

Twelve-year responses of planted and naturally regenerating conifers to variable-retention harvest in the Pacific Northwest, USA

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Abstract: We studied patterns of conifer regeneration over 12 years as part of a regional-scale experiment in variable-retention harvest in the Pacific Northwest, the DEMO Study. We compared survival and height growth of planted conifers and density and seral composition of natural regeneration among treatments with differing retention levels (15% versus 40%) and patterns (dispersed versus aggregated) replicated across a range of latitudes and forest zones. We also assessed plot-scale relationships of natural regeneration with overstory density and basal area, competing vegetation, and slash accumulations. Early (1- to 2-year) survival of planted seedlings was greater in dispersed treatments (*Pinus monticola* Douglas ex D. Don, *Abies* spp.) or unaffected by retention level or pattern (*Pseudotsuga menziesii* (Mirb.) Franco). Later (5- to 12-year) survival did not differ (all species), but growth was distinctly reduced in dispersed treatments and (or) at higher levels of retention. Density of natural regeneration was 1.5–2.5 times greater in dispersed treatments than in the cleared areas of aggregated treatments. Low-level dispersed retention promoted *Pseudotsuga*, the early-seral dominant, presumably by enhancing seed rain within a relatively high-light environment. Dispersed retention favored late-seral conifers. The ability to manipulate retention pattern and level to influence regeneration density and composition provides managers with flexibility in developing structurally complex and compositionally diverse forests.

Résumé : Nous avons étudié les patrons de régénération de conifères pendant 12 ans dans le cadre de l'étude DEMO, une expérience régionale sur les coupes à rétention variable dans la région du Nord-Ouest de l'Amérique du Nord. Nous avons comparé la survie et la croissance en hauteur de plants de conifères ainsi que la densité et la composition de la régénération naturelle entre des traitements se distinguant par le niveau (15% ou 40%) et le type (dispersée ou en bouquet) de rétention et qui ont été répétés sous une gamme de latitudes et dans une variété de zones forestières. Nous avons aussi établi des relations à l'échelle de la placette entre la régénération naturelle et la densité ainsi que la surface terrière du couvert dominant, la végétation concurrente et l'accumulation de débris de coupe. À court terme (1 à 2 ans), la survie des plants était meilleure dans les traitements à rétention dispersée (pour *Pinus monticola* Douglas ex D. Don et *Abies* spp.) ou n'était pas influencée par le niveau et le type de rétention (pour *Pseudotsuga menziesii* (Mirb.) Franco). À plus long terme (de 5 à 12 ans), la survie de toutes les espèces était la même, mais la croissance a été clairement réduite dans les traitements à rétention dispersée ou à niveau élevé de rétention. La densité de la régénération naturelle était de 1,5 à 2,5 fois plus forte dans les traitements à rétention dispersée que dans les aires coupées des traitements à rétention en bouquet. Les faibles niveaux de rétention dispersée ont favorisé *Pseudotsuga*, une espèce dominante de début de succession, probablement en favorisant la pluie de graines dans un environnement avec une luminosité relativement forte. La rétention dispersée a favorisé les conifères de fin de succession. La capacité à manipuler le type et le niveau de rétention de façon à influencer la densité et la composition de la régénération donne de la flexibilité aux gestionnaires pour aménager des forêts structurellement complexes et dont la composition est différente. [Traduit par la Rédaction]

Introduction

Variable-retention harvest has become integral to ecologically sustainable forest management worldwide (Lindenmayer et al. 2012). It emphasizes retention of forest structures through harvest to mimic the processes and outcomes of natural disturbance and succession (Franklin et al. 1997). An implicit goal of variable retention is to balance the ecological and economic values of managed forests (Lindenmayer et al. 2012). Although variable retention can be implemented in diverse ways (Gustafsson et al. 2012), two elements of forest structure, the level (amount) and spatial distribution of retained trees, are hypothesized to play important roles in post-harvest regeneration (Franklin et al. 1997). Studies that isolate the individual and joint effects of retention level and pattern are rare, however (Rosenvald and Lohmus 2008).

Partial retention of the overstory is hypothesized to have direct and indirect effects on the survival, growth, density, and composition of the regenerating cohort. Retained trees can provide direct benefits by ameliorating understory microclimate

(Vanha-Majamaa and Jalonon 2001), increasing seed rain (Beach and Halpern 2001), or facilitating access to mycorrhizae (Luoma et al. 2006). Conversely, they can inhibit regeneration by reducing light (Mitchell 2001), soil moisture, or nutrients (Boyden et al. 2012). Moreover, these influences can change over time, enhancing seed availability early in succession but reducing survival in the longer term (Temesgen et al. 2006). Pattern of retention can also influence the composition of the regenerating cohort. Dispersed retention is thought to favor shade-tolerant species and the harvested matrix among forest aggregates, shade-intolerant species (Franklin et al. 1997).

Partial retention can also shape patterns of regeneration indirectly through effects on post-harvest ground conditions and competing vegetation. For example, variation in cover and depth of logging slash can affect survival of advanced regeneration or post-harvest germination and establishment (Halpern and McKenzie 2001). Retention level and pattern can also influence the growth of herbs and shrubs that compete with regenerating trees (Halpern et al. 2012). Where physical or biotic conditions create barriers to

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Table 1. Physical environments and pre-treatment structural characteristics of forests comprising the six experimental blocks.

Block	Elevation (m)	Slope (%)	Aspect	Stand age (years)	Tree density (no./ha)	Basal area (m ² /ha)	Canopy height (m)	Minor canopy species	Dates of harvest
Watson Falls (WF)	945–1310	4–7	Flat	110–130	310–500	36–52	42–45	Ac, Th, Pp, Pm	June–Oct. 1998
Dog Prairie (DP)	1460–1710	34–62	SW	165	258–475	72–106	45–47	Ac, Am, Cd	July–Sept. 1998
Butte (BU)	975–1280	40–53	E–SE	70–80	759–1781	48–65	30–33	Th, Tp	May–Sept. 1997
Little White Salmon (LWS)	825–975	40–66	NW–NE	140–170	182–335	61–77	53–55	Ag	Mar.–Oct. 1998
Paradise Hills (PH)	850–1035	9–33	Varied	110–140	512–1005	59–87	32–37	Th, Tp, Aa	June–Oct. 1997
Capitol Forest	210–275	28–52	Varied	65	221–562	54–73	45–47	Th, Tp	Dec. 1997 – May 1998

Note: Minimum and maximum values are experimental unit means. Minor canopy species: Ac, *Abies concolor*; Ag, *Abies grandis*; Am, *Abies magnifica* var. *shastensis*; Cd, *Calocedrus decurrens*; Pm, *Pinus monticola*; Pp, *Pinus ponderosa*; Th, *Tsuga heterophylla*; Tp, *Thuja plicata*. Canopy height represents the mean height of trees within the 75th to 95th percentiles of the height distribution.

natural regeneration, planting may be necessary. To what extent level and pattern of retention shape artificial and natural regeneration processes remains a fundamental question in many forest ecosystems.

Here, we present the results of long-term (12-year) studies of planted seedlings and natural regeneration as part of a regional-scale experiment in variable-retention harvest in mature coniferous forests of the Pacific Northwest, USA. Federal standards and guidelines for regeneration harvests in this region require a minimum of 15% overstory retention in each harvest unit, with 70% of this in the form of large (0.2–1.0 ha) aggregates (USDA and USDI 1994). The Demonstration of Ecosystem Management Options (DEMO) Study was initiated in 1994 to test the ecological and silvicultural implications of level and pattern of retention, including the sufficiency of the 15% minimum standard. The experiment consists of operational-scale (13 ha) harvest units replicated at six locations in western Oregon and Washington. Treatments contrast both the level of retention (15% versus 40% of original basal area) and its spatial distribution (trees dispersed versus aggregated in 1 ha patches). Replication across a broad range of latitudes and forest zones offers the opportunity to study responses to a common set of treatments in a diversity of physical and biotic settings. We address the following hypotheses.

Hypothesis 1

Effects of retention pattern and level on survival and growth of planted trees. Early survival of planted trees will be greater in dispersed treatments and at higher levels of retention, i.e., where there is greater amelioration of microclimatic stress. However, longer-term growth and survival will be reduced in these environments, particularly for shade-intolerant species, as resource limitations (shading and root competition) become more important.

Hypothesis 2

Effects of retention level and pattern on density and composition of natural regeneration. Responses will differ for early-seral (shade-intolerant) and late-seral (shade-tolerant) species, which differ in their physiological requirements. Greater retention and presence of dispersed trees will inhibit establishment of early-seral species (including *Pseudotsuga menziesii* (Mirb.) Franco), the dominant canopy species) but will increase density of late-seral species, enhancing survival of advanced regeneration and facilitating post-harvest establishment.

Hypothesis 3

Local influences on natural regeneration density. Local (plot-scale) density of natural regeneration will vary inversely with cover and depth of logging slash and cover of competing shrubs. Effects will be stronger for early-seral species that prefer mineral substrates for germination and greater understory light. In contrast, late-seral species will benefit from greater overstory density or basal area, consistent with responses at the treatment scale.

Methods

Study areas

Six experimental blocks were selected to represent a diversity of physical environments and forest types at low to moderate elevations in western Oregon and Washington (Table 1) (Aubry et al. 1999). Five are in the Cascade Range in southern Washington (BU, LWS, and PH; Gifford Pinchot National Forest) and southern Oregon (WF and DP; Umpqua National Forest); the sixth is in the Black Hills of western Washington (CF; Washington DNR). *Pseudotsuga menziesii* was the dominant canopy species in each block, although stand characteristics, understory, and past management differed among blocks (Table 1). Stands surrounding each block were generally similar in age and structure to the treatment units themselves. Detailed descriptions of forest structure and past management can be found in Aubry et al. (1999) and Maguire et al. (2007).

The climate of the region is maritime; summers are relatively warm and dry and winters are cool and wet. Most precipitation falls between October and April resulting in frequent summer drought (Franklin and Dyrness 1988). Soils vary in depth and texture, but most are moderately deep and well-drained loams to loamy sands derived from andesite, breccia, or basalt parent materials or from pumice deposits (Radtke and Edwards 1976; Pringle 1990; Wade et al. 1992).

Experimental design, retention treatments, and planting of seedlings

The full experiment, a randomized complete-block design, includes six treatments applied to square (360 m × 360 m) or rectangular (320 m × 400 m) harvest units (~13 ha; Aubry et al. 1999). Four treatments are considered in this study.

- (1) 40% dispersed retention (40%D): dominant and codominant trees were retained in a relatively even distribution leaving a residual basal area equivalent to that of 40%A.
- (2) 40% aggregated retention (40%A): trees were retained in five 1 ha circular aggregates (56.4 m radius) spaced ~30 m apart. All other merchantable stems (≥13 cm diameter at breast height (DBH)) were removed to create a cleared matrix (40%A-c) of varying width among aggregates.
- (3) 15% dispersed retention (15%D): dominant and codominant trees were retained in a relatively even distribution leaving a residual basal area equivalent to that of 15%A.
- (4) 15% aggregated retention (15%A): trees were retained in two 1 ha circular aggregates in diagonally opposite quarters of the harvest unit (~115 m apart). All other merchantable stems were removed to create a cleared matrix (15%A-c) considerably larger than that of 40%A-c.

Although submerchantable stems (<18 cm DBH) were left standing in the harvested portions of most experimental units, they were felled at PH and felled if damaged at WF. Logging was com-

Table 2. Planting details including species mix, mean and range of densities within plots (trees/ha), and planting dates.

Block	<i>Pseudotsuga menziesii</i>		<i>Pinus monticola</i>		<i>Abies</i> spp.		<i>Pinus ponderosa</i>		Planting dates
	Mean	Range	Mean	Range	Mean	Range	Mean	Range	
Watson Falls (WF)	204	102–265	84	42–154			159	75–225	14 Apr. – 15 June 1999
Dog Prairie (DP)	332	189–442	65	21–123	110	49–170			24 May – 5 June 1999
Butte (BU)	320	171–475	41	11–69					28 Apr. – 26 May 1998
Little White Salmon (LWS)	217	87–279	57	16–109	24	16–37	38	18–77	1–24 June 1999
Paradise Hills (PH)	169	93–227	45	19–85	63	32–103			1–25 June 1999
Capitol Forest (CF)	586	311–895							27 Jan. – 3 Feb. 1999

Note: Mean and range are densities in the year of planting. *Pseudotsuga menziesii* were 2-0 BR (1-1 at CF), *Pinus monticola* were 2-0 BR (P-1 at LWS), *Abies* spp. (*Abies procera* at LWS and PH and *Abies magnifica* var. *shastensis* at DP) were 2-0 BR, and *Pinus ponderosa* were 1-0 BR (WF) or 1-1 BR (LWS). CF treatment 40%D was planted on 15 March 2000.

pleted in fall 1997 or 1998 (spring 1998 for CF). In addition, to meet minimum requirements for snag density, natural snags felled in the harvested portions of experimental units were replaced by artificially created snags at a density of 6.5/ha. Dominant or codominant stems were selected and were either topped or girdled (methods vary among blocks). Details on yarding methods and treatment of logging slash are presented in Halpern and McKenzie (2001).

To ensure minimum stocking consistent with federal standards (312 stems/ha), conifer seedlings (early-seral species with low to moderate shade tolerance) were planted in the harvested portions of all experimental units (Table 2). Planting densities were lower than in conventional operations so as not to impede natural regeneration.

Sampling methods

Prior to harvest, a sampling grid (7 × 9 or 8 × 8, 40 m spacing) was surveyed in each experimental unit. Permanent tree plots (circular, 0.04 ha) were established at a subset of grid points: alternate points ($n = 32$) in dispersed (D) treatments and varying numbers of points in the cleared areas of aggregated treatments ($n = 22$ in 15%A-c, $n = 12$ in 40%A-c). Plot distances to edge (aggregates or harvest unit boundaries) were considerably greater in 15%A-c than in 40%A-c (greater than two or three tree heights versus often less than one tree height, respectively) (Table 1).

During the first post-harvest growing season (June–October 1999, 1998 at BU), we tagged all planted seedlings and overstory trees (≥ 5 cm DBH) in each plot. Planted seedlings were noted as live or dead and live seedlings were measured for total height and leader growth. Overstory trees were recorded as live or dead and measured for DBH. Measurements were repeated in June–October 2000 (1999 and 2000 at BU), 2003, and 2009 (11–12 years after harvest).

Natural regeneration was sampled in the same permanent plots in five of the blocks (not at CF due to time constraints). Seedlings (< 10 cm tall) were tallied by species in a total of twenty-four 0.2 m × 0.5 m quadrats evenly spaced along four radial transects. Saplings (≥ 10 cm tall, < 5 cm DBH) were tallied by species in 1 m × 6 m subplots defined by the same transects. Sampling occurred before harvest (1994, 1995, or 1996) and 1 year (1998 or 1999) and 10–12 years after harvest (2008 or 2009). Broad-leaved tree species were uncommon and are not considered in this paper.

Analyses

Planted seedling survival and height growth

Analyses of planted seedlings were conducted by species, although *Abies procera* Rehder and *Abies magnifica* var. *shastensis* Lemmon were treated as one taxon (henceforth, *Abies*) (Table 2). *Pinus ponderosa* Douglas ex P. Lawson & C. Lawson was not tested statistically because of limited replication (two blocks) (Table 2). For each species in each experimental unit, we assessed survival and mean height growth (derived from the total height and leader growth of seedlings that survived to the last measurement).

Height growth was chosen as an indicator of potential recruitment into the overstory. Survival and growth were computed for each of two time periods, “early” and “late,” and over the full study period. For survival, the early period represented years 1 and 2 and the late period years 5–11 (6–12 at BU). For growth, the early period represented year 1 (year 2 at BU) and the late period years 4–11 (4–12 at BU).

We used general linear mixed models (GLMM) (McCulloch et al. 2008) to compare survival and growth among treatments (hypothesis 1). Survival models used the binomial distribution (logit link) and growth models, a Gaussian distribution. Models included block (random effect) and treatment (fixed effect). To account for overdispersion (survival model), experimental unit variation was included as a random effect (Browne et al. 2005). Significant models were followed by orthogonal contrasts to test effects of level, pattern, and their interaction.

Natural regeneration density

For each experimental unit, we computed mean densities of seedlings and saplings at three sampling dates: pre-treatment, post-treatment (1 year), and final sampling (10–12 years; times vary among blocks and size classes). Given limited representation of most species across blocks, we summed densities by seral group: early-seral (relatively shade-intolerant pioneer species that fail to establish in closed-canopy forests) and late-seral (shade-tolerant, climax species). *Pseudotsuga*, which dominated the early-seral group, was analyzed separately; the remaining early-seral species were too sparse as a group to analyze statistically.

Analyses were conducted in two stages to evaluate (1) treatment effects (hypothesis 2) and (2) correlates of plot-level variation (hypothesis 3). Felling of submerchantable stems (including advanced regeneration) at PH and WF limited our ability to interpret survival through harvest (i.e., initial disturbance effects). Therefore, we assessed responses to treatments at final sampling using a model that accounted for variation in post-harvest density (i.e., subsequent to felling of submerchantable stems). This approach emphasizes the influences of treatments on post-harvest demographic processes: post-harvest survival of advanced regeneration (seedlings or saplings), seedling establishment, and transitions between size classes, i.e., seedlings to saplings and “loss” of saplings to the overstory (the latter were infrequent and averaged $< 3\%$ of stems among treatments). We used GLMMs (Poisson distribution with log-link) treating block as a random effect and treatment and post-harvest (year 1) density as fixed effects. We accounted for overdispersion by including experimental unit variation as a random effect (Elston et al. 2001). Significant models were followed by orthogonal contrasts to test effects of level, pattern, and their interaction.

We then tested whether plot-level variation in density correlated with overstory characteristics (density and basal area), shrub cover (woody plants > 1 m tall at maturity; Halpern et al. 2012), and slash cover and depth (data from Halpern and McKenzie 2001) (Table 3). Overstory and understory data were contemporaneous with seedling and sapling data (years 10–12), but slash cover and

Table 3. Means and ranges of predictors used in analyses of plot-scale variation in seedling and sapling density in years 10–12.

Predictor	40%D		40%A-c		15%D		15%A-c	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Overstory density (trees/ha)	252	25–2050	162	0–875	190	0–3000	228	0–3650
Overstory basal area (m ² /ha)	34.2	0.6–90.6	1.7	0–11.6	12.2	0–45.4	2.1	0–49.0
Shrub cover (%)	18	4–81	30	0–100	27	0–98	29	0–92
Slash cover (%)	66	0–99	80	13–100	77	14–100	79	30–100
Slash depth (cm)	7	0–24	11	1–37	10	1–38	12	2–46

Note: Means and ranges are based on plot values at final sampling (10–12 years) for overstory density, basal area, and shrub cover and post-harvest values (year 1) for slash cover and depth. The high maximum values of overstory density in 40%A-c and 15%A-c are due to the presence of submerchantable stems (<18 cm DBH) or ingrowth (≥5 cm DBH at final sampling). High values for basal area reflect the presence of large trees that were girdled to create artificial snags but failed to die.

depth were post-harvest values (year 1). We used GLMMs (Poisson distribution with log-link) treating block and experimental unit as random effects and treatment and post-harvest density as fixed effects. We accounted for overdispersion by including individual (plot-level) variation as a random effect. We used an information theoretic approach and model averaging to identify the best-supported model explaining final density within the context of the treatments and post-treatment densities. First, we generated a global model containing all treatment- and plot-level predictors. Because slash depth and cover were correlated, we tested each in a separate global model. We selected predictors for inclusion in the candidate model only if they reduced the Akaike information criterion (AICc) of the global model by ≥2 (Burnham and Anderson 2002). Models with the lowest AICc and highest corrected Akaike weight (w_i) were determined to have the best fit, with all models with a delta AICc (Δ_i) value of ≤2 considered as having substantial support. When a single superior model was not found, we used model averaging to calculate regression coefficients, weighted unconditional SEs, and unconditional 95% CIs (Grueber et al. 2011). Parameter estimates were centered and standardized (2 SD) following Gelman (2008), permitting comparison of coefficients on a common scale. Pseudo- R^2 values were calculated for best-fit models based on the likelihood ratio, adjusted for Nagelkerke's modified statistic (Nagelkerke 1991). Analyses were conducted in R v.2.14.2 (R Development Core Team 2012).

Results

Planted seedling survival and height growth

A total of 58% of planted seedlings survived to final sampling. Survival varied among species (greatest in *Pinus monticola* Douglas ex D. Don, lowest in *Abies*) (Fig. 1). Of total mortality, 57% occurred early (1–2 years) and 22% in the late period (5–11 or 12 years). Survival varied with treatment, partly consistent with hypothesis 1. As expected, early survival was significantly greater under dispersed retention, but only for *P. monticola* and *Abies* (Fig. 1). However, greater retention did not enhance early survival, nor did pattern or level of retention influence later survival. In the two blocks in which it was planted, *P. ponderosa* had lower survival under greater retention. Only for *Abies* did the early benefit of dispersed retention persist to final sampling.

Height growth varied among species and treatments (Fig. 2). On average, 4% (6.2 cm/year) of total growth occurred early (year 1 or 2) and 70% (27.7 cm/year) in the late period (5–11 or 12 years). Responses to retention level and pattern were consistent with expectation. *Pinus monticola* and *Pseudotsuga* experienced late-period growth suppression at higher levels of retention and in dispersed treatments. *Abies* had similar growth reduction, but the effect of pattern was not significant. *P. ponderosa*, which was not tested, responded similarly.

Natural regeneration density

Natural regeneration densities were highly variable among and within blocks prior to treatment and much of this variation per-

sisted through harvest (Fig. 3). In models that account for this variation, final seedling densities did not differ among treatments, although they tended to be greater in dispersed treatments (Fig. 4). In contrast, sapling densities differed significantly among treatments (Fig. 4). We expected early-seral species to be inhibited by greater retention and the presence of a dispersed canopy (hypothesis 2). For *Pseudotsuga* saplings, we observed a significant level × pattern interaction with a distinct peak in 15%D (Fig. 4). Final sapling density (3170/ha) greatly exceeded the post-harvest density of seedlings and saplings (1229/ha), indicating substantial establishment over the study period (Fig. 4). For the remaining early-seral species, sapling density was too low to analyze statistically but suggested greater establishment in dispersed treatments. We predicted that late-seral species would benefit from greater retention and the presence of a dispersed overstory. Responses to pattern, but not level, conformed to this prediction (Fig. 4). Total sapling densities at final sampling exceeded minimum federal stocking levels (312 stems/ha after 5 years) in most experimental units; however, stocking was inadequate in three of four units at DP and in one at LWS, most often in aggregated treatments (A-c).

Models of regeneration density were improved by including plot-scale measures of overstory and understory characteristics (Table 4). However, pseudo- R^2 values were low (0.08–0.13), indicating limited ability to explain variation in regeneration response. Relationships were partly consistent with expectation (hypothesis 3). Sapling densities were negatively correlated with slash cover or depth (*Pseudotsuga* and late-seral species), negatively correlated with shrub cover (*Pseudotsuga*), and positively correlated with overstory density (late-seral species). However, the positive correlation of early-seral *Pseudotsuga* with overstory density was not expected. For seedlings, *Pseudotsuga* density was negatively correlated with shrub cover and overstory density (as predicted) but positively correlated with basal area (not predicted). Density of late-seral seedlings did not correlate with overstory characteristics or slash (Table 4).

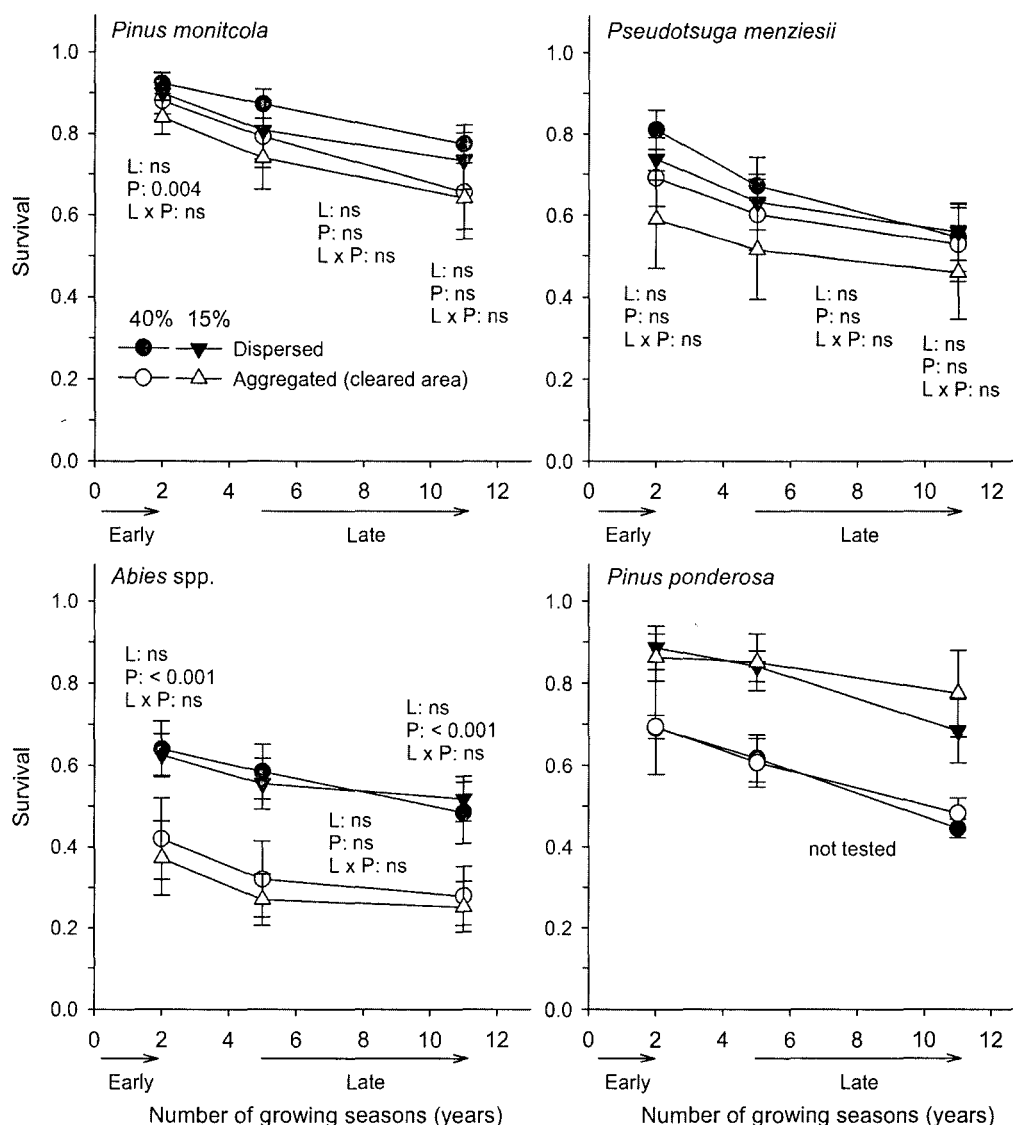
Discussion

The DEMO experiment offers a unique opportunity to explore how residual forest structure can shape early regeneration responses in *Pseudotsuga*-dominated forests of the Pacific Northwest. Although our studies were not designed to compare planted and natural regeneration directly, they allow us to assess the potential for each to meet a diversity of management objectives and the contexts in which these objectives can be met.

Planted seedling survival and growth

Survival of planted seedlings varied markedly among species and treatments. Most mortality occurred within 1–2 years of planting, suggesting a failure to establish rather than gradual suppression of established seedlings. Although high rates of early mortality are likely to reflect inadequate root system develop-

Fig. 1. Survival (mean proportion $\pm$ 1 SE) of planted trees at three points during the study period. Generalized linear mixed models were used to compare survival among treatments for each of three time periods early (0–2 years), late (5 (6)–11 (12) years), and the full study period (0–11 (12) years). Significant differences ($P \leq 0.05$) represent pattern (P: aggregated, A-c, versus dispersed, D) and level $\times$ pattern interaction (L $\times$ P); ns, nonsignificant. *Pinus ponderosa* was not tested due to limited replication (two blocks).

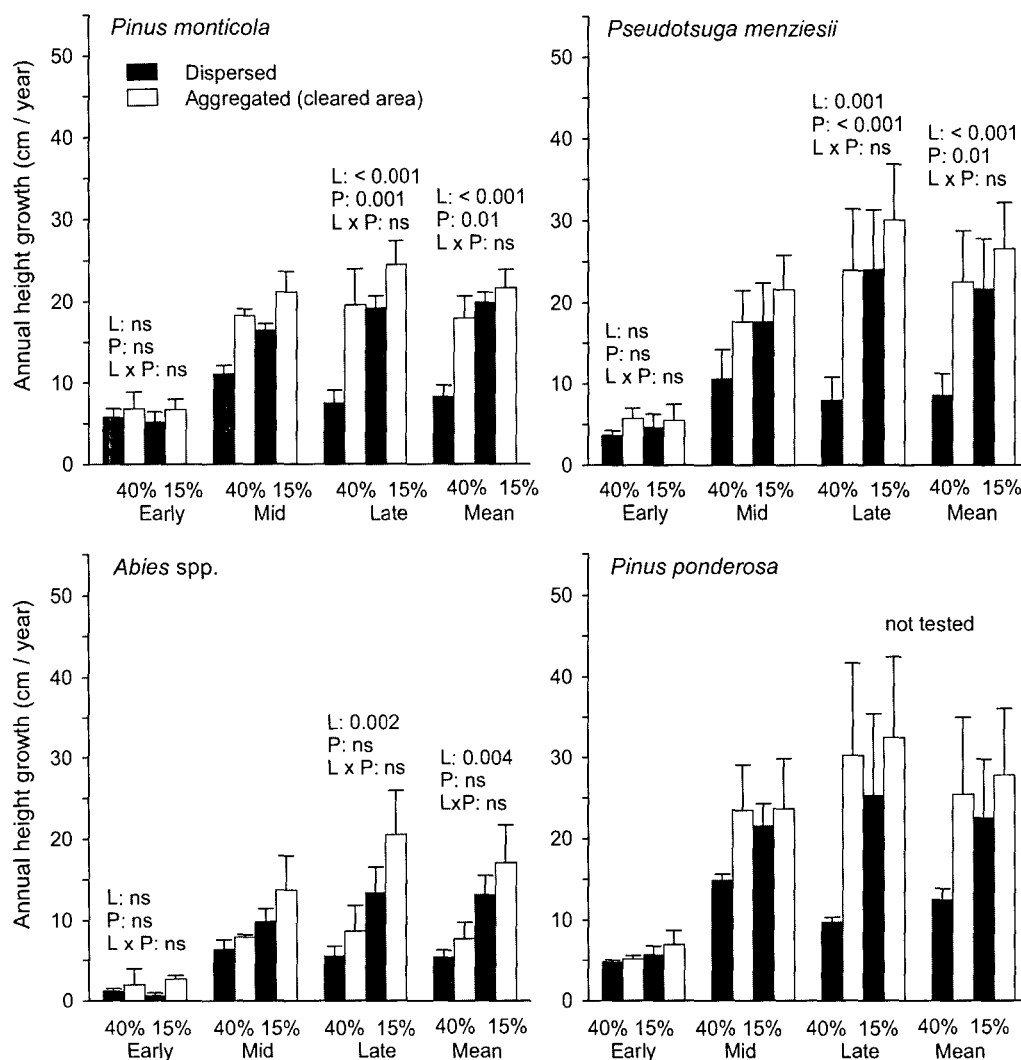


ment, other factors may also be important: quality of planting stock, improper handling, slash accumulations or shrub cover that impede access to planting sites, frost damage (Stathers 1989), or gopher predation (Ferguson 1999).

As hypothesized, dispersed retention enhanced early survival of *P. monticola* and especially *Abies*. *Pseudotsuga* also appeared to benefit, but the effect was not significant due to large variation among replicates. As demonstrated in shelterwood systems, shading from retained trees can temper microclimatic extremes (Childs and Flint 1987), a critical function for newly planted seedlings including drought-sensitive species such as *Abies* (Franklin 1983). Although canopy shading can also benefit survival by suppressing competing vegetation (Paquette et al. 2006), there was little evidence of this mechanism in our system (Halpern et al. 2005). Rates of mortality declined during the late period (5–12 years) but counter to expectation were unaffected by retention level or pattern. As a result, long-term survival varied only in *Abies*, a legacy of its high early mortality in the cleared areas of aggregated treatments. Decade-scale observations in this system thus

support the conclusions of previous studies in which seedling survival is insensitive to a wide range of overstory densities (Paquette et al. 2006) or patterns (Palik et al. 2003). That said, observations of height growth suggest that both factors may limit survival in the longer term. Growth was reduced for all species under higher levels of retention and in dispersed treatments for *P. monticola* and *Pseudotsuga*. Previous studies in this region report similar effects (e.g., growth reductions at 25% retention; Mitchell et al. 2007) but others do not (no reduction at 30% retention; Smith and Beese 2012). Height growth is generally assumed to be regulated by light (Mitchell 2001), although soil resources may become increasingly important below a threshold level of retention (Boyden et al. 2012). For *Pseudotsuga*, light levels <40% of ambient can cause substantial reductions in growth (Drever and Lertzman 2001). Growth reductions in the current study are clearly consistent with reductions in understory light along the retention gradient. Light was reduced by 27% in 15%D and by 60% in 40%D relative to the large openings of 15%A (Heithecker and Halpern 2006).

Fig. 2. Mean annual height growth (± 1 SE) of planted trees during the early (year 1 or 2), mid- (1 (2) – 4 years), and late (5 – 11 (12) years) periods and over the full study (Mean). Generalized linear mixed models were used to compare growth rates among treatments for all but the midperiod. Significant differences ($P \leq 0.05$) represent the results of orthogonal contrasts testing effects of retention level (L: 15% versus 40%), pattern (P: aggregated, A-c, versus dispersed, D), and level $\times$ pattern interaction (L $\times$ P); ns, nonsignificant. *Pinus ponderosa* was not tested due to limited replication (two blocks).



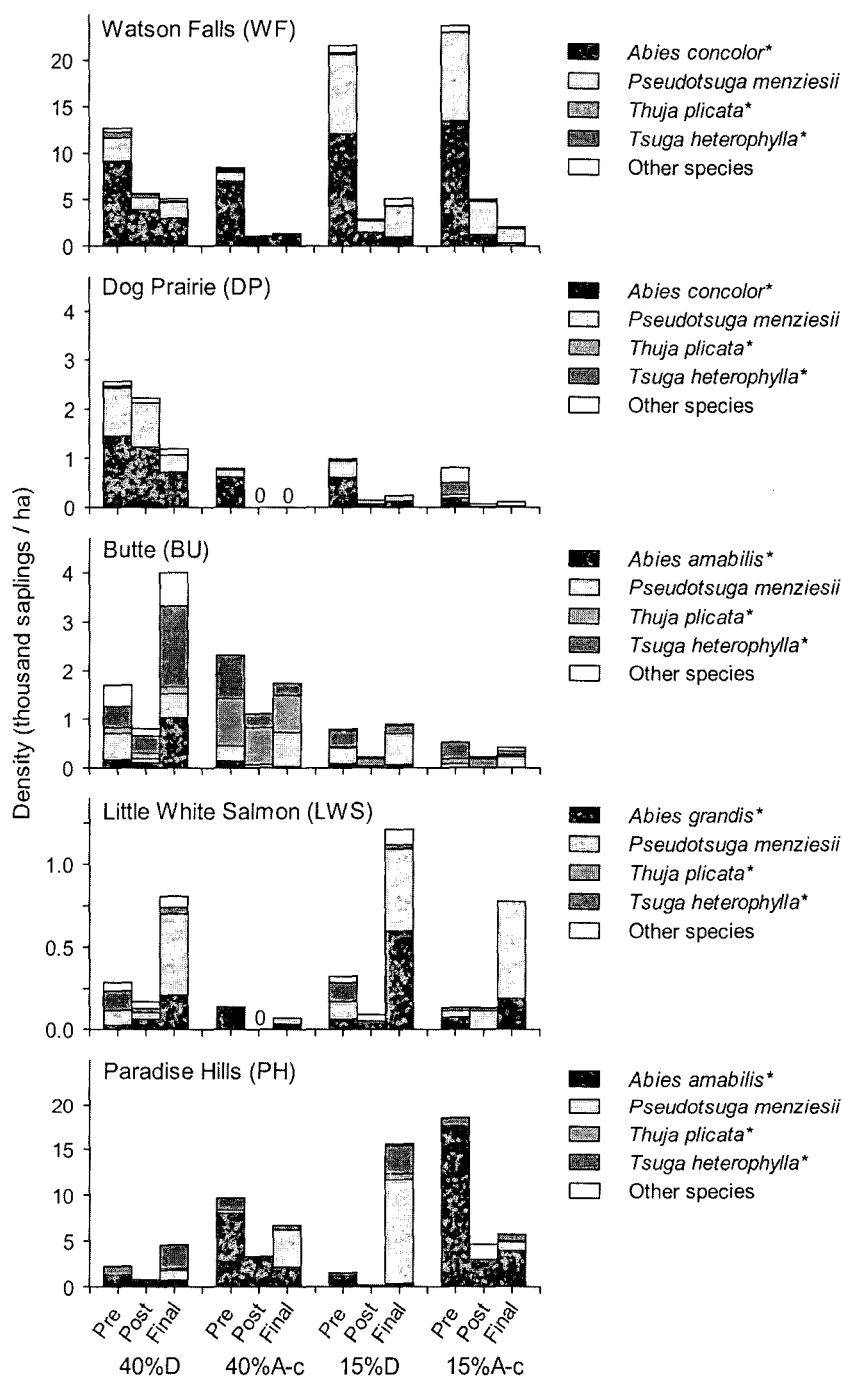
In the longer term, the ability of planted seedlings to maintain current growth rates will depend on resource conditions as stands mature. Under low levels of dispersed retention in this experiment, understory light has increased over time with loss of residual trees to windthrow (Maguire et al. 2006). As a result, future growth may be determined more by competition in the understory than by resource preemption by the overstory. This is an important distinction between retention harvests and silvicultural thinning: in the latter, in the absence of windthrow, crowns expand laterally and vertically to reduce understory light (Anderson et al. 2007).

Natural regeneration density

Patterns of natural regeneration reflect the outcome of many factors: pre-treatment density and composition, losses to logging disturbance, seed availability, and characteristics of the post-harvest environment that inhibit or enhance germination, growth, and survival. In this study, pre-harvest densities varied by one to two orders of magnitude among experimental units (Fig. 4) and felling of submerchantable stems confounded the effects of harvest disturbance. Thus, we focused our analyses on densities at final sampling, contingent on this variation.

We hypothesized that responses to level and pattern of retention would differ for early- and late-seral groups, consistent with the life-history and physiological traits of species. Responses of saplings provided partial support for this hypothesis. Late-seral species were more abundant in dispersed treatments, reflecting an understory microclimate more conducive to establishment, growth, and survival (Heithecker and Halpern 2006). *Pseudotsuga*, the principal early-seral and dominant canopy species, established in profusion under low levels of dispersed retention (15%D), likely reflecting the combined benefits of greater light and a dispersed, locally abundant source of seed. That similar patterns were not evident in seedling populations suggests that opportunities for germination may be constrained in time as competition with understory vegetation increases. Future development of these forests is likely to resemble the natural two-tiered stands studied by Zenner et al. (1998), with an emergent, but sparse canopy of remnant trees from which a younger cohort derives. Whether and when this cohort experiences canopy closure will depend on current densities and less so on competition from residual trees. At PH (>15 000 saplings/ha), closure will be rapid; at DP (270 saplings/ha), it may never occur.

Fig. 3. Mean density (± 1 SE) of saplings before treatment (Pre), after treatment (Post: year 1 or 2), and at final sampling (Final: year 11 or 12). Asterisks denote late-seral species. "Other species" (infrequent or of low density) include one or more of the following: *Abies lasiocarpa*, *Abies magnifica* var. *shastensis*, *Abies procera*, *Calocedrus decurrens*, *Chamaecyparis nootkatensis*, *Picea engelmannii*, *Pinus contorta*, *Pinus monticola*, *Pinus ponderosa*, *Taxus brevifolia*, and *Tsuga mertensiana*.



In contrast with saplings, we were unable to detect treatment-related variation in seedling densities. Although densities were as much as an order of magnitude greater than saplings, they were highly variable among sites and showed little evidence of increase over time. The lack of strong treatment effects and temporal trends is not surprising, however, given the cyclical nature of seed production (Franklin et al. 1974) and high rates of germinant mortality (Leemans 1991).

In addition to the effects of treatments, we hypothesized that regeneration would respond to local (plot-scale) variation in slash,

competing vegetation, and overstory influence. Although these improved the performance of the models, they explained little variation in regeneration density at final sampling. Nevertheless, the nature of the relationships was largely consistent with expectation. Sapling densities were reduced by greater slash, but seedling densities were not, suggesting that inhibitory effects were limited to the early post-disturbance environment, when slash loadings were greatest. Negative correlations between *Pseudotsuga* and shrub cover are consistent with previous observations that competing vegetation can significantly reduce its establishment

Fig. 4. Mean densities (± 1 SE) of seedlings (<10 cm, top row) and saplings (≥ 10 cm, <5 cm DBH, bottom row) before treatment (Pre), after treatment (Post: year 1 or 2), and at final sampling (Final: year 11 or 12). Total densities are partitioned into *Pseudotsuga menziesii* (the dominant early-seral species), late-seral species, and early-seral species other than *Pseudotsuga*. Generalized linear mixed models that accounted for variation in post-treatment density were used to compare densities at final sampling (see Table 4). Significant differences ($P \leq 0.05$) represent the results of orthogonal contrasts testing effects of retention level (L: 15% versus 40%), pattern (P: aggregated, A-c, versus dispersed, D), and level $\times$ pattern interaction (L $\times$ P); ns, nonsignificant. Early-seral seedlings and saplings were too sparse to analyze statistically.

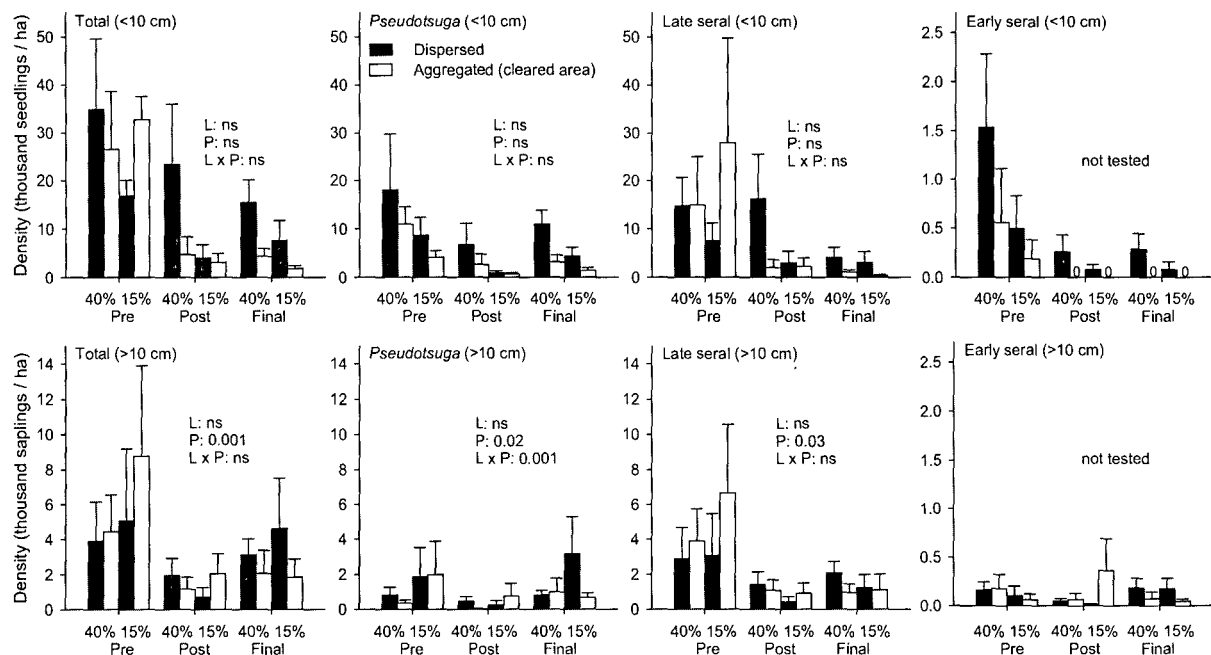


Table 4. Comparisons between best-supported information theoretic models that included plot-scale predictors of natural sapling and seedling densities and base models lacking these predictors.

Size class, seral group	Model	K	AICc	Δ_i	w_i	R^2	Predictor	Coeff (SE)	95% CI
Saplings, <i>Pseudotsuga menziesii</i>	Post + Trt + Tph + Shrub + Slashd	11	982	0	0.52	0.10	Tph	0.54 (0.11)	0.33, 0.76
	Post + Trt + Tph + Shrub	10	983	1	0.24		Slashd	-0.35 (0.18)	-0.69, 0.00
	Base model	8	1010	29	0.0		Shrub	-0.55 (0.26)	-1.07, -0.03
Saplings, late seral	Post + Trt + Tph + Slashc	10	1005	0	0.76	0.13	Tph	0.71 (0.13)	0.46, 0.96
	Base model	8	1044	39	0.0		Slashc	-0.29 (0.14)	-0.50, -0.02
Seedlings, <i>Pseudotsuga menziesii</i>	Post + Trt + Shrub + Tph + BA	11	722	0	0.74	0.11	Shrub	-0.89 (0.24)	-1.37, -0.41
	Base model	8	738	19	0.0		Tph	-0.43 (0.19)	-0.81, 0.06
							BA	0.48 (0.21)	0.07, 0.88
Seedlings, late seral	Base model	8	473	na	na	0.05	None		

Note: Predictors include overstory tree density (Tph), overstory basal area (BA), shrub cover (Shrub), and slash cover (Slashc) and depth (Slashd). All models included post-harvest density (Post) and treatment (Trt) as fixed effects and block, experimental unit, and plot (to address overdispersion) as random effects. Adjusted pseudo- R^2 values (R^2) for best-supported models are based on the likelihood ratio adjusted for Nagelkerke's modified statistic. Standardized model-averaged coefficients (Coeff), weighted unconditional standard errors (SE), and 95% confidence intervals (95% CI) are provided for predictors in the best-supported models. For each model, K is the number of parameters, AICc is the corrected Akaike's information criterion, Δ_i is the difference in AIC units between the lower ranked model and the top model, and w_i is the Akaike weight.

and growth (Harrington 2006). Similar effects were not observed for late-seral species, consistent with our expectation that competitive effects would be stronger for early-seral, light-demanding species. We also hypothesized that greater overstory influence would have a positive effect on regeneration of late-seral species, which typically establish in more shaded environments. Indeed, sapling density was positively correlated with overstory density, but seedling density was not. Overstory shading may have been more critical to regeneration soon after disturbance, when saplings are likely to have germinated and understorey shading was sparse. With rapid recovery of the understorey (Halpern et al. 2012), overstory shading may have been less critical to establishment of seedlings. In contrast, for *Pseudotsuga*, saplings showed a positive response to overstory density, but seedlings showed a negative response. Similar to treatment-scale patterns, overstory influences may switch from positive (enhanced seed rain) to negative

once substrate or competitive environments become less conducive to establishment.

Conclusions and management implications

The results of this large-scale experiment illustrate how level and pattern of retention influence early regeneration processes in *Pseudotsuga*-dominated forests of the Pacific Northwest. For planted seedlings, early survival varied with pattern (in some species), but subsequent survival did not. However, height growth was distinctly reduced in dispersed treatments and at higher levels of retention. Without further silvicultural intervention or natural disturbance, it is unlikely that planted seedlings will attain overstory canopy positions in these treatments. Elsewhere, poor survival of low-density plantings, particularly in *Abies*, suggests limited potential for planted seedlings to contribute to future

stand development. This underscores the importance of natural regeneration when planting densities are low or retention levels are high.

Natural regeneration was significantly greater (1.5–2.5 times) under dispersed retention than in the cleared areas of aggregated treatments. Depending on management objectives, locally dense patches of regeneration may require thinning to reduce competitive interactions and loss of the understory. Although minimum stocking was usually achieved in the aggregated treatments, densities fell below this threshold at DP and in one of two units at LWS. Numerous factors may have contributed to the paucity of regeneration in these units: dispersal limitations, lack of advanced regeneration, deep slash, or competition with residual shrubs (e.g., *Acer circinatum* Pursh). On the other hand, sparse and protracted establishment may be an inherent characteristic of these sites (Tappeiner et al. 1997). In the pre-treatment forests at LWS, trees were widely spaced and open-grown, suggesting a similar pattern of regeneration after stand-replacing fire more than a century earlier. Although not anticipated, the slow pace of regeneration highlights the potential to create and maintain early-seral habitats through retention harvest, habitats that are under-represented in landscapes traditionally managed for rapid reforestation (Swanson et al. 2011).

Our results also support the hypothesis that retention level and pattern can interact to influence the seral composition of regenerating trees. At lower density, dispersed retention promoted *Pseudotsuga*, presumably by enhancing local seed rain within a relatively high-light environment. At higher density, it favored late-seral conifers, enhancing survival of advanced regeneration and facilitating establishment and growth of shade-tolerant species. The ability of managers to manipulate forest structure to influence the density and composition of regenerating species with differing ecological roles lays a critical foundation for maintaining structurally complex and compositionally diverse forest ecosystems.

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