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# Tree regeneration and soil responses to management alternatives in beetle-infested lodgepole pine forests

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ABSTRACT

Recent mountain pine beetle (*Dendroctonus ponderosae*; MPB) outbreaks have caused one of the most widespread and dramatic changes in forest condition in North American forests in more than a century and highlighted challenges facing resource managers. To address uncertainty regarding the consequences of post-harvest woody residue management on soil productivity and tree regeneration following MPB outbreaks in lodgepole pine-dominated forests we compared three treatment prescriptions (bole-only harvest, whole-tree harvest, and whole-tree harvest with scarification) and uncut stands. The study was replicated at twelve sites across a range of operational project areas and stand conditions in northern Colorado. Salvage logging generated a new cohort of lodgepole pine at densities far above the threshold considered adequate to develop into well-stocked stands (1700–2300 t $ha^{-1}$ in logged compared to 537 t $ha^{-1}$ in uncut areas). Regeneration density was generally highest in whole-tree harvested areas. Growth of planted and naturally regenerating lodgepole pine recruits was best in the bole-only, residue-retention treatment, where soil moisture and inorganic nitrogen supply was also highest. However, we found no indication that whole-tree harvesting lowered soil moisture, soil nitrogen supply or pools relative to uncut stands. The density of trees regenerating beneath uncut stands indicates that post-outbreak forest structure should recover without management in these forests. The cohort of trees that regenerated following MPB-related overstory mortality, but prior to harvesting, comprise the fastest-growing component of the growing stock and 30% of its density. The broader watershed-scale outcomes of these treatments and their implications for wildfire behavior and other effects remain uncertain. However, the soil and tree patterns we report during the initial post-treatment period inform on-going decisions regarding harvest and residue retention and create a platform to guide future forest management research.

## 1. Introduction

Recent mountain pine beetle (*Dendroctonus ponderosae*; MPB) outbreaks have caused one of the most widespread and dramatic changes in forest condition in western North American forests in more than a century. The outbreaks have affected lodgepole pine (*Pinus contorta* var. *latifolia*) in forests from Colorado to British Columbia (Raffa et al., 2008; Birdsey et al., 2019) and resulted in tree mortality exceeding 75% in many areas (Collins et al., 2011; Hawkins et al., 2012; Kayes and Tinker, 2012). The widespread disturbance has been attributed to regional increases in air temperature and drought and changes in forest structure (Bentz et al., 2009; Chapman et al., 2012; Creeden et al., 2014). The severity of the outbreaks has created concern from the public and management agencies regarding wildfire and treefall hazard and has prompted widespread salvage logging in the southern Rocky Mountains (Collins et al., 2010) and throughout the outbreak area.

In the southern Rocky Mountains, management actions in beetle-infested lodgepole pine forests typically prioritize crown-fire risk and fuel reduction, mitigation of human safety hazards, and infrastructure protection as well as the capture of economic value from the dead timber (*e.g.,* USDA, 2008). On US Forest Service land, managers are mandated to consider additional objectives (Multiple-Use Sustained-Yield Act of 1960; US P.L. 86–517). Salvage projects, for example, may also include efforts to regenerate forests, and to protect wildlife habitat, watershed conditions, and other ecosystem services, properties and processes. Each management objective has distinct outcomes that compel land managers to confront resource tradeoffs. As one example, removal of MPB-killed trees to maximize fuel-reduction objectives, may not align with watershed, wildlife- and ecosystem-oriented objectives to minimize soil disturbance and retain carbon and nutrients on-site (USDA, 2006 and 2012). Harvesting and post-harvest slash removal and site preparation operations both reduce surface fuel loads, but often promote dense tree regeneration (*e.g.,* ladder fuels) that can generate new wildfire hazard concerns (Pelz et al., 2015; Hood et al., 2017). Pile burning, a commonly used slash removal technique, impacts local air quality and can cause lasting changes in soil and native vegetation (Korb et al., 2004; Rhoades and Fornwalt, 2015). Developing a better understanding of interacting benefits and pitfalls of treatment

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alternatives will help managers determine how to best manage beetle-infested forests.

Managers in the southern Rocky Mountains rely on general guidelines regarding post-harvest wood retention and acceptable soil and site disturbance (USDA, 2012; Napper et al., 2009) but lack information specific to MPB-infested lodgepole pine forests. Removing logging residue, primarily to reduce surface fuels, has been shown to decrease soil C and N and affect tree and understory vegetation under some conditions (Wei et al., 1997; Ranius et al., 2018). Conversely, leaving coarse wood and logging residue within harvest units is commonly considered beneficial for maintaining soil carbon (C), nutrients, soil water, wildlife habitat, and other resources (Harmon et al., 1986). However, residue retention also increases fuel loads and elevates the risk of severe fire effects on soils, can create obstacles to tree recruitment, and has been associated with high N leaching losses in regions with elevated atmospheric N deposition (Akselsson and Westling, 2005; Thiffault et al., 2011). Mechanical scarification is often conducted to promote pine establishment by removing competitive vegetation and exposing a mineral seed bed following harvest operations (Lotan and Perry, 1983; Lotan and Critchfield, 1990), but the consequences of this practices are uncertain in bark beetle-infested forests.

This study compares the outcome of various management treatments on soil resources and tree regeneration density and growth to provide resource managers information to guide land-management decisions in MPB-infested lodgepole pine forests of the southern Rocky Mountains. We engaged US Forest Service hydrologists, soil scientists, fuels specialists and silviculturists to identify practical harvesting and post-harvest prescriptions given the unique ecological and economic conditions associated with the unprecedented level of overstory mortality. The study was replicated across a range of management agencies, operational project areas, and stand conditions in northern Colorado as part of a project aimed at characterizing how the recent MPB outbreak and subsequent logging impacted an array of ecological properties and processes (Collins et al., 2011; 2012; Pelz et al., 2015; Fornwalt et al., 2018). Though MPB-related tree mortality peaked around 2008 (Chapman et al., 2012; Meddens and Hicke, 2014), owing to the slow pace of pine snagfall in these high-elevation forests (Rhoades et al., 2020), salvage logging continues more than a decade later, so this work has relevance to both the current and future outbreaks.

## 2. Methods

### 2.1. Study area

This study was conducted at twelve northern Colorado sites spread across four MPB-salvage projects on the Medicine Bow-Routt and Arapaho-Roosevelt National Forests and the Colorado State Forest. Prior to the outbreak, lodgepole pine comprised 70 to 90% of overstory cover and basal area at all sites with varying amounts of subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*) and quaking aspen (*Populus tremuloides*). Average elevations of the study sites range from 2752 to 2847 m. The region has a continental climate with average annual precipitation ranging from 554 to 702 mm, and mean annual temperature ranging from 1.9 to 2.6 °C (PRISM 2016).

MPB caused widespread lodgepole pine mortality throughout the area starting between 1998 and 2002 (USDA, 2010) with overstory mortality ranging from 60 to 90% before the outbreak abated between 2008 and 2010 (Collins et al., 2012; Pelz et al., 2018). Study sites were selected to minimize differences in forest species composition, stand structure and site conditions between adjacent harvested and untreated stands. We used pre-harvest stand exams (USFS Region 2 and Colorado State Forest Service, unpublished records) and inventories of uncut areas (see Collins et al., 2011; 2012 (Table 3) for additional details) to confirm these similarities. All stands were clear cut in the winters of 2008 and 2009 by logging contractors using tracked feller-bunchers and trees were transported to processing and loading decks by rubber-tired skidders. In accordance to local best management practices, all mechanical operations occurred over a stable snowpack ($>$ 1 m depth) or frozen soils (USDA, 2012).

Each study site consisted of an uncut, MPB-killed stand and an adjacent logged unit containing three experimental management alternatives (described below; see Fornwalt et al., 2018 for additional details). In 2009 treatment alternatives were randomly assigned to adjoining 30 × 30 m areas with 10 m wide border strips separating plots. Equal-size uncut plots were located within 400 m of harvest areas, and their slope aspects and gradients differed from treated areas by $< 25°$ and 8%, respectively. The study compared the following treatment alternatives and management objectives:

***Whole-Tree Harvest to Reduce Canopy and Surface Fuels (WTH).*** Boles, tops and branches were skidded to log processing landings. Merchantable tree boles were delimbed, loaded and transported off site, and all other residue was piled and burned at log landings. This is the most common post-infestation harvesting practice in the southern Rockies and is likely to have similar consequences on tree regeneration as woody biomass-removal harvesting.

***Bole-Only Harvest to Protect Watershed Conditions (BOH).*** Locally known as lop and scatter, BOH removes merchantable tree boles and leaves foliage, tops, branches and small diameter stems within harvest areas. Residue retention helps protect the soil O-horizon and maintain soil productivity by conserving C and nutrients (Wei et al., 1997; Thiffault et al., 2011). Residues also create surface roughness that captures seasonal snow cover and may increase water infiltration (Troendle, 1983; Meiman, 1987). Experimental BOH treatments were created by distributing slash and non-merchantable materials onto WTH treated areas.

***Whole Tree Harvest plus Post-Harvest Scarification to Promote Tree Regeneration (SCAR).*** Lodgepole pine regeneration may be enhanced by mechanical operations that expose a mineral seedbed during or following harvesting operations (Alexander, 1974). Experimental SCAR treatments were achieved by operating tracked equipment within WTH treated areas during dry soil conditions.

***Uncut Control to Retain Bark Beetle-Infested Forest (UNCUT).*** This 'no-action' alternative preserves the legacy of the forest disturbance (Lindenmayer and Noss, 2006). Due to the extent of steep slopes, designated wilderness areas and limited road access, the majority of MPB-infested forests of northern Colorado are likely to remain uncut.

### 2.2. Sampling and analysis

#### 2.2.1. Surface cover and soil properties

We quantified and analyzed various surface cover and soil chemical and physical properties to evaluate potential management treatment and site differences and their relationship with tree regeneration. In summer 2011, we visually assessed soil disturbance following timber harvesting after Napper et al. (2009). Disturbance levels were classified as follows: none - no disturbance, forest floor (O-horizon) intact; light - minor rutting from logging equipment travel and log skidding, O-horizon mostly undisturbed; moderate - O-horizon disrupted and mixed with mineral soil layer; high - mineral soil layers exposed by O-horizon mixing or removal or deep rutting. The level of soil disturbance was observed within 0.1 m radius circular subplots spaced at 1-m intervals along four 20-m transects within each treatment plot, and the highest disturbance class was recorded ($n = 80$ per plot). In addition, we visually estimated surface cover of bare soil, litter, fine fuels (1- + 10-hr lag fuels sizes), coarse fuels (100- + 1000-hr lag fuels sizes), and projected canopy cover of sedges, grasses, forbs and shrubs.

#### 2.2.2. Soil properties

To examine plant-available soil N pools and the production of those forms during the growing season, we sampled and conducted *in situ* incubations in May, July and September 2011. On each sampling date, four 0–10 mineral samples were collected near the corner of each treatment plot, immediately placed in coolers, stored at 4 °C and processed within 72 h. Each sample was sieved (8-mm mesh) to mix them and remove roots and rocks. An initial 10-g subset was then extracted with 50 mL of 2 M KCl and analyzed for $NO_3$-N and $NH_4$-N by colorimetric spectrophotometry (Bundy and Meisinger, 1994; Latchat Company, Loveland, CO). We used closed-top PVC cores to measure *in situ* net mineralization and nitrification rates (Binkley and Hart, 1989). Cores were installed to 10 cm depth on each initial sampling date, retrieved after the 28-day incubation, then prepared, extracted and analyzed as described above. Net mineralization was calculated as the change in $NO_3$-N plus $NH_4$-N between the initial and incubated sample extracts, and similarly net nitrification as the change in $NO_3$-N. For both initial and incubated samples a 10-g subset was oven-dried at 105 °C for 24 h to determine gravimetric soil moisture content.

Samples for the July initial subset were dried for 48 h at 60 °C, ground and analyzed for total C and N by dry combustion (LECO 1000 CHN analyzer, LECO Corporation, St. Joseph, MI, USA). Soil pH also was analyzed in a 1:1 soil to deionized water slurry after one hour of agitation (Thomas, 1996), and texture was measured with the Bouyoucos hydrometer method (Gee and Bauder, 1986).

### 2.2.3. Tree regeneration

We evaluated the consequences of the four management alternatives on tree establishment and growth using naturally regenerating conifers and aspen trees and planted lodgepole pine seedlings. In May 2010, we planted 64 bare root lodgepole pine seedlings in each of the four treatments in six of the twelve study sites. The seedling height and stem diameter averaged 21.6 and 0.37 cm, respectively, at the time of planting. In summer 2015, we recorded seedling survival, total height and stem diameter and measured annual height increments between branch whorls for each growing season since planting (*i.e.,* 2011–2014). We also counted naturally regenerating trees in three randomly placed 5-m radius plots in all treatments in summer 2015. Natural regeneration was tallied by $<$ 50 cm, 50–100 cm, $>$ 100 cm ($<$ 2.5 cm DBH) height classes. We counted branch whorls and annual rings on conifers to determine that trees $<$ 50 cm in height represented new recruits established since salvage operations. The two larger size classes represented trees that regenerated prior to the harvesting (advance regeneration), some of which established since the onset of the MPB outbreak. We measured annual height increment for the five previous growing seasons (2010–2014) for ten randomly selected pine, fir and spruce per plot for trees $<$ 100 cm total height, or for all available trees where $<$ 10 trees were present. Aspen regenerate predominantly from root sprouts following canopy disturbance in these forests (Shepperd, 2001; Long and Mock, 2012; Collins et al., 2012). Due to the species' growth form and ungulate herbivory, we were unable to differentiate annual height increment or sprout age.

### 2.2.4. Statistical analyses

We compared soil properties and tree regeneration density and growth among the four treatment alternatives using generalized linear mixed models. Harvest treatment was the fixed effect and study site (n = 12) nested within MPB salvage project area was the random effect (SPSS, Inc., V 22 IBM, Chicago, IL). Levene's statistic was used to test assumptions of homogeneity of variance; extractable soil N and net mineralization data violated this assumption and were log-transformed prior to analyses. Tree regeneration counts and density were skewed and non-normal so we used a zero-inflated Poisson distribution (Lambert, 1992). Where fixed effects were significant, pairwise Tukey-adjusted comparisons were used to identify differences between treatments. The relations between total soil N and C and soil texture were evaluated using least-squares linear regression for UNCUT stands. We evaluated average growing season conditions rather than seasonal variability on soil moisture and soil N cycling parameters. Throughout the manuscript, statistical significance is reported only when $\alpha \leq 0.05$, unless otherwise stated.

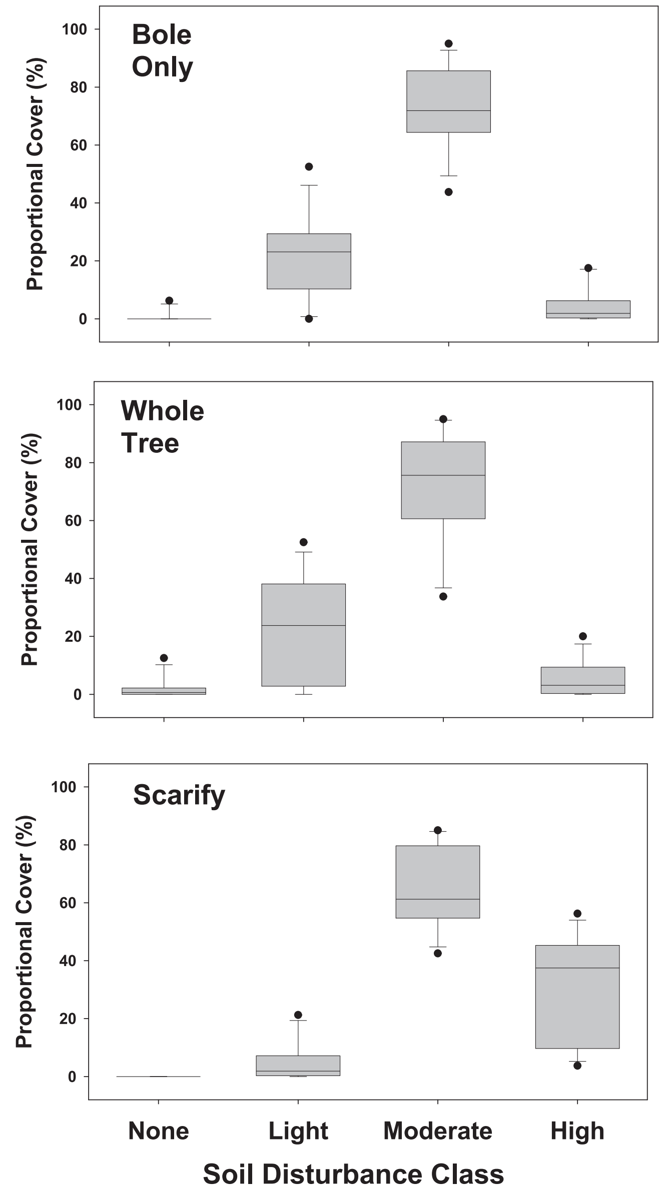


**Fig. 1.** Visual indicators of soil disturbance in salvage-logged clear cut units. Disturbance levels were classified in 2011 as follows: none - forest floor (O-horizon) intact; light - minor rutting from logging equipment travel and log skidding, O-horizon mostly undisturbed; moderate - O-horizon disrupted and mixed with mineral soil layer; high - mineral soil layers exposed by deep rutting, O-horizon mixing or removal (Napper et al., 2009). Boxes denote the 25th, 50th, 75th percentiles, bars denote the 5th and 95th percentiles, and dots denote outliers (n = 80 points per plot).

## 3. Results

### 3.1. Soil and surface cover responses

Salvage logging disturbed the soil surface and altered plant cover compared to UNCUT areas (Fig. 1; Table 1). The BOH and WTH treatments caused similar amounts of light and moderate O-horizon disturbance. The SCAR treatment mixed or removed the O-horizon (high disturbance) on 40% of those treatment plots and increased mineral soil exposure (Table 1). Total understory plant cover was marginally lower in WTH and SCAR compared to UNCUT areas ($P < 0.1$), led primarily by 50% lower cover of the low-statured shrub grouse

**Table 1**
Ground and understory plant cover (%) estimated following bark beetle infestation and salvage logging at twelve study sites in northern Colorado. Data are means and pooled standard errors (in parentheses) estimated by generalized mixed linear models. Where treatment had a significant effect, letters denote which means differed at $\alpha < 0.05$ according to Tukey's-adjusted pairwise comparisons.

| | Bare Soil | Fine Fuels | Coarse Fuels | Sedge | Grass | Forb | Shrubs | Total Understory |
|---|---|---|---|---|---|---|---|---|
| | % in 1 $m^2$ quadrats | | | | | | | |
| Uncut | 0.7 (1.6) a | 6.9 (1.9) a | 6.3 (1.5) a | 11.4 (2.2) | 1.5 (0.8) a | 11.8 (2.0) | 18.8 (2.1) b | 44.1 (3.3) |
| Bole Only | 1.2 (1.6) a | 18.5 (1.9) b | 18.3 (1.5) b | 8.1 (2.2) | 3.1 (0.8) ab | 16.0 (2.0) | 11.4 (2.1) a | 41.3 (3.3) |
| Whole Tree | 6.2 (1.6) b | 15.8 (1.9) b | 6.6 (1.5) a | 9.3 (2.2) | 3.5 (0.8) ab | 12.4 (2.0) | 9.7 (2.1) a | 36.0 (3.3)* |
| Scarify | 9.9 (1.6) b | 18.1 (1.9) b | 5.3 (1.5) a | 6.8 (2.2) | 5.0 (0.8) b | 13.1 (2.0) | 8.8 (2.1) a | 35.3 (3.3)* |
| P-values | < 0.001 | < 0.001 | < 0.001 | | 0.023 | | 0.005 | |

* Means differ from UNCUT at $P < 0.1$.

**Table 2**
Soil moisture, nitrogen (N) and carbon (C) at 0–10 cm depth following bark beetle infestation and salvage logging at 12 sites in northern Colorado. Data are means and pooled standard errors (in parentheses) estimated by generalized mixed linear models for three growing season sample periods (May, July, September 2011) for all response variable except Total C, N, and C:N which were sampled once (September 2011). Where treatment had a significant effect, letters denote which means differed at a < 0.05 according to Tukey's-adjusted pairwise comparisons.

| | | Plant-Available N | | | *In Situ* | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Soil Moisture | $NH_4$ - N | $NO_3$ - N | Sum | Mineralization | Nitrification | Total C | Total N | C:N |
| | % | mg/kg | | | mg/kg/month | | % | | |
| Uncut | 15.8(1.2)a | 3.3(0.4)a | 0.10(0.1)a | 3.4(0.4)a | 2.9(0.7)a | 0.41(0.2)a | 2.6(0.6)b | 0.10(0.02) | 23.6(1.0) |
| Bole Only | 22.2(1.2)b | 5.7(0.4)b | 0.43(0.1)b | 6.1(0.4)c | 3.1(0.7)a | 1.50(0.2)b | 3.8(0.6)ab | 0.12(0.02) | 25.7(1.0) |
| Whole Tree | 16.2(1.2)a | 4.2(0.4)a | 0.21(0.1)a | 4.4(0.4)b | 3.5(0.7)ab | 0.56(0.2)a | 3.2(0.6)ab | 0.12(0.02) | 24.3(1.0) |
| Scarify | 16.1(1.2)a | 4.2(0.4)a | 0.45(0.1)b | 4.6(0.4)b | 5.4(0.7)b | 1.09(0.2)b | 4.5(0.6)a | 0.14(0.02) | 25.1(1.0) |
| P-values | 0.001 | 0.007 | < 0.001 | 0.002 | 0.058 | 0.001 | 0.100 | | |

whortleberry (*Vaccinium scoparium*) (Table 1); total cover was lower in both WTH and SCAR treatments compared to UNCUT areas ($P < 0.1$). SCAR had a statistically insignificant effect on bare soil cover and sedge cover compared to WTH.

Harvesting generally increased soil moisture, plant-available soil N, *in situ* net N production and total soil C and N (Table 2). Moisture declined from spring to fall (data not shown) but was consistently highest in the BOH treatment. Extractable $NH_4$ and $NO_3$ and their sum were highest in BOH relative to UNCUT or the other harvest treatments. Nitrate supplied by net nitrification was roughly 3-fold higher in BOH than UNCUT or WTH. Net mineralization was highest in the SCAR treatment and net nitrification and plant-available N forms were higher than the UNCUT stands. Soil pH averaged 5.6 overall (data not shown) and ranged from 5.3 to 6.0 across the 12 study sites but was not affected by harvest treatment. The SCAR treatment increased total N and C significantly relative to UNCUT stands and the other logging treatments were intermediate. Soil C:N did not differ between UNCUT and harvested areas. Total soil C and N increased linearly with the proportion of clay plus silt in UNCUT forests (Fig. 2), and though post-harvest total Soil C and N also increased across the range of soil texture, the pattern was more variable.

### 3.2. Natural regeneration density and growth

The effects of salvage logging and the specific treatments on natural regeneration density varied by tree species and height classes (Fig. 3). Overall, the density of pine recruits (trees < 50 cm tall) was > 3-fold higher in harvested areas compared to UNCUT stands. The positive responses on pine advance regeneration (trees > 50 cm tall) density were limited to the WTH treatment. The SCAR treatment reduced the density of fir recruits by 88% relative to UNCUT and marginally compared to WTH ($P < 0.1$). Aspen sprouts (< 50 cm class) were stimulated by the SCAR treatment compared to UNCUT or the other harvest treatments.

In lodgepole pine forests of the southern Rockies, a minimum of 370 t $ha^{-1}$ are required to certify that treated areas have regenerated successfully (USDA, 1997). In 2015, six years after harvesting operations, 73% of the individual 5-m radius plots exceeded stocking requirements, considering only new lodgepole pine recruits. Adequate stocking levels were met in 61% of BOH plots compared to the WTH (81%) and SCAR (78%) plots. Pine recruits were absent from BOH treatments in two harvest units. In contrast, 56% of the UNCUT plots were adequately stocked with pine recruits and none were devoid of them.

Average annual height growth of new recruits was generally higher in the harvest areas but varied by species and treatment (Fig. 4). Height growth of pine recruits was highest in the BOH treatment and was marginally higher in WTH ($P < 0.1$) for the other species. Harvesting also increased pine growth for the 50–100 cm height class, but it had no significant effect on the other species or the largest size class. Overall, annual height growth of natural regenerating conifers increased with tree size class.

### 3.3. Planted pine survival and growth

On average, 53% of planted pine trees survived until 2015. Survivorship ranged from 25 to 70% across the study plots but did not differ significantly among sites or treatments (data not shown). Starting after the second growing season, pines planted in the three harvest treatments grew faster than those in the UNCUT stands (Fig. 5). Differences between the harvest treatments increased after that, and on average height increment was 22 and 25% higher in BOH and SCAR compared to the WTH units during 2013 and 2014. Total tree heights in 2015 were 71 and 68 cm in BOH and SCAR plots (data not shown), significantly greater than both those in WTH (55 cm) and UNCUT plots (44 cm). Stem diameters in 2015 followed a similar pattern (data not shown), with larger diameter trees in the BOH treatment (2.1 cm) compared to the other two harvest treatments (1.6 cm) or UNCUT plots (0.8 cm). Total stem height and diameter increased 3- and 5-fold since

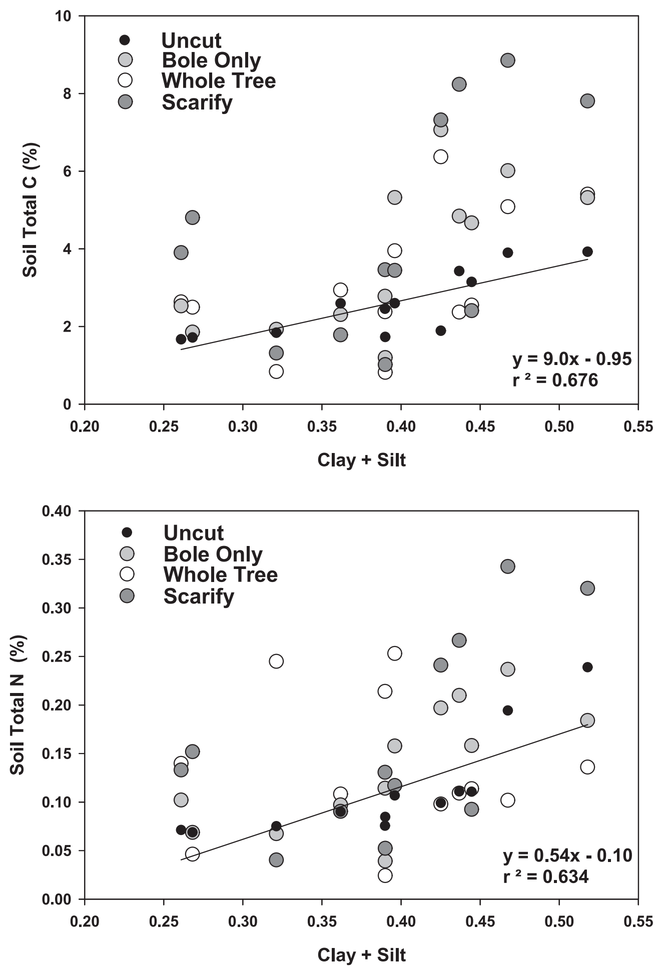


**Fig. 2.** Relation between total soil N and C to soil clay plus silt in salvage-logged clear cut units and nearby uncut, bark beetle-killed forests. Dots are means for twelve sites for the 0–10 cm mineral soil depth sampled in 2011. Linear regressions are fitted for Uncut plots only.

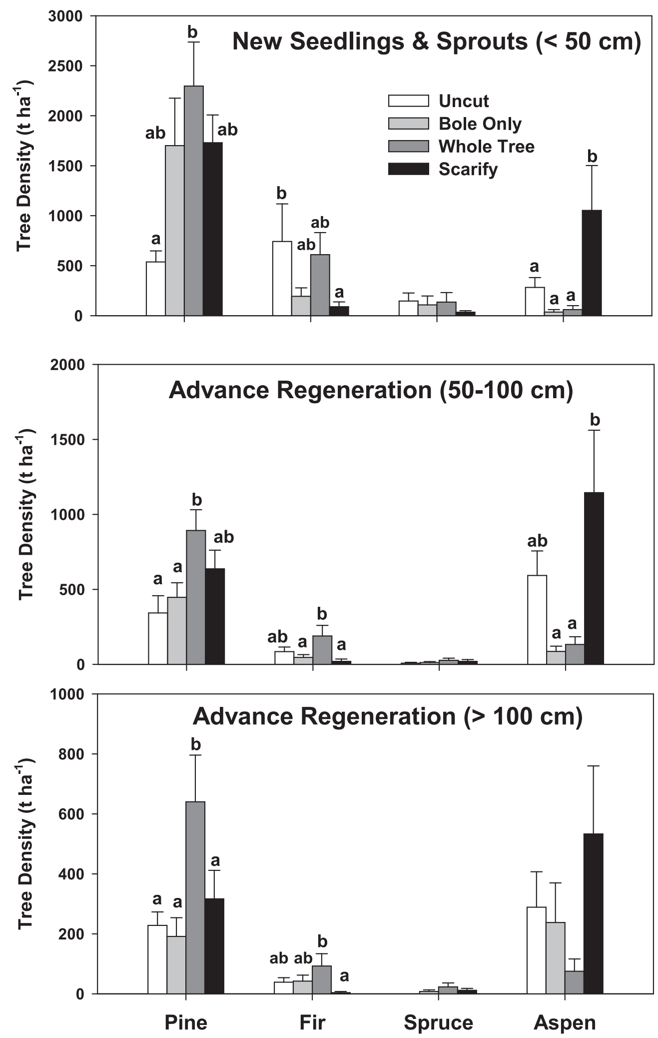


**Fig. 3.** Density of naturally regenerating trees in salvage-logged clear cut units and nearby uncut, bark beetle-killed forests in Colorado in 2015. New conifer recruits and aspen sprouts (< 50 cm total height) generally regenerated after salvage logging and the larger size classes established prior to it. Data are mean and standard error bars at twelve study sites.

trees were planted in BOH plots. In contrast, total tree height and diameter doubled in UNCUT stands and increases were intermediate for the other harvest treatments.

## 4. Discussion

Post-disturbance salvage logging is controversial (Lindenmayer et al., 2004; Leverkus et al., 2018); in this study we found that harvesting met management goals to reduce crown fuels and regenerate new trees without major changes in the measured soil properties. Though shrubs decreased and bare soil cover increased in harvest units (Table 1), soil moisture, N and C and tree density and growth all generally increased (Table 2, Figs. 3 and 4). Previous work showed a shift in understory species composition, relative to untreated stands, but not a large increase in non-native plants (Fornwalt et al., 2018). Like this study, post-MPB harvesting conducted elsewhere increased pine and aspen regeneration (Collins et al., 2010; Pelz et al., 2018; Griffin et al., 2013). Based on initial and more recent stand projections, we expect a return to pre-MPB stand basal area within 80–100 years in both harvested and UNCUT stands (Collins et al., 2011; Hood et al., in review), with a projected divergence in species composition favoring fir in UNCUT and pine in harvested stands. Though harvesting increased the density and growth rate of tree regeneration, the density of new recruits and advance regeneration recorded in UNCUT stands indicate that similar MPB-killed forests will not require harvesting in order to develop into well-stocked conifer forests.

The type, timing and sequence of forest disturbance and management contribute to their ecological outcome, and the specific conditions we observed may not be broadly generalizable to other combinations. Post-MPB salvage, for example, is unlike harvest of live stands that export larger amounts of foliar nutrients (Wei et al., 1997) or post-wildfire harvesting operations following O-horizon combustion and soil erosion (Shatford et al., 2007; Keyser et al., 2009; Wagenbrenner et al., 2016). Beetle-related overstory mortality promotes establishment of new trees (Collins et al., 2012; Pelz et al., 2018), and the winter logging operations conducted during these salvage harvests protected trees in the advance regeneration size classes, that comprised ~30% of the pine growing stock we measured (Fig. 3). Scarification stimulated aspen sprouting in all size classes (Shepperd, 2001; Shepperd et al., 2015). However, trees regenerated following MPB and salvage operations remain susceptible to loss during subsequent wildfire (Rhoades et al., 2018). Dead snags (Page and Jenkins, 2007; Rhoades et al., 2020) and the canopy seedbank (Aoki et al., 2011; Teste et al., 2011) persist for one to several decades after MPB infestation in lodgepole stands, but the efficacy of later-stage salvage logging for fuels and wildfire reduction (Pelz et al., 2015; Leverkus et al., in press) and tree regeneration remains uncertain.

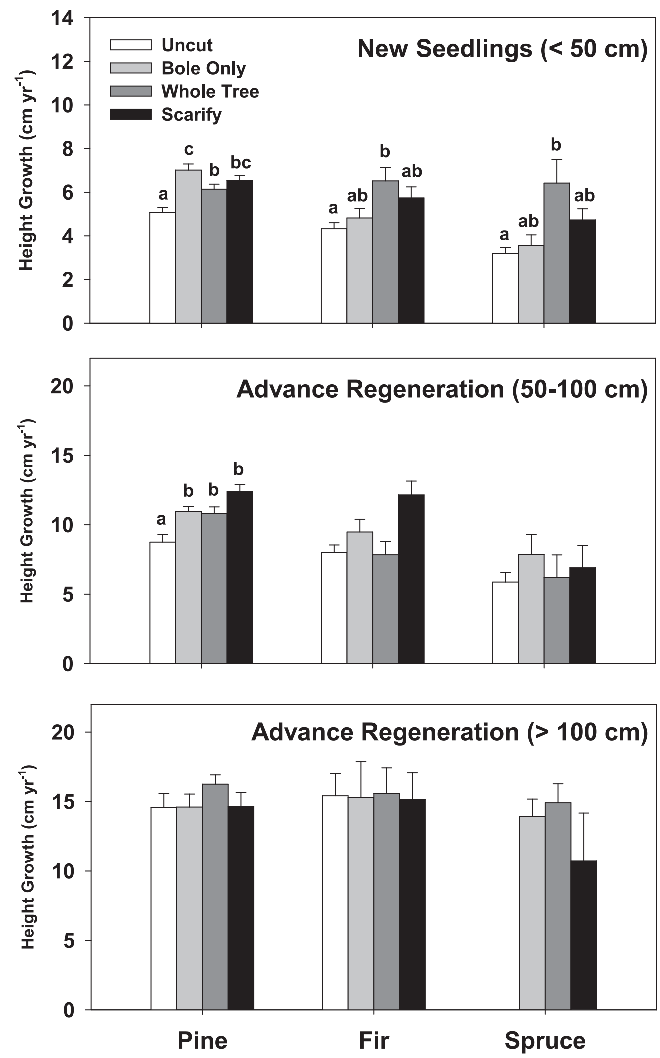


**Fig. 4.** Height growth of naturally regenerating conifers in salvage-logged clear cut units and nearby uncut, bark beetle-killed forests in Colorado. New recruits (< 50 cm total height) generally regenerated after salvage logging and the larger size classes established prior to it. Data are means with standard error bars for annual height increment between 2013 and 2015 at twelve study sites (n = 10 trees per species, size class).

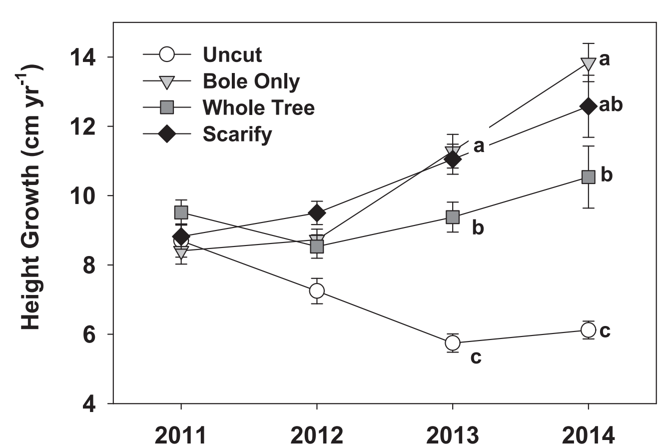


**Fig. 5.** Planted lodgepole pine height growth in salvage-logged clear cut units and nearby uncut, bark beetle-killed forests in Colorado. Data are means and standard errors bars for annual height increment for trees planted in 2010 at six study sites (n = 64 trees per plot).

### 4.1. Ecosystem responses

In addition to tree regeneration, federal land managers must consider how salvage operations influence other natural resources (Ranius et al., 2018; Thiffault et al., 2011). Owing to the low ecosystem productivity and road access constraints, high-elevation forests in the southern Rockies are not a major source of commercial timber (Lynch and Mackes, 2001; Vaughan and Mackes, 2015). However, these ecosystems are critical for the supply of clean water to residents in western states (Brown and Froemke, 2012). Harvesting commonly increases snow accumulation and streamflow in these headwater catchments (Troendle and King, 1985; Troendle and Reuss, 1997; Goeking and Tarboton, 2020). Woody residue retention creates surface roughness that increases snow retention, soil moisture and is consequently linked to water delivery (Troendle, 1983; Meiman, 1987; Murray and Buttle, 2003). We measured higher soil moisture, nitrate and *in situ* net nitrification in the BOH treatment. Elsewhere, the impacts of residue retention on tree seedling establishment and initial growth patterns have been shown to relate to site microclimate, specifically soil temperature and moisture, whereas their effect on soil nutrients and forest productivity became more evident at later stages of stand development (McInnis and Roberts, 1995; Achat et al., 2015; Trottier-Picard et al., 2014). Recruitment and advance regeneration density and growth in the BOH treatment were more than adequate to develop well-stocked stands.

Reduced photosynthesis following tree mortality reduces C capture and may convert beetle-infested stands into net C sources (Kurz et al., 2008; Frank et al., 2014; Birdsey et al., 2019). However, growth of residual canopy and understory trees and other vegetation has been linked to recovery of stand-scale C sink status within a few years of beetle infestation (Romme et al., 1986; Brown et al., 2012; Bowler et al., 2012), and on-site nutrient and water use (Rhoades et al., 2013; Reed et al., 2014; Slinski et al., 2016; Goeking and Tarboton, 2020). Timber harvesting has variable effects on soil C (Johnson and Curtis, 2001; Nave et al., 2010), and there is concern that post-MPB salvage operations may decrease long-term soil and stand productivity. However, we measured higher total soil C and N two years after harvesting activities (Table 2) and total C remained higher for several more years (Avera et al., *in review*). The increases in total soil C and N in both UNCUT and harvested sites scaled with clay plus silt content (Fig. 2) and the largest increase occurred in the SCAR treatment where organic soil was disturbed to the greatest extent.

### 4.2. Woody residue retention

Widespread, high levels of tree mortality during the recent MPB outbreak and the low value of timber in the southern Rockies generated interest in options to utilize wood biomass for energy production (Barrette et al., 2015). It also highlighted the need for guidelines for appropriate levels of woody residue retention. Most existing comparisons of WTH (residue removal) and BOH (residue retention) have been conducted in relatively healthy, green forests (Achat et al., 2015; Thiffault et al., 2011; Ranius et al., 2018). Those studies showed that WTH can increase N and P export in foliage (Wei et al., 1997), alter soil N cycling (Vitousek and Matson, 1985; Hazlett et al., 2007) and reduce tree growth in various forest types (Harrington et al., 2013; Trottier-Picard et al., 2014). In contrast to most previous work, tree needles had senesced prior to harvesting at our sites, or had fallen off during mechanical operations, so foliar nutrients were retained within harvested units. We measured lower soil moisture and plant-available soil nitrate and net nitrification in WTH compared to BOH (Tables 1 and 2), but we found no evidence that WTH reduced the density of any tree species or size class (Fig. 3). In fact, both pine and fir regeneration densities were higher in WTH than BOH for one or both advance regeneration classes. Planted and naturally regenerating pine recruits grew less in WTH than BOH, but the fir and spruce both grew faster in the WTH treatment

(Figs. 4 and 5). Overall, woody residue removal or retention appears to have minor effect on the growth and composition of stands that regenerate following post-MPB salvage logging in these forests. The uncertain implications of these treatments on fuel loads and potential wildfire behavior, and other factors present important management considerations that justifies additional research (Hood et al., 2017; Leverkus et al., in press).

## 5. Conclusions - management implications

Conifers regenerated well in all salvage logging units in these MPB-infested stands (Fig. 3), averaging far above the 370 t $ha^{-1}$ threshold considered adequate for recovery of well-stocked stands (USFS, 2008). Regeneration density was generally highest in the WTH treatment. Pine growth was best in the BOH treatment, where soil moisture and inorganic N supply was highest. There was no sign that WTH lowered soil productivity (*i.e.,* moisture, N cycling, total C and N) relative to UNCUT stands. SCAR did not increase conifer density, though it stimulated aspen sprouting, a common response to mechanical harvest operations in the region (Shepperd, 2001; Shepperd et al., 2015). Natural regeneration beneath UNCUT, beetle-killed stands may be adequate to eliminate the need for harvesting to ensure adequate post-outbreak conifer density. Winter-logging over a stable snowpack and frozen soils is a common best management practice in the southern Rockies that aims to reduce damage to soil and vegation (USDA, 2012). Our study confirmed that advance regeneration was conserved in these winter-logged units and indicates that the larger advance regeneration size class and will be important for recovery of post-harvest forests (Brown et al., 2012; Bowler et al., 2012; Hawkins et al., 2013). The broader watershed-scale outcomes and cumulative effects of these treatments remain uncertain. However, the soil and tree patterns we report during the initial post-treatment period inform on-going decisions regarding harvest and residue retention and create a platform to guide future forest management research.

## Credit authorship contribution statement

**Charles C. Rhoades:** Conceptualization, Writing - original draft, funding acquisition, review & editing **Robert M. Hubbard:** Conceptualization, funding acquisition, review & editing. **Kelly Elder:** Conceptualization, funding acquisition, review & editing. **Paula J. Fornwalt:** Sampling, review & editing. **Elizabeth Schnackenberg:** Conceptualization. **Paul R. Hood:** Sampling, review & editing **Daniel B. Tinker:** Review, editing, & funding acquisition.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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