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Understory vegetation in young Douglas-fir forests: does thinning help restore old-growth composition?

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Abstract

We compared the understory herb and shrub communities of pre-commercially thinned and unthinned young- and old-growth Douglas-fir (Pseudotsuga menziesii) stands. Sites were located in the Cascade Mountains of western Oregon. Young stands were approximately 40 years old at the time of sampling; thinning occurred 20 years earlier. Although tree spacing was wider in thinned than in unthinned stands, faster tree growth in thinned stands meant that thinning had no long-term effect on basal area of P. menziesii. The very large, widely spaced P. menziesii individuals in old-growth stands contributed similar basal area as the smaller trees in young stands; however, old stands had much higher basal area of shade-tolerant conifers. Although low shrubs responded positively to thinning, the difference in cover between thinned and unthinned stands was too small to be statistically significant. Ordination of sample plots in terms of their understory shrub and herb species composition identified a strong gradient in community composition from young to old-growth stands. Understory species associated with old growth included both gap specialists and those that may be dependent on the litter depth and mycorrhizal fungi of old-growth forest floors. Although both thinned and unthinned young stand composition were quite distinct from that of old-growth stands, thinned stands were more similar to old growth than were unthinned stands. Thinned stands had higher frequency of late-seral herbs than did unthinned stands. Forest generalist and release species showed mixed responses to thinning. We conclude that pre-commercial thinning may be a useful management tool to encourage old growth associated understory herbs without precipitating dominance of the understory by low shrubs and weedy species. Although thinning did accelerate tree growth, changes in the understory appear to have been precipitated by the transient increase in resource levels following thinning rather than by any long-term changes in stand structure.

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1. Introduction

The problem of restoration of native biodiversity in planted forests is of global interest (Keenan et al., 1997; Ashton et al., 1998; Moles and Drake, 1999; Stanturf and Madsen, 2002; Zerbe, 2002). Many approaches focus on restoration of tree composition and structure, with the expectation that other components of biodiversity will follow (Allen et al., 2002; Poage and Tappeiner, 2002; Schuler et al., 2002; Vallauri et al., 2002). In the Pacific Northwest of the United States, stands <100-years old, mostly planted, comprise approximately 70% of the forested landscape (USFS, 2002). Young managed stands exhibit very different structure than the old-growth forests

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they replaced, with higher tree densities and lower variation in tree size and canopy height than oldgrowth stands (Spies and Franklin, 1991). In addition, current young forests may be more densely stocked than the young stands that developed into today's old growth (Poage and Tappeiner, 2002). These observations have led to the suggestion that thinning, by fostering development of old-growth stand structure, may accelerate development of ecological communities more similar to those found in old-growth (e.g. Poage and Tappeiner, 2002). We tested this hypothesis for understory herb and shrub communities in 40-yearold managed forests that had been pre-commercially thinned approximately 20 years prior to our sampling.

Pre-commercial thinning is imposed early in stand development, before or around canopy closure and before the trees have reached merchantable size. Commercial thinning operations can occur at any time later in the stand's development. Although forestry practices on industrial lands would generally include both pre-commercial and commercial thinning, lower intensity management on public lands rarely does. Studies of thinning (commercial and pre-commercial) provide an inconsistent picture of long-term (circa 20 year) understory response. Thomas et al. (1999) found that heavy pre-commercial thinning had small but lasting (~ 20 year) positive effects on understory cover despite the absence of a lasting effect on overstory cover, while light thinning had persistent negative effects. In their sites, old-growth associated and mesic-site species responded more positively to intensity of thinning than did release species (species that are released by overstory removal; Halpern, 1989; McKenzie et al., 2000). In areas of dense natural regeneration, heavy pre-commercial thinning can increase understory cover by an order of magnitude even 18 years later (Doerr and Sandburg, 1986). This increase is associated with increased habitat utilization by deer (Doerr and Sandburg, 1986), which browse on understory herbs (Deal, 2001). Dense regeneration of shade-tolerant understory trees following pre-commercial thinning, however, may preclude long-term increases in understory herb and shrub cover (Alaback and Herman, 1988).

Commercial thinning following canopy closure can have larger effects on understory cover and composition than pre-commercial thinning (Bailey et al., 1998; Thysell and Carey, 2001). Release species seem to respond more positively to commercial than to precommercial thinning, perhaps reflecting the more persistent canopy openness that often results from commercial thinning (Bailey et al., 1998; Thysell and Carey, 2001). Bailey et al. (1998) found significant increases in cover of nitrogen-fixing species, grasses and sedges, matted vines and exotic species 7-23 years after thinning in 60-110-year-old stands, while unthinned sites had levels of these species indistinguishable from old-growth. Shade-tolerant forest herbs also increased in response to thinning, but this effect was not statistically significant. In stands with little initial understory cover, Thysell and Carey (2001) found a 7% increase in herb cover associated with two rounds of commercial thinning, 5 and 20 years earlier, with large increases by many exotic and release species and a doubling of cover of the low shrub Gaultheria shallon. While the positive response of G. shallon appears to be a universal response to commercial thinning, other understory herbs and shrubs fail to respond to some commercial thinning operations (He and Barclay, 2000).

Although many argue that young managed stands may require silvicultural manipulation to encourage development of old-growth characteristics (Thysell and Carey, 2001; Poage and Tappeiner, 2002), few present empirical data on the differences in understory composition between young managed and older forests (but see Bailey et al., 1998). Spies (1991) showed that while no herb or shrub species were found exclusively in old-growth, many showed higher frequency or cover in old growth than in mature or young forests that had regenerated naturally after fire. In a smaller but still spatially extensive study, Bailey et al. (1998) found that there was wide and largely overlapping variation in composition among commercially thinned and unthinned planted stands and old-growth stands. The magnitude and nature of these differences should determine the urgency of restoration-oriented action, as well as the kind of intervention that may be needed.

Different measures of herb population performance may show different long-term patterns of response to treatments. Flowering in understory herbs generally occurs only when resource levels are relatively high (Pitelka et al., 1980 and cited references; Winn and Pitelka, 1981; Lubbers and Christiansen, 1986; Hughes et al., 1988; Cunningham, 1997; Geber et al., 1997), and should reflect the current availability of resources in the stand. Frequency, in contrast, may reflect past stand conditions because some understory species tolerate low resource levels (e.g. light, nutrients or water) and may remain present for long periods in unfavorable habitats. Abundance should show intermediate patterns of responsiveness to changes in resource availability.

Our overall objective was to test whether pre-commercial thinning of young Douglas-fir forests fosters development of old-growth understory community composition. To this end, we quantified differences in understory composition between young managed (thinned and unthinned) and old-growth stands. We specifically investigated differences among treatments in: (1) tree basal area, tree species composition and shrub basal area; (2) understory community composition; and (3) frequency, abundance and flowering of individual understory herb species. We discuss the implications of our results for the use of thinning to foster old-growth community composition in young managed stands.

2. Methods

2.1. Study sites and sampling design

Study sites were in the H.J. Andrews Experimental Forest (HJA; 44°N,122°30'W) on the west slope of the Cascade Range in Oregon, USA. This region experiences summer drought, with <10% of the total rainfall of 220 cm falling during the summer months (Bierlmaier and McKee, 1989). Parent materials are volcanic in origin, including ash flows, breccias, basalts and andesites. Stream terraces contain extensive alluvial deposits while steep valley slopes intermix colluvial deposits with occasional exposed bedrock. Soil surface horizons are poorly developed loams with high porosity (Stephens, 1964; Dyrness, 1969). Portions of the forest that have not been harvested support 300-500-year-old stands with a dominant canopy of Pseudotsuga menziesii and a sub-canopy of Tsuga heterophylla.

Young stands originated between 1956 and 1970 after clearcut harvest and broadcast burning of oldgrowth stands and were seeded or planted with *P. menziesii*. Pre-commercial thinning was carried out 15–22 years after planting. Trees averaged approximately 10–15 cm in diameter at breast height at the time of thinning; they were cut with chainsaws and left to decompose where they fell. All hardwoods and shade-tolerant conifers were cut. Before thinning, tree density ranged from 1144 to 7380 trees/ha (mean: \sim 4000); after thinning, spacing of residual trees ranged from 5.5 to 1.8 m (average: \sim 3.6 m), leaving 328 to 2224 trees/ha (average: \sim 600). The sites of Martinez et al. (1992), which comprise about half of our harvest units, were thinned to low (average: 300 trees/ha; 5.5 m spacing) and medium (average: 600 trees/ha; 3.6 m spacing) densities; control stands averaged 3459 trees/ha.

Sampling was carried out in five locations (blocks) within the Lookout Creek Watershed of the HJA, at elevations ranging from 657 to 860 m and on a variety of aspects. Blocks were made up of one or more adjacent second-growth harvest units (established following one clearcut harvest event) and a nearby old-growth area with similar slope and elevation. Thinned and unthinned treatments were interspersed within second-growth harvest units. Thinning treatments were well-documented because they had been installed as experiments to study tree growth; data on tree growth responses to thinning are available for four of the five blocks (Martinez et al., 1992).

In treatment areas with permanently marked study areas we established 9 m radius plots at the center of each marked study area. In all units without permanent study areas, we established 9 m radius plots at random points 50–100 m apart along transects spaced uniformly and spanning the unit. Numbers of plots per unit were selected with a goal of one plot/ha. In total, we sampled 153 plots in five blocks, approximately 10 plots per treatment per block.

2.2. Data collection

Sampling was conducted in June and July 2002. In each plot we recorded the presence of all herb and shrub species, and visually estimated abundance and flowering of 11 focal herb species (Table 1). The 11 focal herb species were chosen because they were abundant, included a mix of late-seral species, forest generalists, and release species, and had phenologies such that flowering was evident throughout the study period. Focal species were divided into three groups.

Species	Family	Species group	Abundance*	Flowering*
Achlys triphylla	Berberidaceae	Late-seral	Ramets	Ramets
Coptis laciniata	Ranunculaceae	Late-seral	Cover	Ramets
Linnaea borealis	Caprifoliaceae	Late-seral	Cover	Inflorescences
Tiarella trifoliata	Saxifragaceae	Late-seral	Ramets	Ramets
Vancouveria hexandra	Berberidaceae	Late-seral	Cover	Ramets
Anemone deltoidea/lyallii	Ranunculaceae	Forest-generalist	Ramets	Ramets
Trillium ovatum	Liliaceae	Forest-generalist	Ramets	Ramets
Hieracium albiflorum	Asteraceae	Release	Ramets	Ramets
Osmorhiza chilensis	Apiaceae	Release	Ramets	Ramets
Trientalis latifolia	Primulaceae	Release	Ramets	Ramets
Whipplea modesta	Hydrangeaceae	Release	Cover	Inflorescences

(*) Abundance estimated visually as number of ramets per plot or percent cover and flowering estimated visually as number of flowering ramets or number of inflorescences per plot.

- 1. *Release species* are subordinate forest herbs and shrubs that are released by overstory removal (Halpern, 1989; McKenzie et al., 2000). They are associated with young or mature rather than oldgrowth forests, or show no stand-age affiliation (Spies, 1991).
- 2. Forest generalists are also associated with younger forests but do not respond positively to overstory removal. These shade-tolerant species decline as a result of clearcut harvest and recover slowly thereafter (Dyrness, 1973), often peaking in abundance in young or mature forests (Spies, 1991).
- 3. *Late-seral species* are associated with old-growth forests (Spies, 1991). These species are generally shade tolerant but respond positively to canopy gaps (Stewart, 1988; St. Pierre, 2000). They decline in abundance at the time of clearcutting but show some recovery in the open-canopy period (Dyrness, 1973; Halpern, 1989).

Scientific names follow Hitchcock and Cronquist (1973). Anemone deltoidea and Anemone lyallii were considered as one taxon because it was not possible to tell non-flowering individuals of the two species apart. Abundance was estimated visually: for species with easily distinguishable ramets we counted the number of ramets in the 9 m radius plot; for other species we estimated percent cover. Number of flowering events per 9 m radius plot was estimated similarly: number of flowering ramets where possible, and number of inflorescences for species without distinct ramets.

We also estimated summed cover of the dominant low shrubs, *Berberis nervosa* and *G. shallon*. In each plot we recorded environmental and stand structural variables including slope, aspect, and basal area of *P. menziesii*, hardwoods (*Alnus rubra, Acer macrophyllum* and *Castanopsis chrysophylla*), and shade-tolerant conifers (*T. heterophylla, Thuja plicata* and *Taxus brevifolia*). Basal area (BA) was estimated from plot center using a BAF-10 (English) prism in young stands and a BAF-20 prism in old growth and then converted to m²/ha. Aspect was re-coded as degrees south from true north (east and west coded the same) to emphasize north-south variation.

2.3. Statistical methods

2.3.1. Data structure

Data from plots from the same treatment area (treatment within block) were averaged to produce a dataset (n = 15) suitable for hypothesis tests on the effects of treatment. The presence or absence data for plots became frequency in treatment areas, the percentage of plots in a treatment area occupied by a species. Rare species (occurring in <10 of 178 plots) were omitted because they can obscure multivariate patterns (McCune and Grace, 2002). All species remaining after this deletion occurred in at least three of the 15 treatment areas.

2.3.2. Multivariate analyses

Multivariate tests for differences in community composition among treatments were conducted using

Table 1

blocked multi-response permutation procedure (MRPP) a non-parametric randomization-based alternative to multivariate ANOVA (PCORD version 4.10: McCune and Grace, 2002). MRPP generates a probability that community composition is more similar within treatment groups than within groups based on random re-assortment of the data. It also yields an effect size A, a measure of the homogeneity (withingroup agreement) of the groups. Within-group agreement ranges from 0 to 1, with 0 denoting as much within-group homogeneity as expected by chance and larger values denoting more homogeneous groups (McCune and Grace, 2002). We used blocked MRPP to test the overall effect of treatment as well as to test pairwise differences between individual treatments; tests were carried out for all three measures of community composition (frequency of all species and abundance and flowering of focal species). An 0.05 probability of type-I error was used for all tests, which is a conservative criterion given the small sample size. However, because no adjustments were made for multiple comparisons, the actual probability of type-I error is somewhat higher than 0.05.

We used non-metric multidimensional scaling ordination (NMS; McCune and Grace, 2002) in PC-ORD version 4.10 (McCune and Mefford, 1999) to examine patterns in community composition within and among treatments. We used Sørensen distance as the measure of compositional dissimilarity between plots. We used the "slow and thorough" autopilot mode in NMS (step length = 0.2, stability criterion = 0.000001, 400 iterations maximum) to generate solutions. and picked the lowest stress solution to interpret. A two-dimensional solution was selected because it had similar stress (a measure of the lack of fit between distances in the full-dimension dataset and the reduced-dimension solution) to the three-dimensional solution and significantly lower stress than solutions derived from randomized data (P = 0.02). The solution was rotated to maximize the loading of treatment differences on Axis 1.

2.3.3. Univariate analyses

We tested for differences in frequency, abundance, and flowering of individual species among treatments in data aggregated to the treatment area level (n = 15) using blocked ANOVA for the overall comparison and *t*-tests paired within blocks for the post-hoc comparisons (S-PLUS version 2000, MathSoft, 1999). The same approach was used to test for differences in stand structure (e.g. tree basal area and low shrub cover) among treatments. Data aggregated to treatment area were always approximately normal.

3. Results

3.1. Stand structure

Thinned, unthinned, and old-growth stands differed in basal area of shade-tolerant conifers and hardwoods, as well as in low shrub cover ($P \le 0.05$, Table 2). Treatments did not differ in basal area of the dominant conifer, *P. menziesii*. Thinned stands, along with old-growth stands, had significantly lower basal area of hardwoods than did unthinned stands (P < 0.05 for pairwise comparisons, see Table 2). Old-growth stands had higher basal area of shadetolerant conifers than did either thinned or unthinned stands; low shrub (*G. shallon* and *B. nervosa*) cover was lower in old growth than in thinned stands (P < 0.05 for pairwise comparisons, see Table 2).

3.2. Community composition

The three treatments (thinned, unthinned and oldgrowth) differed significantly from each other in community composition whether the analysis was based on frequency of all species, or abundance or flowering of focal species (Blocked MRPP *P*-values ≤ 0.01 ; Table 3). Unthinned and thinned stands each differed significantly from old growth for all three

Table 2 Treatment means for tree and shrub variables

Response	Unthinned	Thinned	OG	Р
PSME BA TOL BA HW BA SHRUB	31.88 2.28 ^a 2.79 ^a 23.46 ^{ab}	$31.69 \\ 1.84^{a} \\ 0.443^{b} \\ 31.26^{a}$	26.04 31.6 ^b 0.19 ^b 10.45 ^b	0.20 <0.001 0.01 0.05

Variable definitions: basal area (BA; m²/ha) of *Psuedotsuga menziesii* (PSME), shade-tolerant conifers (TOL), and hardwoods (HW); percent cover of low shrubs. Overall significance from blocked analysis of variance; treatments with different letter superscripts were significantly different in post-hoc paired *t*-tests ($P \le 0.05$).

Blocked MRPP of differences in understory community composition among treatments (main effects and treatment contrasts) for all three measures of herb performance

	Α	Р
Main effect of treatment		
Frequency*	0.12	0.002
Abundance	0.08	0.01
Flowering	0.12	0.002
Unthinned vs. old growth		
Frequency	0.12	0.02
Abundance	0.08	0.02
Flowering	0.12	0.02
Thinned vs. old growth		
Frequency	0.13	0.02
Abundance	0.10	0.02
Flowering	0.12	0.012
Unthinned vs. thinned		
Frequency	0.02	0.02
Abundance	-0.02	0.90
Flowering	0.02	0.11

A, chance corrected within-group agreement (effect size); *P*, probability of randomized groups having as large or larger a within-group agreement. (*) Frequency of all 61 species; abundance and flowering of 11 focal species.

measures of community composition ($P \le 0.02$). However, unthinned stands differed from thinned stands only in terms of frequency of all species (P = 0.02), and the within-group agreement for this comparison was six-fold smaller than those from the contrasts that included old stands. There was suggestive statistical evidence for an effect of thinning on flowering of focal species (P = 0.11); a larger sample size would be needed to adequately test this effect.

Ordination of treatment-area level data on frequency of all species yielded a two-dimensional solution that explained 87% of the variation in the raw data (NMS ordination, final stress = 10.95). Most of the variation (68%) was explained by Axis 1, which separated young unthinned stands (low scores) from old-growth stands (high scores; Fig. 1). In all five blocks, thinned treatment areas were closer to oldgrowth composition than were unthinned areas. The magnitude of difference in species composition between thinned and unthinned treatments varied among blocks, as did the difference between young and old-growth treatments. When the ordination was carried out at the plot level, intensity of thinning was



Fig. 1. NMS ordination of shrub and herb frequency data. Lines connect treatment areas within a block.

not correlated with position in the ordination (data not shown; see Lindh, 2003).

The second axis, which explained 19% of the variation in the data, represented a gradient from mesic sites at lower elevations (low scores) to drier sites at higher elevations (high scores; correlation of scores with elevation equal to +0.81; see Fig. 1). Correlations of species with Axis 2 supported the above interpretation. Taxa with strong (|r| > 0.5) negative correlations with Axis 2 were the mesic-site herbs *Listera* spp. and *Achlys triphylla*, the fern *Blechnum spicant* and the mesic-site trees *A. rubra* and *T. brevifolia*, while species with strong positive correlations included the release herb *Trientalis latifolia*, and the ridge-associated herbs *Synthyris reniformis* and *Xerophyllum tenax*.

Of 61 species examined, 16 showed significant treatment responses (Table 4), and nine reached their highest frequencies in old-growth. The focal late-seral herbs *Coptis laciniata, Tiarella trifoliata, A. triphylla* and *Linnaea borealis* all showed significantly higher frequency in old than young (thinned or unthinned) stands (Table 4, Fig. 2), as did the orchid *Goodyera oblongifolia* (Table 4). Of species peaking in frequency in old growth, all but *G. oblongifolia* responded at least somewhat positively to thinning (Table 4). The focal late-seral herbs *C. laciniata, A. triphylla* and *L. borealis* and the shrub *Vaccinium membranaceum* showed significant positive thinning responses.

Seven of the treatment-responsive species showed peak frequencies in young stands. The focal release herbs *Osmorhiza chilensis*, *Whipplea modesta* and *Hieracium albiflorum* all showed significantly higher frequencies in young thinned and unthinned stands than in old growth (Table 4, Fig. 2), as did the herb *Galium triflorum* and the shrub *Symphoricarpos mollis* Table 4

Mean frequencies and standard errors, by treatment, of species showing significant treatment effects					
Species	Unthinned	Thinned	Old growth	P^*	
Peak in old-growth					
Goodyera oblongifolia	16 ± 7^{a}	$14 \pm 4^{\mathrm{a}}$	$77 \pm 5^{\mathrm{b}}$	0.00007	
Tiarella trifoliata	34 ± 13^{a}	$41 \pm 13^{\mathrm{a}}$	83 ± 9^{b}	0.005	
Chimaphila umbellata	45 ± 7^{a}	$57 \pm 12^{\mathrm{ab}}$	$77 \pm 7^{\mathrm{b}}$	0.01	
Rhododendron macrophyllum	$18 \pm 4^{\mathrm{a}}$	30 ± 8^{ab}	$49 \pm 11^{\mathrm{b}}$	0.01	
Pyrola asarifolia	7 ± 5	13 ± 4	27 ± 9	0.05	
Coptis laciniata	33 ± 12^{a}	$49 \pm 10^{\mathrm{b}}$	$88\pm6^{ m c}$	0.0004	
Achlys triphylla	37 ± 12^{a}	$50 \pm 10^{\rm b}$	$72 \pm 13^{ m c}$	0.0007	
Linnaea borealis	$54\pm 6^{\mathrm{a}}$	$74 \pm 6^{\mathrm{b}}$	$97 \pm 3^{\circ}$	0.001	
Vaccinium membranaceum	$10\pm7^{ m a}$	31 ± 8^{b}	35 ± 11^{b}	0.03	
Peak in young					
Osmorhiza chilensis	$19\pm5^{\mathrm{a}}$	$58 \pm 9^{\mathrm{b}}$	$0 \pm 0^{ m c}$	0.0006	
Symphoricarpos mollis	$42 \pm 17^{\mathrm{a}}$	$74 \pm 15^{\mathrm{a}}$	3 ± 3^{b}	0.005	
Whipplea modesta	71 ± 14^{a}	$64 \pm 17^{\mathrm{a}}$	$22\pm9^{\mathrm{b}}$	0.01	
Hieracium albiflorum	$66 \pm 8^{\mathrm{a}}$	$70 \pm 11^{\mathrm{a}}$	$29 \pm 9^{\mathrm{b}}$	0.04	
Chimaphila menziesii	49 ± 10^{ab}	$57\pm7^{\mathrm{a}}$	31 ± 8^{b}	0.02	
Rubus parviflorus	29 ± 10^{ab}	$43 \pm 4^{\mathrm{a}}$	$12\pm5^{\mathrm{b}}$	0.03	
Galium triflorum	$75\pm3^{\mathrm{a}}$	$69 \pm 5^{\mathrm{a}}$	12 ± 6^{b}	0.00005	

(*) *P*-values are from ANOVA with a block term included. Means with differing superscripts were significantly different ($P \le 0.05$) in post-hoc paired *t*-tests.



Fig. 2. Percent difference between treatments in frequency, abundance and flowering of focal herb species. Percent difference calculated as, for example: (old-growth average – unthinned average)/unthinned average. Stars indicate statistical significance ($P \le 0.05$) of contrasts, based on paired *t*-tests.

(Table 4). Of species with peak frequencies in young treatments, most increased at least somewhat in frequency in response to thinning (Table 4), but the differences were less likely to be statistically significant than were those for the species with peak abundances in old growth. Only the focal release herb *O. chilensis* showed a significant thinning response. Neither of the forest generalist species showed significant treatment effects.

For late-seral and forest generalist species, differences in abundance and flowering between young and old stands were generally larger than differences in frequency (Fig. 2A), but were less likely to be statistically significant. Increases in performance associated with thinning were much smaller than the differences between young and old stands. Late-seral species responses to thinning were consistently positive in terms of frequency, while flowering and abundance showed inconsistent and sometimes negative responses (Fig. 2B). Forest generalist responses to thinning were mixed (Fig. 2B).

Release herbs showed lower frequency, abundance, and flowering in old-growth than young unthinned stands, with all measures showing differences of similar magnitude (Fig. 2A). Most release herbs showed smaller differences in performance associated with thinning than with the unthinned-old-growth contrast; the sign of the difference varied between measures of performance (Fig. 2B). One release herb (*O. chilensis*) responded very positively to thinning, with similar increases in all three measures of performance; only the increases in frequency and flowering were statistically significant.

4. Discussion

4.1. Effects of thinning

In the young forests examined in this study, precommercial thinning appeared to move stands closer to old-growth composition via small increases in the performance of old-growth associated species. These changes in the herb and shrub community observed 20 years after pre-commercial thinning are probably legacies of large differences in stand density immediately following thinning. Thinning treatments removed on average three-quarters of the trees, likely leaving the canopy significantly more open than in unthinned stands. Thinning may also have increased the availability of belowground resources such as nutrients and water (Brix and Mitchell, 1986), which can limit understory plant abundance (Lindh et al., 2003; St. Pierre, 2000). Thinning led to increased rates of tree growth, however, with the heaviest thins exhibiting the highest rates of growth (Martinez et al., 1992). Twenty years after harvest, thinned and unthinned stands exhibited indistinguishable basal areas of *P. menziesii*, the dominant conifer.

While thinning did lead to increased tree size, it did not foster the vertically and horizontally heterogeneous canopy typical of older forests. Shade-tolerant conifers were selectively removed at the time of thinning. Unlike some commercial thins in older stands (Bailey and Tappeiner, 1998), pre-commercial thinning failed to initiate an understory cohort of shade tolerant conifers. Thinning decreased horizontal canopy heterogeneity by lowering the incidence of storm-related canopy gaps (Dave Perry, unpublished data). Significant numbers of trees in steep unthinned areas toppled as a result of snow loads in the winter of 1996, an effect that has been observed in other regions (Nykanen et al., 1997; Wilson and Baker, 2001). The higher incidence of treefall gaps in unthinned stands may have reduced the contrast in understory composition between thinned and unthinned stands.

Different measures of herb population performance yielded different estimates of the magnitude and direction of treatment effects. These differences were largest for late-seral and forest generalist species, which show plasticity of allocation to growth, reproduction and survival (Pitelka et al., 1985; Eriksson, 1993; Damman and Cain, 1998). The responses of these species to thinning were relatively small and individual species showed a range of positive and negative responses for different performance measures. While thinning may have led to short-term increases in frequency, abundance and flowering, subsequent declines in resource availability probably led to rapid declines in allocation to growth and flowering. As a result of this changed pattern of resource allocation, plants may have been able to remain present at high frequencies even as resource availability declined. The range of responses to thinning may reflect variation among species in strategies of resource allocation under conditions of changing resource availability.

In contrast, release species tended to respond to treatments similarly in all three measures of performance, showing neutral or positive responses to thinning. Flowering and abundance are more closely related for these species than for clonal late-seral herbs (Lindh, 2003). The higher resource needs of these species preclude their long-term survival under unfavorable conditions. The overall lack of positive response of release species to thinning suggests that either resource levels were not high enough following thinning for populations to increase or populations increased but then declined again.

4.2. Differences between young and old stands

While compositional differences between young and old stands were large in our study sites, the same suite of species was present in young and old stands. The quantitative rather than qualitative differences between young and old stands suggest that recovery of old-growth composition is possible and may be hastened by manipulation of stand density and tree spacing. Single prescriptions may not work for all species, however, because different groups of understory species may be associated with different aspects of the old-growth forest environment. Some reach high abundance only in canopy gaps, while others may rely on characteristics of the old-growth forest floor. Several clonal species (C. laciniata, T. trifoliata, A. triphylla and L. borealis) are widely but sparsely distributed in young forests (Halpern, 1989; Spies, 1991). Gaps (above or belowground) in old-growth forests allow proliferation of dense clonal patches as well as investment in sexual reproduction (Lindh et al., 2003; St. Pierre, 2000). Populations in younger forests are limited both by the absence of gaps and by slow recovery from declines that occur at the time of clearcut harvest (Halpern, 1989). Abundance and flowering for these species were much higher in old-growth than unthinned stands; thinning led to moderate increases. Our results suggest that thinning may help restore these species in young and mature forests. Achieving population levels like those in old growth forests, however, may be impossible and would certainly require multiple thinning events and the use of patchy prescriptions with gaps.

Other species associated with old growth included ericaceous and orchid species whose old-growth association may reflect reliance on a well-developed forest floor litter layer and/or the availability of mycorrhizal symbionts. These species decline precipitously in response to clearcutting and do not recover noticeably in the open-canopy or young second-growth forest environment (Dyrness, 1973; Halpern, 1989). Ericaceous species such as Chimaphila umbellata rely heavilv on mycorrhizal associations specialized for the decomposition of litter (Read, 1983). Orchids such as G. oblongifolia require mycorrhizae to extract carbon from decomposing litter at least early in their development (Alexander and Hadley, 1985). We believe that species with requirements for specific old-growth associated habitat conditions such as deep litter layers and presence of mycorrhizal symbionts may recover very slowly in second-growth forests, regardless of management intervention.

Young forests differed from old forests not only because they had reduced abundances of late-seral species but also because they had increased abundances of early-seral species. Species with higher frequencies in young stands were generally those that respond positively to canopy removal (Halpern, 1989). These shrubs and herbs occupy high-light microsites in forests but excel in large clearings, reproducing rapidly via vegetative and/or sexual reproduction. Their frequency in our young stands is most likely a legacy of their success during the open-canopy period that followed thinning, rather than evidence of ability to thrive in closed-canopy young-forest conditions. The relatively high abundance of early and mid-seral species in these young stands probably does not preclude re-establishment of old-growth composition: these species appear to decline relatively quickly as stand conditions change.

5. Conclusions

Poage and Tappeiner (2002) suggest that thinning may accelerate the development of old-growth species composition in young stands by creating stand structure more like old growth. In our study sites, thinning did move the composition of the understory somewhat closer to that of old-growth stands, but the formation of old-growth stand structure may not have been the mechanism for this change. Instead, thinning probably affected understory composition by slowing the decline of understory species that would otherwise have occurred following canopy closure. Even if thinning can benefit understory shrub and herb composition, should thinning be widely imposed as a method of accelerating the development of old-growth species composition? Longer-term effects of thinning are unknown, while it is known that old-growth stand structure can eventually develop even from dense unthinned young forests (Winter et al., 2002). Treefall gaps are the aspect of old-growth stand structure that is particularly critical for most forest floor herbs and shrubs. Pre-commercial thinning creates transient openings, but the superior stability of trees in thinned stands may inhibit gap formation over the following decades. Repeated variable-density thinnings (with minimal ground disturbance) may be necessary to simulate gap formation processes. On a longer timescale, however, accelerated growth of larger trees in thinned stands could eventually restore the large tree-fall gaps typical of old-growth forests.

Different thinning prescriptions may be important for different taxa (Muir et al., 2002). Commercial thinning yields merchantable timber and may have large and lasting positive effects on canopy openness and understory cover (Bailey et al., 1998; Thysell and Carey, 2001). Commercial thinning can also encourage the development of understory tree and shrub layers that are important for many taxa, but may facilitate invasion by exotic species, at least temporarily (Bailey et al., 1998). On the other hand, precommercial thinning provides less long-term canopy openness, and therefore less understory tree regeneration than does commercial thinning. However, precommercial thinning accelerates tree growth and can favor late-seral understory species at the expense of low shrubs and weedy species. While no single management strategy will rapidly restore old growth species composition to young stands, a landscapelevel patchwork of thinning intensities and timings may help speed post-disturbance increases in these species.

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