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Tree regeneration and future stand development after bark beetle infestation and harvesting in Colorado lodgepole pine stands

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ABSTRACT

In the southern Rocky Mountains, current mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreaks and associated harvesting have set millions of hectares of lodgepole pine (*Pinus contorta* var. *latifolia* Engelm. ex Wats.) forest onto new stand development trajectories. Information about immediate, post-disturbance tree regeneration will provide insight on dynamics of future stand composition and structure. We compared tree regeneration in eight paired harvested and untreated lodgepole pine stands in the Fraser Experimental Forest that experienced more than 70% overstory mortality due to beetles. New seedlings colonized both harvested and untreated stands in the first years after the beetle outbreak. In harvested areas the density of new seedlings, predominantly lodgepole pine and aspen, was four times higher than in untreated stands. Annual height growth of pine and fir advance regeneration (*e.g.*, trees established prior to the onset of the outbreak) has doubled following overstory mortality in untreated stands. Growth simulations based on our regeneration data suggest that stand basal area and stem density will return to pre-beetle levels in untreated and harvested stands within 80–105 years. Furthermore, lodgepole pine will remain the dominant species in harvested stands over the next century, but subalpine fir will become the most abundant species in untreated areas. Owing to terrain, economic and administrative limitations, active management will treat a small fraction (<15%) of the forests killed by pine beetle. Our findings suggest that the long-term consequences of the outbreak will be most dramatic in untreated forests where the shift in tree species composition will influence timber and water production, wildfire behavior, wildlife habitat and other forest attributes.

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1. Introduction

Recent mountain pine beetle outbreaks (*Dendroctonus ponderosae* Hopkins) have caused an unprecedented amount of overstory mortality in western North American lodgepole pine (*Pinus contorta* var. *latifolia* Engelm. ex Wats.) forests (Raffa et al., 2008). Similar to climate-related increases in forest mortality documented throughout the region (Van Mantgem et al., 2009), increased annual minimum temperatures and persistent drought conditions are implicated in the eruption of bark beetle activity in the southern Rockies during the past decade (Bentz et al., 2010). In Colorado, more than 1.2 million hectares of pine forests were affected by bark beetle infestations between 1996 and 2009 (USDA, 2009). Bark beetles have reduced live lodgepole pine basal area by up to 70% in pine-dominated stands, and overstory mortality often exceeds 90% in mature, even-aged stands in Colorado forests during the current outbreak (Collins et al., 2010; Klutsch et al., 2009). The extent of overstory lodgepole pine mortality from pine beetle has caused concern regarding the future trajectory of beetle-killed forests (Rocca and Romme, 2009). Public concerns about wildfire and risks to infrastructure and human safety from falling trees have prompted active management in heavily infested stands (Fettig et al., 2007; Trzcinski and Reid, 2008). For example, on the Arapaho-Roosevelt National Forest in north central Colorado, salvage of beetle-killed lodgepole pine during the decade since the onset of the mountain pine beetle outbreak has generated more clearcut acreage than in any other decade in the previous century (Collins et al., 2010).

Lodgepole pine regenerates abundantly following canopy disturbance and mechanical harvesting when both seed inputs and exposed mineral seedbed are adequate (Lotan and Perry, 1983). For example, following the 1988 Yellowstone National Park wildfires, lodgepole pine seedling density was 500,000 ha^{-1} in areas with high consumption of forest floor and woody debris, but declined dramatically in areas with more residual surface fuels and less exposed mineral soil (Turner et al., 1999, 2004). Lodgepole also typically regenerates prolifically after harvesting (Alexander, 1986; Collins et al., 2010; Lotan, 1964) except where dense understory vegetation or thick organic soil inhibits seedling recruitment. In such situations, mechanical site preparation treatments are used

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to expose mineral seedbed and stimulate seedling establishment. For example, in Alberta, Canada harvested sites where the ground surface was dominated by moss, scarification increased post-harvest lodgepole pine seedling recruitment 12-fold compared to untreated sites (Landhäusser, 2009).

In contrast to the development of lodgepole pine ecosystems after wildfire or harvesting, we know little about how these forests will respond following bark beetle outbreak. Pine beetle-caused mortality is not accompanied by the immediate loss of overstory canopy, forest floor or vegetative cover common after stand replacing fire and mechanical harvesting. The limited exposure of mineral soil and the residual canopy in beetle-killed forests may both inhibit lodgepole pine recruitment and favor establishment and growth of shade-tolerant species (Claveau et al., 2002). For example, presence of a moss layer was credited for blocking new seedling recruitment for more than a decade following beetle infestation of British Columbia pine forests (Astrup et al., 2008). Studies from Wyoming and British Columbia document increases in the densities of subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) after bark beetles killed the pine overstory (Amman et al., 1988; Astrup et al., 2008; Axelson et al., 2009; Nigh et al., 2008). In Wyoming, residual understory trees, mainly subalpine fir and lodgepole pine, increased growth 3-fold in the decade following overstory loss (Romme et al., 1986).

The current period of extensive canopy mortality and the associated management will impact the development of Colorado forests for the coming century. In north-central Colorado, steep slopes, limited road access and weak timber markets constrain active management; less than 20% of beetle-killed forests are expected to be treated. Greater understanding about forest regeneration in harvested and untreated beetle-killed forests will help land managers project forest recovery from insect outbreaks and determine how to prioritize management actions to meet desired forest conditions. The objectives of this study were to quantify the density and growth of new seedlings and advanced regeneration in untreated and harvested beetle-killed stands, and to assess the effects of management and overstory mortality on the growth of newly established and surviving trees. Results of this regeneration survey were used to estimate changes in stand composition and structure in untreated and harvested beetle-killed stands for two centuries following the current beetle outbreak.

2. Methods

2.1. Study area

This research took place in lodgepole pine-dominated subalpine forests at the US Forest Service, Fraser Experimental Forest, Colorado. The Fraser Experimental Forest (FEF) is a 93 km^2 research forest located 81 km northwest of Denver, Colorado in the Sulphur Ranger District of the Arapaho-Roosevelt National Forest. The elevation at FEF ranges from 2650 to 3900 m above sea level; the study was conducted at sites located between 2700 and 3000 m. The mean annual temperature is 1 °C, ranging between −40 °C and 32 °C annually. Annual precipitation averages 71–76 cm with two-thirds falling as snow (Alexander and Watkins, 1977). Lodgepole pine stands with average site index of 65 (*i.e.*, 20 m height at 100 yrs) dominate the lower elevations and southern aspects (Alexander, 1966). Mixed-species forests of subalpine fir, Engelmann spruce and lodgepole pine occupy valley bottom and north-facing slopes and extend to treeline (3300–3500 m); the dominance of subalpine fir and Engelmann spruce increases as stands mature. Quaking aspen (*Populus tremuloides* Michx.) occurs in small clonal stands, scattered throughout the lower elevations.

The study was conducted in eight pairs of harvested and adjacent uncut, beetle-infested, lodgepole pine-dominated stands. Mountain pine beetle began to cause widespread overstory pine mortality at the FEF in 2002 (Tishmack et al., 2004) and beetle-related salvage operations occurred between October 2007 and March 2008. Harvesting activities were part of the Upper Fraser Valley Forest Health Project administered by the Sulphur Ranger District of the Arapaho-Roosevelt National Forest (USDA, 2008). Project planning stipulated that harvesting conducted on the Fraser Experimental Forest facilitate long-term research; this allowed us to retain uncut stands adjacent to harvest units. Pre-treatment stand examinations indicated similar species composition (>90% lodgepole pine) and overstory timber volume in harvested and untreated study areas (USDA, 2008). All study units were located on well-drained, coarse-textured soils (Ustic Haplocryalfs; NRCS, 2010; USDA, 2005) with relatively flat slopes (0–25%) and southern aspects. Paired treated and untreated stands were situated on similar slope, aspect and soil mapping unit.

All harvesting, skidding and hauling were restricted to winter months in periods with dry or frozen soils or over >1 m of snow. A sanitation salvage overstory prescription, aimed at removal of dead pine to reduce canopy fuels, was conducted in all treated stands. Operations also attempted to maximize structural and species diversity in residual stands. There was no additional mechanical scarification after harvesting. Harvest units varied between 4 and 22 ha in size; untreated stands were located directly adjacent to harvested units and sampled a comparable area.

2.2. Sampling

Overstory, tree regeneration, understory vegetation and surface conditions were sampled on a 150 × 150 m grid that was randomly oriented in each harvest unit and uncut control stand. Tree species composition, diameter and mortality (of trees >2.5 cm diameter at 1.4 m) were sampled on 5 m × 150 m belt transects positioned between grid points ($n = 43$ transects). We enumerated tree recruitment (seedlings and aspen suckers $\leq$3 years old) and advance regeneration (trees <2.5 cm diameter at 1.4 m and >3 years old) in 3.6 m radius circular plots located at each grid point ($n = 83$ circular plots); this equated to a sampling density of 0.5 plots per hectare. We used annual bud scars to differentiate new recruitment from advance regeneration (Murphy et al., 1999). Within each circular plot, we visually estimated the surface cover of woody debris, forest floor, bare soil, rocks, shrubs, forbs, and graminoid species in four 1 m^2 quadrats. Annual height growth was measured on randomly selected lodgepole and subalpine fir seedlings. Overstory composition and seedling recruitment was measured in the fall of 2009, growth of advance regeneration and recruitment was measured in the fall of 2010.

2.3. Forest growth simulation

We used our observations of overstory and tree regeneration as initial conditions to project changes in species composition and stand structure following the bark beetle outbreak. We used the Central Rockies Variant extension of the Forest Vegetation Simulator (FVS) (Dixon, 2002, 2008), a set of allometric equations used to model tree and stand growth in Colorado, New Mexico, Arizona and South Dakota forests. FVS estimates tree growth, mortality and recruitment based on species, stand density, basal area, site index and the influence of overstory crown cover. U.S. Forest Service, Forest Inventory and Analysis data, collected in lodgepole pine stands distributed throughout Colorado, was used to refine FVS estimates of recruitment and mortality over time using the Regeneration Imputation

Table 1
Composition of overstory (>10 cm DBH), understory (2.5–10 cm DBH) and advance regeneration (<2.5 cm DBH and >3 years old) in untreated ($n = 8$ stands) and harvested areas ($n = 8$ stands). Numbers in parentheses represent standard error. Dead lodgepole pine represents trees killed by mountain pine beetle.

	Overstory trees		Understory trees		Advance regeneration
	Basal area (m^2 ha^{-1})	Density (m^2 ha^{-1})	Basal area (m^2 ha^{-1})	Density (trees ha^{-1})	Density (trees ha^{-1})
Untreated					
Lodgepole pine	7.53 (3.79)	416 (7.30)	2.57 (0.81)	832 (20.18)	1207 (348.2)
Dead lodgepole pine	23.09 (2.15)	650 (4.74)	0.14 (0.05)	34 (1.12)	–
Subalpine fir	0.23 (0.12)	16 (0.57)	0.12 (0.06)	63 (1.67)	972 (360.1)
Engelmann spruce	0.10 (0.06)	6 (0.18)	0.02 (0.01)	7 (0.25)	104 (51.3)
Aspen	0.39 (0.28)	11 (0.38)	0.13 (0.05)	70 (2.08)	784 (248.6)
Harvested					
Lodgepole pine	2.26 (0.69)	133 (1.69)	0.42 (0.10)	212 (2.74)	805 (177.2)
Dead lodgepole pine	2.83 (1.12)	175 (3.00)	0.03 (0.02)	8 (0.26)	–
Subalpine fir	0.34 (0.18)	23 (0.74)	0.15 (0.08)	89 (2.53)	491 (143.3)
Engelmann spruce	0.29 (0.21)	9 (0.24)	0.02 (0.01)	10 (0.30)	59 (22.8)
Aspen	0.93 (0.48)	86 (2.52)	0.20 (0.09)	120 (2.76)	1105 (418.6)

Extractor (REPUTE) post-processor (USDA, 2010; Vandendriesche, 2010).

2.4. *Statistical analysis*

We compared recruitment and advance regeneration densities using the multi-response permutation procedure (MRPP), a non-parametric method that does not assume normality or homogeneity of variance and is suited for count data that is not normally distributed (Mielke and Berry, 2001). The null hypothesis under MRPP assumes that observations are independent and identically distributed. Height growth of advance regeneration from 2007 to 2010, on the same individuals, was compared using a paired *t*-test and tested for homogeneity of variance using Levene's test (O'Neill and Mathews, 2002). Statistical significance is reported at the $\alpha = 0.05$ level unless otherwise noted. To assess the statistical significance of ground cover on seedling recruitment and growth we used a backward elimination regression approach in a generalized linear mixed (Neter et al., 1989). Ground cover conditions varied considerably within single harvested and untreated stands, and were not of singular interest; therefore stands were treated as a random effect and overstory and ground cover were considered continuous fixed effects in the regression analysis. Seedling counts were skewed and non-normal, so we used a zero-inflated Poisson error distribution, as recommended for over-dispersed data (Lambert, 1992; SAS, 2008).

3. Results

3.1. *Stand structure*

Lodgepole pine comprised 91–100% of the overstory basal area in untreated stands (31.3 m^2 ha^{-1} for the total of live and dead trees) (Table 1). Bark beetles killed 60–92% of the overstory lodgepole pine (mean = 75%). In these stands, beetle-killed pine was 68% of total stand basal area. Aspen and subalpine fir accounted for approximately 1% of total basal area each and Engelmann spruce constituted less than 1%. In harvested stands, residual overstory basal area comprised mainly of live and dead lodgepole pine averaged 6.6 m^2 ha^{-1}. Aspen was the second most common species in harvested stands, constituting 15% of the basal area; subalpine fir (7%) and spruce (4%) made up the balance (Table 1).

3.2. *Ground cover*

In untreated stands, ground cover was dominated by forest floor (58%) averaging 2.7 cm in depth. Combined cover of forbs, graminiods and shrubs (primarily low-statured *Vaccinium myrtillis*, *V, caespitosum*, and *V. scoparium*) averaged 35% (Table 2). In harvested stands, woody logging debris covered half the ground surface area, on average, and up to 100% of some plots. Average and maximum woody debris depths were significantly greater in harvested compared to untreated stands. Cover of shrub, forb and graminoid plants in harvested areas was less than half that measured in uncut areas (Table 2).

3.3. *Advance Regeneration*

The density of advance regeneration (trees ≤2.5 cm DBH, >3 years old) was similar in harvested and uncut areas (~2850 stems ha^{-1} for all species). Lodgepole pine accounted for 39% of all advance regeneration and occurred on 58% of all study plots (Table 1 and Fig. 1). Subalpine fir and aspen made up 32% and 26% of all advance regeneration stems, and each species was found on about 40% of plots. Engelmann spruce occurred on only 15% of plots.

Table 2
Average ground cover of untreated and harvested areas (3.6 m radius circular plots; $n = 83$). Cover was estimated visually in four 1 m^2 quadrats per plot. Plots were randomly located and evenly distributed across the study units. Woody debris includes 1, 10, 100 and 1000 h fuels, ranging from <1 to >10 cm in diameter. Forest floor consists of fresh litter and organic matter in varying stages of decomposition.

	Woody debris (%)	Woody debris depth (cm)	Forest floor (%)	Forest floor depth (cm)	Bare soil (%)	Rock (%)	Shrub (%)	Forb (%)	Graminoid (%)
Untreated									
Mean	2.2	0.6	58.7	2.7	3.5	0.3	10.9	16.0	8.1
Median	0.0	0.0	60.5	2.0	0.0	0.0	3.0	7.0	2.0
Range	0–64	0–15	0–100	0–33	0–81	0–10	0–75	0–85	0–81
Harvested									
Mean	48.3	3.8	34.7	2.0	2.9	0.3	4.3	5.9	3.6
Median	45.0	3.0	29.0	2.0	0.0	0.0	1.0	2.0	0.5
Range	0–100	0–25	0–99	0–16	0–80	0–17	0–70	0–65	0–78

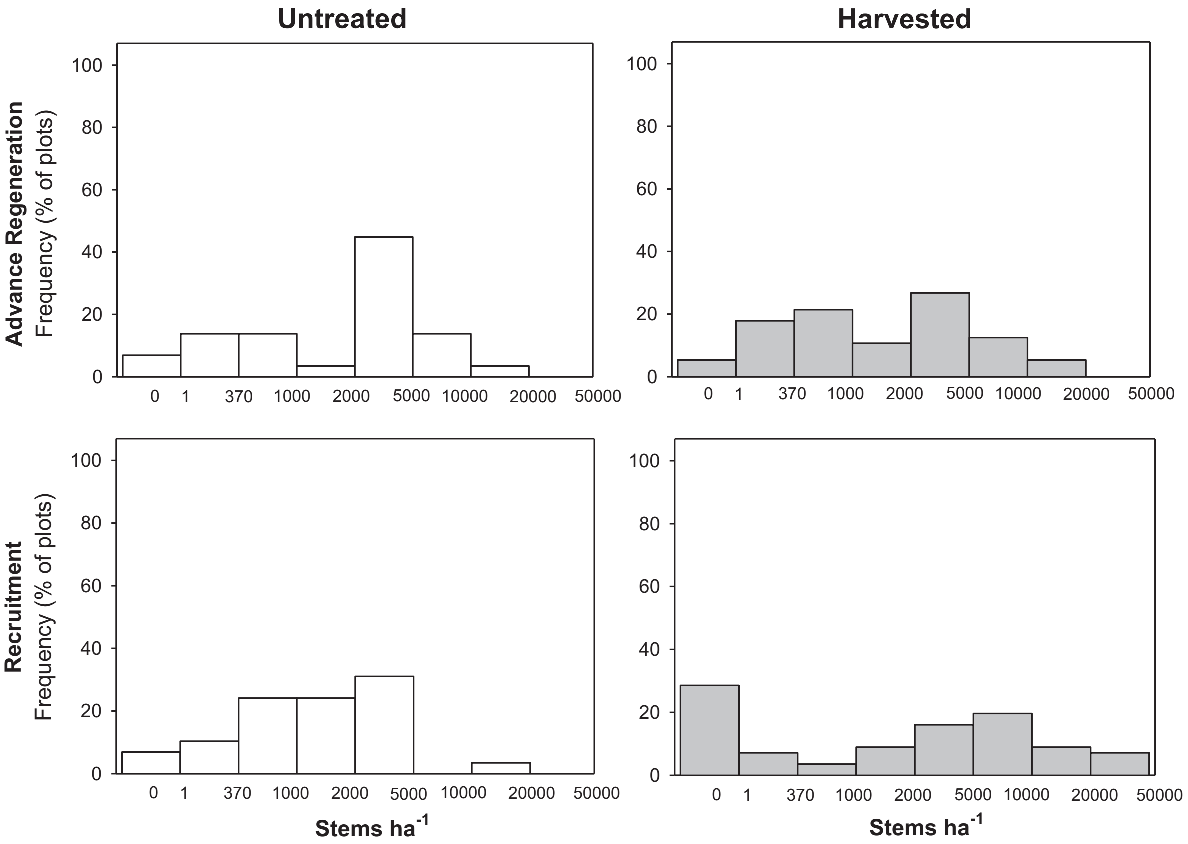

Fig. 1. Advance regeneration (<2.5 cm DBH and >3 years old) and seedling recruitment (≤3 years old) densities of all species in untreated ($n = 29$ plots) and harvested stands ($n = 54$ plots).

3.4. Recruitment

New seedlings (trees ≤3 years old) were four times more abundant in harvested units compared to untreated stands (∼ 5800 *vs.* 1800 stems ha^{-1}; Fig. 2). Lodgepole pine recruits were found on 58% of plots in harvested areas and had an average and maximum density of 3000 and 31,600 stems ha^{-1}, respectively. Lodgepole recruitment was more scarce in untreated areas (875 stems ha^{-1}), though new lodgepole seedlings were found in 50% of these plots. Aspen was the second most common recruit in harvested areas and averaged about 2600 stems ha^{-1} and exceeded 40,000 stems ha^{-1} on some plots. Aspen occurred on 40% of sample plots in harvested stands. Aspen was much less plentiful (499 stems ha^{-1}) in untreated stands. Subalpine fir recruitment did not differ statistically between harvested and untreated stands (262 *vs.* 527 recruits ha^{-1}) (Fig. 2). Subalpine fir was the most widely distributed species of new recruit in untreated areas; we found fir in 54% of plots in untreated stands and measured up to 3000 new fir seedlings ha^{-1}. Engelmann spruce recruitment did not differ between treatments and averaged 19 stems ha^{-1} in harvested and untreated areas.

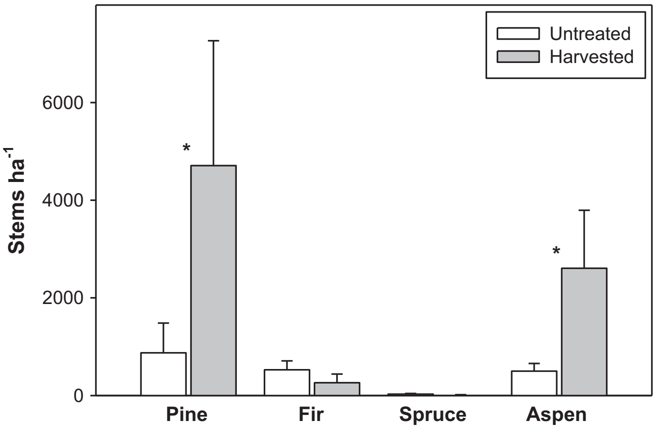

Fig. 2. Density of seedling recruitment that have established since 2008 in untreated ($n = 8$) and harvested areas ($n = 8$). Error bars represent standard error. Asterisks (*) indicate a statistically significant difference between untreated and harvested areas at the $\alpha = 0.05$ level.

3.5. Seedling growth

Annual height increment of lodgepole pine and subalpine fir advance regeneration doubled beneath the beetle-killed overstory between 2007 and 2010 (Figs. 3 and 4); height growth of fir was 15% greater than that of pine ($p < 0.01$). In harvested areas, advance regeneration responded differently. Unlike the increased growth beneath the untreated, standing dead pine canopy, subalpine fir growth declined significantly in harvested areas (Fig. 4). Relative growth (*i.e.*, annual height growth/total tree height) of subalpine fir advance regeneration was constant in untreated stands (*e.g.*, 17.5% year^{-1} on average), but it declined in harvested stands over the course of our study ($p < 0.01$). In harvested areas, lodgepole pine advance regeneration grew at a steady rate during the first two years of the study, then increased by 46% the third year after harvesting (Fig. 3). New seedling recruits added much less height growth than advanced regeneration (*e.g.*, 30–50%), and there was no consistent influence of canopy treatment on either pine or fir seedlings.

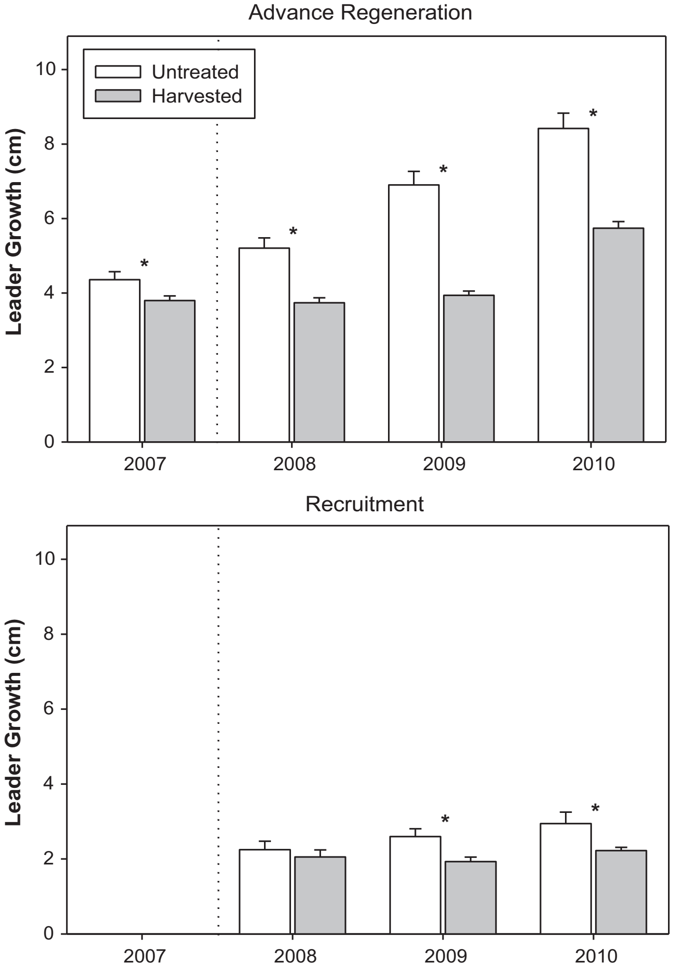

Fig. 3. Growth of lodgepole pine advance regeneration ($n = 538$ trees) and recruitment ($n = 234$) from 2007 to 2010 in untreated and harvested stands. Annual leader growth measured between true branch whorls marked by annual bud scars. Dotted line represents harvest, error bars represent standard error. Asterisks (*) indicate a statistically significant difference between untreated and harvested areas at the $\alpha = 0.05$ level.

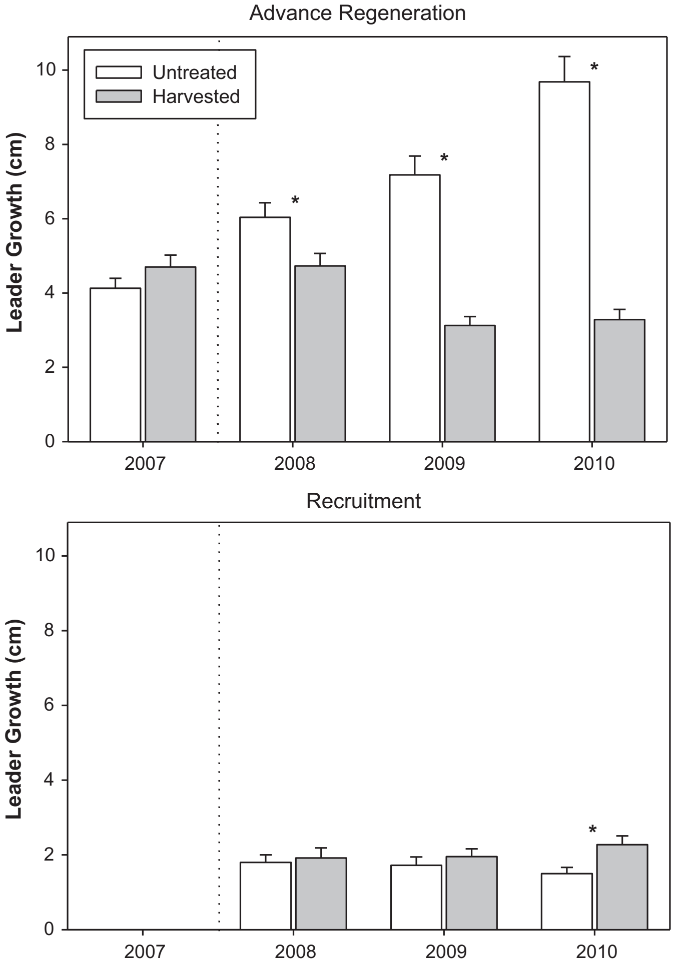

Fig. 4. Growth of subalpine fir advance regeneration ($n = 313$ trees) and recruitment ($n = 21$) from 2007 to 2010 in untreated and harvested stands. Annual leader growth measured between true branch whorls marked by annual bud scars. Dotted line represents harvest, error bars represent standard error. Asterisks (*) indicate a statistically significant difference between untreated and harvested areas at the $\alpha = 0.05$ level.

3.6. *Forest growth simulation*

Our stand growth simulations predicted that total forest basal area will return to pre-outbreak levels ($\sim$34 m^2 ha^{-1}) in untreated and harvested stands after approximately 80 and 105 years, respectively (Fig. 5). In addition to the recruit and advance regeneration density we measured, these simulations were initiated with 11.1 and 4.6 m^2 ha^{-1} of live basal area remaining in untreated and harvested study areas. Aspen is projected to become a significant part of the overstory in harvested and untreated stands the first decades after the infestation. Lodgepole pine will remain the dominant overstory species in harvested beetle-killed stands for at least the next 100–150 years; this is the age range of the forests that were attacked by mountain pine beetles. In contrast, in untreated stands subalpine fir will surpass lodgepole pine as the dominant overstory species.

4. Discussion

4.1. *Regeneration in beetle-killed Colorado forests*

In untreated stands, recovery from bark beetle outbreaks may depend more on advance regeneration (*e.g.*, trees established prior to a disturbance event) than on new seedling establishment. At our sites, we found well-formed, advance regeneration in 93% of plots in untreated stands. Advance regeneration exceeded 1000 stems ha^{-1} on 76% of plots, suggesting that in the absence of management intervention most future stands will be adequately stocked. We also found, however, that new seedlings established in nearly all (*e.g.*, 93%) of our untreated plots since the onset of the outbreak (Fig. 1). In contrast to British Columbia lodgepole stands, where new seedlings were largely unable to recolonize beetle-infested stands owing to the ubiquitous moss layer (Astrup et al., 2008; Landhäusser, 2009), ground cover at our sites consisted of a relatively thin forest floor layer (<3 cm on average), moderate herbaceous plant cover (<25%; Table 2) and no moss. Advance regeneration outnumbered new recruits in our uncut stands (*e.g.*, 3175 and 1896 stems ha^{-1}, of advance regeneration and recruits). Advance regeneration represented the primary source of growing stock in British Columbia stands, but at our Colorado sites the new forest will develop both from advance regeneration and new recruits.

In harvested stands, new seedling recruitment was 4-fold higher than in adjacent, untreated stands and new recruits were three times more abundant as advance regeneration (Figs. 1 and 2). The extent of mineral soil seedbed and the density of competing herbaceous vegetation often regulate post-harvest seedling establishment in lodgepole pine forests (Alexander, 1986; Lotan, 1964, 1975). We found new recruits in 72% of plots in harvested areas

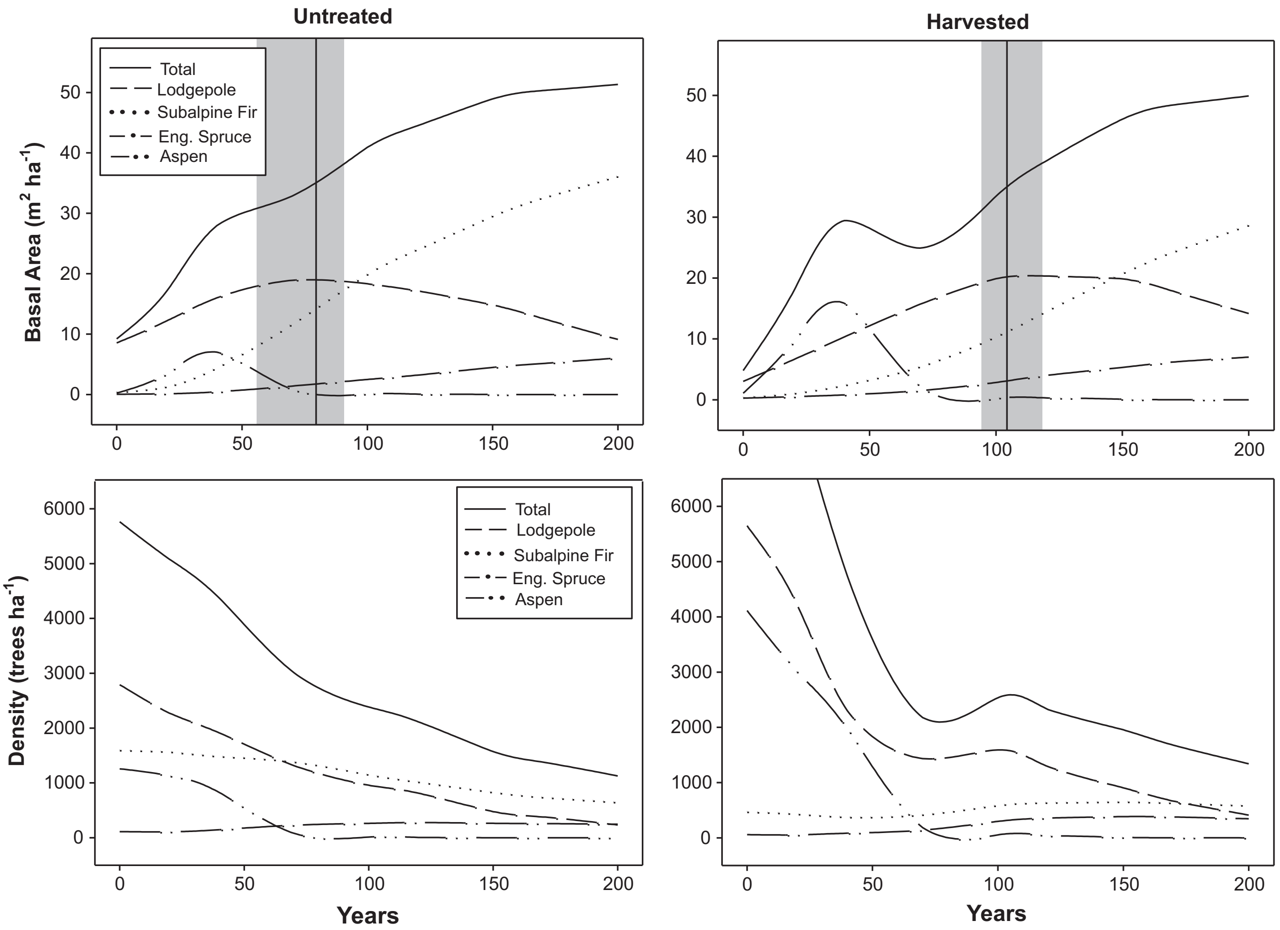

Fig. 5. Projected stand development based on initial observations in harvested ($n = 8$) and untreated ($n = 8$) stands. Vertical line represents basal area equivalent to pre-outbreak conditions, shaded region represents standard error. Growth simulated using the Forest Vegetation Simulator (Dixon, 2002).

and 63% of individual plots exceeded regional seedling stocking density requirements (USDA, 1997) without post-harvest mechanical site preparation, however there were only weak relationships between ground cover and seedling recruitment. Nevertheless, we found that plots with forest floor or woody debris deeper than 5 and 10 cm, respectively, and those with more than 45% herbaceous cover had no new recruits.

The initial growth response of advance regeneration to the declining canopy cover in infested stands is one indication of how these forests will recover after bark beetle infestation. The distinct responses we measured reflect physiological differences between lodgepole pine and subalpine fir and the different environments of uncut and cut beetle-killed stands. The conflicting responses of subalpine fir beneath the dead overstory and in harvested openings is further evidence that this species favors shade during early development and grows poorly in full light (Alexander et al., 1990; Kobe and Coates, 1997). Others have documented that lodgepole pine advance regeneration can respond positively in harvest areas, even after decades of suppressed understory growth (Murphy et al., 1999). Like the results in this study, Murphy et al. (1999) found that lodgepole advance regeneration in Idaho forests did not respond for several years following harvest.

4.2. Forest recovery after bark beetles

The differences we found in species composition, growth rate and density of the growing stock between harvested and untreated stands will likely determine the trajectory of stand development in these beetle-killed forests. High densities of aspen stems, sprouting from existing root structures and lodgepole pine recruits have initiated development of new stands in salvage logged areas. Our forest simulations predicted that following the decline in aspen basal area lodgepole pine would again become the dominant overstory species. Thus, a century after the beetle outbreak, our logged Colorado stands are projected to regain the same basal area and species composition of the even-aged, pine-dominated forests that were attacked by bark beetle. Not surprisingly, in these subalpine forest ecosystems, post-beetle salvage logging, like harvesting of relatively healthy stands, favors regeneration of lodgepole pine (Alexander, 1986; Collins et al., 2010).

In untreated beetle-killed stands, the abundance of subalpine fir advance regeneration that we encountered indicates that future stands are likely to differ from the previous pine-dominated overstory. Though mature subalpine fir-dominated stands are currently uncommon in our study area, growth simulations suggest that this species will replace lodgepole pine as the dominant species in untreated beetle-killed stands (Fig. 5). Studies of other bark beetle infestations in northwestern Wyoming (Amman et al., 1988) and British Columbia (Astrup et al., 2008; Axelson et al., 2009; Nigh et al., 2008) have documented that in the absence of wildfire, the density of shade tolerant species such as subalpine fir can increase in untreated, lodgepole pine stands.

The current bark beetle outbreak is changing various lodgepole pine-dominated forest types. These and our previous findings (Collins et al., 2010) demonstrate that lodgepole stands like those we studied in and around the Fraser Experimental Forest will generally have sufficient regeneration to develop into well-stocked forests. The stand composition and overstory structure of our Fraser study sites are common to other forests across northern Colorado affected by the current bark beetle outbreak. For example, the overstory basal area (27.6–37.6 m^2 ha^{-1}), species composition (86–92% lodgepole, 3–7% aspen and 1–3% subalpine fir) and degree of mortality (79–91%) at three other study locations on the Colorado State Forest, the Routt National Forest and the Parks Ranger District of the Arapaho-Roosevelt National Forest (Rhoades et al., unpublished data) correspond well to the conditions we measured at Fraser. Our findings should have relevance to similar forests across northern Colorado. In contrast, in lodgepole pine stands with sparse understory trees or dense understory vegetation, it is likely that forest recovery will be delayed relative to our findings.

Owing to the complex terrain and limited timber demand in the region, the majority of beetle-affected forests will remain untreated. Based on these conditions, our stand simulations predict a large change in overstory composition across the majority of the landscape in the two centuries after the outbreak. However, because of the susceptibility of subalpine fir to a number of insects and disease agents (Alexander et al., 1990; Nealis et al., 2009) a patchy overstory structure and uneven-age distribution may develop in untreated beetle-killed forests. It is uncertain to what extent the increase in downed wood and the regeneration of ladder and canopy fuels will alter fire risk in recovering beetle-killed forests (Jenkins et al., 2008), but wildfire is likely to regenerate lodgepole pine dominance on a portion of the landscape. Nevertheless our findings suggest that the long-term consequences of the outbreak will be most dramatic in uncut beetle-killed forests where the shift in tree species composition will influence timber and water production, wildfire behavior, wildlife habitat and other forest attributes.

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