Early responses to thinning treatments designed to accelerate late successional forest structure in young coniferous stands of western Oregon, USA

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Abstract: The loss of critical habitat provided by late successional forests has prompted the search for management options that can accelerate the development of late successional forest structure in young stands. We examined operational-scale commercial thinning treatments at seven sites to evaluate if thinning could accelerate development of late successional forest structures in 40–60 year old Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests. Thinning treatments included an untreated control, high density, moderate density, and variable density retention. All thinning treatments had leave islands, and moderate density and variable density included harvest-created gaps. Thinned units, especially moderate density and variable density, had greater spatial variability in tree density, supported lower live branches, had greater tree regeneration and growth, and had slightly lower mortality relative to the control. Canopy gaps extended the range of stand densities and increased growth of trees immediately along gap edges. However, thinning had little effect on growth of the largest Douglas-fir trees and did little to provide large snags or coarse woody debris. These results suggest that thinning treatments can accelerate some aspects, e.g., spatial variability, of late successional forest structures. Other attributes, such as large trees and snags, may prove less responsive to thinning treatments, at least in the short term. Including tree retention levels lower than typical management applications and formation of canopy gaps provide the wide range of conditions that appears beneficial for developing late successional forest structure.

Résumé : La perte d'habitats critiques associés aux forêts de fin de succession a encouragé la mise au point d'options d'aménagement qui peuvent accélérer le développement d'une structure forestière de fin de succession dans de jeunes peuplements. Nous avons étudié des traitements d'éclaircie commerciale à l'échelle opérationnelle effectués sur sept stations pour évaluer si l'éclaircie pouvait accélérer le développement de structures forestières de fin de succession dans des peuplements de douglas vert (*Pseudotsuga menziesii* (Mirb.) Franco) âgés de 40 à 60 ans. Les traitements d'éclaircie incluaient un témoin non traité et la rétention d'arbres à densité forte, à densité modérée et à densité variable. Tous les traitements d'éclaircie comportaient des îlots non traités et les traitements densité modérée et densité variable incluaient des trouées créées par la coupe. Comparativement aux témoins, les unités éclaircies, particulièrement les traitements densité modérée et densité variable, avaient une plus grande variabilité spatiale de la densité d'arbres, supportaient des branches vivantes plus basses, avaient plus de régénération, une meilleure croissance des arbres et légèrement moins de mortalité. Les trouées dans la canopée augmentaient l'étendue de la densité des peuplements et la croissance des arbres situés en bordure. Toutefois, les éclaircies ont eu peu d'effet sur la croissance des plus gros douglas vert et produisaient peu de gros chicots et de débris ligneux grossiers. Ces résultats indiquent que les traitements d'éclaircie peuvent accélérer certains aspects associés aux structures forestières de fin de succession, comme la variabilité spatiale. D'autres attributs, comme les gros arbres et les gros chicots, semblent peu sensibles aux traitements d'éclaircie, du moins à court terme. Des niveaux de rétention d'arbres inférieurs à ceux qui sont associés aux pratiques typiques d'aménagement et la formation de trouées dans la canopée produisent une vaste gamme de conditions qui semblent bénéfiques au développement d'une structure forestière de fin de succession.

[Traduit par la Rédaction]

Introduction

Forest structure influences habitat availability, biodiversity, and disturbance regimes with direct implications for a variety of ecosystem processes and functions (Spies 1998; Puettmann et al. 2009*a*). This recognition has led to widespread efforts to restore structural features in forests throughout the world that have been altered by anthropogenic activities (e.g., Muir et al. 2002; Carey 2003). In many regions, the extent of late successional forests has been reduced by disturbances such as large-scale harvesting resulting in younger stands that lack many structural elements critical for wildlife habitat and bio-

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Table 1. Site characteristics of the seven study sites in the Density Management Study in western Oregon (for more details, see Cissel et al. 2006).

Site	Mean annual precipitation (cm)	Elevation (m)	Ecoregion*	Thinning year	Stand age at thinning (years)	Control mean live basal area year 11 (m^2/ha)	Control mean live trees/ha, year 11
Delph Creek	194	553–725	Cascades	2000	53	71.4	510
Keel Mountain	182	576–798	Cascades	1997	44	75.7	556
Green Peak	195	514–738	Coast Range	2000	56	65.4	438
Ten High	219	430–710	Coast Range	1999–2000	44	69.8	666
O.M. Hubbard	135	341–798	Coast Range	1997	39	47.9	773
North Soup	168	162–426	Coast Range	1998	48	56.5	384
Bottomline	126	210–528	Willamette Valley	1997	55	43.9	373

*According to Thorson et al. (2003).

diversity (Berg et al. 1994; Franklin et al. 2002). Thinning has been widely proposed to reverse this trend and accelerate the development of late successional forest conditions in young managed stands (Carey 2003; Bauhus et al. 2009). However, balancing multiple management objectives may involve complex trade-offs (Franklin et al. 2002), highlighting the need for a better understanding of alternative thinning treatment effects. We examined short-term responses to operational-scale thinning treatments with varying levels of retention and spatial patterns. Specifically, we were interested in measures that assess the potential of these treatments to accelerate the development of late successional forest characteristics in young even-aged homogenous stands.

Accelerating the development of late successional forest structure in young stands will require creating specific structures (e.g., large trees) and promoting vertical and horizontal heterogeneity within the stand (Berg et al. 1994; Zenner 2004). Late successional forests often have multiple canopy layers, a wide range of tree sizes, large live trees, large snags, and abundant coarse woody debris (Franklin et al. 1981; Spies et al. 1988). They also have considerable structural variability with canopy gaps and areas of high tree density (Franklin et al. 1981; Spies et al. 1988). In contrast, young managed stands are often structurally simple with relatively uniform tree sizes, even spacing, few species, and live branches concentrated in the upper canopy (Christensen and Emborg 1996; Franklin et al. 2002). Under natural processes, late successional structure can take 100–200 years or longer to develop (Franklin et al. 1981, 2002). Consequently, many current management activities are based on the assumption that thinning will accelerate development of late successional structures through immediate changes due to tree removal and subsequent changes in environmental conditions that affect key processes such as growth, regeneration, crown development, and tree mortality.

We evaluated whether thinning treatments specified by leave tree densities of varying spatial complexity could move stand structure towards conditions typically found in late successional forests. We give special attention to hardwood species, which have been discriminated against as part of reforestation practices but which provide important habitat for many species in Pacific Northwest conifer forests (e.g., Hagar 2007; Betts et al. 2010). Specifically, we evaluated if thinning affects (*i*) variability in tree density, (*ii*) canopy complexity (expressed in tree diameter distributions, height to the base of the live crown, and tree regeneration), (*iii*) tree growth, especially for the largest trees and trees on the edges of gaps, and (*iv*) tree mortality.

Methods

Study sites

The Density Management Study was initiated in 1994 to evaluate the efficacy of alternative thinning treatments at accelerating late successional conditions in young forest stands that regenerated after heavy harvesting (Cissel et al. 2006). Seven study sites were located in areas managed by the Bureau of Land Management in western Oregon (Cissel et al. 2006). Sites were located in three ecoregions (Thorson et al. 2003): the Coast Range (four sites), the foothills of the Willamette Valley (one site), and the western slopes of the Cascade Mountains (two sites) (Table 1). Mean annual precipitation at the study sites ranges from 135 to 219 cm with dry summers and wet winters (Cissel et al. 2006). Sites were selected based on the presence of relatively homogenous contiguous forest with a minimum size of around 80 ha and conifer dominance, primarily Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), with tree ages ranging from 40 to 60 years at the time of thinning (Table 1). Common conifer tree species included Douglas-fir, western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and western redcedar (*Thuja plicata* Donn ex D. Don). Western hemlock and western redcedar were more common in the Cascade sites than in the Coast Range sites. Hardwood trees were a relatively minor component of the stands and species composition varied considerably among the sites. Common hardwoods included bigleaf maple (*Acer macrophyllum* Pursh), red alder (*Alnus rubra* Bong.), beaked hazel (*Corylus cornuta* Marsh.), Pacific madrone (*Arbutus menziesii* Pursh), Cascara buckthorn (*Frangula purshiana* (DC.) Cooper), and giant chinquapin (*Chrysolepis chrysophylla* (Dougl. ex Hook.) Hjelmqvist). Several sites had been thinned, fertilized, or both 20–40 years prior to selection for this study, thus representing a large range of site conditions typical for the region. A comprehensive overview with individual site histories is provided in Cissel et al. (2006).

Treatments

Treatments were applied to large areas to avoid the need to scale up from experimental plots to operational scales. They were implemented in a randomized block design with operational limitations constraining treatment randomization at a few sites (Cissel et al. 2006). However, based on the site selection criteria and the variety of sites, there is no reason to believe that treatment assignment led to biased results. One replication of each of four thinning treatments (including controls) was applied at each of seven sites for a total of 28 treatment units. Nonthinned control units ranged in area from 16 to 25 ha. Thinning areas ranged from 14 to 58 ha for individual treatment units. The high-density (HD) treatment was thinned to a residual stand density of 300 trees/ha with 3%–13% of the total stand retained in nonthinned circular reserves of different sizes. In the moderate-density (MD) treatment, stand density was reduced to 200 trees/ha. Additionally, 4%–18% of the stand was cut in circular gap openings and 4%–13% of the stand was left in nonthinned 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 HD (300 trees/ha) and MD retention (200 trees/ha) treatments each applied over 25%–30% of the stand and an additional 8%–16% of the stands were thinned to a residual density of 100 trees/ha. Finally, 4%–18% of the stand was left in leave islands and gap openings. Gaps and leave islands in all treatments were a mixture of 0.1, 0.2, and 0.4 ha circular areas. Thinning was completed between 1997 and 2000. All thinning was "from below" focusing on taking out the smaller trees. Subordinate species, especially hardwoods, were preferentially reserved.

Data collection and summarization

Seventy-seven permanent 0.1 ha circular plots were established at each of the seven sites to measure overstory trees. Plot locations were randomly selected across the entire treatment unit including gaps and leave islands with 21 plots in each thinned treatment unit and 14 plots in each control treatment unit at each site. At least part of a plot fell in a leave island about 13% of the time in the HD and MD and about 10% of the time in the VD. About 22% of the plots in the MD and 29% of the plots in the VD included at least a portion of a gap. 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 understory vegetation, including seedlings and saplings. All trees >5 cm diameter at breast height (DBH) were tagged, identified to species, and measured for DBH on the 0.1 ha plots. Clumped hardwood trees were measured as separate trees provided their DBH was >5 cm. Total tree height and height to the live crown were measured on a subset of trees, 10 conifers and six hardwoods per plot, if present. Where more trees in each group were present, trees were sampled systematically to reach the total (e.g., on a plot with 100 conifers every 10th tree was sampled). Height to the live crown was defined as the point where live branches covered at least two thirds of the tree bole. 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. Data were collected in the summer 6 years after thinning (2003–2005) and 11 years after thinning (2008–2010) with sample years varying among sites.

Trees on the edges of gaps were identified in plots that contained at least a portion of a gap. For these plots, tree locations were graphed by their azimuth and distance from the plot center. Gap trees were defined as those with an entire side directly adjacent to the gap with no intervening trees. All species and sizes were included.

Statistical analyses

Prior to analyses, we selected a threshold of $P = 0.05$ for determining statistically significant effects. All analyses were performed in SAS version 9.2 (2008) (SAS Institute Inc., Cary, North Carolina). No pretreatment data were available; therefore, treatment effects are assessed by comparison with the nonthinned control treatments. Because hardwood species were relatively rare and species composition varied considerably among sites, all hardwood species were combined for analyses in this study. Residuals were evaluated for all models to ensure that assumptions of normality, equal variance, and independence were not violated. Square root transformations were applied where needed to meet assumptions. Where significant treatment effects were found, post hoc tests were conducted between each combination of individual treatments with a Tukey correction for multiple comparisons.

We compared basal area (BA), trees per hectare (TPH), and quadratic mean diameter (QMD) among treatments in both year 6 and year 11 using a mixed model approach (Littell et al. 2006) with treatment as a fixed factor and site as a random factor. Hardwoods and all species were evaluated separately. Treatment effects on stand BA growth and the change in TPH for all species from year 6 to year 11 were also evaluated with a mixed model. Data were averaged to the treatment unit level prior to analysis (n = 28 treatment

Table 2. Average stand characteristics for each treatment 6 and 11 years after thinning.

	Live basal area (m^2/ha)		Live trees/ha		Quadratic mean diameter (cm)	
Treatment	Year 6	Year 11	Year 6	Year 11	Year 6	Year 11
All species						
Control	59.0a	61.3a	599a	531a	35.4	38.4
HD	43.8b	47.0b	344b	329b	40.3	42.7
MD	33.3c	36.0c	291b	294b	38.2	39.6
VD	32.0c	34.8c	257b	261b	39.9	41.1
Hardwoods						
Control	1.8	1.7	28	24	29.0	30.0a
HD	1.1	1.1	36	33	20.1	20.1ab
MD	1.5	1.3	42	47	21.2	18.8ab
VD	0.9	0.8	32	34	18.8	17.3b

Note: Different letters indicate significant differences among treatments ($P < 0.05$).

units). A square root transformation was needed to meet assumptions for all species QMD.

We compared the standard deviation in live BA and TPH among treatments 11 years after thinning to evaluate treatment effects on structural heterogeneity. Standard deviations were calculated for each treatment unit from the plots within that unit (14 plots for controls, 21 for thinned treatments). A mixed model was used to compare treatments with thinning treatment as a fixed factor and site as a random factor. Values were weighted based on the number of plots in a treatment unit to account for fewer plots in the control.

We analyzed DBH distributions, height to the base of the live crown, and regeneration (seedlings, saplings, and ingrowth) to evaluate treatment effects on canopy complexity. DBH distributions where analyzed by calculating the number of live TPH for each treatment 11 years after thinning in 10 cm size classes (and an additional class for trees over 70 cm DBH). A contingency table was constructed with the four treatments and seven DBH classes. A χ^2 test was performed to determine if distributions were significantly different among treatments. Due to the large number of trees, all cells had sufficient expected values (>5) to meet assumptions.

Thinning effects on average height to the base of the live crown, density of seedlings, saplings, and in-growth (small trees that were not above the 5 cm diameter cutoff at year 6 but were sampled in year 11) were evaluated 11 years after thinning using a mixed model with data averaged to the treatment unit level ($n = 28$ units). A mixed model was employed with site as a random effect and thinning treatment as a fixed effect. Height to the base of the live crown was compared separately for all species and Douglas-firs only. Regeneration was evaluated for both all species and hardwoods alone.

Treatment effects on plot-level presence or absence of seedlings, saplings, and in-growth were evaluated with logistic regression (PROC GLIMMIX, SAS version 9.2). The number of plots with seedlings, saplings, or in-growth was modeled as the number of "successes", while the total number of plots in each treatment unit was considered the number of trials. Treatment was modeled as a fixed effect and site as a random effect.

Thinning effects on tree growth were analyzed at the individual tree level with a mixed model approach. The analysis focused on trees that were alive and sampled in both post-thinning year 6 and year 11 and frequent species (Douglas-fir, western hemlock, and hardwoods). The change in DBH from year 6 to year 11 was used as the growth response variable. An analysis of BA increment found similar results (data not shown). Initial DBH in year 6 was treated as a covariate with species and treatment as fixed factors. Preliminary analyses and inspection of residuals revealed that a linear effect worked well for approximating the relationship between initial tree size and diameter growth with the data from the young stands. All possible interactions were included in the model. Whether or not a tree was adjacent to a gap (yes or no) was also included as a fixed factor but not included in interactions due to the limited number of trees on the edges of gaps. Site and plot were included as random factors to account for hierarchical nesting of trees with a variance components covariance matrix structure.

We compared height growth among treatments on the subset of live trees with height measured in both years. Height growth was averaged to the treatment unit level and compared with a mixed model with treatment as a fixed effect and site as a random effect. No significant differences were found among treatments ($P = 0.25$). Therefore, we focus on the results and discussion of diameter growth.

The mortality rate was calculated for the 5-year sampling period for each treatment unit as the number of trees that died between the first and second measurements divided by the total number of trees present at the first measurement. We compared mortality rates among treatments using a mixed model with thinning treatment as a fixed effect and site as a random effect. The number of trees dying in each treatment was calculated for each of the major species (Douglas-fir, western hemlock, and hardwoods) in 10 cm DBH classed for a visual representation of snag formation.

Results

As expected, thinning treatments had significantly lower BA and TPH than the control both 6 and 11 years after treatment (Table 2). The MD and VD were not statistically different for any stand variables although both had significantly lower BA than the HD (Table 2). QMD did not significantly vary among treatments. Hardwoods comprised a very small fraction of the total BA (2%–5%) and slightly more of the total TPH (5%–16%) in each treatment (Table 2). Hardwood BA and TPH did not significantly differ among treatments in

Fig. 1. Boxplots of (*a*) basal area and (*b*) trees per hectare for each of the four treatments 11 years after thinning. The center line represents the median, the lower and upper edges of the box the 25th and 75th percentiles, respectively, and the error bars the 10th and 90th percentiles. CON, control; HD, high density; MD, moderate density; VD, variable density.

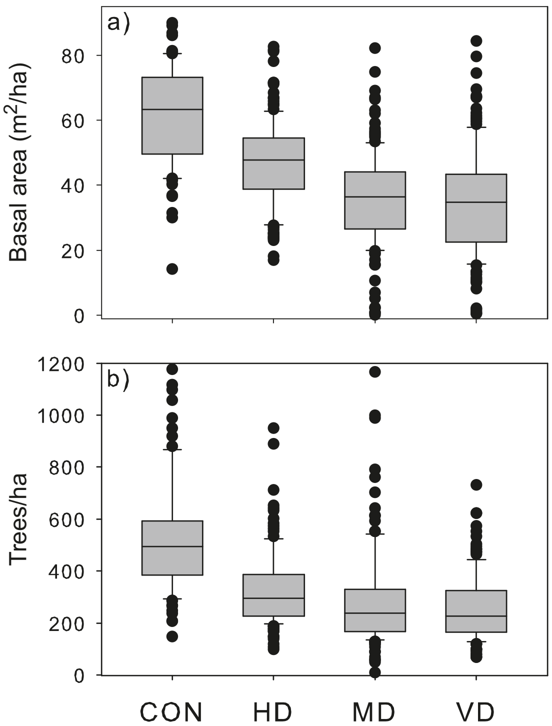


Fig. 2. Live tree diameter at breast height (DBH) distribution in each treatment 11 years following thinning application. CON, control; HD, high density; MD, moderate density; VD, variable density.

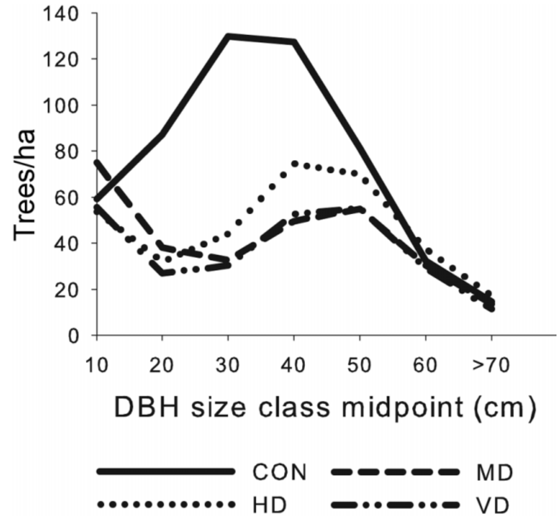


Table 3. Type III tests of fixed effects for comparisons among treatments for seedlings, saplings, and in-growth trees.

Variable	*F*	*P*
Seedling density*	8.69	**<0.001**
Hardwood seedling density	5.83	**0.006**
Sapling density*	6.36	**0.004**
Hardwood sapling density*	4.49	**0.016**
In-growth density*	6.02	**0.005**
Hardwood in-growth density*	1.33	0.294
Seedling probability	14.44	**<0.001**
Hardwood seedling probability	6.34	**0.004**
Sapling probability	7.26	**0.002**
Hardwood sapling probability	5.76	**0.006**
In-growth probability	11.04	**<0.001**
Hardwood in-growth probability	5.83	**0.006**

Note: Significant effects are bolded. Each test had 3 numerator degrees of freedom and 18 denominator degrees of freedom.

*Square root transformed to meet assumptions.

either year (Table 2). Eleven years following thinning, the control had a significantly higher QMD than the VD, although there was no significant difference 6 years following thinning (Table 2). A single atypical plot in one control treatment dominated by hardwoods contributed heavily to the larger tree size in the control.

While total stand BA was higher in the control, stand BA growth from year 6 to year 11 was not significantly different among treatments ($P = 0.59$). Mortality exceeded in-growth (trees that grew to >5 cm DBH) in control and HD treatments, while in the VD and MD, in-growth exceeded mortality. However, there were no significant treatment differences in the change in TPH from year 6 to year 11.

Stand heterogeneity

The large spatial scale of the experimental units was reflected in high variability in tree density on individual plots in all treatments (Fig. 1). For example, density in the controls ranged from 148 to 1206 TPH and from 14 to 90 m^2/ha of BA (Fig. 1). Variability was high both within and among sites. Individual control treatment units averaged from 44 to 76 m^2/ha in BA (Table 1). Within individual control treatment units, plots varied by as much as 45 m^2/ha for BA and 700 TPH.

Thinning significantly affected variability, expressed as standard deviation, in BA among plots within a treatment unit ($P = 0.012$) but did not affect standard deviations in TPH ($P = 0.329$). Standard deviation in BA was significantly higher in the VD (14.7 m^2/ha) than in the control (9.7 m^2/ha) and the HD (10.7 m^2/ha). The MD (13.0 m^2/ha) was intermediate and not significantly different from any other treatment.

Canopy layering

Thinning increased the spatial variability in canopy conditions, as evidenced by both direct and indirect measures of canopy layering. For example, thinning significantly altered DBH distributions ($\chi^2 = 91$, degrees of freedom = 18, $P <$ 0.001). Small trees (5–15 cm) comprised a larger proportion of the total trees in thinned units relative to controls, while the density of moderate-sized trees (20–50 cm) was reduced with thinning, especially MD and VD. This resulted in bimodal DBH distributions for all thinned treatments, a pattern that was not apparent in controls (Fig. 2).

Thinning significantly affected the density of seedlings, saplings, and in-growth trees for all species and hardwood seedlings and saplings 11 years after thinning (Table 3). In

Table 4. Mean (standard error) seedling, sapling, and in-growth tree density per hectare and probability of sampling a seedling, sapling, or in-growth tree on an individual plot in each treatment 11 years following thinning.

Treatment	Seedlings	Saplings	In-growth trees	Hardwood seedlings	Hardwood saplings	Hardwood in-growth trees
Density per hectare						
Control	502 (244)a	114 (32)a	45 (14)a	90 (51)a	15 (9)a	6 (5)
HD	2719 (717)b	527 (197)ab	146 (39)ab	323 (117)b	202 (81)b	40 (27)
MD	2742 (1309)b	815 (329)b	363 (146)b	217 (67)ab	145 (80)ab	156 (137)
VD	4594 (1883)b	747 (214)b	241 (58)b	260 (87)b	181 (81)b	74 (42)
Probability of occurrence on a plot*						
Control	0.60a	0.41a	0.18a	0.22a	0.04a	0.01a
HD	0.93b	0.51a	0.40b	0.50b	0.16b	0.06a
MD	0.88b	0.59ab	0.47b	0.48b	0.20b	0.09ab
VD	0.90b	0.72b	0.56b	0.44b	0.26b	0.16b

Note: Different letters denote significant treatment differences in pairwise comparisons.HD, high density; MD, moderate density; VD, variable density.

*Probabilities are from logistic regression.

each case, the VD treatment had significantly higher densities than controls (Table 4). The MD treatment had significantly higher densities of seedlings, saplings, and in-growth than the control for all species but not hardwoods. The HD treatment had significantly higher densities of all seedlings, hardwood seedlings, and hardwood saplings than the control, but in-growth did not show this trend (Table 4). Seedling, sapling, and in-growth densities never significantly differed among the three thinning treatments.

Thinning also significantly affected the probability of sampling seedlings, saplings, and in-growth trees for both all species combined and hardwoods (Table 3). In each case, the VD treatment had a significantly higher number of plots with regeneration than the control (Table 4). The probability of sampling a seedling or in-growth for any species or hardwood seedlings and hardwood saplings was significantly higher in the HD and MD treatments than in the control (Table 4). The number of plots with saplings of all species and hardwood in-growth in the VD treatment was higher than in the HD treatment (Table 4).

Height to the base of the live crown was highly variable across the study, e.g., averages on individual control plots ranged from 7.6 to 33.8 m. Despite this variability, thinning resulted in significantly lower crowns for all species ($P \leq 0.001$) and Douglas-firs ($P = 0.001$). For all species, MD (mean of 18.3 m) and VD (17.0 m) had significantly lower live crowns than the control (22.3 m), and VD was also significantly lower than HD (19.7 m). For Douglas-fir, both MD (22.0 m) and VD (21.5 m) had significantly lower crowns than the control (25.8 m). The HD (23.2 m) was intermediate and not significantly different from any other treatment for Douglas-fir.

Tree diameter growth

Diameter growth rates varied among species and were a function of initial tree size. Douglas-fir and western hemlock grew more than hardwoods and larger trees grew more than smaller trees, on average (Fig. 3). Growth rates were highly variable among plots. For example, the average growth of trees on individual control plots ranged from about 0.1 to 1 cm in DBH per year.

Fig. 3. Mixed model estimates for diameter growth for each tree species in each treatment for a range of initial sizes. Sizes displayed for each species are the 5th to 95percentiles of initial diameter at breast height. CON, control; HD, high density; MD, moderate density; VD, variable density.

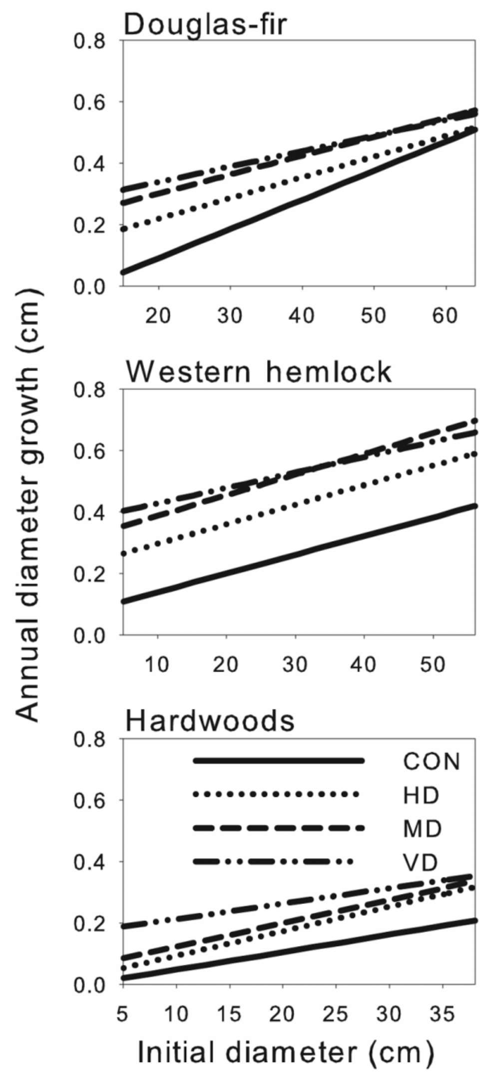


Table 5. Type III tests of fixed effects from the mixed model of diameter growth from 6 to 11 years post-thinning.

Effect	Numerator df	Denominator df	*F*	*P*
Treatment	3	18	9.98	**<0.001**
Initial diameter at breast height (DBH)	1	16 000	431.28	**<0.001**
Initial DBH × treatment	3	16 000	0.35	0.7906
Species	4	16 000	50.01	**<0.001**
Treatment × species	12	16 000	2.18	**0.010**
Initial DBH × species	4	16 000	47.66	**<0.001**
Initial DBH × treatment × species	12	16 000	3.31	**<0.001**
Gap tree*	1	16 000	74.24	**<0.001**

Note: Significant effects are bolded.

*Gap trees defined as trees growing directly on the gap edge, including all species and sizes.

Tree diameter growth response showed expected patterns, with notable exceptions for larger trees and trees adjacent to gaps. Thinning effects varied based on initial diameter and species (significant three-way interaction of species, initial diameter, and treatment; Table 5). Douglas-fir had higher growth in thinned units, especially for smaller trees (Fig. 3). However, large Douglas-firs (>50 cm DBH) grew only slightly more with thinning (Fig. 3). For example, a 25 cm DBH Douglas-fir in the VD averaged more than 250% the diameter growth observed in the control, while a 63 cm DBH Douglas-fir in the VD grew only 8% more than in the control (Fig. 3). In contrast, hardwoods and western hemlocks had higher growth in thinned units regardless of their initial size (Fig. 3). However, Douglas-firs comprised about 86% of the 1000 largest trees in the study (>63 cm DBH). The lower retention MD and VD treatments generally had the highest growth rates (Fig. 3). Trees on the edge of gaps grew significantly faster (about 40%) than trees surrounded by forest (Table 5).

Mortality

Mortality patterns from 6 to 11 years after initial thinning appeared responsive to thinning. A total of 1730 trees died in the 5 years between sampling periods with the highest number of deaths in the control (700) and the least in the VD thinning (230). About 58% of the trees that died were Douglas-firs and nearly one third of the total tree deaths were Douglas-firs <25 cm DBH. Mortality on individual plots within controls was highly variable, ranging from 0% to 40% of trees dying.

Thinning had marginally significant effects on 5-year mortality rates ($P = 0.054$). Average annual mortality rates varied from 1.2% in the VD to 2.2% in the control. Overall mortality in the VD treatment was significantly lower than in the control in pairwise comparisons ($P = 0.036$). The HD (1.5%) and MD (1.7%) treatments were intermediate and not significantly different from any other treatment. Mortality was concentrated in the smaller trees, especially Douglas-firs (Fig. 4). Thinning units had lower mortality for smaller trees, especially Douglas-fir, but had little effect on larger trees (>35 cm DBH), which had low mortality in all treatments (Fig. 4).

Discussion

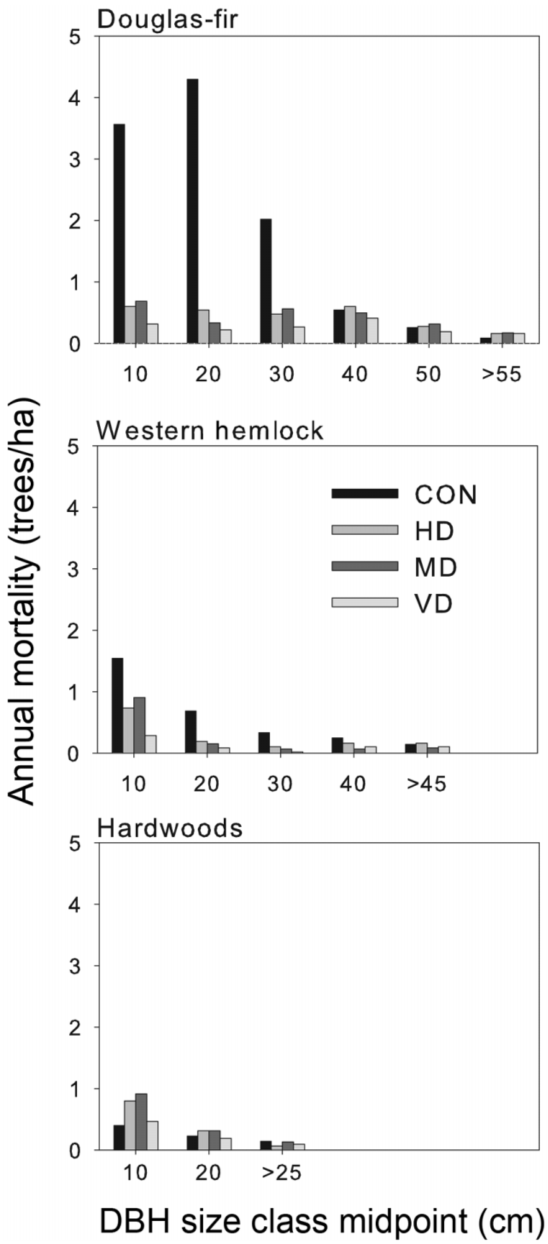
Creating attributes of late successional forest structure in young stands is expected to benefit a variety of species, ecosystem processes, and functions (Bauhus et al. 2009). Within a decade, thinning increased stand variability in BA and canopy layering by facilitating regeneration and slowing crown recession in this study. Thinning also promoted growth of residual trees and habitat diversity as shown by increased regeneration and growth of hardwood species. These changes may translate into habitat for a wider array of species, especially those associated with late successional stand structures. Indeed, other studies have shown that thinning young stands increased diversity or abundance of understory plants (Thysell and Carey 2001), old growth associated lichens (Root et al. 2010), and birds (Hayes et al. 2003), likely in part through modification of forest structure. The operational scale of treatment application and the wide range of site conditions and histories in this study (Cissel et al. 2006) suggest that these results should be generally applicable across a broad range of mesic coniferous forests.

Our results suggest that spatial variability, including gap creation, may have an especially important role in moving young stands toward late successional structure. Gaps are major structural components of many late successional forests but may require centuries to develop without management intervention (i.e., horizontal diversification phase of Franklin et al. 2002). In this study, thinning accelerated the gap creation process and instantly extended the small-scale variability in stand conditions. Gaps additionally may lead to higher diversity of tree sizes and associated canopy conditions, as it leads to increases in tree diameter growth along gap edges, consistent with previous studies (Chen et al. 1992). The open conditions created by gaps and along gap edges may also increase the abundance and diversity of understory species (Fahey and Puettmann 2008), promote seedling establishment (Chen et al. 1992), and provide habitat for late successional species such as epiphytic lichens (Root et al. 2010).

Stand heterogeneity

The role of environmental heterogeneity in maintaining species diversity has been well documented in ecological studies (e.g., Ricklefs 1977; Christensen and Emborg 1996). Species are likely to respond individually to altered environmental conditions created by different levels of thinning (e.g., Thysell and Carey 2001). The increased small-scale heterogeneity in relatively homogenous young forests can provide suitable habitat for a wider variety of species with leave is-

Fig. 4. Annual tree deaths (6–11 years following thinning) in each treatment for 10 cm diameter at breast height (DBH) classes. CON, control; HD, high density; MD, moderate density; VD, variable density.



lands also providing protection for species that are sensitive to thinning (Carey 2003). Creating a variety of stand structures across the landscape by varying levels of density retention (VD) including leave islands and harvest-created gaps could thus provide suitable habitat for many species at a variety of spatial scales (Wilson and Puettmann 2007).

Even the unthinned control stands had considerable variability among individual plots in tree density, height to the base of the live crown, growth rates, average tree sizes, and mortality rates. This contrasts with previous work where young managed stands are often portrayed as homogenous with low variability in tree size and species composition or variability in stand structure (Spies and Franklin 1991; Christensen and Emborg 1996; but see Lutz and Halpern 2006). Processes that create high variability in old stands also may play a role early in stand development (Franklin et al. 2002; Lutz and Halpern 2006). Lutz and Halpern (2006) also documented considerable variability in young stand development and structure in the first few decades following clearcutting. Therefore, silvicultural treatments designed to move stands toward heterogeneous late successional forest structures can be designed to take advantage of high levels of preexisting variability.

Canopy layering

The increase in tree regeneration, longer live crowns, and change in diameter distributions toward a two-storied stand suggest that thinning increased canopy layers. Heterogeneous, multilayered canopies are characteristic of late successional forests (Franklin et al. 1981) and contribute to habitat diversity (Franklin et al. 2002). Thinning often increases tree regeneration (Bailey and Tappeiner 1998; Shatford et al. 2009), thus contributing to the recruitment of lower canopy layers. However, abundant regeneration, especially of shade-tolerant species, may eventually reduce understory species diversity and abundance (Ares et al. 2009). For example, high densities of western hemlock may impede further recruitment of less shade-tolerant species such as Douglas-fir (Shatford et al. 2009). Multiple thinning entries may be necessary to facilitate development of multilayered canopies through continuous recruitment and growth of tree regeneration (Shatford et al. 2009).

While regeneration was similar among the thinning treatments, the heavier thinning in the MD and VD were most effective at slowing crown recession and altering diameter distributions relative to the control. Canopy expansion in residual trees may rapidly reduce light availability, especially with HD retention (Chan et al. 2006; Davis et al. 2007). Increased light availability can slow branch death in the lower canopy (Bailey and Tappeiner 1998; Chan et al. 2006). In species such as Douglas-fir, increased light can also stimulate the growth of epicormic branches, which can become a major component of the total live branches in late successional Pacific Northwest forests (Ishii and Wilson 2001).

Tree growth

Large trees are a hallmark of late successional forests throughout the world and large old Douglas-firs, in particular, provide critical habitat in old forests of the Pacific Northwest (Franklin et al. 1981; Zenner 2004). The results of our study suggest that thinning from below did little to accelerate growth of Douglas-fir trees that were already in the upper part of the diameter distribution, with the possible exception of gap edges. The largest trees in a stand are often not responsive to thinning in the short term (Marquis and Ernst 1991; Walter and Maguire 2004) or may only respond to very high thinning intensities (Davis et al. 2007). However, previous studies indicate that large trees may take more than a decade to respond to thinning treatments (Latham and Tappeiner 2002), suggesting that the full effects of treatment may not yet have been realized. In contrast with Douglas-fir, western hemlock diameter growth responded positively to thinning regardless of initial tree size. However, there were few plots in this study where western hemlocks were among the largest trees.

Diameter growth of smaller Douglas-fir trees was more responsive to thinning than the growth of large Douglas-firs in this study, especially in the lower retention treatments. A positive relationship often exists between the size of an individual relative to the population and growth rate (Schmitt et al. 1987; D'Amato and Puettmann 2004), a pattern also found in this study. Individual tree growth is strongly limited by the number of larger trees near the subject tree (D'Amato and Puettmann 2004; Puettmann et al. 2009*b*). If competition is asymmetric with larger individuals suppressing the growth of smaller individuals, then as population density increases, so should the steepness of the curve between initial size and growth rate (Schmitt et al. 1987). The steeper increase in Douglas-fir growth with increasing size in the control relative to the thinned treatments in this study supports this assertion.

Mortality

The lack of recruitment of large snags and large-diameter coarse woody debris in this study suggests that management of dead wood will be an important component of accelerating late successional forest structure. Dead wood provides habitat for numerous species (Berg et al. 1994), with mortality resulting in recruitment of dead wood habitat in young managed stands where previous management has reduced the quantity of dead wood. While numerous snags were produced over the course of this study, in contrast with old-growth stands (Ares et al. 2012), large snags were mostly absent. Many wildlife species, especially cavity nesters, are associated with large-diameter snags and coarse woody debris (Mannan et al. 1980). Large snags may take more than two centuries to develop in stands without management intervention (Van Pelt and Nadkarni 2004). Active management to create snags has been successfully implemented (e.g., Huff and Bailey 2009) and is planned for the Density Management Study (Cissel et al. 2006). However, heavy thinning around the largest trees selected to become snags may be necessary to accelerate the development of this habitat component.

Thinning can increase resources available to smaller residual trees, thus reducing suppression mortality (Marquis and Ernst 1991), which was likely observed for small Douglas-firs in this study. The mortality rate of just over 2% of the trees in the control per year in this study exceeds rates reported for old-growth forests in the region, which are often under 1% per year (Franklin and DeBell 1988). In contrast, previous studies suggest that thinning can increase physical damage to trees due to wind and snow (Harrington and Reukema 1983), which may be especially pronounced on gap edges (Chen et al. 1992). However, mortality due to physical agents such as wind is often episodic (Lutz and Halpern 2006) or mortality may occur shortly after thinning operations are completed (Chan et al. 2006; Roberts et al. 2007), demonstrating the need for long-term assessments of the often complicated effects of thinning on mortality.

Conclusions and management implications

The increasing recognition that late successional reserves alone will not be sufficient to maintain species populations and biodiversity has prompted the search for silvicultural techniques that can balance wood production and create stands with late successional characteristics (Cissel et al. 2006; Bauhus et al. 2009). In this study, thinning increased stand structural variability, moved stands toward multilevel canopies, and increased residual tree growth. Additionally, thinning treatments provided revenue from timber sales (Cissel et al. 2006), slowed mortality, and had neutral to positive effects on total stand BA growth over 5 years. Collectively, these results suggest that thinning treatments generally can be effective at producing wood products and accelerating the development of several late successional characteristics in young second-growth stands, with notable exceptions. For example, the lack of large-diameter snags or coarse woody recruitment, with or without thinning, suggests that specific actions that create large snags and coarse woody debris may be needed to ensure accelerated development of these late successional structural features.

All thinning treatments evaluated in this study accelerated development of some aspects of late successional forest structure. Lower levels of tree retention generally had larger short-term effects, a pattern consistent with previous studies (Maguire et al. 2006; Davis et al. 2007). Increasing spatial variability, e.g., by creating canopy gaps, appears particularly beneficial for enhancing tree growth and increasing the range of conditions within the stand. The combination of gaps, leave islands of different sizes, and different thinning intensities in the VD treatment appeared particularly effective at increasing structural heterogeneity. This may provide the best opportunity to create suitable habitat for a number of species and lead to differential responses in processes such as tree growth that maintain a trajectory of increasing stand heterogeneity into the future. Monitoring treatment effects over multiple rounds of thinning, as is planned for the Density Management Study (Cissel et al. 2006), will be needed to determine if initial effects persist or if treatments can better facilitate development of large trees and snags over longer time periods.

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