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silviculture

Long-Term Regeneration Responses to Overstory Retention and Understory Vegetation Treatments in the Northern Rocky Mountains

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Classic regeneration cuttings retaining trees at harvest (shelterwood with reserves, group selection) can be analyzed as analogs of variable-retention harvesting. A 1974 silvicultural experiment in the northern Rocky Mountains was analyzed at 38 years to evaluate the long-term effects of retention harvests on stand development, with a focus on both regeneration and retention tree responses. The postharvest understory treatments (understory removed and broadcast burned) effects were also evaluated. Results indicate that overstory retention results in relatively long-term regeneration growth reduction. Compared with the overstory-free condition (clearcut), the shelterwood with reserves and group selection overstories both reduced the regenerated cohort's basal area, 63 and 44%, respectively. Postharvest burning increased regeneration stem density and also decreased mean regenerated tree size; consequently, these treatment effects were somewhat offsetting, as they produced a zero net difference in regenerated cohort basal area. Considerable regeneration growth reduction associated with retained overstory trees in the shelterwood with reserves was partially mitigated by understory vegetation protection measures that conserved advance regeneration. We conclude that both retention treatments somewhat suppressed regenerated cohort development, but that these impacts were lessened when overstory trees were aggregated and cuttings were in groups, rather than regularly dispersed through the cutting unit.

Keywords: western larch forest, biomass harvesting, silviculture, forest stand dynamics, variable-retention harvesting

Contemporary silviculture increasingly targets the conservation of biodiversity for ownerships that emphasize ecosystem management objectives (Seymour and Hunter 1999, Lindenmayer and Franklin 2002, Carey 2003). Because structural heterogeneity plays a critical role in forest biodiversity and other ecosystem functions, creating and promoting complex structures with treatments that mimic natural disturbances has become a major element of silvicultural prescriptions (Bunnell et al. 1999, Seymour and Hunter 1999, Mitchell and Beese 2002). Natural disturbances can generate great structural and compositional complexity (Drever et al. 2006); forest scientists recognize that even stand-replacing natural disturbances create higher structural variability than conventional timber harvesting (Mitchell and Beese 2002, Palik et al. 2014). Strategies such as variable-retention harvesting (e.g., Franklin et al. 1997), green tree retention (e.g., Rose and Muir 1997), irregular shelterwood (e.g., Raymond et al. 2009), and other forms of multiaged management (O'Hara 2014) have been developed (or reevaluated) and promoted in response to this goal. Yet, in many forest types, knowledge about key aspects of the posttreatment stand dynamics associated with these practices remains incomplete (Maguire et al. 2006).

Variable-retention harvesting (VRH) refers to a cutting method that retains live trees at harvest as structural elements for prescribed ecological objectives (Franklin et al. 1997, Helms 1998). One concern over VRH is that the retained overstory trees can hinder regeneration growth (Palik et al. 2014). A number of studies have argued that retention trees reduce the new cohort's growth through competition for limited resources (e.g., Birch and Johnson 1992, Long and Roberts 1992, Rose and Muir 1997, Acker et al. 1998, Elfving and Jakobsson 2006, Temesgen et al. 2006). However, new cohort responses should differ, depending on the spatial arrangement of overstory trees (Coates 2000). Considering the highly flexible attribute of VRH (variable numbers, sizes, and spatial patterns of retention trees), it may be possible to ameliorate reduced regeneration

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growth by manipulating overstory retention spatial patterns to reduce competition impacts, or offsetting them by controlling understory vegetation (Palik et al. 2014). Little is known about retention level effects, spatial pattern effects, and postharvest understory vegetation treatment effects (and their interactions) in many forest types; thus, decision support for forest managers charged with site-specific VRH prescription development is deficient (Zenner et al. 1998, Maguire et al. 2006).

Silvicultural experiments are key to producing that decision support, but relying solely on newly established VRH experiments that require long posttreatment response periods is inefficient and in some cases may be unnecessary. Existing long-term studies of some conventional silvicultural systems can include treatment units that closely resemble structural conditions created by VRH (even though they may not have been conducted originally with VRH in mind) and can therefore enable inferences about retention harvest consequences. For example, the shelterwood with reserves system is structurally comparable to a dispersed-overstory VRH; group selection cuttings produce gaps that are comparable to the openings created by aggregated-overstory VRH.

In 1974, northwestern Montana's Coram Experimental Forest was the site of a research project that aimed to understand the ecological consequences of increased biomass utilization levels in mature mixed-conifer forests subjected to three single-entry regeneration harvests: clearcut, group selection, and shelterwood with reserves (Barger 1980). Each harvest unit was split into thirds and subjected to three postharvest understory treatments. No cuttings were subsequently used and the site was carefully maintained since 1974, thereby providing an opportunity to compare the long-term treatment effects of retention cuttings and understory treatments on understory and overstory dynamics approximately four decades after harvest. We evaluated these retention cuttings as VRH analogs, with the group selection treatment serving as an aggregated retention analog, the shelterwood with reserves serving as a dispersed retention analog, and the clearcut serving as a retention-free control.

For this study, we tested the following predictions:

1. Because the overstory tree retention level is highest in the shelterwood with reserves, growth and vigor of natural regeneration in the shelterwood with reserves should be lowest among the regeneration cuttings.
2. If the postharvest understory vegetation treatments positively influenced shrub biomass production (recovery), then, in turn, shrub biomass should negatively affect (suppress) the development of natural regeneration. By leaving any advance regeneration intact, the understory untreated treatment should result in the greatest regenerated cohort basal area (BA). In addition, we expect to find a similar negative relationship between the postharvest understory treatment and retained overstory tree responses in the shelterwood with reserves.

Methods

Study Area

This study was conducted in western larch (*Larix occidentalis* Nutt.) mixed-conifer forests at Coram Experimental Forest (CEF). CEF is located in northwest Montana, about 9 km south of Glacier National Park. Study units were established on east slopes in Upper Abbot Creek Basin (48°25′ N, 113°59′ W), at elevations of 1,195–1,615 m and at slopes of 30–80%. Soils at CEF consist of Precambrian sedimentary rock, glacial till, and thin surface volcanic ash, classified into the loamy-skeletal soils on materials weathered from impure limestone and argillite (Klages et al. 1976).

The study area climate is a modified Pacific maritime type (Adams et al. 2008) with annual precipitation of 890–1,270 mm (mean, 1,076 mm) (Farnes et al. 1995), occurring primarily as snow during winter. The mean annual temperature ranges from 2 to 7° C (Hungerford and Schlieter 1984), with mean summer and winter temperatures of 16 and −7° C, respectively (Adams et al. 2008). The growing season length near Abbot Creek is 81 days.

The study area is representative of the western larch cover type (Society of American Foresters Cover type 212) (Eyre 1980). Western larch, Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), western hemlock (*Tsuga heterophylla* [Raf.] Sarg.), and western redcedar (*Thuja plicata* Donn ex D. Don) are mixed with several broadleaf tree species such as paper birch (*Betula papyrifera* Marshall), black cottonwood (*Populus balsamifera* L. ssp. *trichocarpa* (Torr. & A. Gray ex Hook. Brayshaw), and quaking aspen (*Populus tremuloides* Michx.). Major shrub species include Rocky Mountain maple (*Acer glabrum* Torr.), Saskatoon serviceberry (*Amelanchier alnifolia* [Nutt.] Nutt. ex M. Roem.), Sitka alder (*Alnus viridis* [Chaix] DC. ssp. *sinuata* [Regel] Á. Löve & D. Löve), mallow ninebark (*Physocarpus malvaceus* [Greene] Kuntze), dwarf rose (*Rosa gymnocarpa* Nutt.), huckleberry (*Vaccinium membranaceum* Douglas ex Torr., *Vaccinium myrtilloides* Michx.), and white spirea (*Spiraea betulifolia* Pall.). The dominant habitat type is the subalpine fir/queencup beadlily (*Clintonia uniflora* [Menzies ex Schult. & Schult. f.] Kunth) (ABLA/CLUN) habitat type (Pfister et al. 1977).

Experimental Design

The basic experimental design of this study was a split-plot design, with three regeneration cutting treatments (whole plots; shelterwood with reserves, group selection, and clearcut) and three postharvest understory vegetation treatments (subplots) (Figure 1). The postharvest understory treatments are understory untreated (U_U), understory removed (U_R), and understory broadcast burned (U_B). For the U_R treatment, shrubs and seedlings were felled, bundled, and extracted manually. Prescription details are described in Table 1. The entire experimental units were replicated twice according to elevation: 1,195–1,390 m for the lower block and 1,341–1,615 m for the upper block.

Trees were harvested in the fall of 1974 and were extracted via a running skyline yarder. Across the two blocks, the shelterwood with reserves units were 14.2 and 8.9 ha in size; clearcut units were 5.7 and 6.9 ha in size. For the group selection units, eight cutting gaps were harvested in each unit. The average gap size in group selection units was 0.3 ha, ranging from 0.1 to 0.4 ha. In the shelterwood with reserves, 36.0% of overstory trees (based on volume) were retained, whereas 0.7% of overstory tree volume was retained in group selection openings and clearcut units on average (Table 2). Diameter and stem density of retained overstory trees averaged 45.9 cm (SE 1.0) and 122.3 tree ha^{-1} (SE 8.7) 38 years after harvest (Table 3). The broadcast burning treatment was conducted in September 1975; however, cool and wet weather conditions prevented the lower shelterwood with reserves unit from being burned (Artley et al. 1978, Schmidt 1980).

In the shelterwood with reserves and clearcut, 10 permanent sample points were systematically established in 5 × 2 (row × column) grids

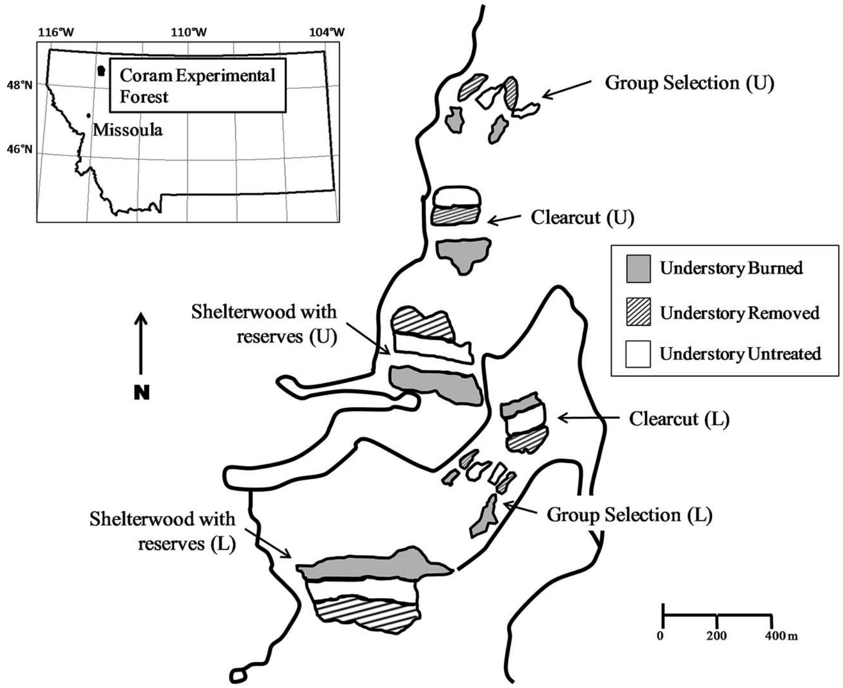

Figure 1. Study site and experimental units at Coram Experimental Forest, Montana. Letters L and U represent the lower and upper blocks of the regeneration cutting treatments. Gray, hatched, and unfilled polygons are the understory burned, understory removed, and understory untreated treatments, respectively.

Table 1. Postharvest treatments within regeneration cutting units.

Postharvest treatment	Abbreviation	Cut trees[1]	Maximum size of retained woody materials[2]
Understory untreated	U_U	>17.8 cm dbh	7.6 cm × 2.4 m
Understory removed	U_R	All trees	2.5 cm × 2.4 m
Understory (broadcast) burned	U_B	All trees	7.6 cm × 2.4 m

[1] Except designated overstory shelterwood trees.
[2] Live and dead down logs (small-end diameter × length); for dead down logs, they were removed if sound enough to yard.

within each subplot (i.e., postharvest understory treatment subplots), at 30.5-m spacing. In the group selection units, five permanent points were located in each cutting gap at various distances, according to the sizes of cutting gaps. Therefore, a total 40 permanent points were installed in each regeneration cutting unit per replicate.

Data Collection

To test the predictions, regenerated cohort BA, stem density, and quadratic mean diameter (QMD) were calculated as stand responses, and tree performance of dominant Douglas-fir trees in that cohort was represented by recent 5-year BA increment and growth efficiency (GE). For prediction 2, shrub biomass was calculated, and initial 5-year BA increment and 38-year BA increment were measured for retained trees in the shelterwood with reserves unit.

Tree species and dbh (1.37 m above groundline) was recorded for all trees taller than breast height in a nested circular plot system in 2012. Trees larger than 25 cm dbh were measured in a 12.62-m (1⁄20 ha) radius plot. Trees less than 25 and 10 cm dbh were measured in 5.64 m (1⁄100 ha) and 2.52 m (1⁄500 ha) radius plots, respectively. At each sampling point, the closest one or two dominant Douglas-fir trees of the regenerated cohort (mean, 15.0 cm dbh; range, 6.5–32.8 cm dbh) were identified. Douglas-fir was used for this analysis because of its ubiquitous presence across all treatment units. From each tree in this sample (n = 114), dbh was measured and foliage samples and two tree cores (perpendicular, at breast height) were taken. In addition, in the shelterwood with reserves units, 20 retained overstory Douglas-fir trees were selected from within each

Table 2. Pre- and postharvest aboveground woody vegetation volumes (>7.62 cm diameter).

Harvesting treatments	Preharvest volume Block 1	Preharvest volume Block 2	Postharvest volume Block 1	Postharvest volume Block 2
	. . . . (m^3/ha)	. . . .		
Clearcut				
Understory untreated	286	222	2	3
Understory removed	173	120	0	1
Understory burned	247	289	0	3
Group selection				
Understory untreated	325	466	11	2
Understory removed	231	320	0	0
Understory burned	432	269	0	2
Shelterwood with reserves				
Understory untreated	239	271	113	129
Understory removed	284	212	21	84
Understory burned	395	303	117	134

Data from Benson and Schlieter 1980. Postharvest treatments are listed in Table 1. Block 1 and 2 are low and high elevation replication, respectively.

Table 3. BA, stem density, and QMD of retention trees in shelterwood with reserves unit 38 yr after harvesting at CEF (n = 2).

Postharvest treatment	BA (m^2 ha^{-1}) Mean	BA SE	Stem density (trees ha^{-1}) Mean	Stem density SE	QMD (cm) Mean	QMD SE
Understory untreated	19.97	1.65	138	13	44.3	1.28
Understory removed	16.98	1.87	97	12	49.2	1.61
Understory burned	18.01	2.78	126	24	44.0	2.35

understory treatment subplot, avoiding trees immediately adjacent to treatment edges, dbh was measured, and two core samples were taken (perpendicular, at breast height).

From the tree cores, bark thickness, recent 5-year tree radial growth, and sapwood length were measured to the nearest 0.01 mm by digital calipers. From those measurements, recent 5-year BA increment and current cross-sectional sapwood area were calculated per tree. Those calculations were also made for the retained overstory trees, plus the 5-year BA increment after harvesting (i.e., BA increment from 1974 to 1979; hereafter, initial 5-year BA increment).

GE was used to estimate tree vigor. GE represents stem volume production per unit leaf area; thus, it is generally expressed as the ratio of a periodic volume growth to total surface leaf area (Waring 1983). In practice, BA increment is a common replacement for stem volume growth in GE (e.g., Waring et al. 1980, O'Hara 1988, Fajardo et al. 2007). In this study, GE was expressed as the ratio of 5-year BA increment to total leaf area (unit: $cm^2\ m^{-2}$). Total leaf area was estimated from cross-sectional sapwood area (Gower et al. 1987), according to the log-linear relationship between the cross-sectional sapwood area of stem and total amount of foliage (Shinozaki et al. 1964).

Shrub biomass was estimated from measurements of canopy cover or root collar diameter. In 1976 (2 years after harvesting) and in 1984, shrub canopy cover was measured from every permanent point using a nested quadrat plot system. Tall shrubs (height $>$2.5 m), medium shrubs (1.5 m $<$ height $\leq$2.5 m), and small shrubs (height $\leq$1.5 m) were measured from 25, 9, and 2.25 m^2 plots, respectively. Shrub crowns were assumed to be cylindroids; thus, height and two diameters of the crown ellipse were measured. In 2012, a revised nested circular sampling system was applied for shrub measurement. From 4 (3rd, 4th, 7th, and 8th) of 10 permanent points, the root collar diameter of each woody shrub species was measured by caliper. Shrubs taller than 1.0-m height were sampled using 1.78-m radius plots; shorter shrubs were sampled using 0.80-m radius plots. Shrub biomass in 1976 (hereafter, "shrub biomass$_{2\ yr}$") and biomass increment during 1976 to 1984 (years 2–10; "shrub biomass$_{2–10\ yr}$") were calculated through equations converting canopy volume to biomass (in situ regression derived in 1974 via destructive sampling; W. Schmidt, Forest Service Rocky Mountain Research Station (retired), August 30th, 1979). Shrub biomass in 2012 was calculated using Brown's (1976) biomass equations for northern Rocky Mountain shrub species.

Data Analysis

Because the experimental design of this study was a split-plot design and included both fixed and random effects, a mixed-effects model was used. The basic model form is as

$$y_{ijkl} = \mu + \alpha_i + B_k + \varepsilon_{(1)ik} + \beta_j + \alpha_i\beta_j + \varepsilon_{(2)ijk} + \varepsilon_{ijkl} \quad (1)$$

where y_{ijkl} is the response variable, μ is the grand mean, α_i is the effect of regeneration cutting (whole-plot effect), B_k is the block effect (random effect), β_j is the effect of postharvest understory vegetation treatment (subplot effect), $\alpha_i\beta_j$ is the interaction between whole-plot and subplot effects, and $\varepsilon_{(1)ik}$, $\varepsilon_{(2)ijk}$, and ε_{ijkk} are the whole-plot error, the subplot error, and the variation among sampling plots in a subplot, respectively. If the interaction term was nonsignificant, the term was removed to test the treatment effects more accurately.

A simpler model was constructed for the retained trees, because they occurred only in the shelterwood with reserves units, and hence there was no regeneration cutting effect. If a significant treatment effect was detected, then linear contrasts among regeneration cuttings (clearcut versus shelterwood with reserves, clearcut versus group selection, and group selection versus shelterwood with reserves) and understory treatments were tested. To assess the understory treatment effects, the understory removal and understory burning treatments were compared against the understory untreated (i.e., U_U versus U_R and U_U versus U_B).

To test prediction 1, regenerated cohort BA, stem density, QMD, recent 5-year BA increment, and GE were tested as response variables. For the latter two responses, dbh was added to the model as a linear covariate to account for the tree size effect. For prediction 2, shrub biomass and recovery and initial 5-year BA increment and 38-year BA increment of retained trees (shelterwood with reserves unit) were compared among the three postharvest understory treatments. Pearson's correlation tests were conducted between shrub biomass and retained tree responses and regenerated tree responses.

All analyses were conducted via R (R Development Core Team 2008). The package nlme (Pinheiro et al. 2014) was used to fit mixed-effects models. Linear contrasts among retention cuttings and postharvest understory treatments were investigated via the multcomp (Hothorn et al. 2014) package.

Results

Regenerated Tree Responses to Retention Cuttings

More than 95% of the regenerated cohort BA was composed of five major species: Douglas-fir (51%), subalpine fir (21%), western larch (8%), paper birch (8%), and Engelmann spruce (7%). Upper and lower blocks differed in composition, with the upper block containing more abundant subalpine fir and the lower block containing more paper birch. Postharvest understory treatment proved a stronger determinant of species composition than cutting treatment. There was no consistent trend in species composition by retention cuttings except for western larch; the greatest abundance of western larch was consistently produced by the shelterwood with reserves treatment regardless of understory treatment (Figure 2).

Thirty-eight years after cutting, tree densities of the regenerated cohort ranged from 2,198 to 4,728 trees ha^{-1}. That cohort's BA in the clearcut was 18.8 $m^2\ ha^{-1}$ (SE 0.61); it was substantially lower in both the shelterwood with reserves (63% less; 7.07 $m^2\ ha^{-1}$, SE 0.63) and group selection (44% less; 10.5 $m^2\ ha^{-1}$, SE 0.73). The regenerated cohort QMDs for the shelterwood with reserves (8.0 cm, SE 0.4) and group selection (8.0 cm, SE 1.0) were reduced by more than 18% to the clearcut (9.8 cm, SE 1.5). The interaction between the regeneration cutting and postharvest treatment had no significant effects on any regeneration variable (Table 4). From the reduced model without the interaction term, a moderate evidence of an effect of regeneration cutting on the regenerated cohort's BA was found ($P = 0.057$).

The mean recent 5-year BA increment (of the regenerated Douglas-fir sample) was greatest in the clearcut (67.7 cm^2, SE 0.1), followed by the group selection (20.0% less at 54.2 cm^2, SE 1.8) and shelterwood with reserves (68.7% less at 21.2 cm^2, SE 0.6). Mean GE was also greatest in the clearcut (1.79 $cm^2\ m^{-2}$; SE 0.02); it was similar in the group selection (1.68 $cm^2\ m^{-2}$; SE 0.04), but was just nearly half as efficient in the shelterwood with reserves (0.91 $cm^2\ m^{-2}$; SE 0.31). The regeneration cutting treatment effect on GE was moderate ($P = 0.068$), whereas it was nonsignificant on recent 5-year BA increment ($P = 0.158$). Collectively, the shelterwood

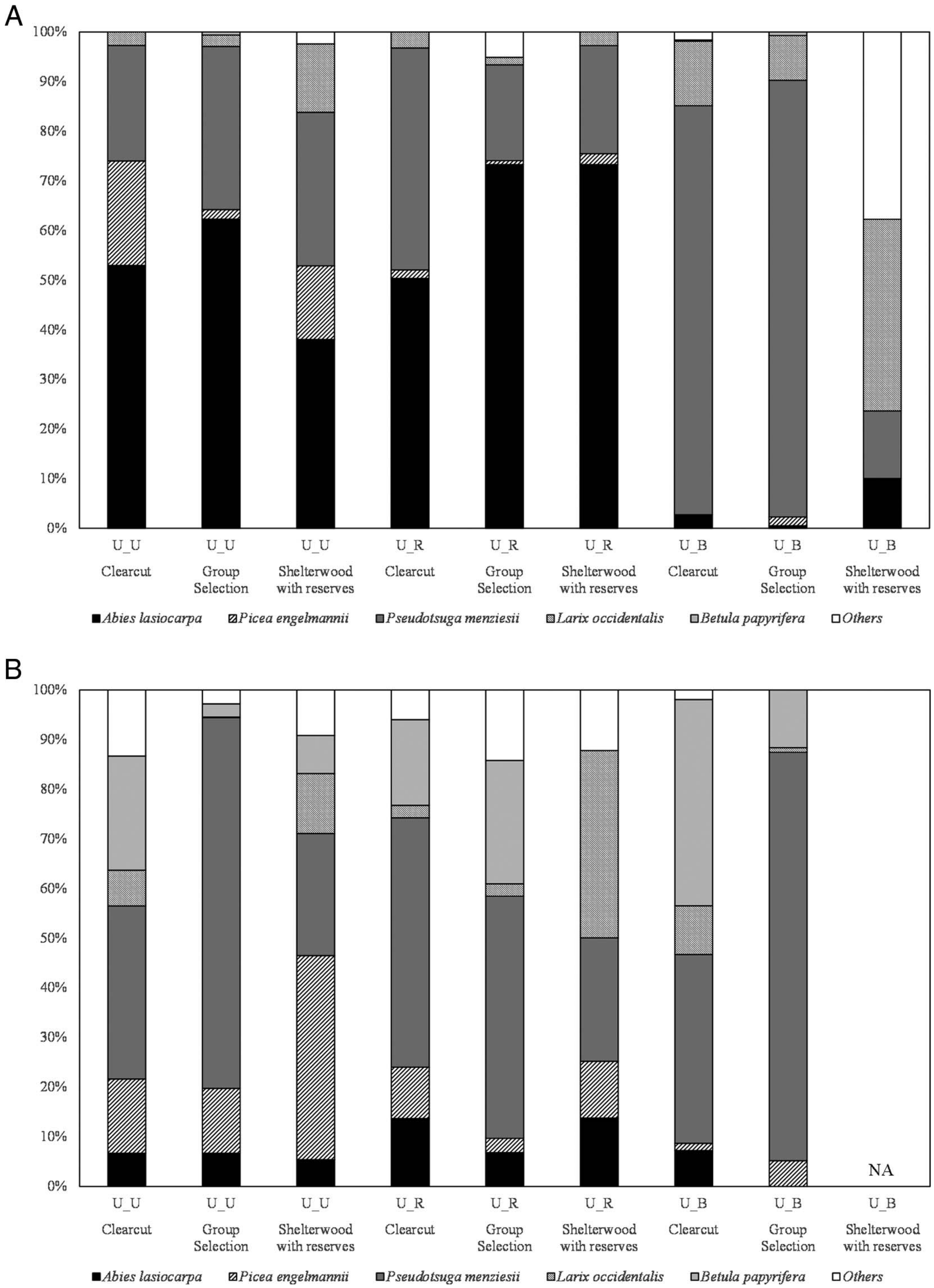

Figure 2. Species composition (percentage of biomass) of regeneration of upper (A) and lower (B) block 38 years after cutting treatment, combined with postharvest understory vegetation treatment.

with reserves and group selection tended to have lower regenerated cohort BA and GE than the clearcut.

Regenerated and Retained Tree Responses to Postharvest Understory Treatments

Postharvest understory treatment influenced both the stem density ($P < 0.001$) and mean size (QMD; $P = 0.004$) of the regenerated cohort, whereas its effect was nonsignificant on BA ($P = 0.931$), recent 5-year BA increment ($P = 0.393$), and GE ($P = 0.352$). Among the understory treatments, the difference in QMD was primarily observed in the contrast between the U_U and the U_B treatments. Across all three regeneration cuttings, the U_B treatment reduced regenerated cohort QMD on average by 68%; (7.0 cm; SE 1.6) and increased stem density by 392% (3,899 trees ha^{-1}; SE 698) relative to the U_U treatment ($P = 0.003$ and $P < 0.001$, respectively).

Shrub biomass in 1976 and 2 years after harvesting (shrub biomass$_{2\ yr}$) was affected by understory treatment ($P < 0.001$): the U_U treatment retained approximately 2.4 times ($P < 0.001$) the

Table 4. Analysis of variance for the responses of BA, stem density, QMD of the regenerated cohort, recent 5-year BA increment, and GE of dominant Douglas-fir trees in that cohort.

Source of variation	ndf	ddf	BA		Stem density		QMD		5-year BA Increment		GE	
			F	*P*[1]	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Model with interaction												
Regeneration cutting (R)	2	2	7.40	0.119	0.10	0.908	3.58	0.218	1.15	0.466	5.37	0.157
Postharvest treatment (P)	2	6	1.43	0.311	2.60	0.154	8.31	0.019*	4.05	0.077	0.25	0.789
Interaction (R × P)	4	6	0.83	0.552	1.64	0.279	1.31	0.364	2.26	0.178	0.99	0.479
dbh	1	95							105.28	<0.001***	1.72	0.193
Model without interaction												
Regeneration cutting	2	2	16.60	0.057	4.304	0.189	1.96	0.338	5.31	0.158	13.79	0.068
Postharvest treatment	2	10	0.07	0.931	17.099	<0.001***	9.80	0.004**	1.03	0.393	1.16	0.352
dbh	1	95							97.14	<0.001***	3.31	0.072

dbh was used as a covariate. ndf, numerator degrees of freedom; ddf, denominator degrees of freedom.
[1] Significance codes: 0 < *** < 0.001 < ** < 0.01 < * < 0.05.

shrub biomass than the U_B treatment and 1.2 times than the U_R treatment ($P < 0.001$). After that initial period, shrub biomass seemed independent of treatment history. During the following 8-year period (shrub biomass$_{2\text{–}10\ \text{yr}}$) it was unaffected by regeneration cutting ($P = 0.202$) or understory treatment ($P = 0.872$). The same was true in 2012 (38 years after harvesting), when shrub biomass was again unaffected by both regeneration cutting ($P = 0.282$) and understory treatment ($P = 0.337$). In 2012, the shrub biomass levels for clearcut, group selection, and shelterwood with reserves were 6.85 (SE 1.43), 10.40 (SE 2.67), and 5.37 (SE 1.85) Mg ha^{-1}, respectively.

None of the regeneration variables were correlated with the current (2012) shrub biomass levels, including regenerated cohort BA ($P = 0.733$), stem density ($P = 0.454$), and QMD ($P = 0.257$). Past shrub biomass levels, however, produced significant but mixed relationships to some current (2012) regeneration variables. For example, the current stem density of the regenerated cohort was negatively correlated with past shrub biomass levels, including both shrub biomass$_{2\ \text{yr}}$ ($r = -0.339$; $P < 0.001$) and shrub biomass$_{2\text{–}10\ \text{yr}}$ ($r = -0.206$; $P = 0.022$). In contrast, the current regenerated cohort QMD was positively correlated with shrub biomass$_{2\ \text{yr}}$ ($r = 0.334$; $P < 0.001$), and shrub biomass$_{2\text{–}10\ \text{yr}}$ ($r = 0.257$; $P = 0.004$). Current BA showed no correlation with either shrub biomass$_{2\ \text{yr}}$ ($P = 0.687$) or shrub biomass$_{2\text{–}10\ \text{yr}}$ ($P = 0.939$).

There was moderate evidence of understory treatment effect on GE of shelterwood retention trees (Douglas-fir) ($P = 0.052$) and strong evidence of its effect on the initial 5-year BA increment ($P = 0.010$) (Table 5). The U_U treatment increased GE by 113% (0.15 cm^2 m^{-2}; SE 0.07) over the U_B treatment ($P = 0.049$). There was no difference in the initial 5-year BA increment between the U_U and U_R treatment ($P = 0.099$). Instead, the initial 5-year BA increment in the U_B treatment was 31.7 cm^2 ($P = 0.009$) less than in the U_U treatment after adjustment for tree size.

Although we found no statistically significant evidence of a persistent understory treatment effect on current BA increment of either regenerated trees (Table 4) or retained trees (Table 5), we did observe an apparent relationship between these two cohorts. In the U_R treatment, the largest positive effect (633.6 cm^2, SE 82.2) on BA increment of the retained trees accompanied the largest negative impact on regenerated trees (-755.1 cm^2, SE 101.6). In contrast, the least positive effect on retained trees observed in the U_B treatment (467.6 cm^2, SE 89.6) resulted in the least negative impact on regenerated tree BA increment (-296.8 cm^2, SE 182.2). The U_U treatment had a moderate impact on both retained and regenerated Douglas-fir tree BA increment (581.0 cm^2, SE 78.7; -726.8 cm^2, SE 101.6, respectively). Using the understory untreated (U_U) as a benchmark, burning reduced the 38-year BA increment of retained trees by 113.8 cm^2 and increased that increment of regenerated trees by 429.9 cm^2.

Table 5. Result summary of analysis of variance for the responses (recent 5-year BA increment, GE, and initial 5-year BA increment) of retained Douglas-fir trees in the shelterwood with reserves units.

Responses	dbh[1]		Retention tree volume after harvesting		Postharvest treatment[2]	
	F	*P*	*F*	*P*	*F*	*P*
Initial 5-year BA increment	37.72	<0.001***[3]	0.93	0.337	4.78	0.010*
Recent 5-year BA increment	21.14	<0.001***	2.76	0.099	2.59	0.080
Total BA increment	12.07	<0.001***	3.53	0.063	2.59	0.080
GE	10.40	0.002**	0.66	0.417	2.72	0.052

[1] In the analysis for initial 5-year BA increment, the inner bark diameter in 1974 was used as a covariate.
[2] Statistics were calculated from the reduced models (i.e., models without the retention tree volume variable).
[3] Significance codes: 0 < *** < 0.001< ** < 0.01 < * < 0.05.

Species composition of the regenerated cohort was substantially influenced by understory treatments, with the early-seral, shade-intolerant (western larch) and mid-tolerant (Douglas-fir) species responding in a manner markedly differently from that of the late-seral, shade-intolerant species (subalpine fir, Engelmann spruce) (Figure 2). Notably, burning (U_B) severely reduced the abundance of subalpine fir and Engelmann spruce and increased the abundance of Douglas-fir and western larch. The U_U treatment did not seem to alter the abundance of the latter two species, relative to the U_R treatment. The U_R treatment affected the two late-seral, shade-tolerant species differently: the U_R treatment consistently increased subalpine fir absolute (BA) and relative (%) abundance, whereas it consistently decreased those metrics for Engelmann spruce.

Discussion

Regenerated Tree Responses to Retention Cutting

Supporting prediction 1, the most substantial reduction of regenerated cohort BA was observed with the shelterwood with reserves (63%). This finding aligns with previous retrospective natural regeneration studies of retention cutting in the Pacific Northwest that observed a negative relationship between retained tree density and regeneration BA (e.g., Rose and Muir 1997, Acker et al. 1998, Zenner et al. 1998, Mitchell et al. 2007). The growth reduction we observed in the shelterwood with reserves was surprisingly great (63%) and exceeds that in most previous reports. Despite this extensive reduction, the absolute regenerated cohort BA in 2012 was sufficient to restock the site and in fact is comparatively greater than that of other studies with similar retention tree densities. For example, our site's regenerated cohort BA in the shelterwood with reserves unit (122 retention trees ha^{-1}) was approximately 7.05 m^2 ha^{-1}, a density far greater than the modest 2.02 m^2 ha^{-1} regeneration density that would be expected using the equation produced by Rose and Muir (1997) based on their findings. Typical of such studies, the inferential value of our site is limited to similar overstory retention levels and similar sites. Regeneration responses to overstory retention levels have been commonly regarded as nonlinear (e.g., Birch and Johnson 1992, Rose and Muir 1997, Acker et al. 1998); thus, extrapolation to heavy retention levels should be implemented with caution.

One striking result of this study is the substantial (44%) reduction of BA observed in the group selection treatment. The overstory was removed in a way almost identical to that for the clearcut, and site conditions were similar, yet its regenerated cohort BA after 38 years was substantially less. This result illustrates the fact that retained trees in the uncut matrix expressed an influence on regeneration dynamics within the cutting gap that has persisted over nearly four decades. The cutting gap sizes (rather small) are probably responsible in this case. In coniferous forests of British Columbia, the 5-year radial growth of coniferous seedlings was positively related to the cutting gap size (Coates 2000). In that study, Coates argued that, especially in small cutting gaps, seedling growth is affected by its specific location within a gap; the largest seedlings were found in the middle of cutting gaps. In our study, the area of group selection gaps were modest, ranging from approximately 0.1 to 0.4 ha. Sampling at our site was conducted in plots scattered throughout each cutting gap; hence, our plot values represented subsamples of the mean cutting gap condition and were not specifically related to position within the gap. Therefore, determining how seedlings performed as a function of their specific positions within the cutting gaps was not possible using this sampling design. Yet some plots were located close to the cutting gap edge, and sampled trees within such plots were probably disproportionately affected by edge trees. Such edge tree effects have been known to increase the within-gap variance in regeneration variables (Shatford et al. 2009, Lam and Maguire 2011). Nevertheless, the statistical significance of the whole-plot effect in this study indicates that the sample size was big enough to encompass the variance. Our plot mean values probably underestimate the potential growth performance of seedlings occurring in a central position within each cutting gap and overestimate the performance of seedlings close to the gap edge.

The net retention effect on regeneration in the shelterwood with reserves seems to reflect an impact not only on seedling recruitment and growth processes but also on regeneration mortality. A previous study conducted at the site in 1992 revealed significantly greater numbers of established regeneration (19,895 trees ha^{-1} by 1992) in the shelterwood with reserves versus the clearcut (6,843 trees ha^{-1}) and group selection (7,168 trees ha^{-1}), a finding that was attributed to abundant on-site seed and shade provided by retained trees (Shearer and Schmidt 1999). However, 20 years later (2012), differences in stem density among regeneration cuttings had reversed. Stem density in the shelterwood with reserves became the sparsest (Figure 3); conversely, regeneration density in the clearcut became the greatest (slightly more than the group selection). The clearcut and group selection seemed not to differ in this regard; there was no statistical difference in regeneration density between the clearcut and group selection in either 1992 (Shearer and Schmidt 1999) or 2012.

Surprisingly, we found that the most shade-intolerant species (i.e., western larch) proliferated in the most shaded (shelterwood with reserves) units. That may be attributed in part to the influence of a local western spruce budworm (*Choristoneura occidentalis* Freeman) outbreak occurring around the year of harvest (1974). Shearer and Schmidt (1999) reported that a spruce budworm outbreak at that time almost eliminated the flowering buds of Douglas-fir and Engelmann spruce (damage to western larch was minor, a fact that could have favored the initial establishment of western larch, along with abundant seed source from retained trees).

Advance regeneration undoubtedly played an important role in regeneration responses, especially in the shelterwood with reserves. In the understory untreated treatment, which theoretically allowed the maximum opportunity for advance regeneration survival, regenerated cohort BA production in the shelterwood with reserves remained equal to that of the more open group selection treatment. This result indicates that the protection of advance regeneration (or presumably, rapid regeneration establishment) can mitigate the adverse impacts of overstory retention on regeneration cohort density, albeit with potentially important species composition differences in the new cohort.

Effect of Understory Vegetation Treatments

Previous research in stands harvested with partially retained overstories has demonstrated a negative correlation between regeneration growth and understory shrub cover (e.g., Harrington 2006, Mitchell et al. 2007, Urgenson et al. 2013, Palik et al. 2014). Our results seem to support this argument, because we found a negative correlation of current regenerated tree density to both shrub $biomass_{2\ yr}$ and shrub $biomass_{2\text{–}10\ yr}$. The result that the burning (U_B) treatment increased stem density over the untreated (U_U) treatment can be explained by the fact that shrubs in the U_U treatment recovered immediately (within 2 years after harvesting, shrub biomass in the U_U treatment had already recovered to over 70% of the preharvesting level, as reported by Schmidt [1980]), an outcome that in turn very likely hindered regeneration in that treatment (Shatford et al. 2007). In contrast, the U_B treatments had low levels ($<$10% of preharvesting level) of shrub biomass, and regeneration responded positively to the diminished competition and increased resource availability.

The trend of regenerated cohort QMD response to retention treatment was consistently opposite that of its density response to the same treatment. The greater regeneration size may be attributed to the preservation of advance regeneration and to reduced competition with other seedlings. As a result, reductions in cohort stem density were compensated for by greater tree sizes, yielding similar regenerated cohort BAs among understory treatments that did not significantly differ.

Regeneration species composition seems to have been affected by postharvest understory treatments, implying the differential responses of each tree species to disturbance regimes represented by the treatment combinations. Among late-seral species in our study site, Engelmann spruce proved most susceptible to disturbance, whereas subalpine fir and Douglas-fir seemed to benefit from the

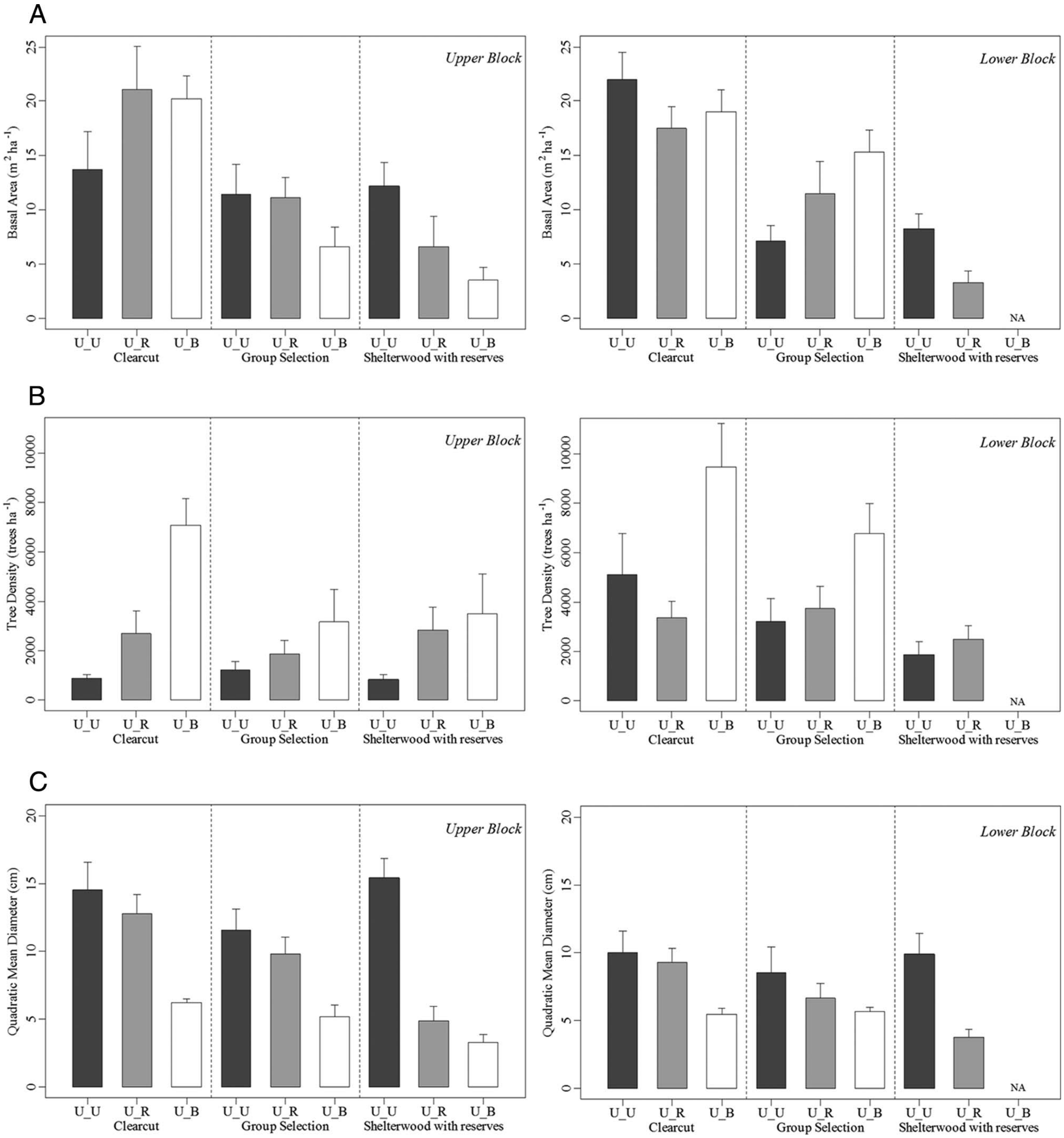

Figure 3. Regenerated cohort BA (A), stem density (B), and QMD (C) by regeneration cutting treatment, combined with postharvest understory vegetation treatment (38 years after harvest). Left and right columns indicate the upper and lower block, respectively.

depletion of Engelmann spruce advance regeneration by the understory removal treatment (Figure 2). On the other hand, both subalpine fir and Engelmann spruce—species of thin bark and low resistance to fire (Fischer and Bradley 1987)—were virtually excluded by the burning treatment, to be replaced by Douglas-fir and western larch. This outcome reinforces the recommendation that, as always, forestland managers should take into account the silvics of each species and its response to specific treatments to best achieve species composition goals in the regeneration cohort.

Retained Tree Versus Regenerated Tree

Among retained trees in the shelterwood with reserves, a significant effect of understory treatment was observed on tree basal area increment during the initial 5 years after treatment and was suggested (but not significant) during the most recent 5-year period and over the total 38-year period, particularly for the burning treatment. Negative impacts of prescribed burning treatment on retained trees can be attributed to many factors, including changes in growth conditions, tree physiological responses due to heat damage, and proliferation of understory vegetation. Adverse impacts of burning treatment on tree growth have been well documented, especially for mature ponderosa pine ecosystems across the Rocky Mountain regions (e.g., Sutherland et al. 1991, Swezy and Agee 1991, Landsberg 1992, Busse et al. 2000). However, several contradictory results have also been published, suggesting there was positive or no burning effect on tree growth (e.g., Wyant et al. 1983, Feeney et al. 1998). In addition, any negative impacts of burning on retained tree growth might be temporary (Sala et al. 2005, but see Monleon et al. 1997).

In our study, burning exhibited a negative impact on retained trees that was persistent even 38 years after treatment. The fire intensities of this study were mild (Artley et al. 1978, Schmidt 1980); therefore, the negative impacts were probably not due to a physiological response to fire. Rather, increased competition with understory vegetation seems to more plausibly explain the burning effect on overstory growth. The burning treatment resulted in a proliferation of regeneration (Shearer and Schmidt 1999) and the shrub community (Schmidt 1980), and hence burning indirectly increased the demand for site resources. Overstory trees possessed an advantage of preoccupancy, but as Harrington (2006) found in shelterwood treatments, root competition can be a stronger limiting factor than light. We believe that a flourishing understory vegetation layer after burning competed against overstory trees for limited belowground resources, and the increment of retained trees was constrained (relative to the unburned treatments) as a result.

Implications for VRH

Given similar forest overstory and understory conditions, we expect that the results of this study can be used to inform VRH application in the northern Rocky Mountain region. Our results over nearly 40 years after retention cutting indicate that:

1. In retention cutting that produces small cutting gaps (such as aggregated variable-retention harvests) and in dispersed retention cutting that retains high overstory levels, it can be expected that regeneration growth will be suppressed below the site's potential (relative to open conditions that are free of retention trees).
2. Retention cutting can reduce the growth efficiency and basal growth increment of regenerated trees. These negative impacts can persist over 38 years after harvesting.
3. Advance regeneration can play an important role in determining the aboveground vegetation growth rates in VRH that resembles a shelterwood with reserves. Protection of advance regeneration during (and after) harvest can thereby ameliorate the negative effect that overstory retention has on the growth of a new cohort. However, the resulting species composition of the new cohort must be taken into consideration, as understory treatments will vary in this regard.
4. Postharvest vegetation control and burning treatments can influence the regenerated stem density, but reduced stem density can be offset by increased regeneration sizes and thereby result in no net difference in total BA of regenerated cohort while also producing larger trees.
5. Postharvest vegetation removal and burning treatments strongly influence some components of regeneration species composition. Therefore, forestland managers should evaluate the response of each species when they prescribe postharvest understory treatments.

Whereas this study produced unusually long-term information to help with the development of silvicultural prescriptions involving overstory retention, its scope of inference has some limitations due to attributes of the original experimental and sampling designs on which it was founded. Our results should inform implementation on other forest types with different management regimes, but due to lack of replicates, they should be applied with caution. For example, relative differences in regeneration performance indicated by this study may be reliable, but the absolute values will probably differ substantially by site. In addition, because the original study design was not built specifically to assess differences in overstory retention levels and patterns, the range of these variables was strictly confined to the two treatments, whereas many variations could exist. For example, gap sizes in the group selection could vary widely between and within stands, with concomitant differences in regeneration conditions. Likewise, various retained tree densities in the shelterwood with reserves should yield a range of regeneration outcomes.

This study's sampling design also was limiting, particularly in the group selection cutting, where sample plots were located only in the cut patches, and none were placed in the uncut matrix. This prevented us from analyzing the growth and mortality occurring among retained trees in that treatment over time. As a result, we focused on the treatments as aggregated versus dispersed approaches to retention (with the zero-retention clearcut as a comparison), while recognizing that with these two retention treatments, overstory retention levels were confounded with the spatial organization of retention.

Yet, those shortcomings also yielded value by helping to suggest best practices for newer studies on this subject. Future studies would ideally be designed with more replicates, and a wide range of overstory retention levels that avoid the confounding of retention density and spatial pattern. In addition, because it is a specific goal of retention cutting to produce structural complexity and because complexity itself affects the resulting stand dynamics, analysis of long-term responses to retention cutting treatments calls for a sampling design that isolates and efficiently captures the variable within-stand microsites that retention cutting produces.

Literature Cited

ACKER, S.A., E. ZENNER, AND W. EMMINGHAM. 1998. Structure and yield of two-aged stands on the Willamette National Forest, Oregon: Implications for green tree retention. *Can. J. For. Res*. 28(5):749–758.

ADAMS, M.B., L. LOUGHRY, AND L. PLAUGHER (COMPS.). 2004; revised March 2008. *Experimental forests and ranges of the USDA Forest Service.* USDA For. Serv., Gen. Tech. Rep. GTR-NE-321 Rev., Northern Research Station, Newtown Square, PA. 183 p.

ARTLEY, D.F., R.C. SHEARER, AND R.W. STEELE. 1978. *Effects of burning moist fuels on seedbed preparation in cutover western larch forests.* USDA For. Serv., Res. Pap. RP-INT-211, Intermountain Forest and Range Experiment Station, Ogden, UT. 14 p.

BARGER, R.L. 1980. The forest residues utilization program in brief. P. 7–26 in *Environmental consequences of timber harvesting in Rocky Mountain coniferous forests: Symposium proceedings, 1979 September 11–13, Missoula, Mont.* USDA For. Serv., Gen. Tech. Rep. GTR-INT-90, Intermountain Forest and Range Experiment Station, Ogden, UT.

BENSON, R.E., AND J.A. SCHLIETER. 1980. *Logging residues in principal forest types of the northern Rocky Mountains.* USDA For. Serv., Res. Pap. RP-INT-260, Intermountain Forest and Range Experiment Station, Ogden, UT. 14 p.

BIRCH, K.R., AND K.N. JOHNSON. 1992. Stand-level wood-production costs of leaving live, mature trees at regeneration harvest in coastal Douglas-fir stands. *West. J. Appl. For*. 7(3):65–68.

BROWN, J.K. 1976. Estimating shrub biomass from basal stem diameters. *Can. J. For. Res*. 6(2):153–158.

Bunnell, F.L., L.L. Kremsater, and E. Wind. 1999. Managing to sustain vertebrate richness in forests of the Pacific Northwest: Relationships within stands. *Environ. Rev*. 7(3):97–146.

Busse, D., A. Simon, and M. Riegel. 2000. Tree-growth and understory responses to low-severity prescribed burning in thinned *Pinus ponderosa* forests of central Oregon. *For. Sci*. 46(2):258–268.

Carey, A. 2003. Biocomplexity and restoration of biodiversity in temperate coniferous forest: Inducing spatial heterogeneity with variable-density thinning. *Forestry* 76(2):127–136.

Coates, K.D. 2000. Conifer seedling response to northern temperate forest gaps. *For. Ecol. Manage*. 127:249–269.

Drever, C.R., G. Peterson, C. Messier, Y. Bergeron, and M. Flannigan. 2006. Can forest management based on natural disturbances maintain ecological resilience? *Can. J. For. Res*. 36(9):2285–2299.

Elfving, B., and R. Jakobsson. 2006. Effects of retained trees on tree growth and field vegetation in *Pinus sylvestris* stands in Sweden. *Scand. J. For. Res.* 21(Suppl. 7):29–36.

Eyre, F.H. 1980. *Forest cover types of the United States and Canada.* Society of American Foresters. Washington, DC. 148 p.

Fajardo, A., J.M. Graham, J.M. Goodburn, and C.E. Fiedler. 2007. Ten-year responses of ponderosa pine growth, vigor, and recruitment to restoration treatments in the Bitterroot Mountains, Montana, USA. *For. Ecol. Manage*. 243(1):50–60.

Farnes, P.E., R.C. Shearer, W.W. McCaughey, and K.J. Hansen. 1995. *Comparisons of hydrology, geology, and physical characteristics between Tenderfoot Creek Experimental Forest (east side) Montana, and Coram Experimental Forest (west side) Montana*. USDA For. Serv., Final Rep. RJVA-INT-92734, Intermountain Research Station, Forestry Sciences Laboratory, Bozeman, MT. 19 p.

Feeney, S.R., T.E. Kolb, W.W. Covington, and M.R. Wagner. 1998. Influence of thinning and burning restoration treatments on presettlement ponderosa pines at the Gus Pearson Natural Area. *Can. J. For. Res*. 28(9):1295–1306.

Fischer, W.C., and A.F. Bradley. 1987. *Fire ecology of western Montana forest habitat types*. USDA For. Serv., Gen. Tech. Rep. GTR-INT-223, Intermountain Forest and Range Experiment Station, Ogden, UT. 95 p.

Franklin, J.F., D.R. Berg, D.A. Thornburgh, and J.C. Tappeiner. 1997. Alternative silvicultural approaches to timber harvesting: Variable retention harvest systems. P. 111–139 in *Creating a forestry for the 21st century: The science of ecosystem management.* Island Press, Washington, DC.

Gower, S.T., C.C. Grier, D.J. Vogt, and K.A. Vogt. 1987. Allometric relations of deciduous (*Larix occidentalis*) and evergreen conifers (*Pinus contorta* and *Pseudotsuga menziesii*) of the Cascade Mountains in central Washington. *Can. J. For. Res*. 17(7):630–634.

Harrington, T.B. 2006. Five-year growth responses of Douglas-fir, western hemlock, and western redcedar seedlings to manipulated levels of overstory and understory competition. *Can. J. For. Res*. 36(10): 2439–2453.

Helms, J. 1998. *The dictionary of forestry.* Society of American Foresters. Western Heritage Co., Bethesda, MD. 224 p.

Hothorn, T., F. Bretz, and P. Westfall. 2014. *multcomp: Simultaneous inference in general parametric models.* R package version 1.3-3. R Foundation for Statistical Computing, Vienna, Austria.

Hungerford, R.D., and J.A. Schlieter. 1984. *Weather summaries for Coram Experimental Forest, northwestern Montana: An international biosphere reserve*. USDA For. Serv., Gen. Tech. Rep. GTR- INT-160, Intermountain Forest and Range Experiment Station, Ogden, UT. 34 p.

Klages, M.G., R.C. McConnell, and G. A. Nielsen. 1976. *Soils of the Coram Experimental Forest.* Res. Rep. 91, Montana State Univ., Montana Agricultural Experiment Station. Bozeman, MT. 43 p.

Lam, T.Y., and D.A. Maguire. 2011. Thirteen-year height and diameter growth of Douglas-fir seedlings under alternative regeneration cuts in Pacific Northwest. *West. J. Appl. For*. 26(2):57–63.

Landsberg, J.D. 1992. *Response of ponderosa pine forests in central Oregon to prescribed underburning.* Doctoral dissertation. Oregon State Univ. Corvallis, OR. 282 p.

Lindenmayer, D.B., and J.F. Franklin. 2002. *Conserving forest biodiversity: A comprehensive multiscaled approach.* Island Press, Washington, DC. 351 p.

Long, J.N., and S.D. Roberts. 1992. Technical commentary: Growth and yield implications of a "new forestry" silvicultural system. *West. J. Appl. For*. 7(1):6–9.

Maguire, D., D. Mainwaring, and C. Halpern. 2006. Stand dynamics after variable-retention harvesting in mature Douglas-fir forests of western North America. *Allg. For. Jagdzt.* 177(6/7):120–131.

Mitchell, A.K., R. Koppenaal, G. Goodmanson, R. Benton, and T. Bown. 2007. Regenerating montane conifers with variable retention systems in a coastal British Columbia forest: 10-Year results. *For. Ecol. Manage*. 246:240–250.

Mitchell, S.J., and W.J. Beese. 2002. The retention system: Reconciling variable retention with the principles of silvicultural systems. *For. Chron*. 78(3):397–403.

Monleon, V.J., K. Cromack, and J.D. Landsberg. 1997. Short-and long-term effects of prescribed underburning on nitrogen availability in ponderosa pine stands in central Oregon. *Can. J. For. Res.* 27(3):369–378.

O'Hara, K.L. 1988. Stand structure and growing space efficiency following thinning in an even-aged Douglas-fir stand. *Can. J. For. Res*. 18(7):859–866.

O'Hara, K.L. 2014. *Multiaged silviculture: Managing for complex forest stand structures*. Oxford Univ. Press. Oxford, UK. 213 p.

Palik, B.J., R.A. Montgomery, P.B. Reich, and S.B. Boyden. 2014. Biomass growth response to spatial pattern of variable-retention harvesting in a northern Minnesota pine ecosystem. *Ecol. Applic*. 24(8):2078–2088.

Pfister, R.D., B.L. Kovalchik, S.F. Arno, and R.C. Presby. 1977. *Forest habitat types of Montana.* USDA For. Serv., Gen. Tech. Rep. GTR-INT-34, Intermountain Forest and Range Experiment Station, Ogden, UT. 174 p.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, EISPACK authors, S. Heisterkamp, B. Van Willigen, and R Core Team. 2014. nlme: Linear and nonlinear mixed effects models. R package version 3.1-117. Available online CRAN.R-project.org/package=nlme; last accessed November 17, 2015.

R Development Core Team. 2008. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Raymond, P., S. Bédard, V. Roy, C. Larouche, and S. Tremblay. 2009. The irregular shelterwood system: Review, classification, and potential application to forests affected by partial disturbances. *J. For*. 107(8):405–413.

Rose, C.R., and P.S. Muir. 1997. Green-tree retention: Consequences for timber production in forests of the western Cascades, Oregon. *Ecol. Applic*. 7(1):209–217.

Sala, A., G.D. Peters, L.R. McIntyre, and M.G. Harrington. 2005. Physiological responses of ponderosa pine in western Montana to thinning, prescribed fire and burning season. *Tree Physiol*. 25(3):339–348.

Schmidt, W.C. 1980. Understory vegetation response to harvesting and residue management in a larch/fir forest. P. 221–248 in *Environmental consequences of timber harvesting in Rocky Mountain coniferous forests: Symposium proceedings, 1979 September 11–13, Missoula, Mont.* USDA For. Serv., Gen. Tech. Rep. GTR-INT-90, Intermountain Forest and Range Experiment Station, Ogden, UT.

Seymour, R.S., and M.L. Hunter, Jr. 1999. Principles of ecological forestry. P. 22–61 in *Managing biodiversity in forest ecosystems*, Hunter, M.L. (ed.). Cambridge Univ. Press, Cambridge, UK.

Shatford, J.P.A., J.D. Bailey, and J.C. Tappeiner. 2009. Understory tree development with repeated stand density treatments in coastal Douglas-fir forests of Oregon. *West. J. Appl. For*. 24(1):11–16.

Shatford, J.P.A., D.E. Hibbs, and K.J. Puettmann. 2007. Conifer regeneration after forest fire in the Klamath-Siskiyous: How much, how soon? *J. For*. 105(3):139–146.

Shearer, R.C., and J.A. Schmidt. 1999. Natural regeneration after harvest and residue treatment in a mixed conifer forest of northwestern Montana. *Can. J. For. Res*. 29(2):274–279.

Shinozaki, K., K. Yoda, K. Hozumi, and T. Kira. 1964. A quantitative analysis of plant form-the pipe model theory. I. basic analyses. *Jpn. J. Ecol*. 14(3):97–105.

Sutherland, E.K., W.W. Covington, and S. Andariese. 1991. A model of ponderosa pine growth response to prescribed burning. *For. Ecol. Manage*. 44:161–173.

Swezy, D.M., and J.K. Agee. 1991. Prescribed-fire effects on fine-root and tree mortality in old-growth ponderosa pine. *Can. J. For. Res*. 21(5):626–634.

Temesgen, H., P.J. Martin, D.A. Maguire, and J.C. Tappeiner. 2006. Quantifying effects of different levels of dispersed canopy tree retention on stocking and yield of the regeneration cohort. *For. Ecol. Manage*. 235:44–53.

Urgenson, L.S., C.B. Halpern, and P.D. Anderson. 2013. Twelve-year responses of planted and naturally regenerating conifers to variable-retention harvest in the Pacific Northwest, USA. *Can. J. For. Res*. 43(1):46–55.

Waring, R. 1983. Estimating forest growth and efficiency in relation to canopy leaf area. *Adv. Ecol. Res*. 13:327–354.

Waring, R., W. Thies, and D. Muscato. 1980. Stem growth per unit of leaf area: A measure of tree vigor. *For. Sci*. 26(1):112–117.

Wyant, J.G., R.D. Laven, and P.N. Omi. 1983. Fire effects on shoot growth characteristics of ponderosa pine in Colorado. *Can. J. For. Res*. 13(4):620–625.

Zenner, E.K., S.A. Acker, and W.H. Emmingham. 1998. Growth reduction in harvest-age, coniferous forests with residual trees in the western central Cascade Range of Oregon. *For. Ecol. Manage*. 102(1):75–88.