

# Ten-year responses of ponderosa pine growth, vigor, and recruitment to restoration treatments in the Bitterroot Mountains, Montana, USA

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## Abstract

Little is known about ponderosa pine forest ecosystem responses to restoration practices in the Northern Rocky Mountains, USA. In this study, restoration treatments aimed at approximating historical forest structure and disturbances included modified single-tree selection cutting, with and without prescribed burning. We compared the effectiveness of restoration treatments on growth, vigor, and composition of recruitment responses with untreated controls. We used a randomized block design to detect treatment differences in mean individual tree basal area increment (BAInc10), growth efficiency (GE), and recruitment abundance between two restoration treatments (Cut-only and Cut-burn) and a Control. We further examined treatment effects by tree age-class (Young, Mature, Presettlement) using a spatial ANOVA model that incorporates the spatial autocorrelation among trees within experimental units. Ten years after implementing restoration treatments, mean individual tree BAI<sub>nc10</sub> and GE were significantly higher for treated units relative to Control units; all three age-classes benefited similarly from restoration treatments relative to the Control, with the greatest response in the Cut-only and moderate response in the Cut-burn. When treated units were compared, Cut-burn negatively affected BAI<sub>nc10</sub> and GE relative to Cut-only. Presettlement trees responded positively to treatment relative to the Control, particularly for BAI<sub>nc10</sub>, demonstrating the potential of these old trees to respond to reduced competition. The Cut-burn treatment, in contrast, negatively affected the BAI<sub>nc10</sub> and GE response of postsettlement trees when compared to Cut-only. Restoration treatments did not reduce the amount of Douglas-fir recruits. In addition, the recruitment of both ponderosa pine and Douglas-fir species was associated with the proximate cover of woody debris in Cut-only and Control treatments. Finally, special consideration needs to be taken for spring Cut-burn treatments, which appeared to dampen growth and vigor, relative to Cut-only, particularly for Young and Mature trees, and increased recruitment of ponderosa pine and particularly Douglas-fir.

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## 1. Introduction

Over the last decade, restoration efforts have generally aimed to reintroduce disturbance and re-establish historical abiotic conditions to promote return of the original plant community (Suding et al., 2004; Young et al., 2005). This is particularly true for lower elevation ponderosa pine (*Pinus ponderosa* P. & C. Lawson) forests in the Rocky Mountains, where prior to Euro-American settlement, natural disturbance dynamics were primarily driven by frequent but low intensity surface fires that

tended to maintain open, multi-aged, and biologically diverse stands (Agee, 1993; Arno, 1988; Covington and Moore, 1994; Mast et al., 1999). In the northern Rockies, understory burns limited more relatively shade-tolerant competitors, particularly Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Mirbel) Franco), from developing in the understory and eventually replacing ponderosa pine (Fiedler, 2000; Thomas and Agee, 1986). In the last century, however, fire exclusion practices have changed the dynamics of these forest ecosystems (Arno and Fiedler, 2005). An increase in understory biomass dominated by shade-tolerant species, along with a decrease of ground flora structure and diversity have been cited as the most striking changes (Arno et al., 1995; Mast et al., 1999; Moore et al., 1999). The increased stocking levels (particularly in the understory) have increased competition for resources, the risk of insect and disease outbreaks, and the potential for stand replacing fires (Arno

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and Fiedler, 2005; Keane et al., 2002). Thinning and prescribed burning are increasingly used to initiate restoration of historical conditions and reduce the risk of stand replacing fires in these forests (Arno et al., 1995; Fiedler et al., 2003; Powers and Reynolds, 2000; Smith et al., 2005). Managers have justified this decision by assuming that presettlement conditions and processes may best represent factors that shaped the evolution of these forest communities (Covington et al., 1997; Moore et al., 1999). However, how these ponderosa pine forests in the Northern Rockies will respond to restoration treatments is not well known.

Studies of ecosystem responses to restoration treatments have led to somewhat contradictory conclusions (Byers et al., 2006; Suding et al., 2004). In Southwest ponderosa pine forests (where fire frequencies are higher than elsewhere) and in the Northern Rockies, treatments such as thinning and prescribed burning have been evaluated based on tree growth and mortality (Feeney et al., 1998; Fiedler, 2000; Skov et al., 2005), as well as on changes in soil nutrient status (Busse et al., 2000; DeLuca and Zouhar, 2000; Gundale et al., 2005; Kaye and Hart, 1998; Monleon et al., 1997; Sala et al., 2005) and understory vegetation composition and structure (Gundale et al., 2006; Metlen and Fiedler, 2006). In some studies, thinning followed by burning has increased soil water availability and improved physiological performance of second-growth (Sala et al., 2005; Skov et al., 2004) and old-growth ponderosa pine (Feeney et al., 1998; Stone et al., 1999). However, in other studies reduced growth and increased mortality have also been reported following prescribed burns (Busse et al., 2000; Landsberg, 1994; Swezy and Agee, 1991). Most of these studies were conducted in second-growth stands or old-growth forest where the focus was on younger trees (Sala et al., 2005) or on presettlement trees only (McDowell et al., 2003), and therefore did not specifically evaluate the response of different age cohorts to restoration treatments (but see Skov et al., 2005).

Ponderosa pine restoration treatments are conducted in part to reduce catastrophic wildfire hazard, but also to improve individual tree vigor, particularly for the conservation of older trees left in the stand (McDowell et al., 2003; Skov et al., 2005; Stone et al., 1999). Improvement in vigor can potentially decrease the vulnerability of these older trees to attacks by insects and pathogens (Coyea and Margolis, 1994; Mitchell et al., 1983). One useful index of tree vigor is the physiologically based measure of growth efficiency, which is the amount of stemwood production per unit leaf area (Coyea and Margolis, 1994; Waring, 1983). Growth efficiency (GE) reflects the average capacity of a tree crown to assimilate carbon, assuming that allocation to stemwood occurs as a lower priority than allocations to defensive compounds and starch storage (Waring and Running, 1998). Growth efficiency has also been examined to measure intensity of competition among individual trees (Mitchell et al., 1983; Waring and Running, 1998), and has increasingly been applied in studies related to tree and stand growth (O'Hara, 1996; Seymour and Kenefic, 2002; Smith and Long, 1989). It has generally been found that GE decreases with increasing tree size and age (Maguire et al., 1998; Seymour and Kenefic, 2002; Waring and Running, 1998),

but this also varies with stand structure and the crown class of individual trees (Maguire et al., 1998; Woodall et al., 2003). Little is known, however, regarding the potential for restoration treatments to promote tree growth and vigor, particularly of older individuals in the Northern Rockies (Latham and Tappeiner, 2002; Skov et al., 2005).

Because old trees are scarce in present-day ponderosa pine forests, and restoration efforts have aimed to conserve them and reinvigorate their growth (Skov et al., 2005). Multi-aged silvicultural practices (i.e., selection cutting) aim to maintain vigorous growth on the reserve growing stock (e.g., older trees) and recruit a new age-class (O'Hara, 1996; Smith et al., 1997). Few studies have examined how individual tree selection cutting and subsequent prescribed burning affect the species composition of regeneration (Bailey and Covington, 2002; Fiedler, 2000). Assuming that one of the goals is to restore presettlement forest composition, we must expect a change in the ratio of recruitment composition. In other words, we expect the application of restoration treatments to dampen the recruitment of the relatively more shade-tolerant Douglas-fir when compared to the seral ponderosa pine. Quantitative data on recruitment of desirable regeneration would improve evaluation of alternative treatments (i.e., the assessment of progress or success of restoration efforts), and promote the adoption of effective restoration practices.

In this study, our general aim was to examine the effects of restoration treatments on the mid-term responses of growth, tree vigor, and post-treatment seedling recruitment in a western Montana ponderosa pine forest. Specifically, we compared basal area increment and growth efficiency of overstory trees, as well as the abundance and composition of recruited seedlings 10 years after the implementation of two restoration treatments, relative to an untreated control. Restoration treatments were conducted using modified selection cutting with and without prescribed broadcast burning. Furthermore, we evaluated the response of different tree age-classes to restoration treatments, for which we conducted a spatial ANOVA model that incorporated the spatial autocorrelation among trees. We addressed the following specific questions: (1) is there a significant growth response of reserve trees following restoration treatments, both in terms of increased basal area increment and improved tree vigor (as indexed by growth efficiency)? (2) Do restoration treatments differ in their effects on growth rate and vigor of reserve trees, as well as on the relative abundance of recruitment composition? (3) Do young, mature, and old (presettlement) trees respond differently to restoration treatments? (4) Is seedling abundance spatially associated with local stand characteristics?

## 2. Study area and methods

### 2.1. Study site and restoration experimental design

The study area is located at the Lick Creek Research/Demonstration Forest in the Bitterroot Mountains of western Montana (46°5'N, 114°15'W), at an elevation of about 1500 m. The mean annual temperature is 7 °C and the mean annual

precipitation is 400 mm with about 30% falling as snow (DeLuca and Zouhar, 2000). The site is dominated by ponderosa pine that ranges from 20 to 250 years of age, with a small component (<10% of total basal area) of interior Douglas-fir that tend to be younger. The selected site represents typical uneven-aged ponderosa pine forests in the Northern Rockies region.

We employed a randomized block experimental design, with three blocks (replicates) established adjacent to each other in reasonably uniform stand conditions (e.g., same aspect and slope). Each block was subdivided into three rectangular, 1-ha treatment units. Each treatment unit within a block was randomly assigned one of three treatments: modified individual tree selection cutting (Cut-only), selection cutting followed by spring prescribed burning (Cut-burn), and no treatment (Control). Restoration treatments applied in 1992 and 1993 initiated the transition toward historical ranges of stand density, structure, and species composition. Restoration targets for these stand characteristics were based on early-1900 inventory data from ponderosa pine stands at the Lick Creek site, descriptions of historical ponderosa pine stands in western Montana (Anderson, 1933), and general management prescriptions for restoring ponderosa pine–fir forests (Fiedler et al., 1992). Reserve trees were marked using a guiding diameter distribution (i.e., reserve basal area of  $9.2 \text{ m}^2 \text{ ha}^{-1}$  for trees between 10 and 50 cm DBH (diameter at breast height), 1.37 m high, maximum diameter of 50 cm, and a 1.2 ratio between number of trees in successively larger 10-cm diameter classes), based on guidelines for uneven-aged management of ponderosa pine (Fiedler et al., 1988). An additional  $2.3 \text{ m}^2 \text{ ha}^{-1}$  of large old trees >50 cm DBH was also reserved to help meet restoration objectives, for a total reserve basal area of  $11.5 \text{ m}^2 \text{ ha}^{-1}$ . All units were reserve-tree marked with tags before treatments were assigned. Trees were reserved on the basis of vigor, crown ratio, and in numbers by diameter class consistent with the guiding diameter distribution. Hence,

tagged trees within Controls were directly comparable to those left after cutting in treated units. Merchantable trees (i.e., >20 cm DBH) not marked for reserve were felled by chainsaw and removed for products in the fall of 1992, and trees <20 cm DBH were thinned and left on-site. Combined selection cutting and thinning reduced pretreatment stocking levels from  $23 \text{ m}^2 \text{ ha}^{-1}$  (in trees >10 cm) to a target reserve basal area of  $11.5 \text{ m}^2 \text{ ha}^{-1}$  for each of the six 1-ha treatment units. Units assigned burning were broadcast burned in the spring of 1993. The goal of prescribed burning was to reduce fuel loads, recycle nutrients bound in the litter and slash, and kill most seedling- and sapling-size Douglas-fir. Logging slash (tops and limbs) and felled sub-merchantable trees were left on-site to provide fuel for the broadcast burn. Immediately before burning, litter averaged 12% moisture content, duff (i.e., partially decomposed and fully humified organic matter) depth averaged 4.3 cm with 30% moisture content, and slash loadings averaged  $28.1 \text{ tonnes ha}^{-1}$  with 75% moisture content. Prescribed burning was accomplished using a strip-head fire technique (Kilgore and Curtis, 1987), with air temperatures ranging from 12 to 21 °C and relative humidity ranging from 48% to 56%. Burning reduced duff depths by 30% and slash loadings by 74%. We recognize, however, that burns might not have been conducted under the historical fuel loads and fuel types, which are unknown for this region.

## 2.2. Field data collection

In summer 2003, we established one square plot ( $50 \text{ m} \times 50 \text{ m}$  to  $60 \text{ m} \times 60 \text{ m}$ ) in the center of each experimental treatment unit for sampling and stem-mapping trees >10 cm in DBH. The plot size varied according to a minimum number of trees needed for the spatial analysis (see below). The total basal area (BA) of trees >10 cm DBH in the Cut-only and Cut-burn plots ranged from  $6.9$  to  $12.7 \text{ m}^2 \text{ ha}^{-1}$  (Table 1). The BA of tagged trees within plots of Control units

Table 1  
Summary of stand characteristics by experimental unit in the Lick Creek Research/Demonstration forest area, western Montana 10 years after treatments were applied

Block	Treatment	Basal area ( $\text{m}^2 \text{ ha}^{-1}$ )				Density (trees $\text{ha}^{-1}$ )				Seedlings (no. $\text{ha}^{-1}$ )		
		Young	Mature	Presettlement	Total	Young	Mature	Presettlement	Total	PP	DF	Total
1	Cut-only <sup>a</sup>	1.1	4.9	2.5	8.6	140	83	13	236	33	127	160
	Cut-burn	0.1	8.4	3.1	11.6	11	125	8	144	67	156	222
	Control	0.2	7.0	5.1	10.3	24	84	24	132			
	Control*	0.2	11.4	7.2	18.8	28	248	52	328	7	117	123
2	Cut-only	0.5	8.8	1.7	11.0	25	114	6	145	86	8	94
	Cut-burn	0.4	6.0	0.6	7.0	27	110	3	140	87	97	183
	Control	0.0	5.5	3.6	9.1	0	120	20	140			
	Control*	0.1	9.2	5.0	14.3	4	272	36	312	4	8	12
3	Cut-only	0.2	3.9	5.4	9.5	7	73	47	127	33	87	120
	Cut-burn	0.3	7.6	4.9	12.7	11	100	26	137	47	50	97
	Control	0.6	3.9	5.1	9.6	32	80	40	152			
	Control*	1.0	5.6	13.7	20.4	72	128	148	348	3	10	13

Data from plots were scaled up to per hectare basis. Seedlings represent seedlings recruited in a 10-year period after treatments were applied. Basal area and tree density values represent all trees larger than 10 cm DBH. Note: blank cells under Seedlings columns and C (Control) rows represent the same figures as C\* (total Control trees, tagged and untagged).

<sup>a</sup> Control: tagged trees only within Controls; Control\*: all trees within Control.

had a similar range (9.1–10.3 m<sup>2</sup> ha<sup>-1</sup>), while total BA of all trees in the Control plots ranged from 14.2 to 20.3 m<sup>2</sup> ha<sup>-1</sup>. Tree density varied from 127 to 237 trees ha<sup>-1</sup> for plots in Cut-only and Cut-burn units, and from 110 to 152 comparable (tagged) trees ha<sup>-1</sup> for plots in Control units (312–348 trees ha<sup>-1</sup> total). For stem maps, the distance and azimuth to the center of each tree (>1.37 m tall) were measured using a laser rangefinder (Impulse<sup>TM</sup>) equipped with an electronic compass module (Laser Technology Inc.). These field measurements were converted to Cartesian coordinates using trigonometric functions. For all trees >10 cm DBH, we measured DBH and extracted an increment core to the pith at breast height to determine age and growth rate. For trees larger than 20 cm DBH, two cores were extracted. Sapwood–heartwood boundaries were visually identified on each increment core in the field. When the sapwood–heartwood boundary was difficult to determine, bromecresol green was used to stain the sapwood (Kutscha and Sachs, 1962).

In the laboratory, increment cores were mounted on grooved boards and hand polished with fine sandpaper. We estimated tree age at breast height by reading annual rings from the cores. Sapwood width, inside-bark bole radius, and annual radial increment of the last 20 years were measured to the nearest 0.01 mm, using a microscope mounted on a dendrochronometer with a Velmex sliding stage and Accurite measuring system. In general, tree rings were very clear and well defined and were cross-dated visually. We computed inside-bark basal area (IBA), sapwood basal area (SA), and 5-, 10-, and 20-year basal area increment (BAInc5, BAInc10, and BAInc20, respectively) by considering DBH and bark thickness at breast height. BAInc10 represented the gain in growth since treatments were applied. We calculated growth efficiency (GE) as an index of tree vigor. Growth efficiency has been defined as the individual tree's stemwood increment per unit of foliage or leaf area (Waring, 1983). However, SA is commonly used as a surrogate for leaf area, based on the established allometric relationship between these two variables (Seymour and Kenefic, 2002; Woodall et al., 2003). In computing GE, we divided the basal area increment of the last 5 years (BAInc5) by the current sapwood basal area (SA). Furthermore, we classified trees into three age-classes: trees older than 100 years (Presettlement), trees between 50 and 100 years old (Mature), and trees younger than 50 years (Young). The designation of trees older than 100 years as "Presettlement" (Moore et al., 1999; Skov et al., 2005) was intended to reflect the disruption of historical fire regimes resulting from fire exclusion efforts initiated about 1900 (Arno et al., 1995).

Each square plot was further divided into 5 m × 5 m subplots to census seedling abundance. To assess post-treatment seedling recruits, we only considered trees less than 10 years old, based on field examination of annual internodes. We also visually estimated the percent cover of shrubs, grasses, and woody debris to the nearest 10%. These local stand variables, along with basal area at breast height (BA) and sapwood basal area at breast height (SA) were used in the analysis of spatial correlation described below. We used stem maps to compute BA and SA per subplot.

### 2.3. Data analysis

We analyzed the data in three different ways. First, we used a randomized block design at the plot level (classical ANOVA) to detect treatment differences in mean plot BAInc10, GE, and recruitment abundance. Second, we further examined treatment effects by tree age-class to detect differences in mean individual tree BAInc10 and GE using a spatial ANOVA model that incorporated the spatial autocorrelation among individual trees within experimental units. And third, we examined the partial correlation of seedling abundance for both species with local stand characteristics using a partial Mantel test.

#### 2.3.1. Analysis of treatment effects using classical ANOVA

We compared differences in the response variables (BAInc10, GE, and abundance of recruited seedlings) among treatments using a randomized block design and plot-level means ( $n = 9$ ). Distributional assumptions of ANOVA were graphically assessed and heteroscedasticity of variances was tested using Levene's statistic (Sokal and Rohlf, 1995). We corrected for heteroscedasticity in BAInc10 and GE using square-root transformations. Additionally, we conducted an ANOVA for BAInc for a 10-year period prior to treatment application. We found non-significant a priori differences among the treatments ( $p = 0.43$ ), and therefore assumed pretreatment similarities across experimental units. Mean comparisons among treatments were performed with a Tukey post hoc procedure ( $\alpha = 0.05$ ). All statistical analyses comparing treatments to Controls (using classical ANOVA) were conducted based on reserve trees in the treated plots and tagged trees in the Controls.

#### 2.3.2. Variation between age-classes using a spatial ANOVA model

We further analyzed the effects of restoration treatments on the individual trees (instead of the individual plots) to determine the role of tree age in such a response. Accordingly, we used individual tree age as a covariate in our analysis. One difficulty with including age-class as a covariate in the analysis is that the experimental unit is actually not a tree, but a plot. By incorrectly considering the trees as the experimental units when treatments were actually applied at the plot level we would be committing what Hurlbert described as "pseudo-replication" (Hurlbert, 1984). As a result, inferences are limited to the nine plots sampled for the tree-level analysis (nine plots sampled, 2527 trees).

If the trees are the experimental units, then they are likely not independent in terms of measured response variables such as BAInc and GE. Indeed, the values of these variables may be the result of a combination of microsite, local competition, and other highly spatially autocorrelated factors (Fajardo and McIntire, 2007; Legendre, 1993). These potential spatial autocorrelations can be accounted for by adopting a more complex covariance structure on the residuals through the use of a spatial ANOVA model. To characterize the spatial autocorrelation present in the response variables among the trees within a plot, we computed empirical semivariograms and



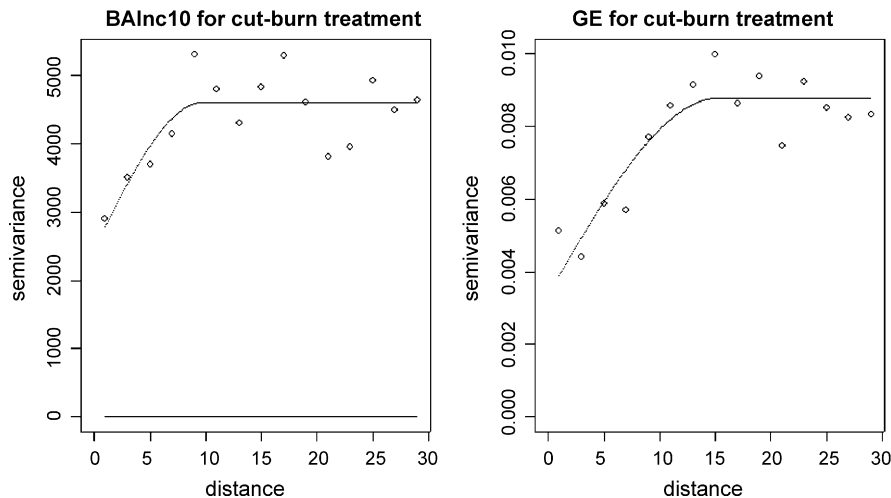


Fig. 1. Empirical and theoretical (spherical modeled) semivariograms showing the existence of positive spatial autocorrelation of basal area increment in the last 10 years (BAInc10) and growth efficiency (GE) for the Cut-burn treatment of individual trees in the Lick Creek Research/Demonstration forest area, western Montana.

modeled the spatial autocorrelation found for BAInc and GE response variables (Fig. 1). Spatial autocorrelation analyses were computed for age-classes with a minimum of ca. 15 tree individuals per plot, which sometimes required the plot size to be enlarged. The fitted semivariogram models can then be used to estimate the covariances between the response values for any two trees. Additional details on the methodological development of the matrix covariances for the spatial ANOVA model and the computation of semivariograms can be seen in Appendices A and B.

### 2.3.3. Spatial correlation analysis of new seedling recruitment

Because seedling abundance data often exhibit spatial autocorrelation, statistical assumptions of independence would be violated if we were to consider each of our  $5\text{ m} \times 5\text{ m}$  subplots as being an independent sample (Legendre, 1993). We therefore used a partial Mantel test (Mantel, 1967) to examine the partial correlation of seedling abundance for both species (ponderosa pine and Douglas-fir) with local stand characteristics. The partial Mantel statistic measures the correlation between two variables in space while controlling for the spatial location (Fortin and Dale, 2005). In our case, the test controls for spatial location in the two variables of interest (seedling abundance and one of the proximate stand variables). Further

details on the computation of matrix correlations for a partial Mantel test can be found in Cressie (1993) and Fortin and Dale (2005). For each  $25\text{-m}^2$  subplot, we recorded BA ( $\text{cm}^2$ ), SA ( $\text{cm}^2$ ), and percent cover (%) of shrubs, grasses, and woody debris. We considered the  $(x, y)$ -coordinates of the subplot center as the spatial location of all the variables. Partial Mantel tests, classical and spatial ANOVA's, and semivariogram modeling were conducted using the statistical software "R" (R-Foundation, 2004). Mean comparisons among treatments for the spatial ANOVA were performed with a Tukey post hoc procedure ( $\alpha = 0.05$ ).

## 3. Results

### 3.1. Treatment effects on individual tree growth and vigor

The alternative restoration treatments (Cut-only and Cut-burn) differed in their effect on the growth increment and vigor of reserved trees. Cut-only treatment had the effect of nearly doubling mean basal area increment for the 10-year period (BAInc10,  $136.58\text{ cm}^2$ ) relative to Control units ( $75.23\text{ cm}^2$ ) (Table 2). Mean BAInc10 values were also higher following Cut-burn treatment ( $106.57\text{ cm}^2$ ) versus Control by 41%, although this difference was not significant based on the plot-level ANOVA (Table 2).

Table 2

Results of classical ANOVA for general treatments and multiple comparison results for basal area (BA) increment of the last 10 years (BAInc10), growth efficiency (GE), abundance of recruited seedlings per hectare for ponderosa pine (PP) and Douglas-fir (DF), and seedling ratio (PP density/DF density) 10 years after the application of restoration treatments in the Lick Creek Research/Demonstration forest area, western Montana

	F-value	P (>F)	Multiple comparisons		
			Cut-only	Cut-burn	Control
BAInc10 (BA-last 10-years ( $\text{cm}^2$ ))	10.51	0.026	136.58 (19.94) a	106.57 (7.05) ab	75.23 (2.43) b
GE (BA-sapwood ( $\text{cm}^2$ ) BA-last 5-years ( $\text{cm}^2$ ) <sup>-1</sup> )	8.86	0.034	0.21 (0.03) a	0.15 (0.01) ab	0.10 (0.01) b
PP seedlings (no. $\text{ha}^{-1}$ )	11.59	0.022	50.93 (17.59) a	67.30 (11.00) a	4.89 (0.89) a
DF seedlings (no. $\text{ha}^{-1}$ )	2.18	0.229	73.89 (34.75) a	101.22 (52.21) a	45.56 (35.57) a
Seedlings ratio (PP/DF abundance)	0.94	0.462	3.80 (3.48) a	0.76 (0.17) a	0.30 (0.13) a

Data are means with SE in parentheses ( $n = 3$ ). Within a row, means with different letters differ at  $P < 0.05$ .

Our measure of tree vigor, mean growth efficiency (GE), yielded similar results among treatments as BAInc10. Mean GE of trees in the Cut-only treatment (0.211 cm<sup>2</sup> cm<sup>-2</sup>) was significantly greater than for Control (0.104) (Table 2), whereas GE values in the Cut-burn treatment units (0.145) were intermediate between Cut-only and Control (Table 2). Block effects were not significant for either BAInc10 or GE.

### 3.2. Variation in basal area increment and growth efficiency with tree age (spatial model)

After adjusting group means to account for autocorrelation with the spatial ANOVA model analysis, similar trends were again detected among the treatment means. Mean BAInc10 values were again highest in Cut-only units and intermediate in Cut-burn, but differences were significant among all treatments due to the increased power of using trees as experimental units. For the analysis of tree vigor, values for mean GE were intermediate in Cut-burn units, and significantly lower than in Cut-only. No significant differences were found between mean GE for Cut-burn and Control units (Table 3 and Fig. 2).

We also detected significant age-class effects (Table 3) for both BAInc10 and GE. Growth rates (BAInc10) were significantly lower in the Young age-class relative to older age-classes; higher mean values were observed for Presettlement trees across all treatments relative to postsettlement trees (Table 3; Fig. 2a). There was not a significant interaction of age-class and treatment for BAInc10 (Table 3). The three age-classes followed the same tendency observed for all trees, i.e., the greatest growth increment in Cut-only and intermediate values in Cut-burn (Fig. 2a). Mature trees displayed the greatest difference in BAInc10 among treatments (Table 3). Mean values for BAInc10 in Cut-only were double the rates in the Control, and for Cut-burn treatment units were over 40% higher than Control (Table 3, Fig. 2a). The Youngest age-class showed no significant differences in mean BAInc10 among restoration treatments ( $p > 0.05$ ).

Mean GE values generally decreased with tree age. GE values were consistently lowest for Presettlement trees across

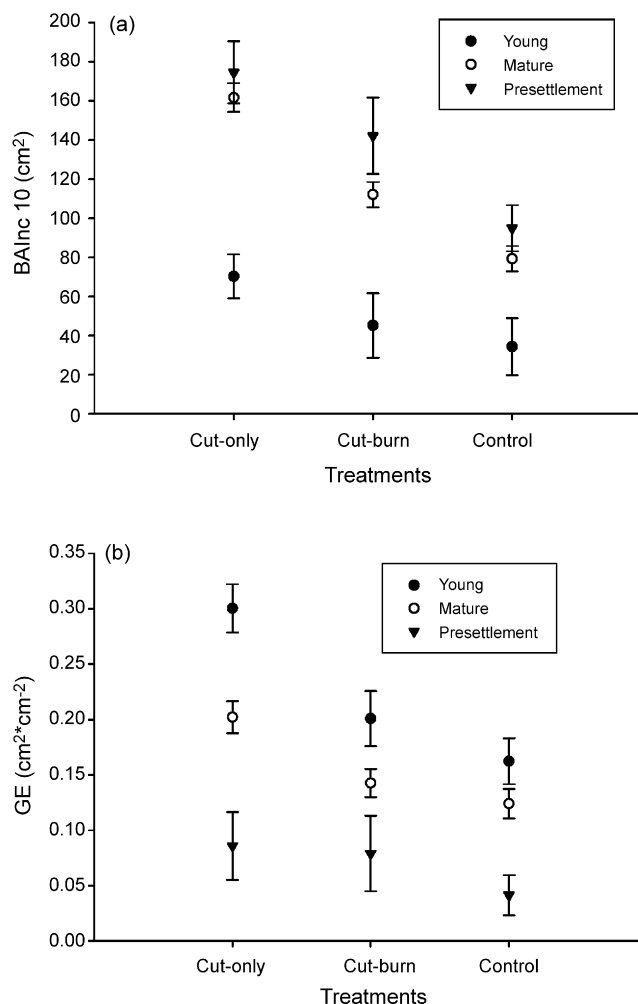


Fig. 2. Mean treatment effects by age-classes on (a) basal area increment in the last 10 years (BAInc10), and (b) growth efficiency (GE) considering the spatial autocorrelation of all the individual trees for each treatment in the Lick Creek Research/Demonstration forest area, western Montana. Error bars represent one standard error ( $n$  varies by treatment and age-class). Age-classes are Young trees (<50 years), Mature trees (between 50 and 100 years), and Presettlement trees (>100 years).

Table 3

Results of spatial ANOVA for multiple comparisons among treatments for basal area increment of the last 10 years (BAInc10) and growth efficiency (GE) by age-class (accounting for spatial autocorrelation), 10 years after treatments were applied in the Lick Creek Research/Demonstration forest area, western Montana

BAInc10	<i>n</i>	Cut-only	<i>n</i>	Cut-burn	<i>n</i>	Control	Total
Young	53	70.28 (11.29) Aa	16	45.20 (16.51) Aa	18	34.31 (14.65) Aa	49.93 (8.26) a
Mature	88	161.68 (7.39) Ab	113	112.15 (6.45) Bb	71	79.29 (6.43) Cb	117.71 (3.91) b
Presettlement	20	174.60 (15.86) Ab	13	142.16 (19.58) ABb	21	94.99 (11.74) Bb	137.25 (9.27) b
Total	161	135.52 (6.67) A	142	99.84 (8.77) B	106	69.53 (6.71) C	

GE	Cut-only	Cut-burn	Control	Total
Young	0.300 (0.022) Aa	0.201 (0.025) Ba	0.162 (0.021) Ba	0.221 (0.013) a
Mature	0.202 (0.014) Ab	0.143 (0.013) Bb	0.124 (0.013) Ba	0.156 (0.008) b
Presettlement	0.086 (0.031) Ac	0.079 (0.034) Ab	0.041 (0.018) Ab	0.069 (0.016) c
Total	0.196 (0.014) A	0.141 (0.016) B	0.109 (0.013) B	

Age-classes are Young trees (<50 years), Mature trees (between 50 and 100 years), and Presettlement trees (>100 years). Data are means with S.E. in parentheses ( $n$  varies by treatment and age-class). Within a row, means with different upper-case letters differ at  $P < 0.05$  for treatments (Tukey post hoc test). Within a column, means with different lower-case letters differ at  $P < 0.05$  for age-classes. Control units include tagged trees only.

all treatments. While mean GE did increase over Control sites for both restoration treatments, only Cut-only differed significantly from Control ( $p < 0.01$ , Table 3; Fig. 2b). For Mature trees, mean GE values were significantly higher in Cut-only relative to both Cut-burn ( $p < 0.01$ ) and Control ( $p < 0.01$ ). Mean GE of Young trees was consistently higher than the other age-classes across all treatments (Table 3).

### 3.3. Recruitment patterns

Recruitment of seedlings was generally higher in the Cut-only and Cut-burn treatments than in the Control (Table 1). The abundance of Douglas-fir (DF) seedlings (no. ha<sup>-1</sup>) was commonly higher than for ponderosa pine (PP) seedlings, i.e., restoration treatments have not produced a reduction in DF recruitment relative to PP. In treated units, density of newly recruited PP seedlings ranged from 33 to 87 ha<sup>-1</sup>. The mean seedling abundance of PP varied significantly among treatments, with higher densities in the restoration treatments than the Control (Table 2). Recruited PP seedlings were approximately 20% higher in Cut-burn when compared with Cut-only, and more than 10 times higher when compared with Control, although none of these differences were significant (Table 2). In contrast, the mean abundance of recruited DF seedlings did not vary significantly among treatments (high variation within treatments; Table 2). We also found that the ratio of PP:DF recruited seedlings did not vary significantly among treatments, and it was highly variable in Cut-only due to the unusually low density of DF seedlings in the second block (Tables 1 and 2).

Results of the partial Mantel correlation analysis indicated that new seedling recruitment was not related to most of the proximate stand characteristics (Table 3). We did not detect any significant Mantel correlation between overstory competition variables, BA and SA, with the occurrence of new seedlings. Similarly, percent cover of shrubs and grasses, which represented competition from understory, did not correlate with seedling abundance after treatments were applied. The only variable that displayed positive significant correlation with the abundance of both species was the percent cover of woody debris, in both Cut-only and Control, but not in Cut-burn treatment.

## 4. Discussion

### 4.1. Growth increment and tree vigor responses to restoration treatments

The multi-aged ponderosa pine forest at our western Montana site responded positively to restoration treatments in the 10 years after treatments were applied, in terms of greater basal area growth increment and improved vigor (i.e., higher GE). Studies on second-growth ponderosa pine forests have reported positive responses in growth increments following restoration treatments (Kolb et al., 1998; Skov et al., 2004). An increase in growth increment for ponderosa pine has been related to reduced competition and increased resource availability (Latham and Tappeiner, 2002; McDowell et al.,

2003). In means separation tests (classical ANOVA contrasts), however, we found that only the Cut-only restoration treatment had significantly higher mean BAInc10 values than the Control. Fiedler (2000) has reported similar conclusions, for a site located in the same region, implying that prescribed burns may reduce or delay tree growth response relative to cutting without burning. In general, these results are similar to results from restoration treatments conducted in northern Arizona, e.g., at the Gus Pearson Natural Area. Studies from northern Arizona ponderosa pine-dominated forests have reported that the Cut-burn treatment frequently is not better than the Cut-only treatment regarding variables used to assess treatment success, e.g., growth, leaf physiology, vigor (Feeney et al., 1998; Hart et al., 2005; Kaye and Hart, 1998; Kaye et al., 2005). This similarity in results suggests that there might be some unifying concepts in the management of ponderosa pine forests across geographic regions.

While surface fire was a frequent natural disturbance in these ponderosa pine forests of the Northern Rocky Mountains, such burns historically occurred during late summer and early fall (Agee, 1993). Prescribed burns in these forests, however, are most commonly applied during spring months when more moist fuel conditions reduce risk of escape and more variable atmospheric conditions enhance smoke dispersal. Negative effects of our spring burning treatment may be related to crown scorching of reserve trees or to damage of tree roots near the surface (Hart et al., 2005). Wyant et al. (1983) found that scorching of lower crown foliage reduced the transpiration surface area, and consequently photosynthetic capacity. Grier (1989) reported that early-season spring burns, conducted while tree root physiological activity is high, can lead to dramatic reductions (~60%) in fine root biomass. Hart et al. (2005) also found that repeated burning (2-year intervals) reduced both fine root length, biomass and mycorrhizal root biomass relative to unburned control in northern Arizona. Reduced growth rates and increased mortality have also been reported for other studies of burning effects in ponderosa pine (Busse et al., 2000; Landsberg, 1994; Swezy and Agee, 1991). Conversely, when prescribed burns were conducted in the fall, some studies have reported no delayed growth response (Feeney et al., 1998).

Growth efficiency (GE) was also highest in the Cut-only treatment, with intermediate levels observed in the Cut-burn treatment. GE is affected by stand structure and light environments within the canopy (O'Hara, 1996; Roberts et al., 1993; Woodall et al., 2003), and trees in Control units presumably experienced higher levels of competition, leading to a reduction in vigor. The lack of significant differences between the Cut-burn and the Control treatments may again be reflecting negative effects of burning. In addition to the potential negative effects of fire on foliage and shallow roots, a mid-term (~10 year) decline in nitrogen availability has been reported (DeLuca and Zouhar, 2000; Monleon et al., 1997; Wright and Hart, 1997) as another potential mechanism explaining the difference in GE between Cut-only and Cut-burn. Thus, we can expect that a release from competition resulting from cutting may be neutralized by the potential alteration of physiological functions caused by burning

(Sutherland et al., 1991; Swezy and Agee, 1991). Although some studies have shown short-term increases in soil nitrogen concentration after fire (DeLuca and Zouhar, 2000; Monleon et al., 1997), several indices of nitrogen availability and transformation rates have exhibited a decline in the mid-term (after ~10 years) (DeLuca and Zouhar, 2000; Kaye et al., 2005; Monleon et al., 1997; Wright and Hart, 1997). Because leaf nitrogen content directly impacts leaf properties and photosynthetic capacity (Reich et al., 1997), direct and indirect effects of different management treatments on soil nitrogen availability may have lasting consequences for the physiological performance of ponderosa pine.

#### 4.2. Trees respond differently to restoration treatments depending on age-class

All three age-classes derived some benefits from restoration treatments relative to the Control for both BAInc10 and GE (i.e., highest values for Cut-only, intermediate for Cut-burn, and lowest for Control). Such differences were not significant among treatments for BAInc10 of Young trees, nor for GE of Presettlement trees. Contrary to long-held assumptions that tree growth rate is limited by age (Kira and Shidei, 1967; Weiner and Thomas, 2001), and that old trees may not respond to reductions in competition, we found that Presettlement trees responded positively to Cut-only treatments for BAInc10. Our findings agree with those of several other studies dealing with old ponderosa pine trees (Fiedler, 2000; Latham and Tappeiner, 2002; McDowell et al., 2003). McDowell et al. (2003) found that stand density reductions resulted in increased growth of individual old trees due to changes in water availability and stomatal conductance. Latham and Tappeiner (2002) reported significant responses after thinning for old-growth trees of both ponderosa pine and Douglas-fir in western Oregon. In northern Arizona, Stone et al. (1999) also found a positive response of old “Presettlement” trees to thinning by increasing growth and the uptake of water, nitrogen, and carbon. However, in the same area, Skov et al. (2005) found a lack of short-term growth response to thinning for older “Presettlement” trees (150–450 years old) three years after treatment.

Our results demonstrate the capability that older trees have to respond to decreased competition through harvest. In this respect, we concur with Latham and Tappeiner (2002) that the commonly held view that old trees do not respond to release treatments may well be because most studies on these trees have focused on stand volume growth rather than individual tree growth (i.e., few individuals of this age-class at the stand level). Additional research is needed to unveil the duration of this positive growth response of old individual trees in the current study area.

The GE of Presettlement trees did not increase in restoration treatments to the same extent as BAInc10. While a slight increase in GE was observed in restoration treatments relative to Control units, the differences were not significant. Across all treatments, we found a lower GE of Presettlement trees relative to younger age-classes; a result that might be associated with the various proposed causes of growth efficiency decline in

older trees, including increasing allocation to foliar respiration and belowground storage components (Binkley et al., 2004; Ryan et al., 2004). Our estimates of GE, based on SA only, do not account for a potential shift toward a greater ratio of SA per unit foliage area in older trees to compensate for hydraulic limitations imposed by tree height (Ryan et al., 2004). While younger age-classes had higher GE values generally, Mature and Young trees appeared to be more negatively affected by burning. Lower-crowned trees may have been scorched during burns, losing some productive capacity with reductions in foliage biomass (Wyant et al., 1983). Although we did not measure scorching levels, we would expect that managers may wish to conduct prescribed burns to control flame lengths and reduce the probability that crowns of Mature and Young trees will be scorched.

We were able to study the effects restoration treatments have on specific tree characteristics (e.g., age-class) by adopting a spatial ANOVA model (Fajardo and Graham, unpublished), where analysis was necessarily conducted at the tree-level. We recognize that the scope of inference of these age-class analysis is limited to the population consisting of the nine 1-ha experimental units, since treatments were applied to plots and not individual trees. However, if additional experiments produce consistent results, our findings can contribute to a larger scope of inference regarding the process being studied.

#### 4.3. Ponderosa pine and Douglas-fir recruitment

Our results suggest that seedlings of both PP and DF were well recruited during the first 10 years after the restoration treatments were applied. We anticipated that restoration treatments would dampen the amount of DF relative to PP, but this did not occur. Recruitment of PP seedlings increased following restoration treatments relative to Control, with the highest levels of both PP and DF recruitment occurring in the Cut-burn treatment. Although the level of recruitment necessary to assure regeneration of these specific forests is unknown (i.e., there is not a standard measure for adequate recruitment under these specific restoration treatments), we believe that the treatments employed here are still inducing the regeneration of both species. We found greater post-treatment seedling density than reported by Bailey and Covington (2002) for northern Arizona, although the time-frame is different. They found only 18–41 seedlings ha<sup>-1</sup> in treated areas (thinning) in the absence of fire, and only 12 seedlings ha<sup>-1</sup> 1-year after burn treatments were applied. Furthermore, we did not find differences in abundance between species 10 years after treatment application. The fact that PP seedling recruitment did not exceed DF, as was expected, may be explained in that a shift of recruitment dominance can be predicted only after periodic fires reduce DF survival rates. We could also speculate that the ponderosa pine system may be ecologically resilient (Gundersen, 2000) to traditional restoration treatments. Suding et al. (2004) stated that strong feedbacks between the biotic and the physical environment can alter the efficacy of successional-based restoration efforts. It is plausible to expect that PP regeneration follows masting periods of seed production and



dispersal, and therefore the time frame of our study may be too short to capture the processes involved. For example, in northern Arizona, Bailey and Covington (2002) documented that a sufficient supply of seeds is available for new ponderosa pine regeneration only once or twice per decade.

In our study, the recruitment of both species appeared to benefit from Cut-burn (in absolute terms), and was locally associated with the percent cover of woody debris in Cut-only and Control treatments. Successful seedling establishment has been reported to depend on the creation of a “safe site” such as the ash bed of a consumed log, where seedlings could establish and grow (Dieterich, 1980; Smith et al., 1997). Additionally, in the absence of fire, the presence of woody debris can also benefit the establishment of PP and DF. Woody debris provides “dead” shade and reduces high temperatures near the soil surface, and may increase humidity levels. In this study we were unable to discern effects of local competition on seedling abundance at the scale examined; no correlation was found between seedling abundance and proximate stand characteristics for either species. The spatial association between saplings of PP and DF and the overstory trees may also depend on the size of overstory trees and the moisture-level of the site (Fajardo et al., 2006).

## 5. Conclusion

The response of ponderosa pine to restoration treatments has been little-studied in the Northern Rocky Mountains. Our results indicate that the growth and vigor of ponderosa pine respond positively to these restoration treatments, particularly cutting without burning. Special consideration needs to be taken for Cut-burn treatments (relative to Cut-only), which appeared to dampen response in terms of growth and vigor, particularly for Mature and Young trees. This treatment also increased recruitment of ponderosa pine, but particularly Douglas-fir. These unwanted effects associated with spring broadcast burning suggest that this treatment needs to be weighed against cutting only or cutting followed by fall burning to determine which treatment approach will best achieve longer-term restoration goals. We also need to consider, however, that the results obtained in the current study represent a mid-term period response, and final considerations about the successful application of restoration treatments need to take into account, for example, the repetition of burning in time.

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## Appendix A. Spatial covariance component

To characterize the spatial autocorrelation present in the response variables among the trees within a plot, we computed

empirical semivariograms that contain information on the spatial autocorrelation among the observations. These semivariogram models can then be used to estimate the covariances between the response variable values for any two trees. These covariances were then formed into a matrix of covariances among all 550 trees. For 550 trees, such a matrix is  $550 \times 550$ , where the  $(i, j)$ th entry represents the covariance between the  $i$ th and  $j$ th tree response values. By denoting this matrix  $V$ , we fit the following linear model with age-class as a covariate for the scenario described:

$$y_{ijk} = \beta_0 + \beta_1 Z_{1jk} + \beta_2 Z_{2jk} + \beta_3 W_{ilk} + \beta_4 W_{i2k} + \beta_5 A_{1k} \\ + \beta_6 A_{2k} + \beta_7 Z_{1jk} W_{1k} + \beta_8 Z_{1jk} W_{2k} + \beta_9 Z_{2jk} W_{1k} \\ + \beta_{10} Z_{2jk} W_{2k} + \beta_{11} Z_{1jk} A_{1k} + \beta_{12} Z_{1jk} A_{2k} + \beta_{13} Z_{2jk} A_{1k} \\ + \beta_{14} Z_{2jk} A_{2k} + \varepsilon_{ijk}, \quad i = 1, 2, 3, \quad j = 1, 2, 3,$$

where

$y_{ijk}$  is the  $k$ th response for the  $i$ th treatment in the  $j$ th block;

$$Z_{1jk} = \begin{cases} 1 & \text{if Cut-only} \\ 0 & \text{if Control} \end{cases}; \quad Z_{2jk} = \begin{cases} 1 & \text{if Cut-burn} \\ 0 & \text{if Control} \end{cases}; \\ W_{ilk} = \begin{cases} 1 & \text{if block 2} \\ 0 & \text{if block 1} \end{cases}; \quad W_{i2k} = \begin{cases} 1 & \text{if block 3} \\ 0 & \text{if block 1} \end{cases};$$

$\beta_i$  the  $i$ th parameter value to be estimated;

$\varepsilon$  is the vector of residuals, where  $\varepsilon \sim N(\mathbf{0}, \mathbf{V})$ .

This generalization of the covariance matrix to include the spatial covariances present affects the parameter estimates, their variances and covariances, and hence all estimated contrasts, ANOVA sums of squares, confidence intervals, and significance tests. Generally speaking, the inclusion of the spatial structure tends to dampen the magnitude of treatment effects by accounting for the spatial redundancy in information provided by individual trees.

## Appendix B. Semivariogram formulation and computing

We used semivariogram models to estimate the covariances between the response variable values for any two trees. The variogram is the variance of the difference between random variables at two units (locations), given by:  $\text{var}(Z_i - Z_j)$  for two sites  $i$  and  $j$ . The empirical semivariogram is one half the estimated variogram, and is defined as

$$\hat{\gamma}(h) = \frac{1}{2N(h)} \sum_{i,j:|x_i-x_j|\approx h} [z(x_i) - z(x_j)]^2,$$

where  $h$  is the distance lag between sampled trees,  $N(h)$  is the number of paired comparisons at lag  $h$ ,  $z(x_i)$  and  $z(x_j)$  are the observed tree variable values at location  $x_i$  and  $x_j$ , respectively (Webster and Oliver, 2001). Under a typical spatial dependence model, two units that are close together will tend to have a smaller variance of the difference. As units get further apart, their differences get larger and usually the variance of the difference gets larger as well. In a semivariogram, the empirical semivariance ( $\hat{\gamma}(h)$ ) is plotted on the  $y$ -axis against lag distance

( $h$ ) on the  $x$ -axis. The lag distance is the step-size used, and the active lag denotes the largest distance considered between points in the semivariance data set, though the whole data set is included in the analysis (Isaaks and Srivastava, 1989; Rossi et al., 1992). We used a minimum lag distance of 1-m, and active lag of 25–30-m on average (i.e., half of the minimum plot dimension). Empirical semivariograms were computed for BAInc10 and GE for each treatment (Fig. 1).

We considered single spherical theoretical models for modeling empirical semivariograms, with three parameters known as the nugget, sill, and range. The nugget is a measure of the microscale variation in the response. The sill, or total sample variance, is the ordinate value at which the semivariogram becomes flat. The range represents the distance beyond which samples are spatially independent (Isaaks and Srivastava, 1989; Webster and Oliver, 2001). We used an iterative non-linear weighted least squares procedure with weights proportional to  $N(h)$  to fit the variogram model to the empirical semivariograms (Cressie, 1985).

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