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Stand dynamics 11 years after retention harvest in a lodgepole pine forest

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ABSTRACT

Structurally diverse forests provide resilience to an array of disturbances and are a mainstay of multiple-resource management. Silviculture based on natural disturbance can increase structural heterogeneity while providing other ecological and economic benefits. One useful silvicultural tool for promoting structural heterogeneity is retention harvesting, whereby a portion of forest stands are left unlogged, transitioning even-aged stands to multi-aged. We report stand and tree dynamics 11 years after retention harvest in a central Montana Rocky Mountain lodgepole pine forest with evidence for a mixed-severity fire regime. Treatments were implemented on 16 experimental units with prescriptions for two 50% overstory basal area retention patterns (Aggregated and Dispersed) crossed with two levels of prescribed fire use (Burned and Unburned). The aim of this study was to identify (1) how retention harvest spatial pattern affects stand dynamics, (2) if stand dynamics after retention treatments are more simply attributable to tree size and competition, or if retention pattern affects dynamics beyond those measures, and (3) how stem and basal area heterogeneity varied over the 11-year measurement period. Retention pattern affected overstory density, growth, mortality, and regeneration density and stocking. After controlling for the fine-scale factors of tree size and competition, overstory mortality, regeneration stocking, and regeneration height growth did not vary by treatment-scale factors. Fine-scaled factors explained significant variation in overstory basal area growth, but at the scale of experimental units, growth was also greater in Dispersed treatments. Prescribed burning interacted with retention pattern to influence overstory tree growth, increased overstory mortality, and increased regeneration height growth. Overstory heterogeneity (e.g., in basal area) degraded more rapidly in treatments with the Dispersed spatial pattern than Aggregated. This study evaluates novel silvicultural treatments in a lodgepole pine forest and highlights the tradeoffs between retention patterns combined with broadcast burning on forest change. Our results are useful for planning silvicultural treatments in multiple-use forests designed to promote structural complexity and resilience to disturbances.

1. Introduction

Forest structural heterogeneity is often associated with resilience to disturbances, including climate change, fire, and bark beetles (Drever et al., 2006; Johnson et al., 2014; Lydersen and North, 2012; Reynolds et al., 2013). Heterogeneity also can improve elements of ecological function, including productivity and biodiversity (Huston, 1979; Seidl et al., 2014; Shugart et al., 2010; Tews et al., 2004). Since increasing resilience to disturbances and maintaining ecological function is so often a management goal for contemporary multiple-use forests, many have recommended increasing structural heterogeneity at tree neighborhood and forest landscape scales (e.g., Beese et al., 2003; Messier et al., 2016).

Many managers increase forest heterogeneity by making structure resemble that which follows a historically typical disturbance event, i.e., natural disturbance-based management (Attiwill, 1994; Drever et al., 2006; Long, 2009). Natural disturbance-based management strategies often aim to concomitantly increase biodiversity, modify forest structure to reduce future disturbance severity, and provide timber for local economies (Bergeron et al., 1999; Churchill et al., 2013; Fiedler et al., 2001; Franklin et al., 2002; Mitchell et al., 2006). Retention harvesting (RH) is a transformative silvicultural strategy for increasing structural heterogeneity and maintaining biological legacies that emulate forest structure after disturbances such as mixed-severity

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fire or insect outbreak (O'Hara, 2014). This type of regeneration harvest is advocated as an ecological alternative to clearcutting and traditional even-aged systems because structural elements (e.g., green trees, snags, riparian areas) are retained to provide biological continuity in forest structures and ecological processes over time (Franklin et al., 1997). Thus, RH increases forest complexity, aesthetic value, and habitat diversity while providing opportunity for timber product extraction (McCaughey et al., 2006; Mitchell and Beese, 2002).

Structural patterns in an RH stand are likely to drive variable stand dynamics. Spatial retention patterns associated with RH are "aggregated" (attributes are retained in patches), "dispersed" (retained attributes are scattered and widespread), or a hybrid of the two, making RH a flexible management option with a multitude of structural outcomes (Beese et al., 2003; Halpern et al., 1999). While North American investigations have characterized forest change given RH in, for instance, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Halpern et al., 2012) and red pine (*Pinus resinosa* Aiton) (Palik et al., 2014), effects of RH strategies on stand dynamics in other systems have been poorly documented to-date. Furthermore, only limited evidence demonstrates how tree growth, mortality, and regeneration processes vary within RH stands, or if retention pattern affects these processes after accounting for typical inventory measures of tree size and competition (e.g., Aubry et al., 2004; Urgenson et al., 2013a, 2013b). These processes might vary because stand-scale and tree neighborhood-scale structure directly mediate stand development processes via competition (e.g., resource availability for growth and survival) and facilitation (e.g., seed source and microclimate moderation) (Oliver and Larson, 1996). Land managers need empirical understanding of stand development by and within retention pattern to assess whether RH prescriptions are viable to meet desired forest conditions.

The RH strategy is particularly appropriate in forests with moderate- (20–70% mortality) and mixed-severity (complex of low, moderate, and high mortality) historical disturbance regimes (hereafter, just "mixed-severity") as these disturbances naturally create stand heterogeneity. Lodgepole pine (*Pinus contorta* Douglas ex Loudon) forests, though typically linked to high-severity disturbances and even aged stands from post-disturbance regeneration pulses (e.g., Turner et al., 2003), are also associated with mixed-severity fire regimes in some regions (Agee, 1993; Barrett, 1993; Horton, 1956). Mixed-severity fires partially kill overstory pines and stimulate regeneration to form a multi-aged stand structure (Axelson et al., 2010) that may in turn be maintained by future mixed-severity fire or reset by stand replacing crown fire (Fischer and Clayton, 1983). Given the ecological precedent of a mixed-severity regime and associated multi-aged forest structure, RH can balance both practical and ecological management goals in lodgepole pine forests (Keyes et al., 2014). As with a number of natural disturbance-based management approaches in fire dependent ecosystems, prescribed burning can be used as a subdued surrogate for natural fire (e.g., Larson and Churchill, 2012; Mitchell et al., 2006; Noss et al., 2006). Pairing RH with prescribed burning can improve site preparation for regeneration, fuel reduction, nutrient release, and environmental heterogeneity, more closely approximating the disturbance modeled after. Since lodgepole pine is a major commercial species with a vast range in North America, it is important to better understand the changes to forest structure under such alternative treatments.

The goal of this study was to evaluate post-RH stand dynamics in lodgepole pine to inform future treatments. We examined forest structure 11 years after experimental RH in central Montana to determine the effects of retention pattern and subsequent prescribed fire on overstory structure, growth, mortality, and regeneration (collectively referred to here as "stand dynamics"). Harvests were prescribed to retain 50% basal area in aggregated or dispersed spatial patterns, and half of the replicates were burned with prescribed fire. We asked the following research questions: (1) what are the 11 year stand dynamics after RH in lodgepole pine, and how do they differ with prescribed burning?; (2) are stand dynamics more simply attributable to fire use, tree size, and plot- and stand-scale competition than harvest pattern?; and (3) does retention pattern perpetuate the variability in structure and growth that treatments establish? First, we expected that stand dynamics would vary with harvest pattern, and that prescribed fire would stimulate the regenerating cohort at the expense of the overstory. However, we also expected that these dynamics would vary within treated stands because of harvest pattern, and that local (i.e., plot scale) environmental and competitive conditions would drive dynamics. Second, we suspected that traditional stand and plot scale covariates may inadequately quantify stand dynamics and that harvest pattern will still explain some of the remaining variation in stand dynamics. Third, we predicted treatments would lead to greater variability in stand structure and dynamics if retention pattern affects post-harvest growth and mortality. The results of this study apply most pertinently to lodgepole pine forests in the Rocky Mountains, but analytical methodology and overstory-understory dynamics will resonate with RH applications in conifer forests throughout the world (Gustafsson et al., 2012).

2. Methods

2.1. Study site

The United States Forest Service's Tenderfoot Creek Experimental Forest is a 3693 ha watershed in the Little Belt Mountains, within the Helena-Lewis and Clark National Forest in central Montana. Elevation ranges from 1840 m to 2421 m. The forest is dominated by lodgepole pine (*Pinus contorta* var. *latifolia* Engelm. ex S. Watson), forming nearly pure stands, roughly half of which are multi-aged (at least two-aged). Associated overstory species are subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), and whitebark pine (*Pinus albicaulis* Engelm.). Associated shrub species are grouse whortleberry (*Vaccinium scoparium* Leiberg ex Coville) and thinleaf huckleberry (*V. globulare* Douglas ex Torr.). Soils are typified by loamy skeletal, mixed Typic Cryochrepts, and clayey, mixed Aquic Cryoboralfs (Adams et al., 2008).

Climate in the experimental forest is generally continental, though it is also influenced by the Pacific maritime climate extending beyond the Continental Divide. Annual precipitation is 880 mm, ranging from 594 mm to 1050 mm across the elevation gradient (Adams et al., 2008). The majority of the precipitation occurs in the form of snow from November to May. Typical mean temperatures range from −9 °C in January to 17 °C in July, with freezing temperatures possible throughout the year. The average plant growing season is estimated to be between 30 and 75 days.

Reconstructed fire history shows evidence of high and mixed-severity fires (Barrett, 1993). For the period of 1580 to 1992, mean fire return interval was 38 years, with large, severe fires interspersed with smaller mixed-severity fires that created even and multi-aged stand structures, respectively. Approximately 72.5% of the treated area was single-aged, though this varied from 10% to 100% (i.e., truly even-aged) within stands. Cohorts within treated stands ranged from 80 to 274 years old upon treatment, forming dense, continuous overstories with open understories.

2.2. Experimental design and sampling

Silvicultural treatments were installed in 16 units, split among two sub-watersheds of Tenderfoot Creek on the Experimental Forest (McCaughey et al., 2006). The harvest prescription called for 50% (range: 40–60%) basal area retention; this retention level was selected for practical (i.e., to pay for management and retain enough growing stock for future harvests) as well as ecological reasons (i.e., to create structural and age-class diversity). Harvests created two spatial patterns: Aggregated and Dispersed (Fig. 1). The Aggregated pattern was characterized by 4–27 large (0.1–0.6 ha) reserves distributed throughout each stand in irregular shapes. In the Dispersed pattern,

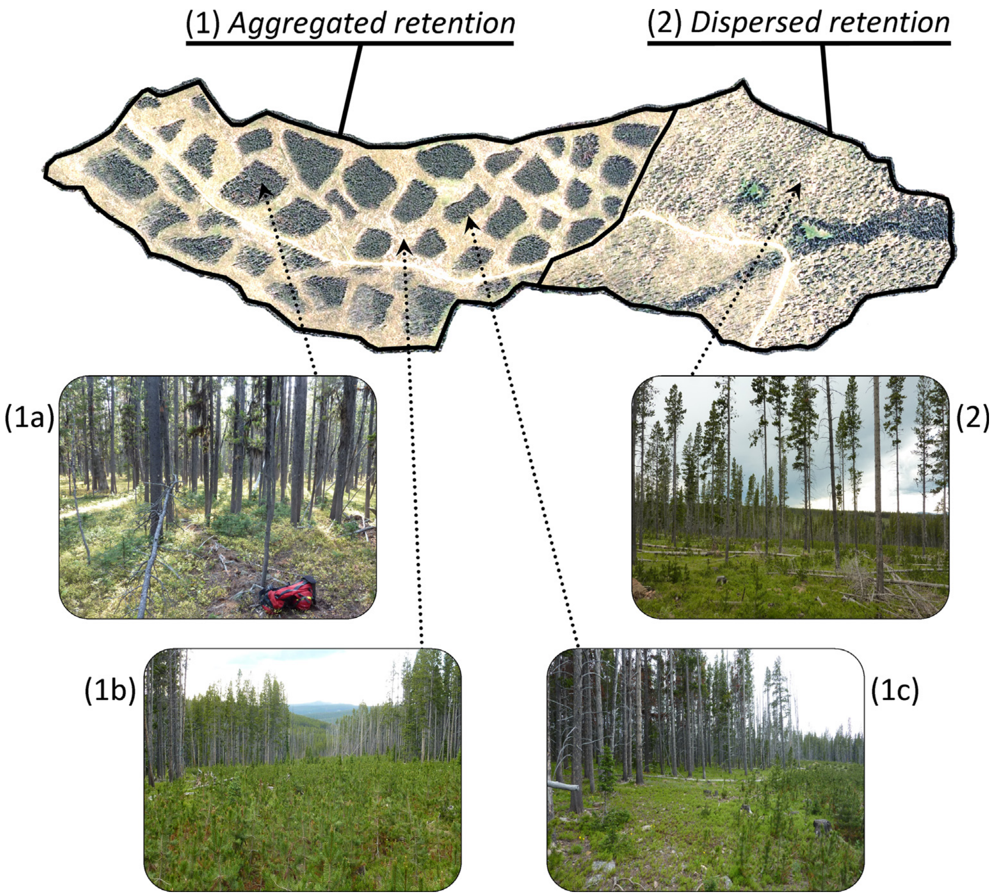

Fig. 1. Diagram of experimental retention harvest treatments at the Tenderfoot Creek Experimental Forest. Aerial photograph shows one replicate of each experimental treatment: Aggregated treatment is on the left and Dispersed treatment on the right; Unburned treatments are above the road and Burned treatments are below the road. Call-out arrows show stand profile at points within treatments: (a) patch interior, (b) opening, and (c) patch edge in Aggregated treatment, and (2) Dispersed treatment.

residual overstory was primarily distributed at an even spacing wide enough for harvesting machinery to navigate. Following harvest, half of the treatment units were broadcast burned in the fall with low-intensity fire (though severity was greater than anticipated; see Hood et al., 2012). Thus, there were a total of 16 experimental units: two RH treatments (Aggregated and Dispersed) × two fire treatments (Burned and Unburned) × two replicates × two sub-watersheds. Harvesting took place in 1999 and 2000; stands selected to be treated with prescribed fire were burned in 2002 or 2003. Pre- and post-treatment (to 2004) stand conditions have been documented in detail (Hood et al., 2012).

We report results from two overstory and regeneration sampling events, measured on 180 nested points/plots (5–17 per unit). Plots were located on a grid, independent of treatment structural attributes. Overstory trees were initially sampled using either 4.59 $m^2\,ha^{-1}$ (Dispersed) or 9.18 $m^2\,ha^{-1}$ (Aggregated) basal area factor prisms (measurement year range: 1997–2000, 0–2 years before treatment). Species, diameter at breast height (1.37 m; DBH), height, and height to live crown were measured for stems ≥10.16 cm DBH. Measured trees were revisited after harvest (prior to prescribed burn) to note which trees were cut and to establish a "post-harvest" dataset with only live, tagged trees. We used this as our "initial" measurement despite a 1 to 2 year lag between measurement and harvest in one experimental block. Another follow-up visit was made one year after burning (2003–2004) to record fire damage on overstory trees. In 2011, we measured overstory trees (species and DBH) in the treatment units using 0.040 ha circular fixed-area plots overlaid over original grid points. Thus, measurements reflect 11–14 year observation periods for overstory growth and mortality, though we simply refer to period as "11 years," which better reflects years since harvest.

Seedlings (height < 1.37 m) were tallied by species in 2004 and 2011 on 0.001 ha circular fixed-area plots which overlaid each of the overstory plot locations. Crop seedlings (tallest lodgepole pine regeneration) were measured in 2011 on four 0.010 ha quadrants of the 0.040 ha overstory plots for stocking and height growth. If at least one crop seedling was present, the quadrant was considered stocked (i.e., a value of 1) at 100 seedlings ha^{-1}; plot stocking was the average of stocked quadrants, ranging from 0 (all four quadrants unstocked) to 1 (all four quadrants stocked). Although stocking at 100 seedlings ha^{-1} is insufficient for even-aged reforestation in the region, we considered it to represent the low end of acceptable stocking in these heterogeneous multi-aged stands. Recent crop seedling periodic annual height growth was the average annual height growth over the period 2006–2010, measured retrospectively by length between whorls. In summary, our regeneration sample reflects an 11 year post-harvest regeneration process (i.e., stocking), and a four year observation period for regeneration height growth.

2.3. Analysis

We addressed our research questions by analyzing changes in the overstory and regeneration attributes over the period since treatment. We examined density and species composition for the overstory and regenerating cohort by summarizing data by treatment (n = 4 unit replicates per treatment) but refrain from statistically testing these given the change in sampling methods (switched from point sample to areal plot sample) over the measurements.

Specific stand dynamics processes (overstory basal area growth and mortality from individual tagged trees, crop regeneration ["crop seedling stocking"], and individual crop seedling height growth) were assessed and tested with general and generalized linear mixed-effects models, with measured plots nested within experimental units. We developed four statistical models for each of the four response variables: (1) a Null model (only watershed block and unit-plot nesting structure included), (2) a Treatment model (RH × fire treatment interaction included), (3) a Descriptive model (best selected model given full suite of immediately post-harvest size, structure, and environmental covariates, including fire treatment but excluding RH treatment), and (4) a Saturated model (Descriptive model plus interaction between RH × fire treatment, and RH × Fire × covariates interactions). We used AIC (Burnham and Anderson, 2002) for model selection within each response; best models were at least two AIC points less than alternative models. For Saturated models, covariates were removed if they no longer reduced AIC after including RH treatment terms. Coefficient P-values were used to identify effects in selected models, assuming $\alpha = 0.05$ means strong statistical evidence. For each model, we report marginal (fixed-effects only) and saturated (including plot and tree random effects) R^2 (Nakagawa and Schielzeth, 2013). We noted covariate explanatory power using a leave-one-out analysis in which models were refit without the covariate of interest to identify effect on marginal R^2.

Covariates used in at least one of the final linear models were: DBH, height, percent live crown, basal area greater, percent basal charring, slenderness (height:DBH), overstory stand density index (SDI), and seedling height (the only seedling metric). Each of these covariates were initial (post-harvest) measurement values (except seedling height, which was retrospectively measured to 2006). Percent live crown was the compacted length of live crown divided by tree height. Basal area greater was the summed basal area of trees with greater DBH than the tree of interest on the 0.040 ha plot. Percent basal charring was the percent of tree basal circumference with char from the prescribed fire. Height:DBH was the ratio of tree height to DBH measured in the same units. Stand density index was the metric conversion of the relative density measure developed by Reineke (1933). Seedling height was the height of the 2006 whorl of crop lodgepole pine regeneration.

The basal area growth models predicted basal area periodic annual increment for overstory trees visited in both the post-harvest and 2011 measurements (n = 122; 93% lodgepole pine). Basal area growth was modeled using lme in R (Pinheiro et al., 2016; R Core Team, 2016). The Saturated basal area growth rate model had the form:

$$y_{BA} = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_4 x_2 x_3 + \beta_5 x_4 + \beta_6 x_5 + \varepsilon_s + \varepsilon_p + \varepsilon_t \quad (1)$$

where y_{BA} was the observed periodic annual basal area growth of individual trees ($cm^2\,yr^{-1}$), β_0 through β_6 were coefficients to be estimated, x_1 was an indicator for watershed block (two levels), x_2 was an indicator for prescribed fire (0 = burned, 1 = unburned), x_3 was an indicator for retention pattern (0 = aggregated, 1 = dispersed), x_4 was percent live crown, x_5 was basal area greater (m^2 on plot), ε_s was the random stand effect (i.e., the experimental unit), ε_p was the random plot effect, and ε_t was the tree-level error. Error terms ε_s, ε_p, and ε_t were modeled as Gaussian and mutually independent. Watershed block was treated as a fixed effect because there were only two levels.

The mortality models predicted tree death between the two overstory measurements (n = 177; 93% lodgepole pine). This response (0 = live, 1 = dead) was modelled as a conditionally binomial process with random stand and plot effects using glmer in R (Bates et al., 2015). Conditional on these random effects, the expected response given the Saturated model is $\frac{e^{\rho_{mort}}}{1 + e^{\rho_{mort}}}$, where

$$\rho_{mort} = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_4 x_2 x_3 + \beta_5 x_4 + \beta_6 x_5 + \beta_7 x_6 + \beta_8 x_7 + \beta_9 x_8 + \varepsilon_s + \varepsilon_p \quad (2)$$

and β_0 through β_6 were coefficients to be estimated, x_1 was an indicator for watershed block (two levels), x_2 was an indicator for prescribed fire (0 = burned, 1 = unburned), x_3 was an indicator for retention pattern (0 = aggregated, 1 = dispersed), x_4 was DBH (cm), x_5 was tree height (m), x_6 was height:DBH, x_7 was percent basal char, x_8 was percent live crown, ε_s was the random stand effect, and ε_p was the random plot effect. Error terms ε_s and ε_p were modeled as Gaussian and mutually independent.

The stocking model predicted 2011 lodgepole pine regeneration stocking at 100 trees ha^{-1}, i.e., the proportion of the four 0.01 ha quadrants of a 0.04 ha circular plot with at least one seedling (n = 129 plots). Since the response was a proportion bounded by 0 (unstocked) and 1 (stocked), it was modelled as a conditionally binomial process with random stand effects using glmer in R. Conditional on these random effects, the expected response given the Saturated model is $\frac{e^{\rho_{stock}}}{1 + e^{\rho_{stock}}}$, where

$$\rho_{stock} = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_4 x_2 x_3 + \beta_5 x_4 + \varepsilon_s \quad (3)$$

and β_0 through β_6 were coefficients to be estimated, x_1 was an indicator for watershed block (two levels), x_2 was an indicator for prescribed fire (0 = burned, 1 = unburned), x_3 was an indicator for retention pattern (0 = aggregated, 1 = dispersed), x_4 was SDI, and ε_s was the random stand effect. Error term ε_s was modeled as Gaussian and independent. Stocking was the only plot-scale response that we modeled in this study; all other models incorporated plot effects to account for within-stand correlations. We verified there was no within-stand autocorrelation for the proportion stocked response using Moran's I (Paradis et al., 2004).

The height growth model predicted recent periodic annual height growth of crop regeneration seedlings, based on up to four years of growth ending in 2010 (n = 333). Height growth was modeled using lme in R. The Saturated height growth rate model had the form:

$$y_{HT} = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_4 x_2 x_3 + \beta_5 x_4 + \beta_6 x_5 + \beta_7 x_6 + \varepsilon_s + \varepsilon_p + \varepsilon_t \quad (4)$$

where y_{HT} was the observed periodic annual height growth ($cm\,yr^{-1}$), β_0 through β_6 were coefficients to be estimated, x_1 was an indicator for watershed block (two levels), x_2 was an indicator for prescribed fire (0 = burned, 1 = unburned), x_3 was an indicator for retention pattern (0 = aggregated, 1 = dispersed), x_4 was SDI, x_5 was seedling height (cm), ε_s was the random stand effect, ε_p was the random plot effect, and ε_t was the tree-level error. Error terms ε_s, ε_p, and ε_t were modeled as Gaussian and mutually independent.

Variability in stand structure by treatment was analyzed by inspecting the distribution of overstory basal area and understory stem densities across and within experimental units via boxplots, quartiles (0, 25, 50, 75, and 100th percentiles), and standard deviations. For example, we compared the treatment average of experimental unit ranges, 75th percentiles, etc., as well as the variability (standard deviation) of these ranges and percentiles. Treatment differences in the variability of stand dynamics processes (i.e., overstory basal area growth, overstory mortality, regeneration stocking, regeneration height growth) were assessed using Levene's test. Although Levene's test is most typically used to identify homoscedasticity for model assumptions, we used it to identify differences in variance (i.e., heterogeneity) across treatment.

3. Results

3.1. Overstory

3.1.1. Stand structure and composition

Mean post-harvest basal area densities in treated stands ranged from 10.4 $m^2\,ha^{-1}$ to 28.0 $m^2\,ha^{-1}$ (Table 1), 27–58% of pre-harvest densities. Immediately after harvest (but prior to burning), plots in the Aggregated Burned treatment had the highest basal area densities, which differed from the Unburned analog despite having the same harvest prescription – this difference in densities may be partly due to the systematic grid sample design and difficulty executing these treatments. Overall, Aggregated RHs had low minima and high maxima, reflecting stand openings juxtaposed with dense retention patches (Figs. 1 and 2). Dispersed RH treatment densities were within the range

Table 1
Post-harvest (~2000) and 2011 overstory structure by retention harvest and prescribed fire treatment (mean and 1 standard error).

Measurement	Retention harvest	Fire	Trees	Basal area	Quadratic mean diameter	SDI	Lodgepole pine
			ha^{-1}	$m^2\,ha^{-1}$	cm	ha^{-1}	% of basal area
Pre-harvest	Aggregated	Burned	1561 (139)	47.9 (5.1)	19.7 (0.7)	1042 (104)	85.6 (8.3)
	Aggregated	Unburned	1138 (330)	36.9 (4.5)	21.6 (1.8)	788 (119)	84.6 (8.9)
	Dispersed	Burned	1428 (141)	47.1 (2.2)	20.7 (1.2)	1008 (44)	85.8 (8.3)
	Dispersed	Unburned	1227 (229)	40.8 (2.0)	21.4 (2.0)	869 (65)	89.9 (8.0)
Post-harvest	Aggregated	Burned	863 (86)	28.0 (1.6)	20.5 (0.7)	603 (38)	84.4 (10.0)
	Aggregated	Unburned	313 (173)	10.4 (2.7)	25.6 (4.1)	218 (71)	83.3 (16.7)
	Dispersed	Burned	411 (157)	15.3 (5.0)	26.5 (4.5)	319 (107)	86.3 (8.0)
	Dispersed	Unburned	296 (149)	11.0 (2.2)	25.4 (3.5)	227 (58)	98.2 (1.8)
2011	Aggregated	Burned	490 (92)	18.3 (3.3)	21.9 (0.2)	383 (70)	86.8 (7.3)
	Aggregated	Unburned	360 (153)	11.2 (2.9)	21.4 (1.4)	241 (71)	80.5 (11.3)
	Dispersed	Burned	105 (27)	4.8 (1.0)	24.7 (1.9)	96 (21)	95.4 (4.1)
	Dispersed	Unburned	193 (25)	8.9 (0.9)	24.4 (1.0)	178 (17)	88.2 (8.4)

of Aggregated treatment densities. Similar to the Aggregated treatments, stands assigned to the Burn treatment in the Dispersed RH treatment initially had greater densities than the stands assigned to the Unburned treatment.

By 2011 (approximately 11 years after harvest and 8 years after prescribed fire), mean basal area densities in the Aggregated RH treatments became more similar following a 35% reduction in Burned treatment basal area and a slight increase in the Unburned treatment (Table 1). In Aggregated RH treatments, basal area densities remained higher in the Burned treatment relative to the Unburned treatment, but in the Dispersed RH treatment basal area in the Unburned treatment became slightly greater than in the Burned treatment, where basal area dropped in response to fire (Fig. 2). The average range of values decreased 40–55% in the Dispersed treatment compared to only a 25% reduction in the Aggregated treatments. Furthermore, variability throughout the Dispersed treatments' distributions (i.e., by quartile) declined substantially (by an average of 48% and 70% for the Unburned and Burned, respectively) but variability among quartiles increased or only slightly decreased in the Aggregated treatments (+40% in Burned or −8% in Unburned). Altogether, this indicates that the Dispersed RH pattern moderated structural heterogeneity changes over time relative to the Aggregated.

Lodgepole pine dominated overstory species composition throughout the duration of this study (Table 1), followed by subalpine

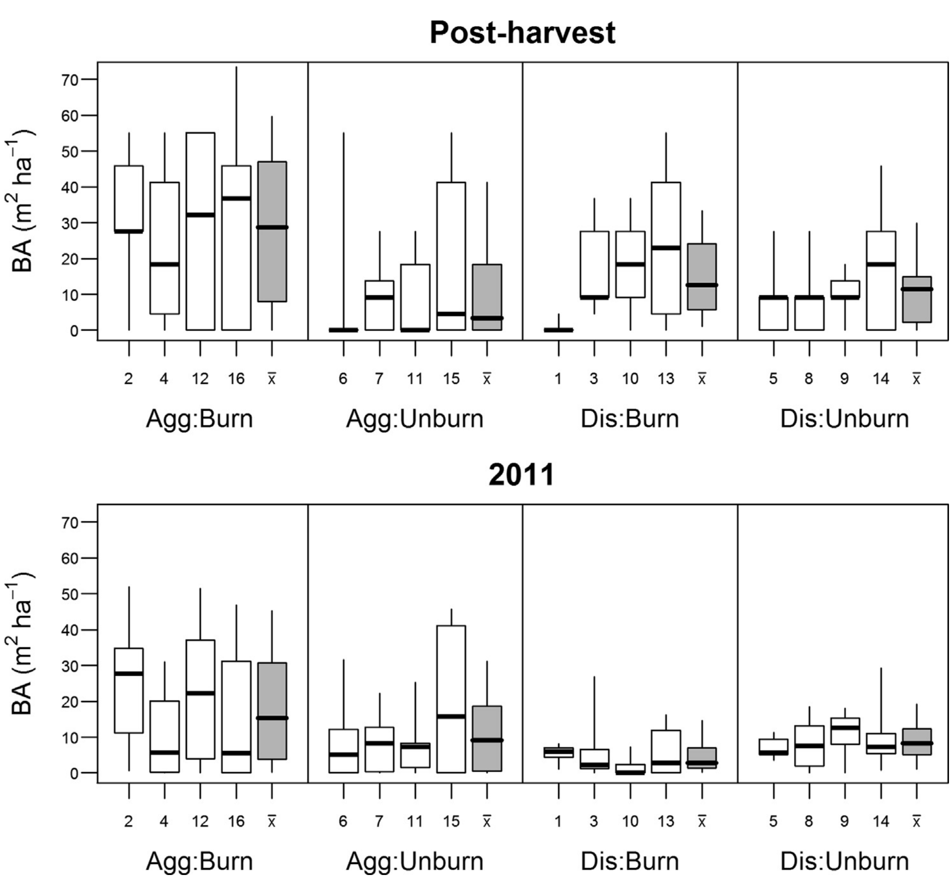

Fig. 2. Boxplots of post-harvest (~2000) and 2011 live overstory basal area by experimental unit and treatment. For white boxplots (labeled by stand number), whiskers extend from minimum to maximum stand values, box shows first quartile, median, and third quartile. Gray boxplots (labeled by $\bar{x}$) illustrate the within-treatment mean of each of those statistics (e.g., average of maximums).

Table 2
Linear regression model coefficients, P values, and fit statistics for four models of annual tree basal area growth (cm^2) between post-harvest (~2000) measurement and 2011. Coefficients for random effects (Unit and Plot within Unit) are not shown.

	Null		Treatment		Descriptive		Saturated	
Predictor	Coef	P value	Coef	P value	Coef	P value	Coef	P value
Intercept	2.726	0.000	2.150	0.000	9.078	0.000	7.771	0.000
Watershed (Sun Creek)	2.099	0.023	1.868	0.016	1.622	0.048	1.580	0.027
RxFire (Unburned)			−0.923	0.284			−1.683	0.057
Retention Pattern (Dispersed)			0.960	0.336			0.647	0.485
RetPattern × RxFire (Disp:U)			2.880	0.062			3.624	0.019
Live crown (%)					0.059	0.006	0.071	0.000
SDI					−0.002	0.026		
BA greater (m^2)					−7.233	0.012	−8.361	0.003
Fit stats								
Marginal R^2	0.07		0.20		0.24		0.31	
Conditional R^2	0.17		0.20		0.36		0.31	
AIC	−1004.5		−1014.7		−1019.7		−1029.5	

fir and Engelmann spruce. Immediately after harvest, overstory lodgepole pine composition was 9% lower in the Aggregated than Dispersed treatments. By the 2011 measurement, average Aggregated treatment lodgepole pine composition was still 9% lower than Dispersed treatments, though composition shifted slightly across treatments.

3.1.2. Overstory tree growth

Treatment terms improved annual basal area growth model fit over the Null model, and there was marginal statistical evidence of the RH × fire treatment interaction ($P = 0.062$; Table 2). Overstory tree annual basal area growth in Aggregated treatments averaged 2.86 cm^2 (95% CI: 1.95–3.77) in Burned and 1.79 cm^2 (0.36–3.21) in Unburned, and Dispersed treatments averaged 3.62 cm^2 (1.89–5.35) in Burned and 5.89 cm^2 (4.47–7.32) in Unburned. Levene's test of homoscedasticity indicated that variance was not different across treatments (P-value = 0.3436).

The Descriptive model indicated that basal area growth was better predicted by post-harvest percent live crown, overstory SDI, and basal area greater than the response tree (Table 2). These covariates had opposite effects, showing that basal area growth increased with relative crown size but diminished with increasing competition (Fig. 3). Percent live crown and basal area greater comprised 27% and 19%, respectively, of the explanatory power of the model. The Saturated model indicated that treatment factors were still important even after accounting for covariates (interaction term, $P = 0.019$), though SDI no longer improved model AIC (Table 2).

3.1.3. Overstory tree mortality

Treatment terms only minimally improved the mortality model over the Null (Table 3). Over the entire period, mortality rates in the Aggregated treatments were 28.0% (95% CI: 14.4–47.4) in Burned and 26.8% (9.1–57.1) in Unburned, and Dispersed treatment rates were 54.9% (27.4–80.0) in Burned and 8.6% (2.0–30.4) in Unburned. Among Burned treatments, tree mortality in the Dispersed retention was especially high because fire thoroughly spread throughout each unit, while fire in the Aggregated treatment generally did not enter into retention patches. Levene's test of homoscedasticity suggested that variability of mortality differed by treatment (P-value = 0.0095). Mortality was most variable in the Dispersed Burned and least variable in the Dispersed Unburned treatment.

Mortality was best predicted with five covariates in the Descriptive model: post-harvest tree DBH, height, slenderness (height:DBH), percent live crown, and percent basal char (Table 3). These covariates indicated that probability of mortality increased with percent basal char, height:DBH, and DBH, but decreased with tree height and percent live crown (Table 3; Fig. 4). Percent basal char was the most influential covariate in this model, comprising 73% of the marginal R^2;

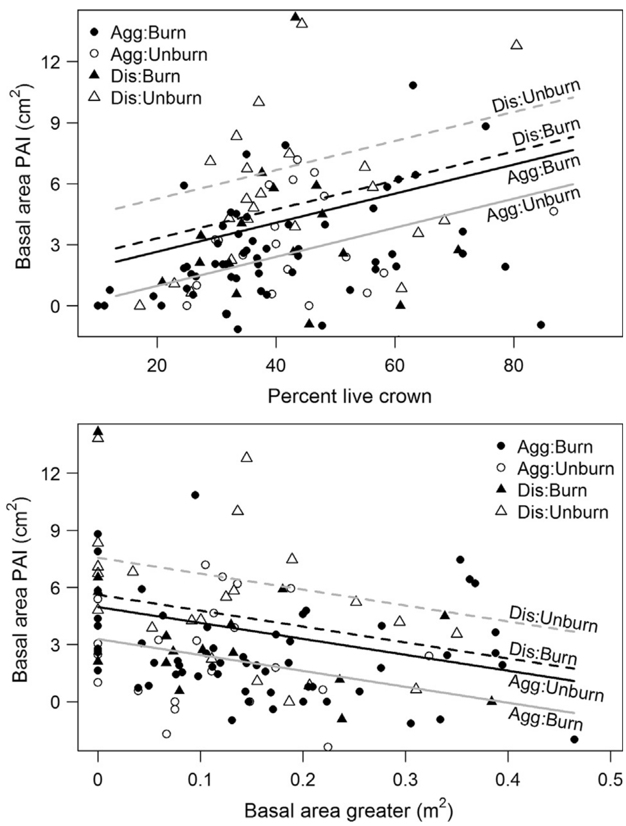

Fig. 3. Treatment partial predictions (assuming median value of other covariate) of basal area periodic annual increment from the Saturated model as a function of percent live crown (top panel) and basal area greater (post-harvest basal area of neighboring stems greater than individual tree; bottom panel).

height:DBH comprised 22% of the explanatory power. After accounting for these covariates in the Saturated model, prescribed fire and RH treatment factors were no longer significant predictors (Table 3).

3.2. Regeneration

3.2.1. Abundance and composition

Natural regeneration was abundant in all the treated stands in 2004 and 2011 with lowest average abundance over 5000 seedlings ha^{-1} (Table 4). In 2004, Aggregated treatments had 50% more seedlings than Dispersed treatments, and Burned treatments had 31% more than Unburned. By 2011, pooled seedling density decreased by 26%, except in

Table 3
Logistic regression model coefficients, P values, and fit statistics for four models of overstory tree mortality between post-harvest (~2000) measurement and 2011. A predicted value of 1 indicates a 100% probability of mortality. Coefficients for random effects (Unit and Plot within Unit) are not shown.

	Null		Treatment		Descriptive		Saturated	
Predictor	Coef	P value	Coef	P value	Coef	P value	Coef	P value
Intercept	−1.096	0.006	−1.080	0.022	−21.512	0.001	−22.274	0.001
Watershed (Sun Creek)	0.339	0.563	0.416	0.476	0.611	0.419	0.478	0.514
RxFire (Unburned)			−0.093	0.906			1.756	0.115
Retention Pattern (Dispersed)			1.100	0.138			−0.068	0.942
RetPattern × RxFire (Dis:U)			−2.493	0.055			−1.094	0.465
DBH (cm)					0.497	0.002	0.476	0.002
Tree height (m)					−0.448	0.025	−0.428	0.032
Ht:DBH					0.162	0.002	0.155	0.002
Basal char (%)					0.059	0.000	0.064	0.000
Live crown (%)					−0.033	0.154	−0.039	0.103
Fit stats								
Marginal R^2	0.01		0.10		0.52		0.54	
Conditional R^2	0.37		0.43		0.73		0.73	
AIC	216.4		214.1		163.9		164.2	

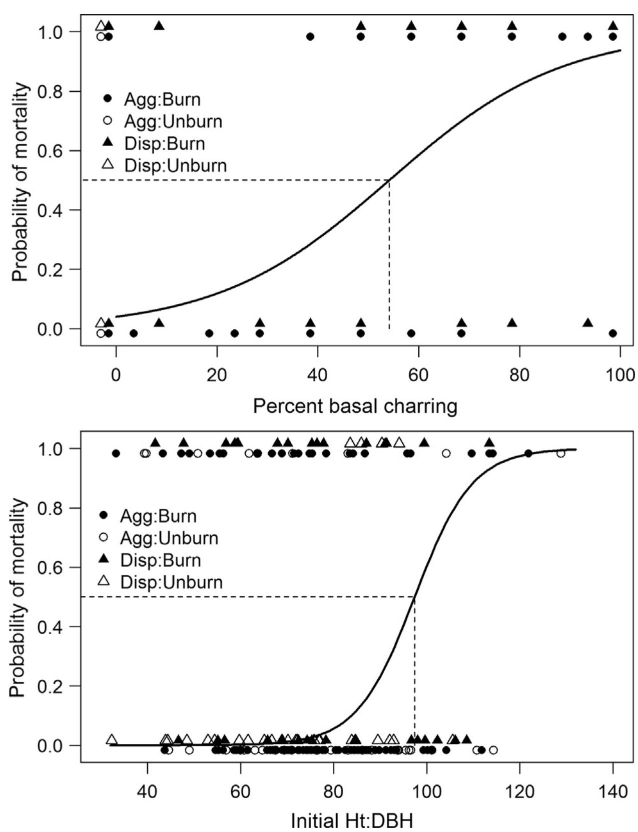

Fig. 4. Partial predictions (assuming median value of other covariates) of periodic stem mortality from the Descriptive model as a function of percent basal charring (top) and post-harvest height:DBH (bottom). Dashed line illustrates 50% probability of mortality.

the Dispersed Unburned where it increased 54%. Burned treatments had 79% greater in-stand variability than Unburned in 2004, but by 2011 variability decreased by 46%, except in Dispersed Unburned where it increased 50%. In-stand variability was only substantially less than the mean (coefficient of variation < 1) in 2011's Aggregated Unburned treatment. Lodgepole pine comprised 51% of seedlings across treatments in 2004, while the remainder was predominantly subalpine fir. Between 2004 and 2011, the proportion of lodgepole pine seedlings decreased by 44% and was eclipsed primarily by subalpine fir. Combined Engelmann spruce and whitebark pine seedling composition was never greater than 5.5% in the 2004 measurement, and not more than 13.3% in 2011 (both in the Dispersed Burned treatment).

3.2.2. *Crop seedling stocking*

The Treatment stocking model was only slightly more appropriate than the Null model (Table 5). In 2011, lodgepole pine seedling stocking in Aggregated treatments was 60.9% (95% CI: 32.2–83.6) in Burned and 72.2% (42.7–90.0) in Unburned, and in Dispersed treatments was 97.4% (78.6–99.7) in Burned and 86.4% (60.1–96.4) in Unburned. Levene's test of homoscedasticity indicated that variability in stocking differed by treatment (P-value = 0.0005). Burning caused both high (in Aggregated) and low (in Dispersed) variability in stocking estimates.

Post-harvest SDI was the sole covariate that explained seedling stocking in the Descriptive model (Table 5). The SDI covariate indicated that the relative density of the overstory hindered crop seedling stocking (Fig. 5). Treatment terms were included in the Saturated model, but it was not more appropriate than the simpler Descriptive model. Yet, the marginally significant retention pattern term (P-value = 0.062) indicated that SDI may be unable to fully account for variability in stocking across treatments.

3.2.3. *Crop seedling height growth*

The Null height growth model was just as appropriate as the Treatment model (Table 6). Recent periodic annual height growth of lodgepole pine seedlings by 2010 was 17.3 cm (95% CI: 15.2–19.3) in Burned and 18.0 cm (15.5–20.5) in Unburned Aggregated treatments, and 16.2 cm (14.3–18.1) in Burned and 14.1 cm (12.0–16.2) in Unburned Dispersed treatments. Levene's test of homoscedasticity suggested that variability in growth did not significantly differ across treatments (P-value = 0.0946).

According to the Descriptive model, height growth was best predicted by post-harvest SDI, prescribed fire occurrence, the square root of the seedling height at the beginning of the recent period (as early as 2006), and the interaction between prescribed fire and seedling height (Table 6). We used the square root transformation of initial height because it reduced model AIC by 3.4 points and visually improved fit on the partial prediction plot (Fig. 6). These covariates indicate that overstory competition reduced height growth, that seedling height had a diminishing improvement on growth for Burned treatments, and that height growth was largely independent of seedling height in Unburned treatments (Fig. 6). After accounting for these covariates in the Saturated model, RH treatment factors were still not statistically significant (Table 6).

Table 4
Natural regeneration abundance mean, in-stand standard deviation, and composition in treated units in 2004 (1–2 years after burning) and in 2011. Values in parentheses are 1 standard errors.

Measurement	Retention harvest	Fire	Mean	In-stand st.dev.	Lodgepole pine	Subalpine fir
			Stems ha^{-1}	Stems ha^{-1}	%	%
2004	Aggregated	Burned	10,441 (4026)	14,119 (3184)	48.9 (26.2)	50.7 (25.9)
	Aggregated	Unburned	8961 (2243)	10,394 (2589)	51.8 (22.5)	46.0 (21.8)
	Dispersed	Burned	7906 (1904)	13,711 (2591)	46.8 (16.5)	47.6 (13.6)
	Dispersed	Unburned	5017 (1109)	5160 (3572)	57.4 (18.4)	39.8 (18.9)
2011	Aggregated	Burned	8494 (2890)	8445 (6486)	36.6 (26.2)	61.7 (25.6)
	Aggregated	Unburned	6550 (3500)	4893 (1922)	13.5 (11.0)	86.3 (11.2)
	Dispersed	Burned	5414 (1988)	7548 (2008)	22.7 (16.4)	64.0 (15.6)
	Dispersed	Unburned	7714 (3557)	7758 (1134)	42.8 (24.6)	51.4 (23.8)

4. Discussion

Our study demonstrates the importance of both retention pattern and prescribed fire in driving stand dynamics, especially for overstory tree growth, overstory tree mortality, and regeneration stocking. All treatments had ample regeneration and high in-stand variability throughout the study period, although subalpine fir regeneration composition was disproportionally greater than its presence in the overstory. Second, we identified that retention pattern did not contribute to the mechanistic understanding of overstory tree mortality, nor regeneration height growth, and only marginally for regeneration stocking; instead, combinations of overstory competition, tree size, and tree form more directly explained the effect of treatment on those processes. Third, Aggregated retention treatments maintained overstory spatial heterogeneity better than Dispersed retention treatments over the measurement period.

This study examines stand structures and processes following a retention harvest experiment. Although the experiment prescribed 50% basal area retention, our data indicate that the prescription was not met across treatment type. This inconsistency may be an artifact of our sample design, but it also indicates the difficulty in executing such a prescription in this forest type. We note that contrasts between Aggregated and Dispersed treatments are not just due to harvest pattern, but also to differences in forest density. Thus, our inference most appropriately applies to treatments prescribed for 50% retention; our interpretations do not assume actual retention levels are constant across harvest pattern.

4.1. Stand dynamics by treatment

Eleven years after treatments, overstories were still dominated by lodgepole pine despite a slight decline. Lodgepole pine overstory dominance was greater in Burned treatments likely due to a loss of subalpine fir, which has slightly thinner bark and greater sensitivity to light fire than lodgepole pine (Hood et al., 2008; Lotan and Critchfield, 1990; Ryan and Reinhardt, 1988). Fischer and Clayton (1983) identified that low-intensity fires maintain lodgepole dominance (and self-succession) in unmanaged Douglas-fir, subalpine fir, and Engelmann spruce habitat types east of the Continental Divide by reducing stem density, fuels, and shade-tolerant species (see also Agee, 1993). Without shade-tolerant species removal by wildfire or silvicultural treatments, overstory composition will eventually transition to a fir-spruce forest, thus failing to perpetuate the multi-aged lodgepole pine structure associated with mixed-severity fire that treatment was modeled after.

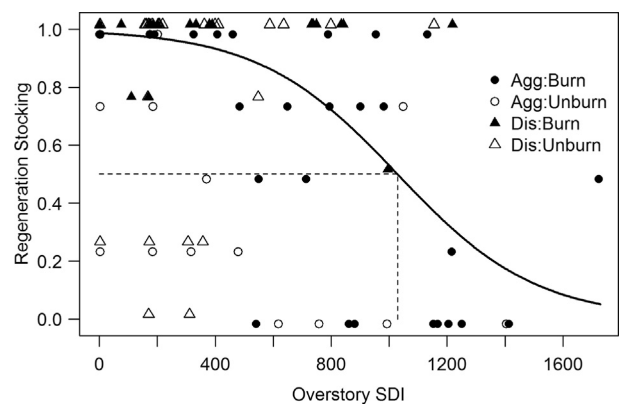

Fig. 5. Predicted regeneration stocking from the Descriptive model by post-harvest overstory SDI. Dashed line illustrates 50% probability of stocking.

It was surprising that lodgepole pine was a minority in 2011's seedling species composition, 11 years after harvest. Since treatments removed 42–73% of initial stand basal area, and residual overstory composition was over 80% lodgepole pine, we expected more

Table 5
Logistic regression model coefficients, P values, and fit statistics for four models of crop seedling stocking in 2011. A predicted value of 1 indicates 100% stocked with 100 regenerated lodgepole pine per hectare. Coefficients for random effects (Unit and Plot within Unit) are not shown.

	Null		Treatment		Descriptive		Saturated	
Predictor	Coef	P value	Coef	P value	Coef	P value	Coef	P value
Intercept	0.942	0.068	−0.123	0.853	3.209	0.001	2.817	0.021
Watershed (Sun Creek)	1.294	0.115	1.356	0.065	1.094	0.354	1.310	0.214
RxFire (Unburned)			0.427	0.611			−1.243	0.336
Retention Pattern (Dispersed)			3.258	0.015			3.444	0.062
RetPattern × RxFire (Disp:U)			−2.274	0.151			−2.082	0.341
SDI					−0.004	0.000	−0.004	0.000
Fit stats								
Marginal R^2	0.08		0.33		0.36		0.55	
Conditional R^2	0.35		0.45		0.68		0.71	
AIC	132.3		129.0		100.9		99.5	

Table 6
Linear regression model coefficients, P values, and fit statistics for four models of recent (up to 4 year) annual crop seedling height growth (cm) by 2010. Coefficients for random effects (Unit and Plot within Unit) are not shown.

	Null		Treatment		Descriptive		Saturated	
Predictor	Coef	P value	Coef	P value	Coef	P value	Coef	P value
Intercept	16.780	0.000	17.608	0.000	13.300	0.000	13.947	0.000
Watershed (Sun Creek)	−1.145	0.301	−1.166	0.220	−1.541	0.180	−1.562	0.139
RxFire (Unburned)			0.230	0.864	2.559	0.241	3.108	0.206
Retention Pattern (Dispersed)			−0.869	0.509			−1.420	0.325
RetPattern × RxFire (Disp:U)			−1.753	0.343			−0.740	0.709
SDI					−0.003	0.003	−0.003	0.005
$\sqrt{\text{start height}}$ (cm)					5.654	0.000	1.036	0.000
RxFire (Unburned) × $\sqrt{\text{start height}}$					−4.445	0.011	−0.828	0.009
Fit stats								
Marginal R^2	0.01		0.05		0.11		0.15	
Conditional R^2	0.47		0.47		0.45		0.46	
AIC	−314.9		−313.8		−337.6		−337.1	

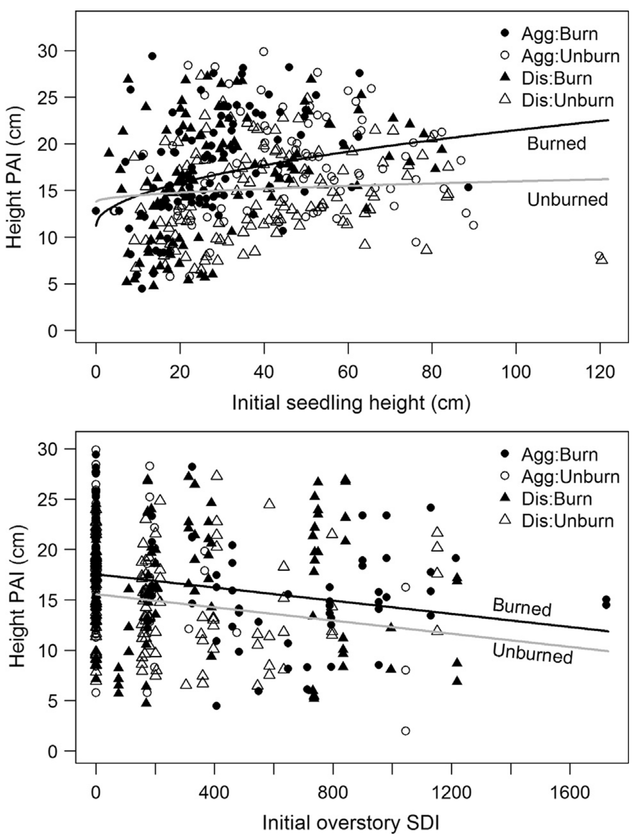

Fig. 6. Treatment partial predictions (assuming median value of other covariates) of crop regeneration height periodic annual increment from the Descriptive model as a function of initial seedling height (top) and post-harvest overstory SDI (bottom).

regeneration from the shade-intolerant species (but see similar compositional shift in Day (1970)). The heavy shade-tolerant composition (subalpine fir and Engelmann spruce) may have been mostly advance regeneration (more than 27,000 seedlings ha^{-1} prior to treatment versus only 265 seedlings ha^{-1} of lodgepole pine, data not shown), but this study did not document regeneration age nor losses due to logging equipment and prescribed fire. Lodgepole pine may also be the minority in composition because of an asynchrony between cone production and treatment schedule, limited lodgepole pine seed release, or destruction of regeneration by treatment. Northern Rocky Mountain lodgepole pine in mixed-severity fire regimes has semi-serotinous cones (generally considered 50% serotinous; Lotan and Perry, 1983; Muir and Lotan, 1985), and we expected open-cone seed to be supplemented with seed from serotinous cones that opened from burning or with elevated forest floor temperatures in the summer (Lotan, 1964). We found no consistent stocking trend by prescribed fire treatment, so it is apparent that cone serotiny at least did not limit widespread regeneration success at 100 seedlings ha^{-1}. Lodgepole pine's rapid early height growth may lead to height stratification over the shade-tolerant species despite its compositional minority (Cobb et al., 1993; Fahnestock, 1976). Traits that make lodgepole pine an adept colonizer after mixed-severity fire (i.e., prolific regeneration, cone serotiny, and rapid early height growth) may also stimulate thriving cohorts in stands managed with RH, though this study shows that lodgepole pine may not be dominant in the first decade after treatment.

Retention pattern and prescribed fire impacted overstory basal area growth and mortality over the measurement period. Namely, trees in the Unburned Dispersed treatment had greater growth and survival than expected from either treatment factor alone. Greater residual tree growth after Dispersed RH has been documented in other studies. For instance, Douglas-fir dominated stands in the Demonstration of Ecosystem Management Options (DEMO) study showed greater volume growth with dispersed retention (Maguire et al., 2006; Urgenson et al., 2013b). This was accompanied with more overstory mortality, but the effect on Douglas-fir mortality was moderated by retention level. In Minnesota red pine, biomass growth was also slightly greater after dispersed retention, but mortality rates did not differ by treatment (Palik et al., 2014). However, these retention studies did not investigate the effects of prescribed fire, nor are studies of underburning in lodgepole pine forests common, so our study adds depth to both retention and lodgepole pine studies.

Our results suggest why there are few experiments studying burning in this forest type: lodgepole pine survivorship is sensitive to even low-intensity fire if it chars more than half of the bole. These results are consistent with the argument by Lotan et al. (1985) who make the case that broadcast burning in lodgepole pine forests achieves multiple-use management objectives, but then caution that burning should be implemented with special care to avoid mortality. Although burning may have increased the proportion of overstory lodgepole pine, our data suggests that combining broadcast burning with a Dispersed pattern conflicts with treatment objectives in this forest type because of the substantial overstory loss. Median basal area densities in the Dispersed Burned treatment were a third of those in the Dispersed Unburned treatments in 2011, and mean basal area was only 13% of pre-treatment density. Whereas 10% to 15% overstory retention may be desirable for other forest types or objectives (e.g., Baker and Read, 2011; Mitchell and Beese, 2002), the extensive overstory mortality and accumulation of forest fuels (Crotteau et al., 2016) in these burned stands was not the original management intention. More research is needed to evaluate the benefits that broadcast burning has on wildlife habitat, biodiversity, hydrology, disturbance resilience, and aesthetics in lodgepole pine forests to adequately consider management tolerance for diminished stand-scale growth and increased mortality in the Dispersed overstory.

This study also showed that crop seedling stocking was greatest in Dispersed treatments, but that height growth was similar across all treatments. In the DEMO study, planted seedling mortality was greater in the Aggregated treatment for mid- and shade-tolerant species (Maguire et al., 2006), and though stocking was typically sufficient, it was occasionally low in the Aggregated treatment (Urgenson et al., 2013a). In contrast, planted seedling survival did not vary by treatment in a similar red pine experiment (Palik et al., 2014). As for height growth, the DEMO study showed greater height growth for shade intolerant species in the Aggregated treatment (Maguire et al., 2006). At the red pine experiment, seedling biomass growth was not statistically different by treatment, though it was greater in the openings of Aggregated treatments (Palik et al., 2014). In Alberta, regeneration growth was negatively impacted by increasing levels of dispersed overstory retention in the Ecosystem Management Emulating Natural Disturbance (EMEND) experiment (Gradowski et al., 2008). We expected greater regeneration growth in Aggregated than Dispersed treatments because Dispersed treatments had similar structure to an even shelterwood, which casts shade over the forest floor and promotes even distribution of stocking but hinders regeneration growth (Nyland, 2016). However, height growth was similar across treatments, likely because overstory survival was so low in Dispersed treatments, making regeneration conditions similar to the open environments in the Aggregated treatments.

4.2. What drives differences in stand dynamics?

Tree basal area growth is important for overstory resistance to wind damage and continued function of two-storied stands. Basal area growth is also a measure of tree vigor, which may improve resistance to successful bark beetle attack (Larsson et al., 1983). Our Saturated basal area growth model indicated that both competition (basal area greater) and percent live crown were important predictors of overstory tree growth. These were expected results (e.g., per Hann and Larsen, 1990; Wykoff, 1990), but we were surprised that absolute measures of tree size such as basal area, height, and volume were excluded from the final model. Although basal area periodic annual increment is mechanistically explained by measures of crown size and competition, the significant treatment factors in the Saturated model illustrated there was some unmeasured element that contributed to variability in growth across treatment. Since greatest growth was in the Dispersed treatments, it is likely that the significant treatment factor accounted for the more diffuse competition in those treatments than the Aggregated, where competition was densely clumped.

The Descriptive mortality model showed that mortality was linked to tree DBH, height, height:DBH, percent basal char, and percent live crown. The positive influence of DBH on mortality was counter-intuitive because large trees typically out-compete smaller neighbors. As such, our model suggests that competition has not been the primary driver of mortality during this measurement period, an idea confirmed by the absence of competition covariates in the models. Fire was the predominant mortality agent in this study, as shown by the predictive power of the basal char term. These results confirm that the impact prescribed fire has on tree mortality (Hood et al., 2008; Ryan and Reinhardt, 1988) persists over a long measurement period, and that fire damage is still an important predictor of mortality even after controlling for tree size and competitive environment. Our model predicts 50% probability of mortality at 54% basal charring, which emphasizes that lodgepole pine tolerates fire poorly, and that patchy prescribed fire in this forest type can radically improve tree survival by retaining unburned refugia. Additionally, the height:DBH model term suggests that wind was a significant mortality agent (as expected by Alexander, 1966) since high height:DBH values (slender trees) are associated with wind damage (Cremer et al., 1982; Wonn and O'Hara, 2001). This confirmed observations made by Hardy et al. (2006), who provide anecdotal evidence of wind-induced mortality shortly after initiating the Tenderfoot Project. Lavoie et al. (2012) identified that height:DBH was a significant predictor of mortality associated with Dispersed retention in eastern Canada, but not with Aggregated retention patterns. Our model did not discriminate by retention pattern, and suggested trees with height:DBH of 97 had a 50% probability of mortality. However, tree slenderness moderated mortality less than we expected, as a height:DBH of 80 is recognized as a threshold for wind damage (Wonn and O'Hara, 2001). Finally, since treatment factors were not significant, we identified that mortality was closely tied to tree size, shape, and charring, and not to competition or an unmeasured attribute of treatment-scale spatial structure.

Regeneration stocking was limited by post-harvest overstory density, which was greatest in the Aggregated Burned treatment. We expected a significant overstory density coefficient because overstory competition inhibits successful regeneration of shade-intolerant lodgepole pine (Lotan and Critchfield, 1990). Surprisingly, our model predicts 50% stocking at an overstory SDI of 960, 55% of the maximum SDI for lodgepole pine and well beyond site occupancy where we expect lodgepole regeneration to flourish (McCarter and Long, 1986). Although McCarter and Long (1986) found that lodgepole pine regeneration stocking improved with overstory removal intensity, Alexander (1966) also found 53% stocking of advance regeneration in the uncut control, suggesting that stocking is less sensitive to residual overstory than regeneration abundance and growth are. Overstory tree presence, as a seed source, may have had a positive impact on stocking if retention level in these treatments was lower or more clumped (for instance, Cochran (1973) recommends openings less than two tree heights for optimum regeneration stocking in non-serotinous lodgepole pine). However, canopy openings in this study were small enough for adequate wind-based seed dispersal. The marginally significant treatment term adds explanatory power to the fit beyond the effect of overstory density, but not enough to suggest causality of an unmeasured covariate that varies systematically by treatment. Therefore, 2011 crop seedling stocking in this study is primarily a function of post-harvest overstory density, but predictive capacity was slightly improved by treatment factors. This is important because stocking (i.e. regeneration presence) increases stand resilience to bark beetles. Mountain pine beetle populations generally do not amplify to outbreak levels in cohorts less than 20 cm DBH or 80 years old (Axelson et al., 2010; Safranyik and Carroll, 2006), so regeneration secures stand resilience even if overstory is lost in a bark beetle outbreak.

Like the overstory tree growth model, the seedling height growth model supports our expectation that competition hinders growth. We correctly anticipated that seedling size influences growth rate (Stage, 1975). The square root function effectively characterized the relationship between size and growth because increments in size improved height growth more for small trees than for larger trees in the regenerating cohort. We did not expect that starting height would improve growth in one treatment (Burned) but not the other (Unburned), although the Unburned treatment had slightly greater average starting heights. We suspect that the combination of seedling size and burning treatment may be due to a post-burn nutrient pulse through the soil profile that only the early-initiated regeneration were able to utilize (Vitousek and Matson, 1985). Giardina and Rhoades (2001) observed a positive seedling growth response to burned soils in the laboratory, but failed to find it in the coupled field study, partially supporting our results but also suggesting that growth response to burning is complex and variable. Since retention tree spatial pattern (and its interaction with prescribed fire) did not significantly influence regeneration growth, we confirm that overstory density is paramount for regeneration height growth.

4.3. Treatment influence on spatial heterogeneity

Stand scale resistance and resilience to both bark beetle outbreak and crown fire may increase with spatial and structural heterogeneity (Crotteau et al., 2016; Johnson et al., 2014; Ziegler et al., 2017). Retention harvests created heterogeneous, non-normally distributed basal area distributions in treated units, especially in the Aggregated treatments where structure transitioned from retention patch to opening across very short distances. These distributions are not fully characterized by treatment means and standard errors. Rather, the data quantiles are more informative for identifying structural differences between some of these stands. Post-harvest variability in stand structure differed by retention pattern: although Dispersed overstory density minima were similar to Aggregated minima, Dispersed maxima were lower than Aggregated maxima because Dispersed treatment prescription specifically prevented residual stand clumpiness. Furthermore, pattern-induced differences broadened over time. Our basal area data show that both within-treatment and within-stand variability dramatically decreased over time in the Dispersed units. Johnson and Fryer (1989) found that natural lodgepole pine-Engelmann spruce stands also became more homogeneous over time (lower coefficient of variation), and that increased mortality rates accelerated the transition from structural heterogeneity to homogeneity. Similarly, Kashian et al. (2005) identified that structural variability converged with undisturbed lodgepole pine stand age. Both retention patterns lost variability, but the accentuated loss in the Dispersed retention pattern is an undesirable side effect for managers that want to perpetuate structural heterogeneity within the stand and across the landscape.

Spatial variability in seedling density was greater in Burned treatments in 2004, but in 2011 the prescribed fire effect was only evident in the Aggregated pattern. It was surprising that 2011 in-stand variability in the Aggregated Unburned treatment was both the lowest of the treatments and the lowest relative to its mean, since the clumpy nature of gaps and retention patches in the Aggregated treatments theoretically drives clumpy and highly variable regeneration. Seedling density will affect that cohort's subsequent patterns of canopy closure, crown recession, and competition-based stem mortality (Oliver and Larson, 1996; Schaedel et al., 2017). Taken one step further, variability in the cohort's density will be important for crown class differentiation at the neighborhood scale and height mediation at the homogeneous patch scale. Inconsistency in regeneration density is undesirable where well-distributed growing stock is a management goal, but the high variability in the Dispersed treatments and in the Aggregated Burn treatment provides a gradient of stand dynamics processes characteristic of a multiple-use forest or mixed-severity fire regime (in crown differentiation, snag creation, woody debris deposition, understory reinitiation, precipitation interception, etc.; Puettmann et al., 2009). However, it is likewise possible that the within-stand variability is of no value in the long run if regeneration is so dense that stagnation of the new cohort is inevitable. For instance, Trappe and Harris (1958) recommend densities less than 1980 seedlings ha^{-1} to avoid negative crowding effects in lodgepole pine stands. Total regeneration densities were over 3 times this recommendation for most of our treatment units in 2011, suggesting that pre-commercial thinning may be necessary to foster ecological or timber objectives.

Variance of overstory mortality and regeneration stocking differed by treatment, but variance of overstory basal area growth and regeneration height growth did not. Thus, RH and prescribed fire treatment influences variability in population dynamics and structure, but not growth. Variability in mortality was driven more by prescribed fire than by retention pattern, but the opposite is true for regeneration stocking. This variance partition suggests that managers can choose treatment types (prescribed fire and/or retention pattern) based on the cohort (overstory or understory) in which post-treatment heterogeneity is desirable. Furthermore, since variability in growth is not impacted by treatment, growth can be forecasted with similar precision across treatments.

4.4. Conclusion

We analyzed stand structure and dynamics 11 years after retention harvesting in lodgepole pine. Treatment goals were to improve stand resilience to disturbances by increasing age and structural complexity. The retention and prescribed fire treatments successfully increased complexity by converting stands to two-canopied, multi-aged stands. This study did not specifically aim to show treatment effect on resilience to disturbances, but our results clearly showcase a multi-aged structure with a newly developing cohort. While the multi-aged structure increases resistance to mountain pine beetle (one of the primary disturbance agents in lodgepole pine forests) by reducing mature overstory density and homogeneity, the new cohort increases stand resilience to the insects because young trees are unsuitable for beetle reproduction and therefore not preferred (i.e., killed) by them. Another major disturbance in this forest type is wildland fire. Although developing regeneration will increase ladder fuels and potential for torching in the near term, increased canopy patchiness following treatment will likely limit horizontal crowning during a wildfire event until the overstory redevelops connectivity.

We found the Aggregated retention pattern better preserved live overstory density and variability than the Dispersed pattern because trees in the Dispersed pattern were subject to increased mortality from prescribed fire and windthrow. However, high mortality in the Dispersed treatments led to greater overstory tree growth, regeneration, and seedling height growth than in the more dense Aggregated treatments. We speculate that a hybrid Aggregated-Dispersed retention pattern may help managers maintain fast growing individuals and high overall survivorship. Additionally, we found that most stand dynamics processes (i.e., overstory mortality, regeneration [stocking], and seedling growth) were more simply explained by competition, size, and fire instead of retention harvest treatment, demonstrating that tree and neighborhood-scale drivers best explain forest development in complex stands. Management that emulates forest structure associated with historical disturbance regimes may bolster resilience to future disturbances, but these treatments have unique effects on stand dynamics. Our results are useful for planning silvicultural treatments in multiple-use forests that aim to increase resilience to mixed-severity fire and insect disturbances.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.foreco.2018.05.013.

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