Natural Regeneration in Thinned Douglas-fir Stands in Western Oregon

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ABSTRACT. In response to interests by land management agencies to transform even-aged stands to structurally mimic old-growth forests, we evaluated whether thinning in 40- to 80-year-old Douglas-fir (*Pseudotsuga menziesii*) stands influenced amount and composition of advanced regeneration 5 to 7 years following treatment. We used data from two large-scale management experiments (Density Management Study and Young Stand Thinning and Diversity Study) conducted in western Oregon. Thinning focused on the removal of Douglas-fir, while maintenance of minor species was encouraged. Although both experiments showed higher tree regeneration after thinning, we found that variation in regeneration density was too high (3 orders of magnitude) to find statistical differences among thinning intensities. While seedlings

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of the major species, Douglas-fir and western hemlock (*Tsuga heterophylla*), were always present and dominated regeneration on nearly all sites, species trends were driven by high spatial and compositional variation throughout all units, treatments, and sites. Thinning increased the number of species within the regeneration layer. Hereby, species diversity was strongly related to overstory composition, suggesting seed source limitations for minor species. Hence, favoring rare species during thinning operations may be an effective method to increase regeneration species richness. Local conditions, as defined by overstory density appeared more influential than regional climate patterns in determining seedling densities. Shrub and grass competition did not prevent seedling establishment as their cover values were generally not as high as typically found in clearcuts in the region. The high variation in seedling density and species richness within the seedling stratum in the thinned stands may set the stage for development of structural complexity in even-aged Douglas-fir plantations.

KEYWORDS. Natural regeneration, composition, thinning, Oregon, *Pseudotsuga menziesii*, multivariate analysis

The majority of mature and old-growth forests in western Oregon and Washington have been replaced by young second-growth stands because of widespread harvesting and artificial reforestation in the 20th century (Aubry, Halpern, & Maguire, 2004; Bolsinger & Waddell, 1993; Cissel et al., 2006). These stands are comprised of mostly homogenous, even-aged Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) that lack the rich structural complexity typical of late-successional forests in this region (Spies, 1990; Spies & Franklin, 1988). Public concerns over the long-term effects of forest practices and the resulting emphasis on Ecosystem Management (Gilmore, 1997; U.S. Department of Agriculture [USDA] & U.S. Department of the Interior [USDOI], 1993) shifted the management focus on public lands from timber production to a complex set of objectives, including a special emphasis on late-successional structure (Kessler, Salwasser, Cartwright, & Caplan, 1992). Consequently, enhancing and fostering structural complexity in young plantations, while maintaining timber production, has become a research focus (Cissel et al.; Reutebuch, Harrington, Marshall, & Brodie, 2004; USDA & USDOI, 1994).

Observations that old-growth forests initiated with lower densities than current plantations (Tappeiner, Huffman, Marshall, Spies, & Bailey,

1997) have led suggestions that thinning may become a tool to accelerate the development of late-successional features in young stands (Carey & Curtis, 1996; McComb, Spies, & Emmingham, 1993). While thinning activities appear to promote and enhance the establishment of some late-seral stand attributes, such as large trees and large snags (Barbour, Johnston, Hayes, & Tucker, 1997; Davis, Puettmann, & Tucker, 2007), abundance and composition of understory vegetation appear to follow more complex trends in time and regarding thinning intensities (e.g., Bailey, Mayrsohn, Doescher, Pierre, & Tappeiner, 1998; Davis & Puettmann, in press; Lindh & Muir, 2004; Thysell & Carey, 2001). Since tree regeneration is typically managed through reproduction cutting (Smith, Larson, Kelty, & Ashton, 1997), it has received little attention after thinning operations.

Generally, regeneration studies in young Douglas-fir forests are limited in scope because of a retrospective approach, limited severity, and extent of canopy disturbances, or a focus on single study sites. Several studies highlighted different trends after thinning. For example, greater seedling densities in thinned than unthinned stands have been defined and conditioned by high variability over time (Maas-Hebner & Emmingham, 1998) and great spatial variation (Chan et al., 2006; Gerstein, 1999). Seedling density and frequency (i.e., proportions of plots with seedlings) increased with thinning intensity in even-aged stands (Bailey & Tappeiner, 1998) and stands managed by selection thinning (Miller & Emmingham, 2001). On the other hand, studies on partial harvesting or partial overstory mortality from wildfires showed that greater overstory densities appear to be favorable on harsh or exposed sites (Minore, Abee, Smith, & White, 1982; Seidel & Cooley, 1974; Tesch & Mann, 1991) especially facilitating regeneration of shade-tolerant species, such as western hemlock (*Tsuga hetrophylla* (Raf.) Sarg.) and western redcedar (*Thuja plicata* Donn ex D. Don) (Keeton & Franklin, 2005; Larson & Franklin, 2005; Zenner, 2000). Low levels of diversity in overstory species were reflected in the low species diversity of tree regeneration (Buermeyer & Harrington, 2002; Rose & Muir, 1997).

Several large-scale management experiments (e.g., Monserud, 2002), which cover large treatment units on multiple sites, offer an opportunity for a comprehensive study of the effects of different thinning prescriptions on natural regeneration patterns. We used data collected from two thinning experiments to characterize natural regeneration established shortly after thinning in second-growth Douglas-fir forests. To understand regeneration patterns and factors responsible for such patterns, we used the following approach:

1. To understand whether thinning practices are an opportunity to initiate development of an understory tree layer, we developed a detailed description of the amount and spatial distribution of natural regeneration patterns (quantity and composition).
2. To test whether thinning intensities vary in their effects on tree regeneration, we compared impacts of different thinning treatments on regeneration densities and species diversity (thinning response).
3. To quantify patterns of regeneration densities and species diversities, we characterized species composition by identifying structural regeneration groups (structural groups).
4. To better understand mechanisms that drive regeneration after thinning in homogenous, even-aged stands, we related these structural regeneration groups to environmental and ecological variables (environmental interpretation).

METHODS

Study Sites

We used data from two large-scale management experiments in western Oregon in this study: Density Management Study (DMS) and Young Stand Thinning and Diversity Study (YSTDS). The DMS was initiated in 1996 (Chan, Anderson, Cissel, Larsen, & Thompson, 2004; Cissel et al., 2006) in 50- to 80-year-old, unthinned Douglas-fir-dominated stands and contained four thinning treatments of 15 to 70 ha each, replicated once on each of seven sites, located up to 300 km apart. Treatments consisted of an unthinned control (CON, ~ 600 trees per ha [t ha^{-1}]), a high density retention (HD, ~ 300 t ha^{-1}), a moderate density retention (MD, ~ 200 t ha^{-1}), and a variable density retention (VD, ~ 100–300 t ha^{-1}). Leave tree islands (0.1, 0.2, or 0.4 ha) were included in all the thinning treatments, whereas gaps (0.1, 0.2, or 0.4 ha) were created in the MD and the VD treatments only. For logistical reasons, harvests were staggered among sites between 1996 and 2000. Measurements taken 5 years after the harvest were used in this study. Thinning operations focused on removing major species (primarily Douglas-fir), retaining minor species that made up less than 10% of the overstory. The seven study sites, located in three ecoregions in Oregon (Coast Range, Willamette Valley, and Cascades), are described in detail by Cissel et al. The YSTDS was initiated in 1994 and installed in unthinned 35- to 45-year-old Douglas-fir-dominated stands. The four thinning treatments, 15 to 50 ha each, are replicated once on each of four sites, located up to 30 km apart. Treatments consist of an unthinned control (CON, ~ 600 t ha^{-1}), a light thin (LT, ~ 250–300 t ha^{-1}), a heavy thin (HT, ~ 125 t ha^{-1}), and a light thin with 20% of the area in gaps (GAP, 0.2 ha openings). Thinning operations were implemented between 1994 and 1996, and data were measured in 2001 (i.e., 5–7-years post harvest). Like the DMS, thinning in the YSTDS focused on major species (primarily Douglas-fir), retaining the minority species. The four study sites, located in the Willamette National Forest at the western slopes of the Central Cascades in Oregon, are described in Hunter (2001) and Beggs (2005).

Sampling Procedures

The DMS sampling design consisted of 0.1-ha of randomly distributed circular overstory plots. Fourteen overstory plots were installed in controls with 21 plots within each thinning treatment. To increase information on openings, two additional overstory plots located within small artificial gaps were added in the MD and VD treatments of four study sites (gap plots). Within overstory plots, four circular regeneration subplots (20.25 m^2) were installed 9 m in each cardinal direction from the plot center.

Data collection in the YSTDS was also based on 0.1-ha circular overstory plots. To cover approximately 7.5 percent of the respective treatment areas, 13 to 30 overstory plots were installed within the treatment units. Plots in the LT, HT, and CON treatments were randomly located along transects that were systematically placed throughout the treatment units. To sample sufficiently the three sub-treatments (matrix, edge, gap) in GAP treatments, 30 sample plots were placed inside each randomly selected gap, at the edge and in the adjacent forest matrix (Beggs 2005). Regeneration data was collected within two regeneration subplots (14.5 m $\times$ 1.5 m) placed 7.25 m from the plot center in opposite directions (Beggs).

For both DMS and YSTDS, all trees with a diameter at breast height (dbh) greater than 5 cm in the overstory plots were identified by species; dbh was measured; and stand basal area (m^2 ha^{-1}) was calculated. In the regeneration subplots, all live naturally regenerated conifer and hardwood seedlings (15–137 cm in height for DMS, 10–200 cm in height for YSTDS) were counted by species. This count may have included seedlings that established before the thinning operation; however, high initial mortality rates of naturally regenerated seedlings (Battles, York, & Levin, 2000) suggest that the majority of seedlings in our counts were established in the last 5 to 7 years. Regeneration subplot tallies belonging to the same overstory plot were averaged for all analysis. For analysis of our first two objectives, quantity and composition and thinning response, average values were calculated for each treatment unit. A set of environmental variables were measured and summarized in Table 1.

Data Analysis

Both studies were analyzed separately. For the multivariate analysis the original species matrices contained 554 and 365 overstory plots (site-treatment-plot number combinations as rows) and 15 and 17 species (columns) for the DMS (including gap plots) and YSTDS, respectively. Values of the "species-by-samples" matrices were equal to the total seedling count for a specific plot-species pairing. These basic matrices were analyzed to address our first two objectives, quantity and composition and thinning response. Seedlings were grouped into shade-tolerance classes for this purpose (see Table 2 for composition of tolerance classes). Descriptive statistics and ANOVA regarding site and treatment differences were performed with the SAS software package (SAS, 2002–2003). Differences were tested via Tukey's multiple comparison test.

To reduce the bulk and noise in the data when addressing objective 3 species occurring in less than 5% of the plots in one of the original matrices were deleted. As plots without any seedlings provided no information for determination of structural groups, the software was not equipped to analyze these plots and they had to be removed (McCune & Grace, 2002), To accommodate the dominance of single species, the great range of seedling densities, and the large number of zero values in both data sets, the reduced matrices were transformed with the Beals smoothing function (Beals, 1984; McCune, 1994). This transformation replaced presence-absence species data with the probability of a species occurring on a certain plot.

The reduced and transformed DMS matrix had 433 plots and 10 species. The proportion of zeros shrank from 89.5% to 0.5% and the beta diversity from 9.5 to 1.0. Coefficients of variation of plots and species decreased from 273.5% and 273.9% to 9.2% and 86.2%, respectively. The final

TABLE 1. Environmental predictor variables for both experiments, unless otherwise noted

Variable	Resolution	Description
Disturbance		
TRT	Treatment unit	Treatment: CON = control, HD = high density retention[a], MD = medium density r. [a], VD = variable density r. [a], LT = low thinning[2], HT = high thinning[b], GAP = gap opening[a]/light thinning with gap openings[b]
LOGCAT[a]	Treatment unit	Logging procedure: A = no logging, B = cable yarding, C = ground yarding
Climate		
HEAT	Overstory plot[a]/ Treatment unit[b]	Heat index: equation #3 of McCune and Keon (2002)
PREC[a]	Overstory plot	Site precipitation adjusted to elevation
Topography		
ELEV	Overstory plot[a]/ Treatment unit[b]	Elevation in ft
ASPECT	Overstory plot[a]/ Treatment unit[b]	Transformed aspect (Beers, Dress, & Wensel, 1966)
SLOPE	Overstory plot[a]/ Treatment unit[b]	Slope in percent
PHYS[a]	Overstory plot[a]/ Treatment unit[b]	Slope position: A = mtn peak or ridge top, B = lower sidehill, C = dry bench or terrace, D = alluvial flat or swamp
Overstory		
CRCOVER[b]	Overstory plot	Crown cover (incl. boles and snags)
BArSpecies[c]	Overstory plot	Basal area by species in m^2 ha^{-1}
BArShToSp[c]	Overstory plot	Basal area of shade-tolerant species in m^2 ha^{-1}
BArTOTAL	Overstory plot	Total basal area in m^2 ha^{-1}
Neighborhood		
percentCOVER	Regeneration plot	Averaged plot ground cover of ROCK and stones, BARESOIL, DUFF[a] or fine litter, MOSS, GRASSes[a] (incl. sedges and rushes), FORBs[a], FERNs[a], HERBs[b], low shrubs and tall ferns < 1 m (LOWSHR[b]), tall shrubs > 1 m (TALLSHR[b]), SHRUBs[a], and LOGs[a] (woody debris)
SAPLINGS	Regeneration plot	Total number of saplings

(*Continued*)

TABLE 1. (*Continued*)

Variable	Resolution	Description
Others		
COM	Overstory plot	Forest communities of the *Tsuga heterophylla* Zone of western OR based on understory vegetation: from A = driest association to F = wettest association, (Franklin & Dyrness, 1973)
SINDEX[b]	Treatment unit	Site index
REMARKS[a]	Regeneration plot	Special plot remarks: A = no remark, B = slash, C = (skid) road, D = stream, E = deer or bear traces, F = gap patch, G = leave island

[a]DMS.
[b]YSTDS.
[c]See Table 2 for species listing and abbreviations.

YSTDS matrix had 335 plots and 10 species. The proportion of zeros was reduced from 86.2% to 0.1% and the beta diversity from 7.2 to 1.0. Coefficients of variation of plots and species decreased from 120.9% and 144.3% to 5.7% and 71%, respectively.

The reduced and transformed matrices were analyzed via Cluster Analysis (CA) with Euclidean distances and Ward's group linkage method (McCune & Mefford, 1999; Ward, 1963; Wishart, 1969). CA produces an agglomerative, hierarchical classification of plots, so-called groups, based on similarities of species composition within each single unit. The final number of groups was based on within-group composition analysis and regenerating patterns of Douglas-fir-dominated forests, as established in the literature. Indicator Species Analysis (ISA) determined the species characterizing structural groups (Dufrêne & Legendre, 1997). Randomization Monte Carlo tests (1,000 permutations) revealed significance of every single (maximum) indicator value for each species of both reduced matrices. Discriminant analysis (DA) was used to find and redefine misclassified plots (McCune & Grace, 2002). DA was computed with the PROC DISCRIM procedures of the SAS software package (SAS, 2002–2003). Data transformation, as well as CA and ISA, was performed with PC-ORD multivariate analysis software (McCune and Medford).

TABLE 2. Number of sites, percentage of plots occupied by seedlings, and average number of seedlings per hectare of tree seedling species. Numbers in parentheses show the range among study sites

Species		Code[a]	DMS[b]			YSTDS		
			Number of Sites	Percent occupied plots	Seedlings ha^{-1}	Number of Sites	Percent occupied plots	Seedlings ha^{-1}
Shade-intolerant								
Red alder	*Alnus rubra*	ALRU	7	5.0 (1–2)	35.2 (2–189)	2	1.9 (0–6)	14.5 (0–45)
Pacific madrone	*Arbutus menziesii*	ARME	2	6.5 (0–44)	45.1	2	1.6 (0–4)	28.3 (0–54)
Oregon ash	*Fraxinus latifolia*	FRLA			0	1	0.3 (0–1)	5.0 (0–17)
Western white pine	*Pinus monticola*	PIMO			0	4	5.8 (1–12)	15.1 (3–35)
Black cottonwood	*Populus balsamifera*	POBAT			0	2	1.4 (0–4)	14.5 (0–45)
Bitter cherry	*Prunus emerginata*	PREM	4	4.5 (0–25)	19.1 (0–106)	3	23.0 (0–61)	477.4 (0–1345)
Douglas fir	*Pseudotsuga menziesii*	PSME	7	41.2 (22–68)	232.7 (58–613)	4	49.6 (36–67)	479.9 (215–1005)
Willow	*Salix* spec.	SALIX			0	1	0.3 (0–1)	8.8 (0–43)
Shade-tolerant								
White fir	*Abies concolor*	ABCO	1	0.4 (0–3)	0.5 (0–3)			0
Grand fir	*Abies grandis*	ABGR	5	7.4 (0–42)	69.0 (0–463)	2	1.1 (0–3)	3.8 (0–11)
Bigleaf maple	*Acer macrophyllum*	ACMA	6	14.9 (0–29)	49.2 (0–99)	4	24.7 (2–65)	1078 (18–3377)
Incense cedar	*Calocedrus decurrens*	CADE			0	3	4.7 (0–9)	28.3 (0–43)
Giant chinquapin	*Chrysolepis chrysophylla*	CHCHC	6	8.9 (0–20)	30.6 (0–90)	3	14.2 (0–47)	258.2 (0–1048)
Pacific dogwood	*Cornus nutallii*	CONU	2	0.4 (0–1)	0.5 (0–2)	2	3.0 (0–7)	27.7 (0–71)
Cascara buckthorn	*Frangula purshiana*	FRPU	3	8.9 (0–33)	32.9 (0–136)	4	11.8 (1–35)	119.7 (6–380)
Pacific yew	*Taxus brevifolia*	TABR	2	0.4 (0–1)	0.9 (0–5)	4	10.4 (4–19)	61.7 (10–150)
Western red cedar	*Thuja plicata*	THPL	7	8.9 (3–26)	23.2 (3–95)	4	26.6 (11–56)	297.3 (73–818)
Western hemlock	*Tsuga heterophylla*	TSHE	7	43.6 (1–87)	1293 (3–5581)	4	54.8 (35–68)	623.5 (145–1066)
California laurel	*Umbellularia californica*	UMCA	1	1.1 (0–8)	1.6 (0–11)			0

[a]Without gap plots.
[b]Abbreviations used in analyses.

Ordination with nonmetric multidimensional scaling (NMS) and classification tree analysis was used to address objective 4, understanding the mechanisms driving regeneration patterns. NMS using Euclidean distances was applied to find structural and environmental gradients (Kruskal, 1964a, 1964b; Mather, 1976). A medium thoroughness autopilot test checked both matrices to find the best of one- to four-dimensional solutions (McCune & Mefford, 1999). After these preliminary runs, the recommended solution was checked in a second step to improve reliance by minimizing stress and lowering instability to less than 0.001 (McCune & Grace, 2002). Both the first and second step of the NMS analyses involved Monte Carlo tests with 30 and 50 runs of randomized versions of the matrices, respectively. The final two-dimensional NMS solutions selected for either experiment had final stresses significantly lower than would have been obtained by chance ($P = .0196$), minimizing the measure of departure from perfect fit to 14.0 (DMS) and 13.4 (YSTDS). NMS was conducted with PC-ORD multivariate analysis software (McCune & Medford).

Classification tree analysis (Breiman, Friedman, Olshen, & Stone, 1984) was used to explore and indicate which environmental variables are responsible for differences among structural groups obtained by CA. A set of 50 cross-validation runs and the 1-SE rule were applied in order to determine the optimal level of "tree pruning" and to find the best and most frequently occurring tree for both data sets (De'ath & Fabricius, 2002; Feldesman, 2002). Predicting accuracy was assessed with misclassification tables (McCune & Grace, 2002). The R statistical package "mvpart" was used to conduct classification tree analysis (De'ath, 2006; R Developmental Core Team, 2005; Therneau & Atkinson, 1997).

RESULTS

Natural Regeneration Densities and Spatial Patterns

Overall tree regeneration was abundant and highly variable at different scales, but the majority of plots (i.e., average of subplots) were well stocked. A total of 7,976 and 5,623 seedlings were counted on the 537 DMS and 365 YSTDS plots, respectively. In general, regeneration was higher in the YSTDS than in the DMS: The mean seedling density on YSTDS plots was 3,542 ha^{-1} and 1,832 ha^{-1} on DMS plots. Despite these large averages, the variation in seedling density revealed important patterns at multiple spatial scales. Large differences in seedling densities were not only found between the two experiments, but also within experiments across sites and within sites across treatments (Tables 3 and 4). Average overall seedling density for individual treatment units ranged from 9 to 9,777 seedlings ha^{-1} for DMS and 470 to 10,291 seedlings ha^{-1} for YSTDS. Eight percent of the YSTDS plots, and 22% of the DMS, plots contained no seedlings. Half of all DMS plots, and one fifth of YSTDS plots, had a seedling density lower than 500 ha^{-1}, a density considered the minimum level for full stocking in Oregon (Oregon Department of Forestry, 1994). The variability across sites appeared to be related to overstory and understory conditions. For example, sites with comparatively large proportions of shade-tolerant species in the overstory, primarily western hemlock and western redcedar (e.g., Keel Mountain and Delph Creek in the DMS and Mill Creek and Sidewalk Creek in the YSTDS), showed the greatest total seedling densities. On the other hand, Bottomline, a site where the understory is dominated by sprouting shrubs, had the lowest seedling density.

A wide variety of tree species regenerated under the range of conditions found in the experiments (Table 2), exibiting consistent patterns regarding tree species. Douglas-fir, western hemlock, and western redcedar—the three tree species indicative of the *Tsuga heterophylla* Zone (Franklin & Dyrness, 1973)—grew on all study sites. These three species comprised about 64% of the total number of seedlings. Red alder (*Alnus rubra* Bong.), bigleaf maple (*Acer macrophyllum* Pursh), and bitter cherry (*Prunus emerginata* (Dougl. ex Hook.) D. Dietr.) also grew on the majority of sites. But California laurel (*Umbellularia californica* (Hook. & Arn.) Nutt.), western white pine (*Pinus monticola* Dougl. ex D. Don), and incense cedar (*Calocedrus decurrens* (Torr.) Florin) were found on few sites and not in both experiments.

Regeneration on most sites was dominated by shade-tolerant species (see Table 2 for composition of shade-tolerance classes). In the DMS, western hemlock was the dominant species, comprising nearly three fourths of the seedlings, followed by Douglas-fir with 13%. Despite their differences in numbers, the spatial distribution of these two species was similar, as shown by the seedling densities and proportion of plots within the sites that contained regeneration (Table 2). Both species grew on every DMS site and in nearly half of all plots. Bigleaf maple and Pacific madrone (*Arbutus menziesii* Pursh) were the most abundant hardwoods, comprising approximately 3% each. Species patterns were different in the YSTDS: Bigleaf maple was the most abundant species, comprising

TABLE 3. Regeneration density (average number of seedlings per hectare) on DMS and YSTDS sites

	DMS								YSTDS				
	P	Bottomline	Delph Creek	Green Peak	Keel Mountain	North Soup	OM Hubbard	Ten High	*P*	Christy Flats	Cougar Reservoir	Mill Creek	Sidewalk Creek
Intolerant	0.233	230	285	861	250	361	470	652	0.058	2444	237	438	1168
Tolerant	0.001	10a	5682b	26a	2455ab	433a	495a	584a	0.035	470a	1453ab	4948b	2762ab
Total	0.005	240a	5967b	887a	2705ab	794a	965a	1236a	0.245	2914	1690	5386	3930

Note. Numbers with different letters indicate significant differences at $P \leq .05$.

TABLE 4. Regeneration density (average number of seedlings per hectare) and species richness (average seedling species numbers) within DMS and YSTDS treatments (see Table 1 for treatment abbreviations)

	DMS					YSTDS				
	P	CON	HD	MD	VD	*P*	CON	LT	HT	GAP
Seedling density										
Intolerant	0.070	68	530	458	596	0.479	167	1096	1193	1574
Tolerant	0.414	169	1211	1950	1813	0.639	1588	3928	3010	1750
Total	0.251	237	1741	2408	2409	0.348	1755	5024	4203	3324
Species richness										
Intolerant	0.000	0.6a	2.1b	2.9b	2.6b	0.999	5.5	5.8	5.5	5.5
Tolerant	0.001	2.4a	3.7ab	5.3b	4.9b	0.272	2.0	2.8	2.5	3.5
Total	0.000	3.0a	5.9b	8.1c	7.4bc	0.915	7.5	8.5	8.0	9.0

Note. Numbers with different letters indicate significant differences at $P \leq .05$.

roughly one third of the total seedlings and was followed by western hemlock, Douglas-fir, and bitter cherry (all around 15%). Spatial patterns, however, were similar to the DMS for western hemlock and Douglas-fir: These species were found on all sites and half of all plots in the YSTDS. On the other hand, bigleaf maple, bitter cherry, and western redcedar regenerated on approximately 25% of all the plots and on at least three of the four YSTDS sites.

Plots with the highest seedling densities were dominated by regeneration of western hemlock (DMS and YSTDS), bigleaf maple (YSTDS), or bitter cherry (YSTDS). Generally, seedlings of shade-tolerant species were more common. The Christy Flats site in the YSTDS was an exception because it contained a large amount of shade-intolerant bitter cherry in the overstory (Table 3).

Comparison of Thinning Treatments

Thinning resulted in significantly higher seedling densities than found in the controls, but thinning treatments did not differ significantly from each other. Treatment patterns were consistent for both experiments (Table 4). Both shade-intolerant and shade-tolerant species groups had greater seedling densities in thinned treatments than in controls, even though the differences were never significant. Although shade-intolerant seedling numbers increased with thinning intensity, and density of shade-tolerant species peaked in treatment units with medium overstory densities, these trends were not significant and consistent across all sites. The coefficient of variance at the plot level in the DMS ranged from 166% to 563%, while values varied between 118% and 364% for YSTDS. Throughout the study, variability of seedling densities was high. For example, low seedling densities for species from both shade-tolerance classes were not limited to the controls, but were found on various sites and treatments in both experiments. On the other hand, high regeneration numbers only appeared in thinned units.

The diversity of regenerating tree species was higher in thinning treatments. In the DMS, significantly higher species numbers were found in thinned units for both shade-tolerance classes (Table 4). On average, twice as many species regenerated in thinned units compared to the control. In the YSTDS, differences in seedling densities between thinned and unthinned stands were less pronounced. They were limited to shade-intolerant species and not statistically significant.

Patterns of Species Composition

Analysis of species composition through determination of structural regeneration groups revealed consistencies and similarities within and among both experiments. CA and ISA identified several structural regeneration groups in both experiments (Table 5):

- Groups D-1 and Y-1 are dominated by Douglas-fir and bigleaf maple, in conjunction with a high seedling density of giant chinquapin (*Chrysolepis chrysophylla* Dougl. ex Hook.).
- Groups D-3 and Y-3 are defined by bigleaf maple as indicator species and higher seedling densities of cascara (*Frangula purshiana* (DC.) Cooper) and Douglas-fir.
- Groups D-4 and Y-4 have western redcedar as the major indicator species and western hemlock has the second-largest indicator species values.
- Groups D-5 and Y-5 are characterized by western hemlock as the only regenerating species.

Structural groups D-2, D-7, Y-2, and Y-6 were each limited to one of the two studies and within studies generally limited to one or two sites. These groups were defined by species that were relatively rare and limited in occurrence (Table 5). The majority of the structural groups were associated with specific sites, rather than a specific treatment, affirming that they were mainly determined by local site characteristics. On the other hand, species composition of D-3, D-6, D-7, and Y-3 showed structural characteristics that could be linked to higher disturbance intensities. They were defined by high seedling densities of cascara, bigleaf maple, red alder, or bitter cherry. Plots of these groups were not restricted to heavily thinned units; however, despite these species needing greater canopy and ground disturbances to regenerate.

Additionally, CA dendrograms (not shown) suggested that several groups can be combined into higher ranking meta-groups. One DMS meta-group (D-I) includes D-1, D-2, and D-3, and the second meta-group (D-II) consisted of D-4 to D-7. Similarly, YSTDS meta-group Y-I consisted of Y-1 and Y-2, while Y-II comprised Y-3 to Y-6. Evaluation of ISA results revealed that the meta-group types are distinguished by their proportions of the two major coniferous species. D-I and Y-I had high densities of Douglas-fir and comparatively small amounts of western hemlock seedlings, while the hemlock-dominated meta-groups D-II and

TABLE 5. Indicator species and average number of seedlings per hectare for each structural group

Species	Group	DMS							YSTDS					
		D-1	D-2	D-3	D-4	D-5	D-6	D-7	Y-1	Y-2	Y-3	Y-4	Y-5	Y-6
	n	101	36	64	43	75	58	56	78	45	83	44	30	55
Shade-intolerant														
Bitter cherry		0	0	0	*0*	*0*	**192**	0	*869*	**1895**	61	0	0	293
Douglas-fir		**561**	*257*	255	210	0	181	507	*772*	**1328**	368	157	0	322
Pacific madrone		*93*	**418**	0	0	0	2	0						
Red alder		4	3	0	*17*	*0*	23	**293**						
Western white pine									*0*	**117**	3	0	0	0
Shade-tolerant														
Bigleaf maple		*28*	*0*	**353**	14	0	19	20	*289*	0	**4204**	0	0	397
Cascara buckthorn		1	0	*93*	0	0	**234**	0	0	31	**507**	*0*	*0*	4
Giant chinquapin		**136**	*31*	15	17	0	2	0	124	72	116	*0*	0	**1304**
Grand fir		*55*	**878**	2	0	0	4	0						
Incense cedar									0	0	**125**	0	*0*	0
Pacific yew									0	0	42	*0*	0	**347**
Western red cedar		1	0	0	**264**	0	*45*	0	206	56	36	**951**	0	*819*
Western hemlock		397	3	160	*1367*	**1847**	*6192*	3005	442	102	886	*1118*	**950**	681

Note. Maximum indicator values for each species are highlighted in bold type, second largest indicator values are highlighted in underlined italic.
n = number of plots.

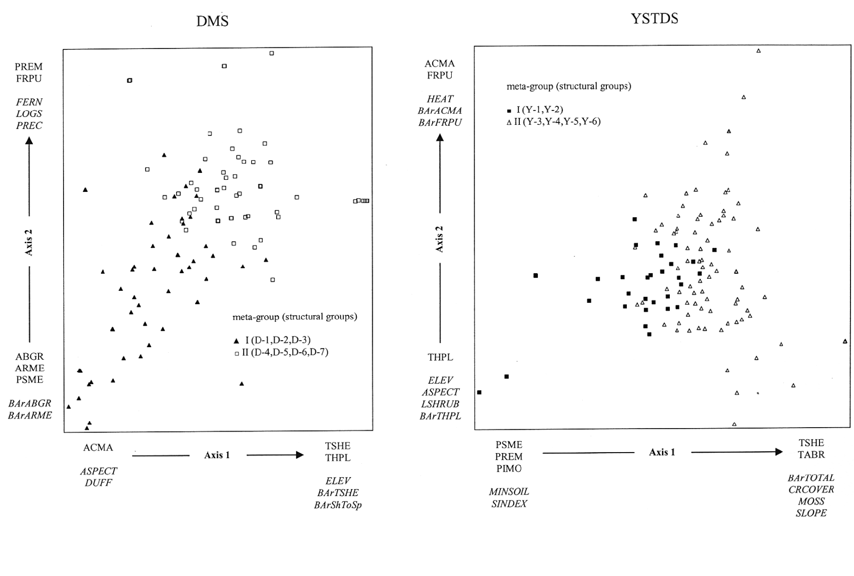
Y-II show the inverse ratio of both species (Table 5). In addition, western redcedar is indicative of meta-group II.

Factors Influencing Regeneration Patterns

NMS and classification tree analysis confirmed the expected strong influence of the residual overstory trees on tree regeneration. On the DMS sites, the seedling density was almost exclusively related to mature tree density and composition. Even in the YSTDS, where they were more important, environmental variables linked to climate and geography generally had inferior predictive power than those related to overstory features.

Pearson's *r*-correlation coefficients of NMS axes and seedling species frequency (converted into Beals probability of occurrence) were high, reaching maximum values over 0.8 in both solutions. In contrast, predictor variables correlated to a much lesser extent with the NMS axes. The best correlations of both variable classes are displayed in Figure 1. In consideration of these best correlations, NMS revealed structural gradients within the samples of both experiments. Axis 1 of the DMS solution corresponded to a gradient of decreasing light and temperature from left to right. DMS

FIGURE 1. NMS graphs of DMS and YSTDS datasets. Overlaying meta-group type based on structural groups identified by Cluster Analysis. See Tables 1 and 2 for list of regeneration species and environmental predictor (in italic) variables.



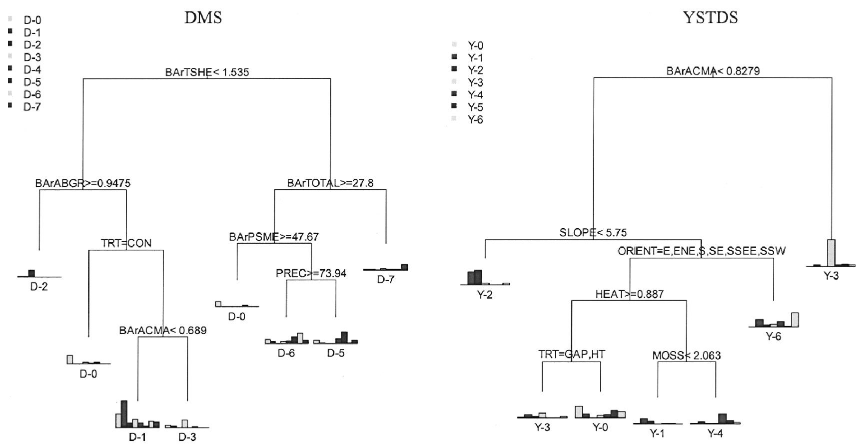
axis 2 was correlated with variables indicative of a moisture and disturbance gradient. YSTDS solution axis 1 could be defined as a gradient for increasing light and moisture stress from left to right, and axis 2 corresponded to a gradient of increasing temperature and disturbance. Axis 1 explained 54.7% and 45.3%, while axis 2 represented 36.4% and 46.2% of the variation of the DMS and the YSTDS solution, respectively.

As indicated by ISA, overlaying Douglas-fir and western hemlock abundance on the NMS graphs (Figure 1) subdivided both scatterplots. Both meta-groups were clearly separated in both experiments. Meta-groups D-I and Y-I, with a higher Douglas-fir/western hemlock ratio, were on the left side of the respective graphs, indicating species preferences for light and disturbance conditions. Meta-groups D-II and Y-II, with a lower Douglas-fir/western hemlock ratio, were found on right portion of the NMS graphs, indicating species preferences for shady and cool-humid conditions. A high density of one of these species was correlated with low proportion of the other one on the same plot. Plots with a much more equal but lower density of both species existed in both experiments nonetheless.

Final classification trees supported the notion of structural groups, as identified by CA (Figure 2). This analysis included additional groups (D-0 and Y-0) without any regeneration. At the first split of both classification trees conspecific, overstory basal area of the most common seedling species was identified as the most important distinction variable. The basal area of overstory trees was the most important element to define the composition of regeneration. The majority of plots without any tree regeneration was linked to high overstory basal area, as found in the control and low intensity thinning units. Other lower level predictor variables used as splitting criteria reflected environmental factors, such as sun radiation and moisture stress (orientation, slope, heat) and water availability (precipitation, moss).

Compared to the null model, the misclassification rate improved for both final trees (null = 78% and 77%, final model = 54% and 48% for DMS and YSTDS, respectively). Misclassification rates of individual structural groups were mostly similar to the percentage of the overall trees. But groups D-1, Y-0, Y-2, and Y-3 had distinctly lower rates, averaging just 21%. Despite being identified as compositionally distinctive by CA and ISA, groups D-4 and D-7, as well as Y-1 and Y-5, were commonly misclassified. Even plots in these groups were mistakenly classified into groups within the same meta-group class (data not shown). Only plots of Y-5 did not match this trend. The frequent misclassification of Y-5 plots

FIGURE 2. Pruned classification trees for Cluster Analysis identified structural groups of plots with (D-1 to D-7 and Y-1 to Y6) and without (D-0 and Y-0) regeneration on environmental predictor variables for DMS and YSTDS. Terminal nodes show predicted structural group distribution resulting from splitting criteria chain, as well as the name of the most abundant group within each distribution. Each split is labeled with its predictor variable and splitting value. Variables appearing near the top of the tree are more important than variables invoked lower in the tree. The vertical distance between nodes is proportional to the amount of variation explained by the predictor variable associated with the split.



into the Y-0 group was indicative of the similarity of environmental conditions between plots dominated by western hemlock (Y-5) and plots without any regeneration (Y-0).

DISCUSSION

In contrast to shelterwood and seed tree cuts and their usually distinctly lower residual densities, thinning is traditionally not aimed at tree regeneration (Smith et al., 1997) and the dearth of information on the topic reflects this. Our study covered a wide range of geographical conditions and thinning treatments in western Oregon and showed that thinning homogenous young second-growth Douglas-fir stands can lead to dense and diverse tree regeneration. Regeneration patterns are highly variable; however, especially when overstory treatments are designed to enhance structural complexity, as in these studies. Highly variable seedling densities appear to be an inherent feature of natural regeneration (Buermeyer & Harington, 2002; Chan et al., 2006; Franklin, 1963; Gerstein, 1999; Shatford, Hibbs, & Puettmann, 2007), not only in Douglas-fir dominated stands (Daniels, 1978; Fiedler, McCaughey, & Schmidt, 1985; Graney, 1989; Rudolph & Lemmien, 1976; Seidel & Head, 1983; Wickman, Seidel, & Starr, 1986). Thinning resulted in average seedling densities that are considered too high in managed forests, but they were highly variable and irregularly distributed. In both experiments, heavily stocked regeneration plots were found in the same sites as plots without any seedlings. Reforestation stocking rules of the Oregon Forest Practices Act (Oregon Department of Forestry, 1994) require reestablished Douglas-fir stands seedling densities of at least 500 ha^{-1}. Even when considering conifer and hardwood species together, half of all DMS plots and one fifth of the YSTDS plots had tree seedling densities lower than this standard. As expected, the majority of these inadequately stocked plots were in control units (Chan et al., 2006). Other studies within the same region also reported consistently lower seedling densities and frequencies in areas with a high overstory tree density after homogenous (Bailey & Tappeiner, 1998) and selection thinning (Miller & Emmingham, 2001).

In both experiments, thinning greatly influenced regeneration patterns, but the actual thinning intensity had little influence on tree regeneration. Where similar results have been observed for understory vegetation patterns in the YSTDS (Beggs, 2005) and the DMS (Berryman, Fahey, & Puettmann, 2005), other long-term retrospective studies found higher seedling densities in stands with lower residual densities (Bailey & Tappeiner, 1998; Miller & Emmingham, 2001). This apparent contradiction may be because only 5 to 7 years had expired between treatment implementation and regeneration measurements in our studies. Early establishment is influenced by seed availability and dispersal (Brokaw & Busing, 2000; Clark, Macklin, & Wood, 1998; Keeton & Franklin, 2005), seed size (Leishman & Westoby, 1994; Schupp, 1995), and fine-scale microsite conditions, such as local seedbed conditions (Gray & Spies, 1997). These factors are not strongly impacted by differences in resource levels found under various overstory densities, such as light and moisture regimes and microclimate conditions. On the other hand, resource and microclimate differences influence growth and mortality of seedlings over time (Brandeis, Newton, & Cole, 2001; Puettmann & Saunders, 2000;). Thus, impacts of varying overstory densities may only be detectable after a longer period.

Species composition of seedlings showed patterns that provide insights into regeneration patterns of Douglas-fir dominated forests in the Pacific Northwest. The dominance of Douglas-fir and western hemlock became apparent, not only in overall seedling numbers and frequencies. These two species were also responsible for separating the meta-groups, while rare species were responsible for the distinction of regeneration groups. Our results revealed and verified the value of the ratio of Douglas-fir and western hemlock (and western redcedar) densities in representing regeneration patterns in west-side Douglas-fir forests (Larson & Franklin, 2005). It has been hypothesized that partially because of larger seeds, Douglas-fir establishment is less sensitive to microsite conditions, resulting in a commanding role of this species within early regeneration of thinned conifer forests in the Pacific Northwest (Bailey & Tappeiner, 1998; Gray & Spies, 1997; Hemmond, 1969; Witler, 1975). As predicted and described by Hansen et al. (1995) and Larson and Franklin, our results show that regeneration of shade-tolerant western hemlocks and redcedars increases with overstory density and lower drought stress, thereby replacing Douglas-fir as dominant regenerating species.

Especially in thinned stands, the overall species diversity of the seedlings was surprisingly high, given that the study sites were selected to represent "homogenous" Douglas-fir stands (Beggs, 2005; Cissel et al., 2006). Thinning prescriptions encouraged leaving rare species and overstory species composition, especially the presence of rare species, was reflected in regeneration patterns in the thinned stands. These trends are apparently not limited to conifer stands and are also found in thinned conifer-hardwood forests (Shelton, 1997) and mixed hardwood stands (Minckler & Woerheide, 1965). In our study, the impact of rare overstory species was not only evident for shade-tolerant conifers (Miller & Emmingham, 2001), but also light-demanding hardwoods.

Mature trees of shade-tolerant coniferous species (primarily western hemlock and western redcedar) are especially uncommon in managed young second-growth forests, suggesting that seed sources are a limiting factor for regeneration of these species (Beach & Halpern, 2001; Gray & Spies, 1996; Keeton & Franklin, 2005; Schrader, 1998). We found that even a small number of seed-producing trees of these species can change regeneration patterns dramatically (Bailey & Tappeiner, 1998). Based on similar findings, Buermeyer and Harrington (2002) concluded that a lack of diversity among reserve trees is the major factor responsible for limited tree species diversity in a naturally regenerated stand 12 years after harvesting. In addition, an increase in proportions of rare species in the overstory is positively related to the proportion of these species in the regeneration layer (Buermeyer and Harrington). Their results and our findings therefore suggest that regeneration composition of apparent "homogenous" stands, such as used in this study, can be influenced by favoring selected rare species during thinning operations. Because seed availability appears to be a major driver, management of seedbed conditions and competing vegetation could be locally important and could be managed to provide conditions for the variety of desired species.

Aside from overstory density and composition, several environmental factors have influenced tree regeneration in this and previous studies. Species-specific drought resistance and tolerance to direct sunlight (as well as fire tolerance) are known to be major determinants of forest composition in the Pacific Northwest (Ohmann & Spies, 1998; Poage & Tappeiner, 2005; Waring & Franklin, 1979; Wimberly & Spies, 2001; Zobel, McKee, Hawk, & Dyrness, 1976). Hence, after seed source and overstory densities, environmental factors related to drought and heat—such as precipitation, aspect, slope, and elevation in our study—were identified as decisive factors, influencing seedling establishment and regeneration patterns (Bever, 1954; Goslin, 1997; Gray & Spies, 1997; Larson & Franklin, 2005; Minore et al., 1982; Zenner, 2000). While commonly a dominant influence in clearcuts or shelterwoods (Bailey & Tappeiner, 1998; Buermeyer & Harrington, 2002; Isaac, 1943; Rose, Ketchum, & Hanson, 1999; Wagner & Radosevich, 1998), shrub and grass cover appear to have less impact on seedling establishment in thinnings (Gerstein, 1999; Miller & Emmingham, 2001) and small gaps (Gray & Spies, 1997). On the other hand, vegetation cover has been shown to facilitate regeneration in exposed portions of larger gaps, mainly through increased germination rates (Gray & Spies, 1997). Shrub cover values in our thinned stands were generally not as high as typically found after clearcutting in the reasons (Rose et al., 1999). In addition, other aspects, such as seed availability, may overshadow competition as a driver of regeneration.

Impacts of environmental factors on natural regeneration patterns are not easily detected. The same site conditions that influence regeneration patterns likely influenced the development of the existing overstory; and overstory composition is, at least partly, reflected in the regeneration (see above). Additionally, microsite controls operating on smaller scales than seed dispersal seem to be secondary to seed source availability, at least after extensive overstory mortality (Keeton & Franklin, 2005). Furthermore, overstory cover often overlays principal environmental influences, modifying and blurring primary growth conditions (Goslin, 1997; Minore et al., 1982; Seidel & Cooley, 1974; Zenner, 2000). Environmental variables, however, were more important in predicting YSTDS regeneration groups. Likely differences in overstory composition, and thus seed availability, were not as prevalent in this study compared to DMS. In addition, the lower resolution of environmental information for major factors in the YSTDS, such as aspect and slope, characterized plots conditions less concisely.

Lastly, our data were limited to short-term conditions (5 to 7 years) and seedlings presence in highly dynamic stands. For long-term stand development, it is important to consider that shade-intolerant species, such as Douglas-fir, red alder, or bitter cherry, need continuously open conditions to ensure growth and survival beyond the seedling stage. Although Douglas-fir has been shown to survive fairly heavy shading for longer periods (Del Rio & Berg, 1979), competing shade-tolerant species—such as western hemlock or redcedar—may replace Douglas-fir as understory trees. Under these circumstances, maintaining shade-intolerant species demands repeated thinnings to ensure a steady and adequately open canopy for continuously sufficient light levels in the understory (Bailey & Tappeiner, 1998; Witler, 1975). In addition, diseases and selective herbivory may further influence species composition and regeneration success (Hobbs, 1996; Weisburg & Bugmann, 2003).

CONCLUSIONS

Natural regeneration appears in thinned Douglas-fir stands, but is highly variable and irregularly distributed leading to a mix of over- and understocked stand portions. While this provides for spatial diversity, it can also be a major drawback when uniform regeneration is desired. The dominant overstory species, Douglas-fir and western hemlock, commonly also dominated the regeneration. However, leaving rare species during thinning operations increased regeneration diversity due to greater seedling species richness. That seemingly applied to shade-tolerant as well as more light-demanding species, at least during the first few years after thinning. While local overstory composition and density was influential on regeneration development, larger scale environmental variable seemed to be less important. Also, shrub and grass competition in thinned stands appeared not to be limiting tree regeneration, as often found in clearcuts in the region.

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