

forest management

Multiscale Controls on Natural Regeneration Dynamics after Partial Overstory Removal in Douglas-Fir Forests in Western Oregon, USA

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We examined natural regeneration following operational-scale variable density retention treatments in 40–60-year-old Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests at seven sites for a decade following treatment. Treatments included residual overstory densities of 300, 200, and 100 trees/ha, with leave islands and gaps of three sizes (0.1, 0.2, and 0.4 ha) and an untreated control (~600 trees/ha). Natural regeneration was influenced by factors from multiple spatial scales including broad-scale differences in overstory composition among sites, mesoscale variability in topographic position, and fine-scale variability in overstory and understory competition. High local basal area (BA) decreased the probability of seedling establishment, though some seedlings established even under high BA, particularly shade-tolerant western hemlock. In contrast, recruitment of saplings (> 1.37 m height) required lower residual overstory density (i.e., 100 trees/ha), especially for shade-intolerant Douglas-fir. Understory vegetation had little effect on saplings but was negatively related to seedling densities, particularly when overstory density was low. Variable density prescriptions can take advantage of the importance of fine-scale variability to promote regeneration of desired species mixtures, though other factors such as site overstory species composition and variation in topographic position will also influence regeneration dynamics. Including heavy overstory removal or gap creation could facilitate rapid recruitment of saplings, especially for shade-intolerant Douglas-fir.

Keywords: seedling bank, thinning, density management, Douglas-fir, western hemlock

Tree regeneration is an essential component of silvicultural systems and shapes stand trajectories such as the development of multilayered canopies typical of late-successional forests (Franklin et al. 2002, Van Pelt and Nadkarni 2004, Dial et al. 2011). Worldwide declines in late-successional forest and reductions in associated species has spurred interest in utilizing partial harvests to better balance wood production with ecological and social objectives (Bailey and Tappeiner 1998, Franklin et al. 2002, Muir et al. 2002). Concurrently, an increasing emphasis has been placed on natural regeneration, both to reduce costs associated with planting and to reverse trends of increasing homogeneity typical of plantations (Harmer 2001, Swanson et al. 2011, Donato et al. 2012). However, in many forested regions practices such as clear-cutting and planting have dominated land management, resulting in a relative lack of information regarding natural regeneration processes following partial overstory removal (Rose and Muir 1997, Buermeyer and Harrington 2002). A better understanding of natu-

ral regeneration is needed to assess the feasibility and efficacy of partial overstory retention for balancing multiple objectives.

Overstory density reductions may benefit regeneration by creating favorable sites for seedling establishment and increasing resources needed for subsequent growth (Chan et al. 2006, Shatford et al. 2009, Newsome et al. 2010). While overstory removal can promote natural regeneration, it is often patchy and highly variable, making it less reliable for managers (Harmer et al. 2001, Kuehne and Puettmann 2008, Newsome et al. 2010, Urgenson et al. 2013). Regeneration is influenced by processes operating at a variety of spatial scales (Clark et al. 1999), contributing to the high variability observed among and within studies. For example, regeneration dynamics may be affected by factors that vary at relatively large spatial scales such as species composition (Nabel et al. 2013) and site productivity (Drever and Lertzman 2001, Larson et al. 2008), to very small-scale microsites required for establishment (< 10 cm; Gray and Spies 1997). Local effects of residual overstory trees and

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Table 1. Site characteristics for the DMS study sites. Stand age, basal area (BA), and seedling and sapling density values are from year 11 posttreatment.

Site	Site index (m) ^b	Stand age (yr)	TSHE ^a BA (%)	TSHE seedlings/ha	TSHE saplings/ha	Elevation (m)	Ecoregion ^c
Bottomline	42	55	0.4	5	7	210–528	Willamette Valley
Delph Creek	37	53	31.0	6,631	1,483	553–725	Cascades
Green Peak	37	56	0.7	7	22	514–738	Coast Range
Keel Mountain	39	44	53.3	6,192	444	576–798	Cascades
North Soup	40	48	14.5	519	250	162–426	Coast Range
OM Hubbard	36	39	1.3	15	91	341–798	Coast Range
Ten High	38	44	13.5	792	226	430–710	Coast Range

^a*Tsuga heterophylla*.

^bKing (1966).

^cFollowing Thorson et al. (2003).

understory vegetation are also likely important for regeneration development (Balandier et al. 2006, Royo and Carson 2006, Devine and Harrington 2008), but effects remain poorly understood for variable retention harvests. A better understanding of multiscale influences on regeneration dynamics is needed to understand the potential for management use of natural regeneration in heterogeneous forest conditions.

Additionally, conditions that are suitable for one life stage of plants may not be suitable for another (i.e., Adili et al. 2013). For example, similar to the “seed-seedling conflict” (*sensu* Schupp 1995), conditions suitable for seedling establishment may not be sufficiently open for recruitment into the sapling layer and lower canopy. Evidence suggests this conflict maybe particularly pronounced for less-shade-tolerant species such as Douglas-fir (Isaac 1943, Williamson 1973, Raymond et al. 2006, Cole and Newton 2009). Thus, increased seedling establishment initially following partial overstory removal will not necessarily accelerate the development of multilayered stands without subsequent growth and recruitment into lower canopy positions. A better understanding of natural regeneration development over time under different levels of overstory retention is needed to understand the potential for variable density retention to not only initiate regeneration but also to understand effects on subsequent growth.

We used replicated operational-scale field experiments in 40–60-year-old Douglas-fir forests of the Pacific Northwest to examine multiscale influences on natural tree regeneration following variable density harvesting. Specifically we examined (1) if variability in regeneration densities among sites is related to site productivity or overstory tree species composition, (2) whether small-scale variability in residual overstory basal area or understory vegetation cover affect tree regeneration, and (3) how seedling (< 1.37 m) and sapling (≥ 1.37 m height, ≤ 5 cm dbh) densities change over a decade at different levels of overstory retention.

Methods

Study Sites

The Density Management Study (DMS) was initiated in 1994 to evaluate variable retention harvest effects on accelerating late-successional conditions in young stands (Cissel et al. 2006). Seven study sites were located in forests managed by the Bureau of Land Management in western Oregon (Cissel et al. 2006, Ares et al. 2009). Sites were located in three ecoregions: the Coast Range (four sites), the boundary between the Willamette Valley and the Coast Range (one site), and the western slopes of the Cascades Mountains (two sites; Table 1). All sites were at least 81 ha and dominated

by conifers, primarily Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), with varying levels of western hemlock (*Tsuga heterophylla* (Raf.)) in the overstory (Table 1). Stands ranged in age from 40–60 years at the time of harvest (Table 1). Common conifer species included Douglas-fir and western hemlock with infrequent western redcedar (*Thuja plicata* Donn ex D. Don). Hardwood trees were also a relatively minor component of the stands by tree density (Dodson et al. 2012) although species composition varied considerably among sites. The most common hardwoods included *Acer macrophyllum* Pursh, *Alnus rubra* Bong, *Corylus cornuta* Marsh, *Arbutus menziesii* Pursh, *Frangula purshiana* (DC.) Cooper and *Chrysolepis chrysophylla* (Douglas ex Hook.) Hjelmq. Management histories were highly variable among sites. Some sites were precommercially thinned, fertilized or both 20–40 years prior to selection for this study, thus representing a large range of site conditions typical for forests of the region (Cissel et al. 2006).

Treatments

Treatments were implemented in a randomized block design with one replication of each treatment (including controls) at each of the seven sites for a total of 28 treatment units. Operational constraints limited treatment randomization at some sites (see Cissel et al. 2006 for details), but we have no reason to suspect a systematic bias in overstory, understory, or regeneration conditions. Live overstory density in untreated control units ranged from 500 to 800 trees/ha, in areas of 16–25 ha. Treated unit area ranged from 14–58 ha for individual treatment units. Residual density in the high density (HD) treatment was about 300 trees/ha following harvest. The HD included 3–13% of the treatment unit (values varied by site) retained as unharvested circular leave islands. The moderate density (MD) treatment reduced residual stand density to 200 trees/ha in the majority of the stand. Additionally 4–18% of the stand was cut in circular gap openings and 4–13% of the stand was left in unharvested circular leave islands. The variable density (VD) treatment was designed to create the maximum spatial variability and complexity within the stand. This treatment included both the high density retention (300 trees/ha) and moderate density retention (200 trees/ha) each applied over 25–30% of the stand. Additionally, 8–16% of area in the stands was reduced to a residual density of 100 trees/ha. Finally 4–18% of the stand was left in leave islands and gap openings, respectively. Gaps and leave islands in all treatments were a mixture of 0.1, 0.2, and 0.4 ha circular areas. Harvesting was completed between 1997 and 2000. Harvests preferentially removed smaller trees of dominant species (primarily Douglas-fir). Subordinate species and any remaining remnant old trees (present

Table 2. Overstory characteristics for the DMS study 11 years following treatment application. The first value is the treatment mean. Values in parenthesis represent the 5th and 95th percentile values for each treatment from individual 0.1 ha plots, respectively.

Treatment	Basal area (m ² /ha)	Quadratic mean diameter (cm)	Height ^a (m)
Control	61 (37,81)	40 (26,51)	34 (25,42)
High	47 (25,68)	44 (31,57)	33 (24,41)
Moderate	36 (11,59)	42 (22,60)	33 (17,43)
Variable	35 (10,64)	42 (27,57)	30 (19,39)

^aHeight averages only include conifers, measured on 10 trees per 0.1 ha plot, if available.

on some sites) were preferentially reserved. Posttreatment stand characteristics varied considerably within and among treatments (Table 2). More detail about the study sites and treatments can be found in Cissel et al. (2006).

Data Collection and Summarization

To investigate the influence of site factors and local mechanisms driving natural regeneration, we used 539 permanent 0.1 ha circular “treatment” monitoring plots. These plots were measured twice (6 and 11 years after treatment), with plot locations randomly selected using geographic information systems (GIS) with 21 plots in each harvest treatment unit and 14 plots in each control unit at each site. The random placement of treatment plots resulted in inclusion of leave islands and harvest-created gaps in several plots (Dodson et al. 2012). Slope and azimuth were measured for each plot in the field. All trees (> 5 cm dbh) present on the 0.1 ha plot were tagged, identified to species, and dbh was measured. Clumped hardwood trees were measured as separate trees provided dbh was > 5 cm. Distance and azimuth from the plot center were collected for all trees. Four permanent circular 0.002 ha subplots were established in each plot at 9.1 m in each cardinal direction from the plot center to sample vegetation, including seedlings and saplings. Saplings (at least 1.37 m tall and < 5 cm dbh) and seedlings (between 15 and 136 cm tall) were tallied by species on the four 0.002 ha subplots. Vegetation cover was estimated at each subplot for each understory life-form (shrubs, graminoids, ferns, and forbs) to the nearest cover class (i.e., 1, 5, 10%, and thereafter to the nearest 10%). Total understory cover was determined for each subplot by summing values from individual life-forms. Data were collected in the summer 6 years after harvest (2003–2005) and 11 years after harvest (2008–2010) with sample years varying among sites (Cissel et al. 2006). Site index was collected for each site following King (1966).

Additionally, we used a subset of 0.1 ha “overstory retention” plots (“thinning” plots per Cissel et al. 2006) that were established nonrandomly (20–34 plots per site) right after treatment application and measured three times to evaluate regeneration over time at target overstory densities. These overstory retention plots were established where tree densities were within 20% of prescribed values (300, 200, and 100 trees/ha for high, moderate, and low density retention, respectively) and to maximize spatial coverage within each treatment unit (Cissel et al. 2006). Four permanent circular 0.002 ha subplots were established in each plot at 15.24 m in each cardinal direction from the plot center to sample vegetation, including seedlings and saplings. Saplings (at least 1.37 m tall and < 5 cm dbh; dbh) and seedlings (between 15 and 136 cm tall) were tallied by species on the four 0.002 ha subplots. Overstory retention plots

were sampled three times: 1–3 years following harvest (initial sampling varied among sites), 6 years following harvest, and 11 years following harvest. More detail about the measurement protocol can be found in Cissel et al. (2006).

The fine-scale basal area around each subplot was calculated from stem-mapped trees in a 90 degree wedge (i.e., 45–135 degrees around the east subplot) extending from the plot center to the edge of the plot, including the subplot area. Potential direct incident radiation (PDIR) was calculated for each plot from latitude, slope, and aspect using nonparametric multiplicative regression equations (McCune 2007).

Statistical Analyses

Prior to analyses we selected a threshold of alpha = 0.05 for determining statistically significant effects. All analyses were performed in SAS (SAS Institute, Inc. 2008, version 9.3, Cary, NC). No pretreatment data were available; therefore, treatment effects are assessed by comparison with an unharvested control. We cannot rule out the possibility of systematic variation due to factors other than treatment; however, the considerable range of conditions within and among the seven sites makes this unlikely.

Site-Level Variability

We used simple linear regression to examine the relationship of seedling and sapling densities with site index (King 1966) and the percentage of overstory basal area comprised by western hemlock. For this cross-site analysis, data were averaged at the site level ($n = 7$) from plots (calculated across all treatments). Residuals were inspected to ensure assumptions of normality, equal variance, and independence were not violated.

Fine-Scale Controls on Regeneration

We modeled the probability of seedling establishment and the probability of sapling recruitment separately using generalized linear mixed logistic regressions (SAS PROC GLIMMIX). These models related the presence or absence of seedlings and saplings (i.e., whether at least one seedling or sapling was sampled on a subplot) 11 years following harvest to local BA, plant cover, and the interaction thereof. PDIR was included as a covariate at the plot level ($n = 539$ plots). Treatment was modeled as a fixed factor at the treatment unit level ($n = 28$ treatment units) with four levels: control, high density retention (300 TPH), moderate density retention (200 TPH), and variable density retention (areas with 300, 200, and 100 TPH). Site, treatment unit, and plot were included as random terms to account for the hierarchical nesting of subplots. The subplots covered a wide range of overstory and understory conditions as random assignment of plots within treatments resulted in some plots in gaps as well as unharvested leave islands (Dodson et al. 2012).

Though there was high variability in BA in all treatments (Table 2; Dodson et al. 2012), treatments significantly reduced BA (Dodson et al. 2012) and increased plant cover (Ares et al. 2009). Thus, the inclusion of treatment in the model tests if treatment explains additional variation not accounted for by BA and plant cover, which were modeled at the subplot level. Preliminary analyses revealed that subplot BA and plant cover were not strongly correlated suggesting the effects could be evaluated separately ($r = 0.2$). Separate analyses were performed for seedlings and saplings and for all species together and the two most common conifer species individually (western hemlock and Douglas-fir). Full models were fit with all possible predictors. No Douglas-fir saplings were sampled in the

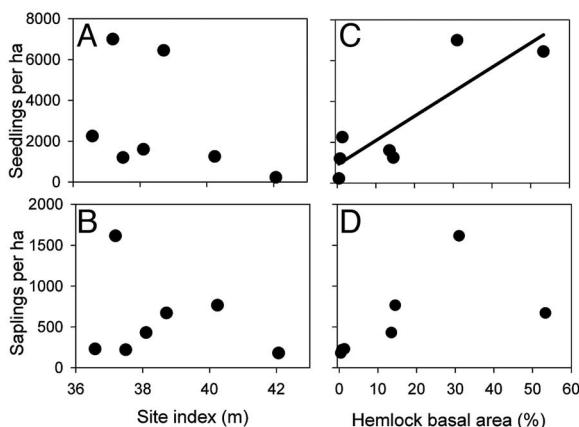


Figure 1. Exploratory relationship of seedling and sapling density with site index (A, B) and relative western hemlock BA (C, D). Trend lines are simple linear regression fits shown for only significant ($P < 0.05$) effects. Scatterplot points are values for individual sites.

control; therefore, treatment comparisons used only the three harvest treatments for the analysis of saplings with this species. When treatment was found to be significant, post hoc tests were performed among treatments with a Tukey adjustment for multiple comparisons.

Overstory Density Treatment Effects on Regeneration Densities over Time

A repeated measures mixed effect analysis of variance (ANOVA) was used to evaluate temporal trends in seedling and sapling density in the overstory density plots, (i.e., at target densities of 300, 200, and 100 trees/ha, respectively). All data were averaged at the treatment-unit level prior to analyses. We evaluated effects of residual overstory density, which was modeled as a fixed factor with four residual densities: high retention (300 trees/ha), medium retention (200 trees/ha), low retention (100 trees/ha), and control (no harvest, ~ 600 trees/ha). Plots in variable density treatment were assigned to their given residual density level (300, 200, or 100 trees/ha). Residual overstory density, year, and their interaction were modeled as fixed effects, while site was modeled as a random effect. Where significant year by treatment interactions were found, post hoc tests within years between residual density levels were performed with a Tukey correction for multiple comparisons. Seedlings and saplings were modeled separately. Residuals were evaluated for all models. A square root transformation was required to ensure assumptions of normality, equal variance, and independence were not violated for both seedlings and saplings.

Results

Site-Level Variability

Regeneration density varied considerably among the seven sites 11 years following harvest. For example, densities ranged from an average of 225 to 7,000 seedlings/ha and 180 to 1,615 saplings/ha among the seven study sites (Figure 1A and B, respectively). However, site differences in seedling and sapling density were not significantly related to productivity (both P values > 0.3). Instead, total seedling density was related to the percentage of western hemlock BA at a site ($P = 0.01$), though sapling density was not ($P = 0.15$).

Table 3. Type III tests of fixed effects from mixed model logistic regression results for seedlings at the subplot scale. Significant effects are in bold type.

Effect	Regression coefficient ^a	Standard error	d.f. ^b	<i>P</i>
All seedlings				
BA	-0.005	0.001	2,024	<0.001
Plant cover	-0.016	0.003	2,024	<0.001
Plant cover \times BA	0.00003	0.000	2,024	0.049
Treatment ^c			18	<0.001
PDIR ^d	-0.143	0.586	398	0.808
Douglas-fir seedlings				
BA	-0.006	0.002	2,024	<0.001
Plant cover	-0.017	0.004	2,024	<0.001
Plant cover \times BA	0.000	0.000	2,024	0.291
Treatment ^c			8	0.005
PDIR ^d	1.609	0.770	263	0.0375
Western hemlock seedlings				
BA	-0.008	0.002	2,024	<0.001
Plant cover	-0.021	0.005	2,024	<0.001
Plant cover \times BA	0.0001	0.0000	2,024	0.014
Treatment ^c			13	0.481
PDIR ^d	-3.054	0.789	349	<0.001

^aEstimated regression effect size on the odds ratio.

^bd.f. = Denominator degrees of freedom.

^cTreatment was modeled as a fixed factor with four levels.

^dPDIR = potential direct incident radiation calculated following McCune (2007).

Western hemlock BA explained 78% of the variation among sites in seedling density, with increasing seedling densities at sites with more hemlock (Figure 1C), due primarily to higher numbers of hemlock seedlings at these sites (Table 1).

Fine-Scale Controls on Regeneration

Eleven years following treatments seedlings were found on 54% of the 0.002 ha subplots in the randomly established plots (across all treatments) with densities ranging up to 100,000/ha. Western hemlock and Douglas-fir comprised the majority of the seedlings (82%), though 20 species were sampled. Western hemlock occurred on about 27% of the subplots, with densities up to 100,000 seedlings/ha. Site-level variability in western hemlock seedling densities was strongly related to the amount of western hemlock in the overstory (Table 1). Douglas-fir occurred on about 20% of the subplots, with densities as high as 15,500 seedlings/ha. Across the study sites, hemlock comprised over 75% of the seedlings sampled in the control, with an average density of 399 seedlings/ha despite low densities on sites with few hemlocks in the overstory (Table 1). Douglas-fir seedlings were basically absent in controls, occurring in the control at only two of the seven sites and comprising only 2% of the total seedlings in the control with an average density of 11 seedlings/ha.

Saplings (> 1.37 m height, < 5 cm dbh) were less frequent, occurring on about one quarter of the randomly established 0.002 ha subplots with densities ranging up to 35,500/ha. Western hemlock and Douglas-fir comprised over 70% of the saplings. Western hemlock saplings occurred on about 16% of the subplots, with densities as high as 35,500 saplings/ha. Douglas-fir occurred on only about 4% of the subplots, with densities as high as 3,000 saplings/ha. No Douglas-fir saplings were sampled in the control, while western hemlock comprised 83% of control saplings.

The probability of seedling establishment on a subplot was related to BA and understory plant cover for all seedlings, western hemlock, and Douglas-fir (Table 3). The probability of seedling

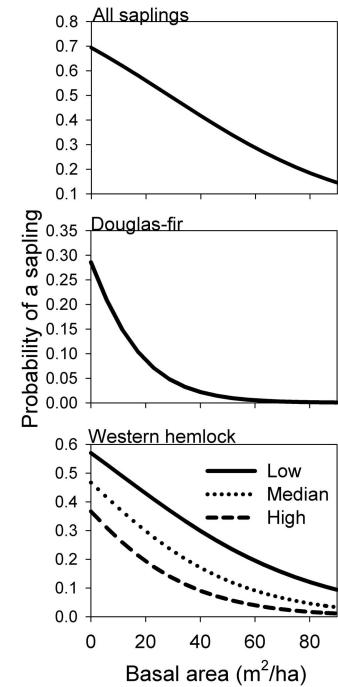
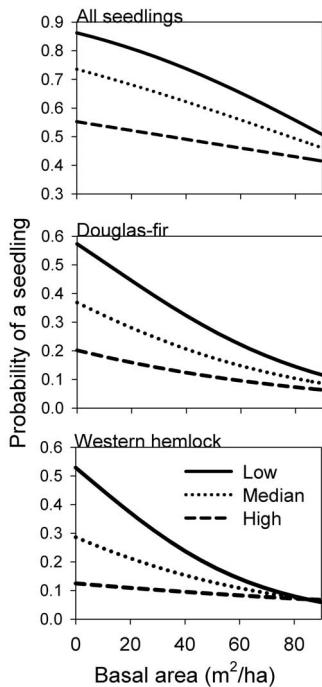


Figure 2. Modeled values from mixed model logistic regression predicting the probability of sampling at least one seedling on a subplot (0.002 ha), as a function of BA and total understory cover for seedlings of all species, Douglas-fir, and western hemlock. Understory cover values are the 10th percentile (low), median, and 90th percentile (high) from field data. Lines represent overall means from all sites; hemlock seedling probabilities varied significantly among sites (see text).

establishment increased with decreases in residual BA but decreased with associated increases in the cover of understory vegetation locally (Figure 2). Interactions between overstory BA and understory cover were significant for all species combined and western hemlock (Table 3).

After accounting for local BA and understory cover, treatment still had significant effects for Douglas-fir and all seedlings but not western hemlock (Table 3). All thinned treatments had a significantly higher probability of seedling establishment of any species or a Douglas-fir seedling than the control (all P values < 0.01 in pairwise comparisons), but the three harvest treatments were not significantly different (all P values > 0.5). PDIR was positively related to Douglas-fir seedling establishment and negatively related to western hemlock seedling establishment and, therefore, not related to the pattern of seedling establishment for all species combined (Table 3). Sites with a large component of western hemlock in the overstory (Delph Creek and Keel Mountain; Table 1) had significantly higher (both P values < 0.05) probabilities of the establishment of western hemlock seedlings than the overall site mean.

The probability of sapling recruitment for Douglas-fir, western hemlock, and all species combined was negatively related to residual overstory BA (Figure 3). In contrast to seedling establishment, understory cover did not affect sapling recruitment, except for western hemlock (Table 4) where increases in understory cover reduced the probability of sapling recruitment (Figure 3). Sapling recruitment increased markedly for Douglas-fir when BA was reduced beyond a threshold of 20–25 m²/ha (Figure 3). PDIR was negatively related

Figure 3. Modeled values from mixed model logistic regression predicting the probability of sampling at least one sapling on a subplot (0.002 ha), as a function of BA and total understory cover for saplings of all species, Douglas-fir, and western hemlock. Understory cover values in the western hemlock model are the 10th percentile (low), median, and 90th percentile (high) from the field data. Understory cover was not significant for all saplings and for Douglas-fir saplings.

Table 4. Type III tests of fixed effects from mixed model logistic regression results for saplings at the subplot scale. Significant effects are in bold type.

Effect	Regression coefficient ^a	Standard error	d.f. ^b	P
All saplings				
BA	−0.006	0.002	2,012	<0.001
Plant cover	−0.002	0.003	2,012	0.592
Plant cover \times BA	0.000	0.000	2,012	0.656
Treatment ^c			18	0.554
PDIR ^d	−1.211	0.602	467	0.045
Douglas-fir saplings				
BA	−0.022	0.005	1,249	<0.001
Plant cover	−0.006	0.006	555	0.379
Plant cover \times BA	0.000	0.000	1,418	0.103
Treatment ^c			8	0.220
PDIR ^d	2.821	1.373	118	0.042
Western hemlock saplings				
BA	−0.006	0.002	2,012	<0.001
Plant cover	−0.008	0.004	2,012	0.047
Plant cover \times BA	0.000	0.000	2,012	0.187
Treatment ^c			18	0.454
PDIR ^d	−1.658	0.710	450	0.020

^aEstimated regression effect size on the odds ratio for continuous variables.

^bd.f. = Denominator degrees of freedom.

^cTreatment was modeled as a fixed factor with four levels.

^dPDIR = potential direct incident radiation calculated following McCune (2007).

to all sapling recruitment for all species combined and western hemlock but increased the probability of recruiting Douglas-fir saplings (Table 4). Treatment did not significantly affect sapling recruitment after accounting for BA and understory cover (Table 4).

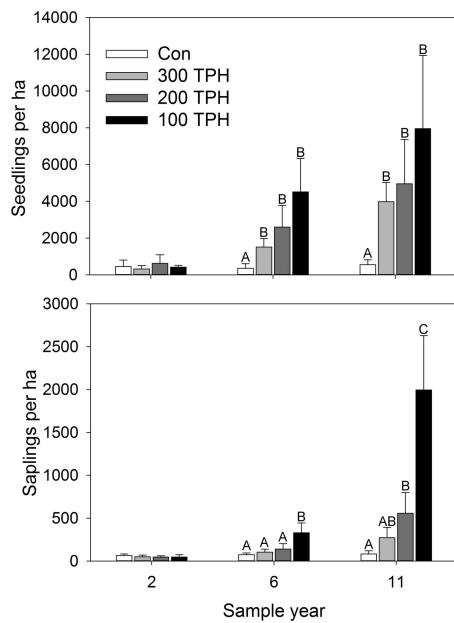


Figure 4. Mean density (plus one standard error) for (A) seedlings and (B) saplings for each sample year under different overstory retention levels from the nonrandomly established plots. Different letters represent significant differences among treatments within a sample year. Sample year 2 varies from 1 to 3 years following treatment, depending on site. Con = Control with an average of 600 overstory trees/ha (TPH).

Overstory Density Treatment Effects on Regeneration Densities over Time

Seedling and sapling density increased in treated areas throughout the 10 year study period on nonrandomly established overstory retention plots (Figure 4). Residual overstory density treatments significantly affected seedlings and saplings, but effects varied with sample year (both P values < 0.01). Post hoc tests of treatments within years revealed no differences in seedling or sapling densities 1–3 years following treatment (Figure 4). In contrast, at 6 and 11 years following treatment, there were more seedlings in all harvested treatments than the control. Eleven years after harvest the control averaged just over 500 seedlings/ha, while all residual densities in the harvested treatments averaged $> 3,900$ seedlings/ha (Figure 4). Though seedling densities tended to increase with decreases in overstory residual density (Figure 4), there were no significant differences among residual density treatments (Figure 4A). In contrast, the lowest level of overstory retention (100 TPH) had greater sapling densities than all other residual densities both 6 and 11 years following treatment (Figure 4B), averaging nearly 2,000 saplings/ha 11 years following harvest (Figure 4). The high retention (300 TPH) was never significantly different than the control in sapling density, while the moderate retention (200 TPH) had higher sapling densities than the control (average of 474 more saplings/ha) 11 years following harvest but was not significantly different at 6 years (Figure 4B).

Discussion

Variability in natural regeneration in this study was influenced by factors from multiple spatial scales, including broad-scale differences in species composition, landscape position, and fine-scale heterogeneity in overstory and understory vegetation, likely owing to preharvest conditions and influenced by variable density retention

(i.e., Dodson et al. 2012). These patterns provide insights into the processes leading to high variability in regeneration patterns within treatments and among sites (i.e., Alaback and Hermann 1988, Bailey and Tappeiner 1998, Miller and Emmingham 2001, Kuehne and Puettmann 2008, Nabel et al. 2013, Urgenson et al. 2013). The importance of factors that vary at spatial scales both larger and smaller than typical harvest operations (i.e., 10–100 ha) highlights the need to develop understanding beyond stand level averages for forest management (Puettmann et al. 2009). Our results show that foresters can benefit from considering the spatial scales of processes driving regeneration patterns, such as seed rain, germination, neighborhood competition, and regional environmental conditions, providing a quantitative example of the importance of cross-scale interactions in forest ecosystems (Levin 1992, Puettmann et al. 2013).

Regeneration variability has important implications for future stand development, affecting both future timber productivity, as well as the development of habitat structures. Areas of high regeneration density may eventually undergo stem exclusion (Oliver and Larson 1996, Franklin et al. 2002) while areas with low regeneration densities may encourage more rapid recruitment of large trees (Porage and Tappeiner 2002). In contrast to natural regeneration patterns, treeplanting coupled with vegetation control can ensure target densities, species composition, and distribution of regeneration and, therefore, has often been preferred for forest management (Harmer et al. 2001, Chan et al. 2006). However, high heterogeneity in stand density is also a common feature of late-successional forests, which often include both gaps and areas with dense trees (Franklin et al. 2002). High variability in the establishment phase, including sparse regeneration and gaps without regeneration, could function to accelerate the development of the heterogeneity characteristic of late-successional forests in young stands (Donato et al. 2012).

Sapling recruitment was less sensitive to understory competition than seedling establishment in this study but appeared more sensitive to local competition from overstory trees. Despite high annual precipitation, summer water limitations for plant growth are common in Pacific Northwest Douglas-fir forests (Lindh et al. 2003, Devine and Harrington 2008). Herbaceous and grassy vegetation has been shown to be very competitive to young seedlings in clearcut settings (Wagner and Radosevich 1991, Rose et al. 1999). Our results and previous studies suggest this is also the case in understory settings (Smidt and Puettmann 1998, Cole and Newton 2009). As seedlings grow into saplings or trees they are less shaded by understory vegetation and roots may reach deeper soil layers than herbs and grasses, competitive relationships become asymmetric, with a greater effect of saplings and trees on understory species than vice versa (Lindh et al. 2003, Balandier et al. 2006). In contrast, overstory trees compete asymmetrically with tree regeneration for light, soil resources, and space, having a greater and longer-lasting effect than understory vegetation (Balandier et al. 2006, Devine and Harrington 2008). However, belowground competition from understory vegetation may continue to be important even for overstory trees on some dry sites (Price et al. 1986).

These results, suggesting that variable density retention that includes patches with heavy overstory removal, gaps, or both is required for sapling recruitment, are consistent with those from previous studies (Raymond et al. 2006, Adili et al. 2013). At the extreme, heavy partial harvesting that retains only a few residual trees (i.e., $< 15/\text{ha}$) may not significantly reduce growth of regeneration relative to clearcuts over decadal time scales (Rose and Muir

1997). Alternatively, subsequent treatments may be required to maintain growth of seedlings where initial harvests leave higher residual basal area (Devine and Harrington 2008, Shatford et al. 2009).

The dominant species in this study, Douglas-fir and western hemlock, showed disparate responses that are generally consistent with their physiology and life history traits. The high shade tolerance of western hemlock allows it to regenerate in mature Douglas-fir forests in the absence of canopy gaps when a seed source is present (Spies et al. 1990, Antos et al. 2005) consistent with the dominance of this species in the control. The lack of Douglas-fir seedlings in the control is consistent with the long-recognized importance of disturbance for Douglas-fir regeneration (Isaac 1943, Williamson 1973, Gray and Spies 1997). Harvest benefits for Douglas-fir seedlings exceeded the direct effect of reductions in basal area in this study (significant treatment effect after accounting for changes in basal area), likely due to creation of favorable seedbeds such as mineral soil (Minore 1979, Spies and Franklin 1989). Douglas-fir regeneration was also more prevalent on plots with higher potential direct incident radiation, suggesting regeneration of Douglas-fir is likely to vary depending on the local topographic position. In contrast, western hemlock is limited by moisture in the Oregon Coast Range (Gavin et al. 2006) and establishment is highly sensitive to substrate moisture (Williamson 1976, Gray and Spies 1997), which may explain the negative relationship of hemlock seedlings with potential radiation in this study. The potential for western hemlock to form a seedling bank and respond strongly to harvest may result in dense hemlock regeneration that can suppress understory vegetation, compete with regeneration of other conifer species, and limit subsequent regeneration under a hemlock dominated canopy (Farr and Harris 1971, Alaback and Hermann 1988, Shatford et al. 2009). Therefore, sites with a higher proportion of western hemlock in the overstory may require alternative management approaches (Nabel 2013).

Understory competition with tree regeneration has been well documented (i.e., Balandier et al. 2006, Royo and Carson 2006), but strong understory competition is not universal (Harmer et al. 2001, Balandier et al. 2006, Montgomery et al. 2010). In this study, understory competition with tree regeneration was most evident when residual BA was low. Similarly, Montgomery et al. (2010) found that shrubs competition with tree regeneration was much stronger in gaps while under a forest canopy facilitation was more common. Stands that are near stem exclusion may have shaded out much of the understory vegetation, limiting vegetative responses (Cole and Newton 2009). Furthermore, residual overstory trees may limit competition from understory vegetation thus serving effectively as vegetation control mechanism (Smidt and Puettmann 1998, Balandier et al. 2006). Indeed, previous studies have also found limited benefit of vegetation control in partial harvests (Harmer et al. 2001), suggesting that partial harvests could facilitate natural regeneration without the need for vegetation control, which may have negative ecosystem consequences (i.e., Relyea 2005). Our study suggests that decisions about weed control could benefit from assessments at neighborhood scales.

In even-aged stands that initiated after heavy harvesting, advanced regeneration is critical for generating the variety of tree sizes and multiple canopy layers that are characteristic of late-successional forest (Franklin et al. 2002, Van Pelt and Nadkarni 2004, Dial et al. 2011). The development of late-successional forest characteristics may be faster on sites with high productivity (Franklin et al. 2002,

Larson et al. 2008), including more rapid growth of regeneration at productive sites when overstory density is reduced (Drever and Lertzman 2001). The relatively few sites in this study (seven) spanned a relatively large geographical range (> 200 km), including a large range of site histories, environmental and soil conditions, and varying amounts of western hemlock in the overstory (Cissel et al. 2006; Table 1), perhaps confounding the relationship between site productivity and regeneration density previously found at smaller spatial scales (i.e., within a watershed; Larson et al. 2008). Also, while reflecting a large portion of the Douglas-fir sites in western Oregon, sites in this study did not span a large productivity gradient (measured as Douglas-fir site index) relative to total variability present in the large natural distribution of Douglas-fir, which made it harder to detect statistically significant relationships. Another key structural attribute of late-successional forests, large trees, was similarly not strongly influenced by site productivity at 28 sites that covered a similar geographic scope as our study (Poage and Tappeiner 2002). This lack of a clear pattern for specific attributes associated with late-successional forests (i.e., multiple canopy layers and large trees) suggests further studies are needed to better understand how development of these structural attributes varies along environmental gradients, including site productivity, to better understand forest responses across the wide range of conditions and guide management prioritization of treatments.

Conclusions

The results of this study contribute to the growing body of evidence that partial overstory removal can facilitate natural regeneration without vegetation control (e.g., Miller and Emmingham 2001, Shatford et al. 2009). In addition, our study provided insights into processes controlling regeneration at multiple scales that typically result in variable and patchy distributions of natural regeneration (e.g., as reflected in numerous studies in the region: Alaback and Hermann 1988, Bailey and Tappeiner 1998, Urgenson et al. 2013). Foremost, the differential response of seedling and saplings overstory density within stands suggests different stages of regeneration, such as germination, establishment, and subsequent growing conditions should not simply be combined (as a result of a seedling-sapling conflict; *sensu* Schupp 1995). Additionally, results illustrate how these fine-scale processes associated with seedling establishment and recruitment are constrained by broad-scale variability in overstory composition and mesoscale variability in topography. Understanding multiscale controls on regeneration will facilitate the development of variable retention and vegetation management prescriptions that lead to desirable quantities and patterns of regeneration and subsequent development of desirable stand structures. Such prescriptions may vary depending on overstory composition and topography, which appears to influence the composition of regenerating seedlings.

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