Forest Ecology and Management 108 (1998) 99–113

Forest Ecology
and
Management

Effects of thinning on structural development in 40- to 100-year-old Douglas-fir stands in western Oregon [1]

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Received 7 July 1997; accepted 10 December 1997

Abstract

We studied the composition and structure of the understory in thinned and unthinned Douglas-fir/western hemlock stands on 32 sites in western Oregon. These stands had regenerated naturally after timber was harvested between 1880 and 1940; they were thinned between 1969 and 1984. Commercially thinned stands had 8–60% of their volume removed 10–24 years before the study. Undisturbed old-growth Douglas-fir stands were present for comparison on 20 of these paired sites. Conifer regeneration density and frequency were consistently greater in thinned than unthinned stands. For example, average seedling density in thinned stands (1433/ha) was significantly ($p \leq 0.001$) greater than in unthinned stands (233/ha), but very similar to that in old-growth stands (1010/ha). Seedling density and frequency were strongly related to the volume removed and to stand density index (and other measures of overstory density) just after thinning. In thinned stands, the density of small trees (intermediate crown class overstory trees and advanced regeneration) was 159/ha, significantly ($p \leq 0.001$) greater than in unthinned stands (90/ha), but not significantly different from that of old-growth (204/ha). The live crown ratio of these trees in thinned stands (66%) was greater than in unthinned (44%) and old-growth (48%) stands. Cover and stem density of shrubs was variable in all three stand types. There was significantly less tall shrub cover in unthinned stands than in either thinned or old-growth stands, which did not differ. Thinned stands had the most low shrub cover. Salal and bracken fern cover was greater in thinned stands than in the other stand types, but there was no difference in sword fern and Oregongrape cover. Leaf area index in thinned stands (6.6) was not significantly different from that in unthinned (6.8) and old-growth stands (7.1); however, there was more leaf area in shrubs in the thinned stands. Thinning young Douglas-fir stands will hasten the development of multistory stands by recruitment of conifer regeneration in the understory as well as by enabling the survival of small overstory trees and growth of advanced understory regeneration. Thinning will also help develop the shrub layer by increasing tall shrub stem density and cover of some low shrubs.

Keywords: Stand structure; Old-growth; Stand density; Understory vegetation

1. Introduction

Much is known about the effects of thinning on stand characteristics such as volume growth and rates of overstory tree mortality, as well as on individual tree characteristics such as diameter growth

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[1] Paper 3207, Forest Research Laboratory, Oregon State University.

PII S0378-1127(98)00216-3

and live crown ratio (Smith, 1986). Several long-term studies have related tree and stand development to such measures of stand density as basal area, stand density index (Reineke, 1933), and relative density. Drew and Flewelling (1979) developed diagrams for assessing stand and tree development based on size and density of overstory trees, and they used those diagrams to evaluate the effects of thinning for several case studies.

Only a few studies, however, have examined the effects of thinning on understory tree regeneration; these studies include Witler (1975), Del Rio and Berg (1979), Barrett (1982), Alaback and Herman (1988), Fried et al. (1988), and Tappeiner and Zasada (1993). All authors found increased survival of regeneration; most found increased growth rates. Del Rio and Berg (1979) found regeneration height growth to be positively correlated with light penetration through the canopy. Maintenance of an enhanced light environment is particularly important for the less shade-tolerant species such as Douglas-fir. Such species may germinate under reduced light conditions, but their growth and survival are low under a canopy of older trees (Hermann and Lavender, 1990).

Understory shrub response to thinning is similarly important because shrubs: (a) interfere with conifer and hardwood seedling establishment in the present stand or at the end of a rotation (Daniel et al., 1979); (b) are a major component of wildlife habitat (Mannan and Meslow, 1984; Carey and Johnson, 1995; Hayes et al., 1995; Hagar et al., 1996); (c) affect nutrient cycling, especially rates and amounts of nutrients recycled (Tappeiner and Alm, 1975; Fried et al., 1988); and (d) may affect fire behavior. Huffman et al. (1994) found increased rates of rhizome expansion and aerial stem growth in salal (*Gaultheria shallon* Pursh) in response to thinning; O'Dea et al. (1995) found increased layering of vine maple (*Acer circinatum* Pursh). Likewise, the densities of seedlings of salal, vine maple, bigleaf maple (*A. macrophyllum* Pursh), and salmonberry (*Rubus spectabilis* Pursh) were inversely related to stand density (Messier, 1992; Tappeiner and Zasada, 1993; O'Dea et al., 1995).

These studies and those on overstory trees cited above generally involved individual species in small experimental plots on which overstory density was carefully controlled. Understory vegetation is composed of many species, however, and its composition and density may vary considerably throughout a stand because of differences in overstory canopy and stand history. Thus, while these studies provided important information on the response of individual species, they do not reflect the way an understory responds to the operational realities and spatial scale of actual thinning operations.

In the Pacific Northwest, the effects of thinning young Douglas-fir stands, along with their potential for understory development, are of particular interest because most of these forests have regenerated after harvest during this century. This has resulted in many dense, rapidly growing young stands with 750 + trees/ha: sufficient density for repeated commercial thinnings within a rotation. Without thinning, these stands typically pass through an extended stem exclusion stage (Oliver, 1981), causing mortality of smaller overstory trees and suppression of most understory regeneration and shrub communities.

Newton and Cole (1987) demonstrated that thinning such dense stands can encourage development of overstory structure similar to that of the old-growth forests described by Franklin and Spies (1991), with concomitant benefits for species associated with older forests (McComb et al., 1993). Thinning young stands may also stimulate development of understory structures characteristic of old-growth forests through a combination of: (a) stimulating tree regeneration in the understory; (b) increasing the survival and growth of suppressed and intermediate trees, both of which would lead to a multi-story stand; and (c) fostering the development of diverse shrub layers. In this study, we compared regeneration, understory trees, and shrubs among operationally thinned, unthinned, and old-growth stands. In addition, we related the development of these characteristics to stand density and thinning intensity.

2. Methods

2.1. Study area

This study was conducted in young and old-growth Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests of the Coast and Cascade Ranges of western Oregon (Fig. 1). The young stands regenerated naturally following disturbance associated with clear-cutting and burning in the late 1800s through 1940. They were dominated by one age cohort of Douglas-fir in the overstory with few, if any, large trees or snags remaining from a previous stand. Old-growth stands dated from before 1800 and showed little evidence of recent human disturbance (e.g., stumps or roads). Elevations ranged from 250 to 800 m, with

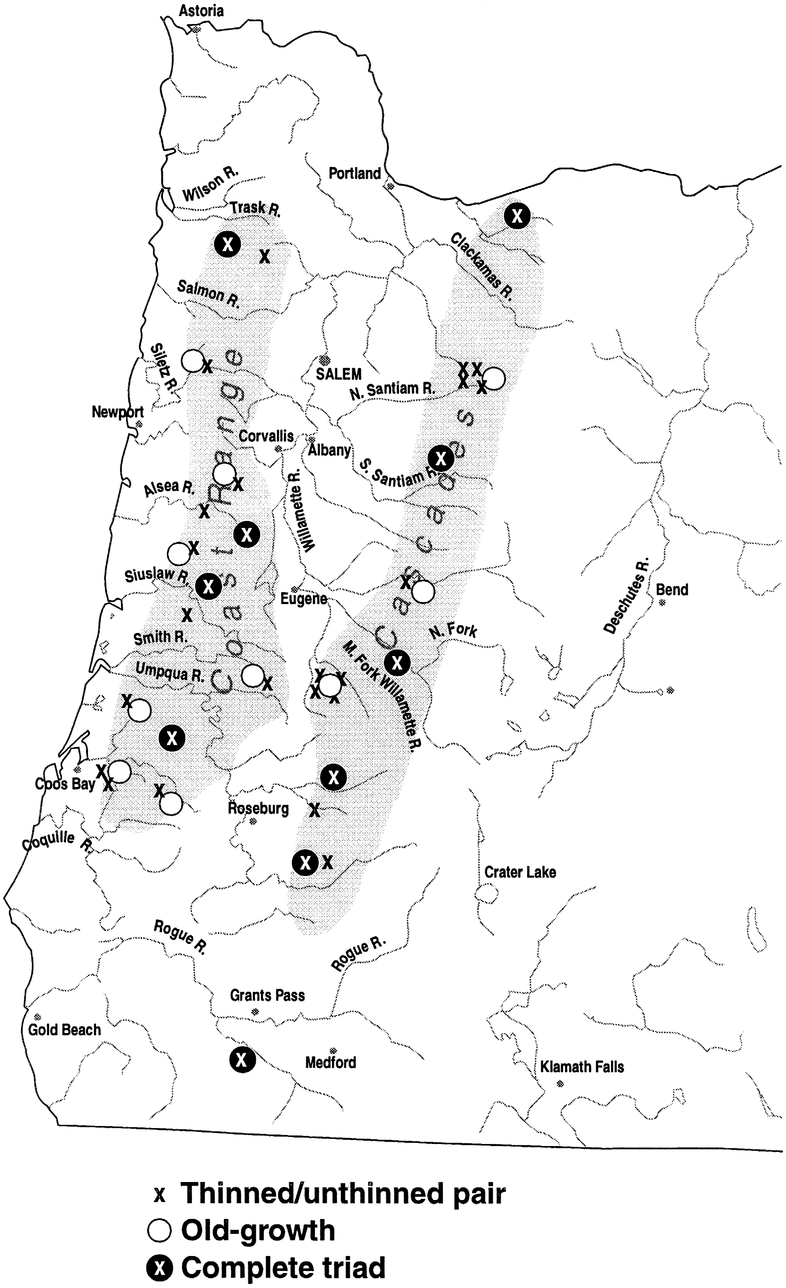

Fig. 1. The study site locations in western Oregon, USA.

precipitation primarily in the form of rain (100–300 cm). Most sites were in the Western Hemlock Zone (Franklin and Dyrness, 1984), where western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) is considered climax. However, Douglas-fir is the likely climax on drier sites on the eastern edge of the Coast Range and in the southern Cascades. The most southern sites were in or near the Douglas-fir Zone (Franklin and Dyrness, 1984).

Using Bureau of Land Management and Oregon Department of Forestry inventory data, we located and sampled 32 pairs of thinned and unthinned stands meeting the following criteria: (1) stand ages ≥ 50 years; (2) operational thinnings conducted 10–25 years before this study in part of the original stands, leaving an adjacent unthinned control area; (3) records available to document the time and intensity of thinning; (4) thinned stands similar to unthinned stands (e.g., slope and aspect); and (5) no additional treatments conducted in either stand. Twenty of these pairs were located near old-growth stands (200 + years) with the characteristics described by Franklin and Spies (1991), and we compared old-growth understories with those of both young stand types. The resulting 32 pairs of young stands, 20 of which were associated with old-growth stands as 'triads,' included a broad range of stand densities, productivity (King, 1966), and ages (Table 1). Thinnings ranged from light to extremely heavy (8–60% of merchantable volume removed). Stand basal areas in thinned stands averaged 32 m^2/ha (range 15–54 m^2/ha), about 21 m^2/ha less than in unthinned stands (53 m^2/ha, range 26–81 m^2/ha).

2.2. Data collection

We inventoried pairs and triads from mid-June to September in 1993–1995, 10 to 25 years after thinning. We established 6–12 (typically 10) points on a systematic grid at 50- to 75-m intervals in an interior area of each >20 ha stand. All sampling occurred at least 75 m from the nearest stand edge, in 10 or more

Table 1
The stand-average overstory characteristics for three stand types (data range in parentheses)

	Thinned ($n = 32$)	Unthinned (32)	Old-growth (20)
Age (years)	80 (50–120)	80 (50–120)	na[a]
Time since thinning (years)	18 (10–24)	na[b]	na[b]
Volume removed (%)	32 (8–60)	na[b]	na[b]
Site index (50)[c]	35 (24–43)	35 (24–43)	36 (24–43)
Stand conditions immediately after year of thinning			
Density (trees/ha)	173 (72–346)	378 (136–847)	–[d]
Basal area (m^2/ha)	32 (15–54)	53 (26–81)	–
RDI[e]	0.31 (0.18–0.50)	0.55 (0.28–0.90)	–
Current stand conditions			
Density (trees/ha)	148 (59–289)	274 (109–541)	99 (40–215)
Basal area (m^2/a)	40 (20–58)	51 (27–70)	62 (40–81)
RDI[e]	0.37 (0.23–0.60)	0.55 (0.30–0.73)	0.50 (0.35–0.67)
Volume (m^3/ha)	92 (51–184)	128 (52–184)	172 (100–288)
Coefficients of variation			
Density (trees/ha)	42 (18–65)	45 (23–78)	52 (22–90)
RDI[e]	30 (13–50)	30 (15–51)	34 (19–49)

Stand conditions immediately after thinning were reconstructed by subtracting diameter growth since the time of thinning from current conditions. Current conditions were determined from measurements in this study

[a] Tree ages are variable.

[b] No trees or volume removed.

[c] See King (1966); base age 50, height in m.

[d] Not reconstructed.

[e] See Reineke (1933).

ha of interior stand conditions. To ensure an unbiased sample, we used aerial photographs to establish the first point on the basis of a pre-assigned stand entry location, direction, and distance that avoided stand boundaries.

Living dominant and co-dominant overstory trees (> 20 cm) were tallied on variable-radius (prism) points within a modified ORGANON sampling template (Hester et al., 1989). Species, diameter at breast height (DBH), total height, height to live crown, and crown radius of each overstory tree were recorded directly into an electronic spreadsheet. Five-year radial growth and radial growth since the year of thinning were determined for three trees per point by coring a range of tree diameters. To calculate site index (King, 1966), we measured breast height age on five to eight dominant and co-dominant trees and total height on 40–50 such trees. A metric equivalent to Stand Density Index (SDI; Reineke, 1933) and Relative Density Index (RDI; Drew and Flewelling, 1979) were calculated from density and diameter values; Live Crown Ratio (LCR) was calculated from total height and height to live crown. Estimates of tree density, basal area, SDI, and RDI in the year immediately following thinning were reconstructed for each stand on the basis of current density of living and standing dead trees and backward projection of average diameter at the time of thinning based on the sample of increment cores.

For seedlings and understory trees, we used fixed-radius plots. The five 2.37-m radius subplots for the seedlings were nested within the five 4.75-m radius plots for understory trees. One plot was located at the point center and the other four were 15 m distant, one in each cardinal direction.

Tree seedlings (< 2.5 cm DBH, > 15 cm height) were tallied on the small subplots. We recorded number and height of seedlings for each species. Total age and 5-year height growth were determined by whorl counts on Douglas-fir and true fir species; ages for other seedlings were calculated from discs taken from the largest individual of that species on each plot. For understory trees (2.5–20 cm DBH and below the main canopy), we recorded the same information as for overstory trees.

Understory shrubs were also measured on each subplot, segregated into two layers: ‘tall shrubs’ (higher than 150 cm) and ‘low shrubs’ (50 to 150 cm high). For tall shrubs (e.g., vine maple), the number of stems and their average height and crown radius (± 15 cm) were recorded by species on each subplot. For the low shrub layer, which included bracken fern (*Pteridium aquilinum* (L.) Kahn.) and sword fern (*Polystichum munitum* (Kaulf.) Presl) and other species, % cover of all species was visually estimated by 5% classes; trace cover was recorded as 1%. Low shrub cover could total up to 100%, but it typically included some empty space (i.e., bare ground).

Leaf Area Index (LAI) was estimated for the overstory canopy and tall and low shrub layers at each point center with a LICOR 2000 canopy area meter (Licor, Lincoln, NE). This instrument uses the difference between full sunlight and under-canopy readings of light intensity to estimate LAI.

2.3. Data analysis

Statistical comparisons of means between paired stands in observational studies assume that stands were initially identical and that observed differences are due to treatment effects (Cochran et al., 1983). In this study, detailed pre-treatment data that would have established similarities between stands were not available, although the broad classifications of habitat type and the aerial-photo-based overstory classifications were identical for each pair prior to thinning. Every effort was made to ensure compliance with this fundamental assumption of observational studies. Our strongest statistical comparisons were therefore treatment effects between individual pairs of thinned and unthinned stands (i.e., *t*-tests that treated points as the experimental units). Three-way ANOVA comparisons among thinned, unthinned, and old-growth stand types were done to test for differences in present condition even though they violate the shared-past assumption described by Cochran et al. (1983). This violation is considered minor because the focus shifts from testing for treatment effects to testing for differences among stand types.

We analyzed density and frequency (% of subplots with one or more individuals) for seedlings and tall shrubs; LCR, density, and radial growth rates for understory trees; and cover for short shrubs. Thirty-two independent pair-wise comparisons and 20 independent three-way ANOVAs were performed for each of the variables (one for each pair and triad), with points (within stands) used as the experimental units (Snedecor and Cochran, 1980). For many dependent variables (e.g., shrub cover), data were averaged from a collection of five equally weighted subsamples.

Most density (count) data for seedlings and tall shrubs, understory tree data, tall and low shrub LAI, and cover of less common low shrubs were non-normally distributed within and across stands (i.e., they were skewed by the predominance of zeroes or low values). These data typically showed markedly different variances among stand types as well. We, therefore, used Wilcoxon rank-sums comparisons classified by pair or triad with a Kruskal–Wallis χ^2 approximation test for significance (SAS Institute, 1989). Blocking by triad was used for all three-way comparisons. We present *p*-values for stand type effect only.

We used stepwise regression to find the best predictor of understory vegetation characteristics from among four measures of stand density: overstory basal area and trees/ha, SDI (Reineke, 1933), and RDI (Drew and Flewelling, 1979). We also included % volume removed, obtained from inventory data, as a measure of thinning intensity. Average seedling frequency for each young stand was plotted on a modified stand density diagram (Reineke, 1933) based on reconstructed stand-average DBH and density.

Comparisons of stand averages across stand types were used to explore differences among the stand types that were consistent across many pairs and triads. Pairwise *t*-test comparisons of stand averages across the 32 pairs, along with ANOVA comparisons with blocking across the 20 triads, were used for normally distributed data with equal variances (e.g., DBH, understory tree height, and canopy and total LAI). Most point data, including count and cover data, were non-normal and required Wilcoxon rank-sums comparisons classified by pair or triad with a Kruskal–Wallis χ^2 approximation test for significance (SAS Institute, 1989). *p*-values for such comparisons are presented. Multivariate stepwise regressions of stand-level averages used age, site index, time since thinning, % volume removed, and four measures of current and past stand density (discussed above) as independent variables. For seedling height–age regressions, we determined ln(height) and reciprocal of age to be the best transformation for fitting the data, except for Douglas-fir in thinned stands (linear model).

3. Results

Variability among pairs and triads was an important consideration for all analyses of overstory and understory data. Pairwise comparison of thinned and unthinned stands was necessary to detect differences between the two stand types for all comparisons. Blocking by triad was significant for nearly all three-way comparisons; we found only two cases in hundreds of comparisons where blocking by triad was not significant at $p \leq 0.10$. Bailey (1996) likewise established that site-to-site differences exerted more influence than stand type differences on multivariate data ordination of shrub and herbaceous communities on these same study sites.

Variability within stand types had similar effects on analyses, creating unequal variances among samples. Coefficients of variation (CVs) for overstory tree density and stand relative density showed that old-growth stands were the most variable (Table 1). Only five older, unthinned stands (with distinct areas of self-thinning mortality and/or natural disturbance) and seven heavy thinnings exceeded the average CV found in old-growth. Young unthinned stands were remarkably homogeneous; light and moderate thinnings typically homogenized overstory tree spacing even further, reducing spatial heterogeneity within the stand. Variability within stands increased only with the heavier thinnings ($>30\%$ volume removal) on these sites.

3.1. Understory conifer seedlings (<2.5 cm diameter)

Understory conifer seedling density and frequency were greatest in thinned stands, and these responses were the largest and most consistent differences measured between thinned and unthinned stands (Fig. 2, Table 2). Seedling densities (primarily of Douglas-fir and western hemlock) were significantly higher in thinned stands for 24 of the 32 pairs; no pair had more seedlings in the unthinned stand.

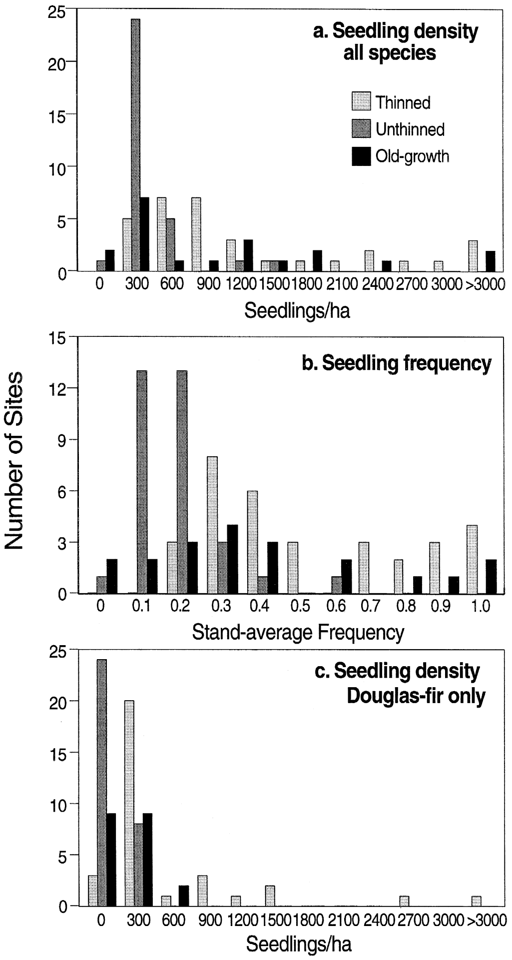

Fig. 2. Conifer seedling (a) density and (b) frequency of all conifer seedling species in three stand types. (c) Douglas-fir seedling density. Distributions were constructed from 32 thinned and unthinned stand pairs and 20 old-growth stands. The *x*-axis shows the uppermost value for each frequency class.

Thinned stands had greater seedling densities across all pairs ($p \leq 0.0001$), and seedling density was negatively correlated with SDI following thinning ($r = -0.62$). Seedling frequency averaged 0.51 (range 0.3–1.0) in thinned stands and 0.14 (range 0–0.2) in unthinned stands; the differences were significant across all pairs ($p \leq 0.0001$) and were negatively correlated with relative density following thinning ($r = -0.69$). 'Heavy' thinnings (half of the sites, from which $> 30\%$ of the overstory volume was removed) averaged > 2000 seedlings/ha, with a frequency of > 0.60, which was significantly greater than the averages for all thinnings. The corresponding unthinned stands averaged only 185 seedlings/ha, with a frequency of 0.14, which did not differ from the averages for all 32 unthinned stands. 'Light' thinnings ($\leq 30\%$ volume removed) were intermediate, with < 800 seedlings/ha and frequency < 0.40, although these numbers were still significantly greater than those in unthinned stands.

Compositional changes were as dramatic as density and frequency differences. Of the 32 thinned stands, 29 had Douglas-fir seedlings in the understory; only seven unthinned stands had such regeneration, all at densities of less than 300 seedlings/ha (Fig. 2c). Most of these seven pairs were in southwestern Oregon or along the drier fringe of the Willamette Valley. Shade-tolerant western hemlock and western red cedar (*Thuja plicata* Donn ex D. Don) comprised nearly all of the regeneration in unthinned stands, with hemlock seedlings dominant in unthinned stands, and light thinnings at more northern sites. Douglas-fir seedlings outnumbered western hemlock and other species only in heavy thinnings and in southwestern Oregon thinnings.

Seedling density and frequency in old-growth stands were intermediate between and different from both thinned and unthinned stands at $p \leq 0.0001$ (Fig. 2c). On individual sites, seedling density and frequency in old-growth and thinned stands did not differ on 7 of 20 triads. However, the percentage of shade-tolerant species was higher in old-growth stands, with Douglas-fir seedlings uncommon.

The pattern of seedlings—the relationship between density and frequency within a stand (Kershaw and Looney, 1985)—was similar among the three stand types (Fig. 3). At any given frequency within a stand (y-axis), stand-average densities were similar. The greatest difference among stand types was the range of densities and frequencies, as discussed above. Thinned stands averaged 3.8 seedlings/plot and unthinned stands 2.0 seedlings/plot, a significant difference across all pairs ($p = 0.0036$). Old-growth stands, however, averaged 2.9 seedlings/plot, which did not differ significantly from either stand type. These small differences in plot level density compared with large differences in frequency demonstrate the importance of frequency in evaluating the status of tree regeneration in the understory.

Table 2
The stand-level averages and standard errors (in parentheses) for understory characteristics from 32 paired thinned and unthinned stands and 20 old-growth stands

Characteristic	Thinned stands	Unthinned stands	Old-growth stands
Seedling density (stems/ha)	1432 (52)	232 (4)	1010 (57)
Seedling frequency	0.51 (0.01)	0.14 (0.01)	0.38 (0.02)
Tall shrub density (stems/ha)	2085 (40)	1336 (28)	2429 (67)
Tall shrub frequency	0.82 (0.01)	0.56 (0.01)	0.93 (0.02)
Tall shrub LAI	0.44 (0.01)	0.23 (0.01)	0.42 (0.01)
Salal cover (%)	23 (0.5)	12 (0.4)	10 (1)
Bracken fern cover (%)	7 (0.3)	2 (0.7)	1 (0.1)
Sword fern cover (%)	13 (0.5)	17 (0.4)	14 (1)
Oregongrape cover (%)	10 (0.5)	10 (0.3)	10 (1)
Total low shrub cover (%)	56 (1)	42 (1)	38 (1)
Low shrub LAI	1.40 (0.02)	0.91 (0.02)	0.78 (0.02)

Differences in seedling frequency (condensed into frequency classes) display well on the stand density diagram of Reineke (1933) (Fig. 4). The highest frequencies of conifer seedlings were found in stands with SDI values of 300–665, equivalent to RDI values of 0.20–0.45 (SDI is based on trees/ha when mean diameter is 25 cm). These stands are primarily thinned stands with > 30% of their overstory volume removed. Stands with SDI values > 815 (RDI values of > 0.55)—the 'zone of imminent mortality' (Drew and Flewelling, 1979)—had zero or low frequencies of seedlings. These stands were comprised exclusively of unthinned stands. Half of the stands with medium frequencies of seedlings had relative densities > 0.55, and most seedlings were western hemlock. Some of the stands that were reduced by thinning to SDI values as low as 370 (relative density = 0.25) produced only moderate frequencies of seedlings. Such a lack of regeneration could be related to seed source availability or competing vegetation.

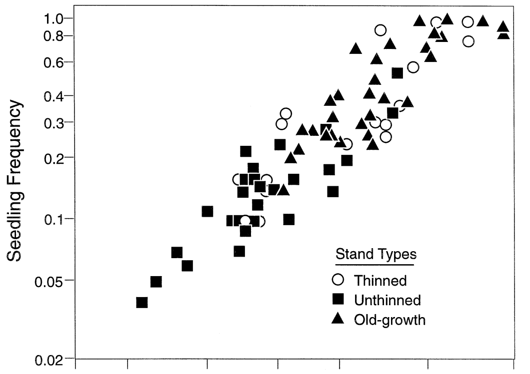

Fig. 3. Seedling density vs. seedling frequency on a log–log scale, by stand type.

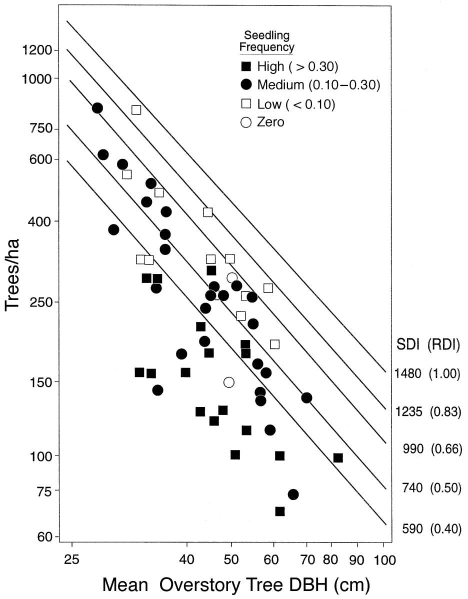

Fig. 4. The stand-level seedling frequency in thinned and unthinned stands plotted on a stand density chart (after Reineke, 1933). The maximum SDI for Douglas-fir is 1480 trees/ha (600 trees/acre) at 25 cm DBH. RDI values are in parentheses. Points are based on reconstructed diameter and density for the year immediately following thinning.

Both seedling density and frequency were strongly and negatively related to shrub cover ($p \leq 0.0001$) in thinned stands. Although there was no distinct threshold above which seedlings were precluded, seedling densities at shrub covers $> 70\%$ averaged only about 40% of those at covers of 20% or less (Fig. 5). Seedling density was likewise related to shrub cover in old-growth stands ($p = 0.002$) but unrelated in unthinned stands ($p = 0.2$). As with most seedling variables, the trends in old-growth data appear more similar to thinned than to unthinned stand data (Fig. 5).

Stand-average height growth rates did not differ between thinned and old-growth stands for either Douglas-fir or western hemlock seedlings (Fig. 6). At age 12, Douglas-fir seedlings averaged 1.3 m in height and were growing an average of > 0.11 m/year in both stand types. This growth rate was constant in thinned stands but slowing in old-growth stands. Douglas-fir seedlings in unthinned stands also averaged 1.3 m in height at age 12, but only 0.03 m/year current height growth. Western hemlock seedlings at age 12 were < 1.3 m in height and averaged ≤ 0.05 m/year growth in all three stand types. Within all stand types, there were individual seedlings of both species that well exceeded these stand averages in terms of height growth. For example, 25-year-old seedlings of both species in thinned stands exceeded 3 m in height and grew at 0.13 m/year; Douglas-fir seedlings grew < 2.5 m in height by age 25 in old-growth and unthinned stands. Regressions of individual seedling height vs. age within sites were significant ($p \leq 0.0001$) for both species; they explained 47–62% of the variation for Douglas-fir height, but only 35–44% for western hemlock. Annual height growth of Douglas-fir seedlings in all three stand types was quite variable among sites (Fig. 7a) and among individual seedlings within sites (Fig. 7b). Douglas-fir seedling height

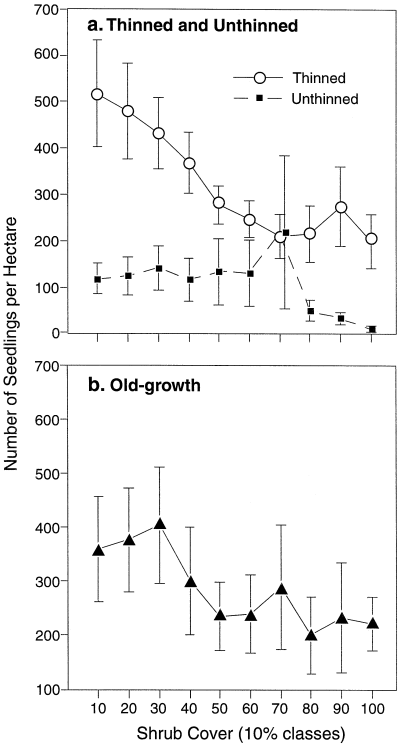

Fig. 5. The relationship between shrub cover (by 10% classes) and seedling density in (a) thinned and unthinned stands and (b) old-growth stands of Douglas-fir. $N = 1599$ in thinned stands, 1430 in unthinned stands, and 937 in old-growth stands. Vertical lines represent standard errors.

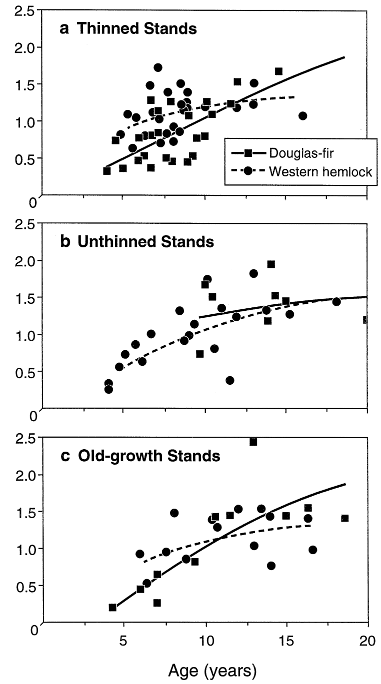

Fig. 6. The stand-average age vs. height of Douglas-fir and western hemlock seedlings based on data for (a) thinned, (b) unthinned, and (c) old-growth stands.

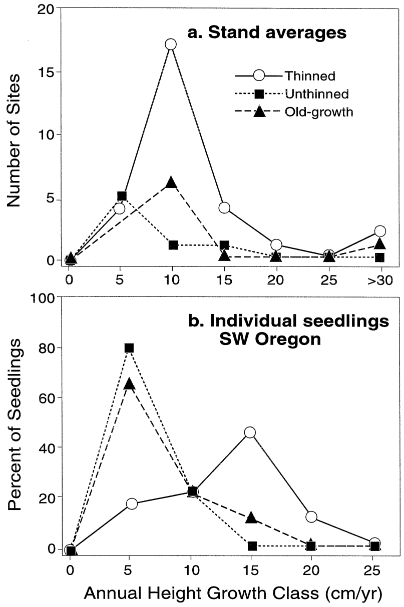

Fig. 7. The Douglas-fir seedling annual height growth (vigor) for three stand types for: (a) stand-level averages from all stands with Douglas-fir regeneration, and (b) all seedlings within a subsample of southwestern Oregon stands with a high density of Douglas-fir regeneration.

growth in old-growth stands was intermediate between that in thinned and unthinned stands (Fig. 7).

3.2. Understory trees

Understory trees averaged 158 trees/ha in thinned stands, compared with 88/ha in unthinned stands ($p = 0.01$). In addition, dead understory trees averaged 34 trees/ha in thinned stands, compared with 81/ha in unthinned stands ($p = 0.001$). In thinned stands, understory trees were predominantly new conifer saplings regenerated after thinning, with a few live understory trees from the original overstory. In sharp contrast, understory trees in unthinned stands were mainly suppressed trees from the overstory with a very few (< 10/ha) young saplings. Consistent with these observations, understory tree LCR was significantly greater in thinned stands in 20 of the 32 pairs, and across all sites it averaged 60% in thinned stands compared with 44% in unthinned stands, significant at $p \leq 0.0001$. Understory tree density and the percentage of standing stems alive were both significantly correlated with relative density immediately after thinning ($r = -0.68$). Equations using relative density explained 55% of the variation in % living understory trees and 72% of understory tree density. As expected, numbers of dead standing stems were strongly correlated with the density of the stand immediately after thinning, with trees/ha alone explaining 80% of the variation.

Thinning intensity had a major effect on the density and characteristics of understory trees. Percent volume removal explained 39% of the variation in understory trees/ha. Heavy thinnings (> 30% of volume removed) averaged 250 understory trees/ha (93% living), with an average LCR of 63%. On the more northerly sites, most of these trees were western hemlock, while Douglas-fir was the principal understory tree on southwestern and interior sites. We found no understory Douglas-fir saplings in unthinned stands.

Understory tree density in old-growth stands was intermediate between that in the two younger stand types and not significantly different from either ($p = 0.6249$), although the character of these trees (i.e., younger and smaller, with a mix of shade tolerance) was more similar to that in thinned stands (Fig. 8). The percentage of living trees and the density of standing dead trees did not differ between thinned and old-growth stands; unthinned stands had lower percentages of living trees and higher densities of standing dead trees across all 20 triads ($p \leq 0.0001$

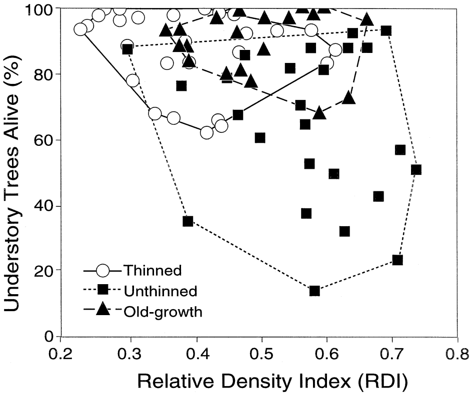

Fig. 8. The % of understory trees alive at different overstory densities (based on RDI values) by stand type for 32 young-stand pairs (thinned and unthinned) and 20 old-growth stands. Stand types are delineated to show the data range for each.

for both variables). Low percentages of living trees were typically associated with stand RDI values > 0.55 in unthinned stands, but not in old-growth stands. Thinned stands had the greatest understory tree LCR across all triads ($p \leq 0.0001$). Understory tree LCR was less in old-growth than in thinned stands in 8 of 20 triads. There was no significant difference between unthinned and old-growth stands. Variability in understory tree density was not consistently different among young and old stand types.

3.3. *Shrub cover*

Shrub density was related to thinning intensity and stand density, but it was more variable than conifer seedling density and frequency (Table 2). Tall shrub stem density was significantly greater in thinned stands in 14 of 32 pairs; it was significantly greater in five unthinned stands. Tall shrub frequency was greater in thinned stands in 21 of 32 pairs (lower in 4 of 32 pairs). Density and frequency of tall shrubs were significantly greater in thinned stands across the combined 32 pairs ($p \leq 0.0021$). Both density and frequency were negatively correlated with relative density ($r = -0.31$ and -0.21, respectively) and trees/ha ($r = -0.41$ and -0.36). Equations using these variables explain only 13–17% of the variation in tall shrub frequency and density.

Across the combined 20 triads, thinned and old-growth stands had similar stand-average measurements (which were significantly greater than for unthinned stands) for tall shrub density ($p = 0.0181$), frequency ($p = 0.0107$), and LAI estimates ($p = 0.0002$). Thinned stands had the greatest tall shrub LAI in 3 of 20 triads, unthinned stands in 1 triad, and old-growth in 4 of 20 triads.

Total low shrub coverage also increased consistently with thinning (Table 2). Thinned stands had greater low shrub cover than unthinned stands in 16 of 32 pairs, and cover was significantly greater in thinned stands across the 32 pairs ($p = 0.0003$). The higher shrub cover in thinned stands was mainly due to cover of salal, which was greater in thinned stands for 17 of 32 pairs ($p \leq 0.0001$), and bracken fern, which was greater in 22 of 32 pairs ($p \leq 0.0001$). Three unthinned stands had greater low shrub cover than their thinned counterparts, mainly because of differences in sword fern and Oregongrape (*Berberis nervosa* Pursh). In pair-wise comparisons, sword fern cover was significantly greater in six thinned stands, but also in eight unthinned stands; among all stands, its cover was marginally greater in unthinned than thinned stands ($p = 0.1539$). Oregongrape cover was inconsistent across all the pairs ($p = 0.6065$), with significantly greater cover in three thinned and six unthinned stands.

Low shrub cover was significantly related to trees/ha ($r = -0.25$), but not to relative density. An equation using both trees/ha and stand age (both with negative coefficients) explained 23% of the variation in low shrub cover. Low shrub LAI was greater in thinned stands for only 11 of 32 pairs, but was greater in thinned stands across the combined pairs ($p \leq 0.0001$).

Total low shrub cover was greater in thinned stands than in either unthinned or old-growth stands for 11 of 20 triads, as was LA1 for 10 of 20 triads; both were higher across all triads ($p \leq 0.0001$ for both variables). Unthinned and old-growth stands did not differ for either variable, nor did the cover of individual low shrub species. Across the 20 triads, total low shrub cover averaged 52% in thinned stands, significantly greater ($p \leq 0.0001$) than in either unthinned (42%) or old-growth (37%) stands, which did not differ from each other. Average covers of salal and bracken fern in unthinned and old-growth stands were similar, about one-third to one-half that in thinned stands. Average covers of sword fern and Oregongrape were nearly identical in the three stand types (Table 2).

4. Discussion

The ranges of thinning density, relative density, and basal area in the operational thinning treatments in this study were very similar to those reported by Curtis and Marshall (1986) and Marshall et al. (1992). These ranges of thinning intensity are also compatible with the management of Douglas-fir stands for wood production. Despite the ranges in stand density, time since thinning, site quality, and geographical distribution of the stands, we were able to detect major differences in understory characteristics among the three stand types.

4.1. Conifer regeneration

The increased seedling frequency in thinned stands indicated that the higher densities of seedlings were well distributed throughout the stands, not clumped in small patches. This suggests that soil disturbance associated with thinning, along with the reduction of overstory density, created rather uniform conditions for seedling establishment. Positive relationships between volume removal and both seedling density and frequency, as well as their negative relationships with stand density immediately after the stand was thinned, suggest that greater thinning intensities (greater amounts of wood removed) created more microsites for seedling establishment over a longer time period. These data were consistent with work on natural conifer regeneration showing that mineral soil and shaded seed beds favor seedling establishment in clearcuts (Hermann and Chicote, 1965), shelterwoods (Williamson, 1973), and in partially cut stands (Tappeiner and Helms, 1971; Seidel, 1983). Some western hemlock regeneration occurs on decaying logs and stumps, as documented by Christy and Mack (1984) and Harmon and Franklin (1989), but regeneration is not restricted to those microsites.

Conifer regeneration following thinning was not limited to shade-tolerant species such as western hemlock. Douglas-fir seedlings were common on drier sites in southwestern Oregon and along the edge of the Willamette Valley and were scattered among western hemlock on mesic sites. Del Rio and Berg (1979) also reported Douglas-fir seedling establishment in a thinning experiment in 40-year-old Douglas-fir plots. They found seedling densities of up to 10,000 seedlings/ha and height growth rates of 4.0–7.5 cm/year in light and heavy thinnings. Our observations of Douglas-fir regeneration and recent research on Del Rio and Berg's plots by Beer (1997) suggest that the future survival and growth rates of Douglas-fir seedlings and their relationships to overstory density are uncertain. It appears likely that many will die as the overstory canopy closes. Additional thinning may be needed to ensure future growth, particularly in lighter thinnings and on highly productive sites.

Seedling density decreased as shrub cover increased (Fig. 5); however, there were considerable numbers of seedlings in areas with as much as 50% shrub cover. Shrub cover increased substantially after thinning, so current densities do not reflect densities at initial seedling establishment. Species such as salal and bracken fern are capable of rapid development through expansion of rhizomes below ground and initiation of aerial stems from the resulting bud bank (Huffman et al., 1994). The current low shrub cover in most young unthinned stands suggests that these species were at the stem exclusion stage (Oliver, 1981) when thinning occurred. Thus, lack of shrub cover (along with some soil disturbance) created the conditions necessary for seedling establishment for a number of years following thinning. Given the current shrub cover, it is unlikely that future thinning or other disturbances within the next several decades would lead to rates of seedling establishment as great as those we measured. However, shrub cover probably will subside as overstory and understory trees grow.

Douglas-fir seedlings grew to greater heights and lived longer in thinned and old-growth stands than in unthinned stands. Annual growth rates over the last 5 years were slightly higher in thinned stands than in other stand types, but growth rates of 0.15–0.20 m/year are still remarkably low compared with those for more open-grown individuals. Thinning appeared to ensure at least some survival of Douglas-fir. Western hemlock growth rates in thinned stands were twice those in other stand types (Fig. 6), and seedling heights were slightly greater than those for Douglas-fir of the same age. Where a seed source is available, western hemlock makes a major contribution to understory development over time, particularly as shade from the overstory canopy increases with time after thinning.

4.2. Understory trees

Understory tree density was greater in thinned stands than in unthinned or old-growth stands for two reasons. The larger understory trees (12–20 cm DBH) responded well to overstory thinnings that reduced stand densities to RDI values of below 0.55, the point at which suppression-related mortality is likely to occur (Drew and Flewelling, 1979). In addition, where conditions were very good for rapid height growth (older, more intense thinnings and larger gaps), new saplings emerged from the seedling class. At RDI values greater than 0.55, the density of most unthinned stands, the percentage of live understory trees is much smaller (Fig. 8). In contrast to unthinned stands, the proportion of living understory trees in old-growth stands did not decrease sharply at RDI values above 0.55. This lack of understory suppression is presumably due to the patchier distribution of overstory trees in old-growth stands relative to young, unthinned stands, which allows sufficient light penetration into the understory for survival. The spatial arrangement of a given density of overstory trees appears important to the growth of understory trees. The greatest LCR in understory trees occurred in thinned stands, indicating that these trees are likely to persist and form a multi-layered stand.

4.3. Understory shrubs

The differences between shrub layers in thinned and unthinned stands were consistent with those in studies of shrub regeneration on similar sites. Vine maple density increases following thinning as slash from felled trees pins its long, drooping aerial stems to the forest floor (O'Dea et al., 1995). These stems then layer and produce new aerial stems and cause an increase in the extent and density of vine maple clones. Seedlings of vine maple are also more common in thinned stands, but growth is likely to be too slow to affect understory density 10 to 20 years after thinning (O'Dea et al., 1995). Because these species can maintain their cover by replacing dying aerial stems with new ones from a belowground bud bank, it is likely that once established in the understory they will persist for many years (Tappeiner et al., 1991; Huffman et al., 1994). Indeed, this may explain the high densities and frequencies of tall shrub species in old-growth stands.

Huffman et al. (1994) found that salal rhizome growth and clonal development increased as overstory density decreased; rhizome growth of 1 m/year was common in thinned stands, consistent with the two-fold increase of salal in our thinned stands (Table 2). In contrast, Oregongrape cover did not differ in our three stand types. Its rhizome growth and clonal development are much slower than that of salal (Huffmann and Tappeiner, in preparation). Oregongrape invasion following disturbance depends primarily on seedling establishment and subsequent slow clonal development.

4.4. Structural development in thinned stands

Thinned stands were similar to old-growth stands in understory seedling density and frequency, density of trees 2.5–20 cm diameter, and tall shrub density. Low shrub cover was greater in thinned stands because of increases in salal and bracken fern. Additional work on these sites has shown that overstory tree size, LCR, and density are all more similar between thinned stands and old-growth stands than between unthinned and old-growth stands (Bailey, 1996). Also, native understory herb frequency and richness are similar among all three stand types. Thus, thinning appears to set young stands on a trajectory toward achieving overstory and understory attributes similar to those in old-growth stands. The rate at which stands proceed on this trajectory will depend on initial stand density, intensity of thinning, and site productivity, as well as natural disturbance from wind, fire, ice storms, and root diseases and insects.

4.5. Management implications

This study was conducted in large stands that had received operational thinnings, not small experimental plots designed to test specific activities. Thus, the consistent responses seen in this study are strong evidence that thinning initiates and promotes tree regeneration, shrub growth, and the development of multi-storied stands even when the treatments focused mainly on management of overstory/crop tree density and spacing. Such understory development can address several objectives related to stand regeneration and forest and wildlife management. Treatments designed to purposely favor legacy structures (large remnant trees, snags, and downed wood) and/or overstory hardwoods would further hasten development of old-growth forest characteristics.

Acknowledgements

Funding for this project was provided by the Bureau of Land Management through the Forest and Rangeland Ecosystem Science Center, Corvallis, OR.

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