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Initial Response of Understory Vegetation to Three Alternative Thinning Treatments

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This study compares initial understory vegetation response among three thinning treatments and a control in 30- to 50-year-old even-aged Pseudotsuga menziesii *(Mirbel) Franco (Douglas-fir) stands. It was conducted on four sites on the western slope of the central Oregon Cascades. Treatments included a control (no thinning), a light thinning, and two treatments designed to encourage development of understory vegetation: a light thinning with gap creation and a heavy thinning. Vegetation response was measured during the first post-treatment growing season and 5–7 years later. At a treatment-scale, vegetation structure and composition differed between thinned and unthinned stands but varied little among thinning treatments. Thinnings resulted in initial declines of bryophytes, tall shrubs, and low shrubs followed by subsequent recovery and growth. Herbs displayed little initial response, but a release of early-seral species was evident in thinned stands by 5–7 years posttreatment. The addition of gaps resulted in differentiation of plant composition across the gradient from gap center to*

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the thinned forest matrix, but this was only statistically detectable at a within-treatment scale. The causal mechanisms driving initial post-thinning response are discussed to better understand long-term implications and potential roles of thinning in managing for understory vegetation.

KEYWORDS forest management, understory vegetation, thinning, density management, forest structure, forest composition, late-seral, ecosystem management, gaps, Douglas-fir

INTRODUCTION

Understory vegetation plays a key role in forest ecosystems by providing wildlife habitat, epiphyte substrate, and contributing to nutrient cycling and forest productivity (e.g., Yarie, 1980; Carey, 1996; Hagar, McComb, & Emmingham, 1996; Muir et al., 2002; Converse, White, & Block, 2006). Though understory vegetation is a major component of stand structure in old-growth forests in the Pacific Northwest (Alaback, 1982; Spies & Franklin, 1991), it is often scarce in young (~ 30 to 80 yr) managed *Pseudotsuga menziesii* (Mirbel) Franco (Douglas-fir) forests (Franklin et al., 2002). Consequently, young managed forests often have reduced levels of ecological functions provided by an understory layer and potentially offer less suitable habitat for a variety of species, especially species relying on late-seral forest structure (Duffy & Meier, 1992; Carey & Johnson, 1995; Hayes et al., 1997).

Thinning dense young stands has been suggested as a silvicultural tool to increase growth and heterogeneity of understory vegetation by increasing resource availability (Thomas, Halpern, Falk et al., 1999; Lindgren, Ransome, Sullivan et al., 2006; Melten & Fiedler, 2006). However, understory vegetation response to overstory disturbance is complex and varies with initial conditions, disturbance intensity, and its spatial distribution (e.g., Anderson, Loucks, & Swain, 1969; Meier, Bratton, & Duffy, 1995; Berger & Puettmann, 2000; Collins, Wein, & Philippi, 2001). In addition, thinning could potentially produce unintended negative effects, such as increasing abundances of exotic species by creating conditions favorable for invasion (e.g., disturbed soil, increased light availability; Bailey, Mayrsohn, Doescher et al., 1998; Mack et al., 2000; Thysell & Carey, 2000).

Such issues raise questions about the efficacy of traditional thinning prescriptions (i.e., prescriptions with the main objective of improving timber yield) for management of understory vegetation and what types of modifications, if any, result in thinning prescriptions that better achieve understory management objectives. In particular, information is lacking about potential impacts of higher intensity thinnings on understory vegetation and about the role of canopy gaps in influencing understory dynamics due to their localized effect on understory structure and composition (Chen, Franklin, & Spies, 1992; Brandeis, Newton, & Cole, 2001; Godefroid, Koedan, & Rucquij, 2006). To elucidate these uncertainties, we compare effects of a control (no thinning) and traditional low thinning aimed at timber production with two thinning regimes aimed at increasing ecosystem complexity by encouraging development of understory vegetation in young managed forests while also achieving timber goals. Compared to the traditional thinning prescription, both of these regimes result in lower residual stand density, where the additional tree removal is either evenly spread throughout the stand or spatially concentrated in gaps.

In addition, this study investigates vegetation response to thinning at a large-scale (treatment areas average 31 ha), making it directly and immediately relevant to forest managers as well as researchers investigating large-scale ecological questions. While large-scale management studies face many unique challenges in regard to design, implementation, and analysis (Ganio & Puettmann, 2008), they provide a valuable but rare opportunity to gain insights into stand level responses without the need to "scale-up" (Monserud, 2002). This study is one of few that provide ecological responses to treatments applied within an operational (i.e., stand level) context. The size of treatment units and treatment applications ensure incorporation of variability inherent in operational settings into the study results. The results, therefore, are not laden with extrapolation problems commonly associated with small research plots (Bruce, 1977), but are more directly applicable to management conditions within the region.

In this publication we evaluate the response of understory vegetation to different intensities and spatial distributions of operational-scale thinning in young, managed stands by comparing understory vegetation cover and composition among three thinning treatments and an unthinned control. Specifically, we examine short-term (1 yr and 5–7 yr after thinning) impacts on (a) understory vegetation structure, including the herb, low shrub, tall shrub, and forest floor bryophyte cover; and (b) plant community composition. We separately examine the response of exotic species to address concerns regarding potential post-thinning increases in exotic species (e.g., Bailey et al., 1998). Similarly, we evaluate species associated with late-seral habitat to address specific management goals targeted at increasing late-seral habitat (United States Department of Agriculture [USDA] Forest Service, 1994).

Furthermore, the treatment that includes creation of canopy gaps was intended to enhance within-stand heterogeneity. The design of this treatment, its large treatment areas, and its stratified sampling regime permit us to investigate thinning effects for this treatment at a finer spatial resolution (within-treatment scale: inside gap versus gap edge versus thinned forest matrix) in addition to the treatment-level comparisons previously described. Such analysis provides important insights into understory responses to this treatment and allows for a simulation study to assess the impact of higher gap densities. It also provides a linkage between within-stand level and stand level response to highlight the influence of the choice of spatial scales when assessing treatments that are specifically designed to create heterogeneous conditions (Ganio & Puettmann, 2008).

METHODS

Study Description and Design

The study was located in the Willamette National Forest, on the western slope of the Cascade Range in central Oregon. This area fell within the *Tsuga heterophylla* (Raf.) Sarg. (Western Hemlock) zone (Franklin & Dyrness, 1973). The climate of the area is maritime, with mild, wet winters and warm, dry summers. The mean annual precipitation is 230 cm, with only 6% falling between June and August. The average yearly temperature is 10.1°C, with average minimum temperatures ranging from −5.5°C in January to 11.9°C in August and average maximum temperatures ranging from 5.5°C in January to 23.3°C in July (Bierlmaier & McKee, 1989). Soils are generally well-developed, ranging from thin shotty loams/clay loams to thin gravelly loams. Soil series throughout the study area include: Klickitat, Kinney, McCulley, Peavine, Honeygrove, Oxford, Olympic, and Cinebar.

The study used a randomized block design comprised of four blocks: CR (Cougar Reservoir), MC (Mill Creek), CF (Christy Flats), and SC (Sidewalk Creek). Each block contained one replication of four treatments, providing a total of 16 treatment units. Blocks consisted of *P. menziesii* forests that were clearcut harvested between the mid-1940s to mid-1950s and replanted or interplanted by the late 1950s. Criteria for block selection included similarity in overstory composition, stand age, management history, and size (> 56 ha). Within blocks, treatment units were similar in size, elevation, slope, aspect, site index, soil type, and dominant plant association (Beggs, 2005). Across all blocks, treatment units ranged in size from 15 to 53 ha (average = 31 ha), are midelevation (approximately 600–900 m), and had varied slopes and aspects.

Pre-thinning stand conditions were assessed using USDA Forest Service stand exam data collected prior to harvest in 1993. Analysis of these pre-treatment data indicated that initial basal area (BA) and density (trees per hectare [tph]) were similar among treatment units within blocks (data not shown, see Beggs, 2005). Therefore, pre-treatment conditions within each block were assumed to be similar and analysis focused on differences among treatments.

Treatment Description

Each block contained four randomly assigned treatments: Control, Light thinning, Heavy thinning, and Light with Gaps thinning (hereafter abbreviated as Control, Light, Heavy, and LtGaps, respectively). Treatments were applied between 1995 and 1997 (for detailed description of timing of treatments, see Beggs, 2005). At the CR and MC blocks, treatments were applied using a combination of tractor and skyline systems. A ground-based harvester and forwarder system was used at the CF block and a skyline system was used at the SC block.

All thinning treatments used a low-thinning prescription (Smith, Larson, Kelty et al., 1997) with the added direction to maintain diversity by retaining hardwoods and conifer species other than *P. menziesii*. The Control maintained stand densities of approximately 750 tph (density estimates include hardwoods) and provided a reference for stand development without management intervention. The Light reduced stand densities to approximately 300 tph, a density similar to a typical "commercial thin" at the time. The Heavy opened the canopy substantially more—approximately 200 tph—and reflected recent findings that many old-growth stands may have initiated at very low densities (Tappeiner, Huffman, Marshall et al., 1997; Poage & Tappeiner, 2002; but see Winter, Brubaker, Franklin, et al., 2002). The LtGaps treatment was intended to provide within-stand spatial diversity by creating open patches (0.2 ha circular gaps evenly dispersed every 2 ha). The stand matrix was thinned to the same density as the Light treatment, resulting in an overall post-treatment density of approximately 250 tph. If present, overstory hardwood species were retained in gaps to maintain species diversity. However, gaps generally contained none or few trees. For analysis purposes, areas within the LtGaps treatment are stratified into 3 post-treatment habitat units: (a) Gap, (b) Edge, and (c) Stand Matrix (Figure 1).

Sampling Methods

Initial post-treatment vegetation sampling occurred in the summer of 1995, 1996, or 1997, depending on time of harvest completion (for detailed harvest schedule, see Beggs, 2005). Generally, sampling was done during the first post-treatment growing season, with a few exceptions where plots were sampled during the second growing season posttreatment (Beggs). For simplicity, these data will collectively be referred to as "1997" data. Resampling was completed during the summer of 2001, depicting vegetation response 5–7 growing seasons postharvest ("2001" data).

In Control, Light, and Heavy treatment units, approximately 7.5% of the area was sampled using 0.1 ha (17.8-m radius) permanent plots. In these units, transects were systematically placed through treatment units and sampling plots were located randomly along each transect. In LtGaps treatment units, 10 gaps, 10 edges, and 10 areas within the stand matrix (Figure 1) were randomly selected and one plot was placed in each (30 total plots) to ensure adequate sampling of rare habitats (e.g., gaps) that can be undersampled

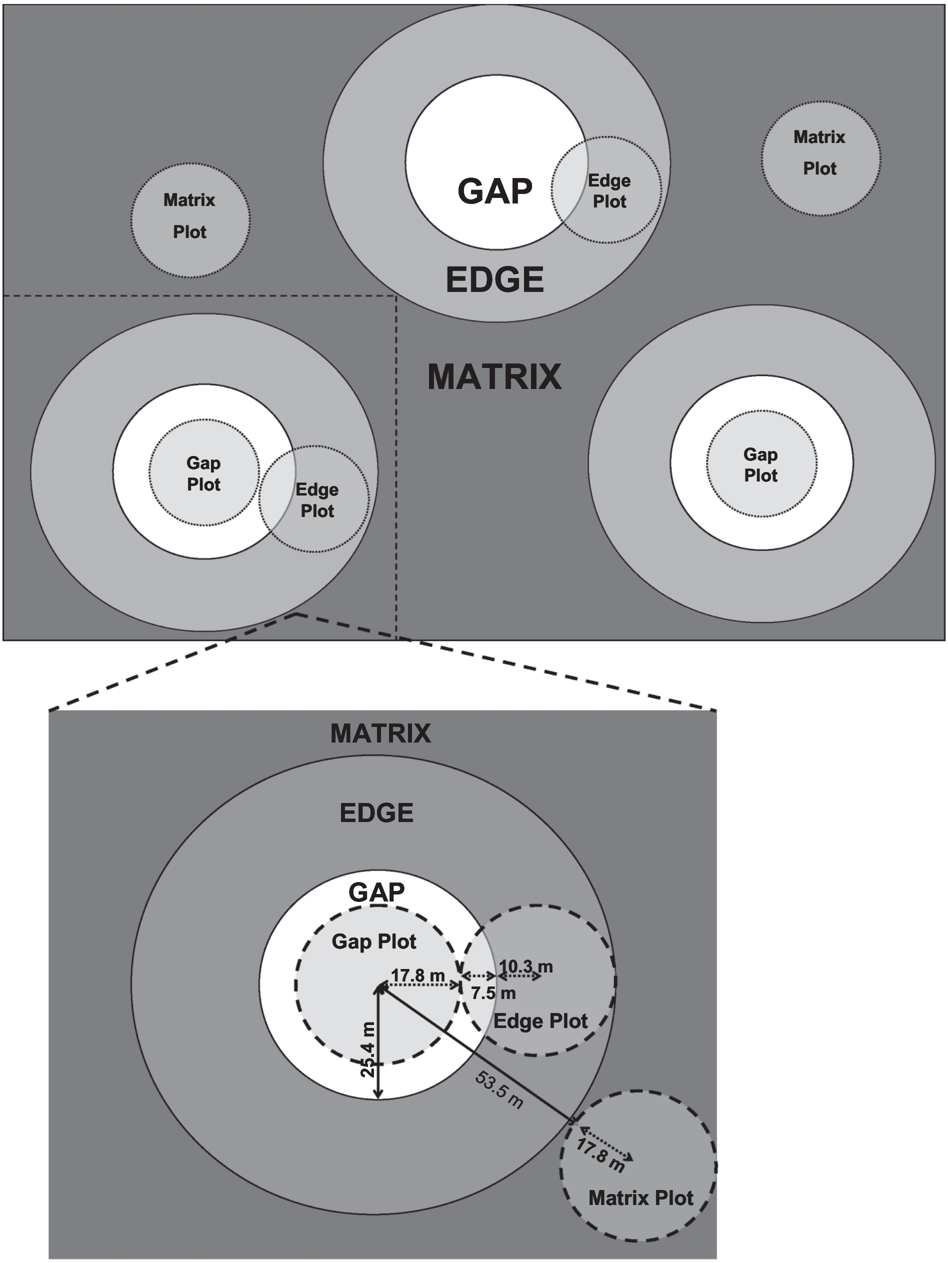

FIGURE 1 Schematic of sampling design and plot layout in LtGaps treatment. Not drawn to scale.

using strict random sampling. Gap plots were centered in the gap, edge plots were centered in a random direction 35.7 m from gap center, and matrix plots were randomly placed throughout the remainder of the treatment (Figure 1).

Within each permanent 0.1-ha circular plot, overstory cover was measured at plot center and at four locations 10.25 m from plot center in each cardinal direction using a “moosehorn” densiometer (Cook, Stutzman, Bowers et al., 1995). The presence of all understory species was also recorded in each plot. Two parallel 14.5-m transects were nested within each plot (see Beggs, 2005 for plot diagram). Eight 0.1 m^2 subplots were evenly spaced along each transect, providing a total of 16 subplots per plot (see Beggs, 2005). In each subplot, cover (percent) of herbaceous and low shrub species, graminoids and forest floor bryophytes; and ground surface features including exposed mineral soil, coarse litter, and fine litter was visually estimated to the closest percentage. Graminoids and bryophytes were identified only as taxonomic groups. Along each transect, the line intercept method was used to estimate understory tall shrub and small tree (diameter at breast height [dbh] < 5 cm) cover. Low shrub/tall shrub designation was based on potential stature of plant at maturity (typically low shrubs < 1 m < tall shrubs). Taxonomic nomenclature followed Hitchcock and Cronquist (1973) in the field and was updated using the USDA PLANTS database (USDA Natural Resources Conservation Service [NRCS], 2004).

Understory Structure

Understory structure was characterized by cover and variation of four vegetative layers: (a) forest floor bryophytes, (b) herbs, (c) low shrubs, and (d) tall shrubs/small trees. The cover of vegetative layers was not measured directly; therefore, cumulative covers of species within each layer were used as a surrogate. Tall ferns (i.e., *Polystichum munitum* [Kaulfuss] K. Presl and *Pteridium aquilinum* [L.] Kuhn) were included in the low shrub layer due to their similar functional and structural roles (Bailey et al., 1998; Hagar, Howlin, & Ganio, 2004).

Understory Composition

Understory composition was described by: (a) overall plant community composition, (b) exotic species abundance, and (c) frequency of late-seral associated species. Overall plant community composition included investigation of abundance of all understory species identified in the study. Exotic species were defined as all species non-native to the western United States (Hitchcock & Cronquist, 1973; USDA, NRCS, 2004). The abundance of exotic species was assessed collectively rather than by individual species. Species identified in previous studies as late-seral associates (Spies, 1991; Halpern & Spies, 1995; Lindh & Muir, 2004) were used as representatives of late-seral species composition.

Data Analysis

Although sparse pre-treatment understory vegetation data existed for the treatment units from initial stand exams, these stand exams utilized a different plot design from post-treatment data, focused on only a few species, and the data was often incomplete. Thus, pre-treatment data were determined to be insufficient for inclusion in a formal analysis. A decision was made to focus the analysis on post-treatment data as robust assessments of treatment effects were still possible through replicated comparisons to a reference condition (the control) since assignment of treatments was unbiased. To accommodate residual concerns about the lack of pre-treatment data, we focused our results and interpretations on species groups or community patterns and used responses of individual species to highlight broad ecological trends rather than to predict species-specific responses to thinning.

Data aggregation: Treatment-scale

Prior to statistical analysis, data were aggregated to the treatment unit level. With the exception of LtGaps treatment units, treatment unit means for cover of each species and ground surface features (e.g., exposed mineral soil) were calculated by averaging plot means. In LtGaps treatment units, Gap, Edge, and Stand Matrix habitats were equally sampled but did not occupy an equal proportion of the total treatment unit area. Therefore, LtGaps treatment unit means were calculated using a weighted average of habitat means. Weights for each habitat were based on the proportion of each habitat in the total treatment unit area. (For example, if the gap center occupied 8.5% of the total treatment unit area, the gap center average value was multiplied by 0.085 to compute the weighted gap center average. The weighted gap center average was then added to the weighted averages of the gap edge and stand matrix to compute a weighted treatment unit mean.) This calculation produced an unbiased estimator necessary for statistical comparison of treatments.

The impacts of thinnings on abundances of late-seral species were difficult to assess because all species had cover values below 1% in all treatment units; therefore, frequency was used as an indicator of occurrence. The 2001 data were used because they represented time of maximum recovery from harvest disturbance. Because frequency in the LtGaps treatment could be overestimated due to relatively intensive sampling in this treatment (Gleason, 1925), the LtGaps treatment was excluded and the frequency analyses were re-run. Results did not change and therefore only results that included the LtGaps treatment are reported.

Statistical analysis: Treatment-scale

Treatment comparisons of abundance and variation (CV) of vegetation layers, abundance of exotic species, and frequency of late-seral species were performed using SAS v. 8.2 statistical software (SAS Institute, 2001). Analysis was performed with ANOVA using a randomized complete block model in conjunction with the Tukey-Kramer adjustment for all multiple comparisons (PROC GLM). A repeated measures analysis was used to examine variation over time in cover of vegetation layers and exotic species. For this analysis, a Time × Treatment interaction was used to determine if the interaction of treatment and time was equal among treatments (PROC MIXED). If this interaction was significant, ANOVA comparisons of change over time among treatments were performed (PROC GLM). Data aggregated to the treatment unit level (n = 16 treatment units) were approximately normal; therefore, no transformations were performed.

An exploratory sensitivity analysis was conducted to determine if doubling or tripling the gap area in the LtGaps treatment altered the response of understory structure to thinning treatments. To do this, a hypothetical treatment was simulated in which the proportional area of gaps in each LtGap treatment unit was doubled (or tripled). The remainder of the treatment unit was considered edge (when gaps area comprised more than approximately 15% of the treatment area, the corresponding increase in edge area eliminated the stand matrix). These proportions were then used to calculate hypothetical weighted means for the LtGaps treatment as previously described and data analyses for understory structure were repeated.

To examine plant community composition, multivariate community analysis was conducted using PC-ORD v. 4.0 (McCune & Medford, 1999). Differences in community composition among treatments and between years (1997 versus 2001) were tested using multi-response blocked permutation procedure (MRBP; Mielke, 1979). In addition to testing for differences among groups, MRBP also provides an effect size, A, that measures within-group agreement relative to random expectation. Composition was tested for differences among all treatments and differences among thinned treatments only. The tests were performed separately for 1997 and 2001 data. Additionally, compositional change in treatments over time was examined by separately testing each treatment for a difference between 1997 and 2001.

To illustrate plant community patterns, an ordination of treatment units in species space was conducted with non-metric multi-dimensional scaling (NMS; Kruskal, 1964). Skewness in the data was adjusted for by deleting species that occurred in less than 2 treatment units and log transforming the data (McCune & Grace, 2002). Zero values were retained by adding 0.001 (derived from McCune & Grace, 2002) to all cover values prior to transformation. Environmental variables were not compared statistically but correlations with axis scores were used to aid interpretation of the ordination (Table 1). Overstory cover and exposed mineral soil were used as surrogates for canopy openness and harvest-related soil disturbance, respectively.

TABLE 1 Average 1997 Cover (%, ± 1 *SD*) of Environmental Variables (Overstory Cover and Exposed Mineral Soil) Used in Interpretation of Ordinations for Each Treatment/Block (Treatment-Scale) and Each LtGaps Habitat/Block (Within-Treatment Scale)

Environmental variable and treatment (treatment-scale) or habitat (within-treatment scale)	Block			
	CR	MC	CF	SC
Treatment-scale				
Overstory cover (%)				
Control	82 (6)	82 (10)	80 (14)	70 (14)
Heavy	25 (13)	45 (20)	17 (9)	31 (19)
Light	50 (15)	62 (15)	37 (15)	53 (18)
LtGaps	40 (15)	50 (14)	36 (14)	42 (20)
Exposed mineral soil cover (%)				
Control	2 (3)	2 (2)	1 (2)	1 (2)
Heavy	6 (9)	4 (8)	8 (7)	1 (2)
Light	9 (12)	2 (5)	9 (8)	2 (6)
LtGaps	5 (2)	2 (1)	4 (1)	5 (3)
Within-treatment scale (LtGaps only)				
Overstory cover (%)				
Matrix	48 (13)	60 (8)	42 (19)	44 (16)
Edge	42 (19)	49 (12)	39 (20)	46 (16)
Gap	1 (3)	15 (25)	0 (0)	5 (12)
Exposed mineral soil cover (%)				
Matrix	2 (3)	1 (2)	10 (3)	0 (9)
Edge	6 (7)	2 (4)	2 (1)	6 (12)
Gap	3 (4)	6 (7)	10 (12)	3 (7)

Note. Values for 2001 (not shown) followed similar patterns. CR = Cougar Reservoir block; MC = Mill Creek block; CF = Christy Flats block; SC = Sidewalk Creek block.

Indicator species analysis (Dufrêne & Legendre, 1997) was used to identify species indicative of treatments and also of years. Due to lack of strong differentiation among thinned treatments (see Results), comparisons were made only between "thinned" (i.e., all thinned treatments were grouped) and "control." Treatment (i.e., Control and thinned) indicator species were identified separately for 1997 and 2001. Temporal (i.e., 1997 and 2001) indicator species were identified separately for Control and thinned stands.

DATA AGGREGATION: WITHIN-TREATMENT SCALE (LTGAPS ONLY)

Stratified sampling of habitats within the LtGaps treatment units also permitted within-treatment examinations of impacts of small-scale spatial variation in the overstory on understory structure and composition. For this analysis, each LtGap habitat unit (Gap, Edge, and Matrix) was treated as a separate treatment unit (n = 12; 3 habitats in each of 4 blocks). Habitat means for overstory cover, ground surface features, individual species, vegetative layers, exotics, and late-seral species were calculated by averaging plot means within each habitat.

STATISTICAL ANALYSIS: WITHIN-TREATMENT SCALE (LTGAPS ONLY)

Within-treatment scale statistical analyses of vegetative layers, late-seral and exotic species, and plant community composition for the LtGaps treatment (including MRBP and indicator species analysis) employed the same techniques as described for treatment-scale analyses. At the within-treatment scale, habitat means were used in place of treatment unit means. For univariate analyses, data aggregated to the habitat unit level were approximately normal ($n = 12$); therefore, no transformations were performed.

An ordination of habitat units in species space was also used to illustrate compositional variation among habitats. Methods and data were identical to those described for the treatment-scale analysis, except that a value of 0.01 (instead of 0.001) was added to cover values of all species prior to log transformation in order to retain zero values (derived from McCune & Grace, 2002). Values for environmental variables that facilitated interpretation of the ordination are displayed in Table 1.

RESULTS

Structure—Treatment-Scale

Five to 7 years following thinning, most understory layers have recovered from initial decline after harvest (Figure 2a). Tall and low shrubs in all thinned treatments and bryophytes in the Heavy treatment had significantly less cover than the Control in 1997 but recovered to levels similar to that of the Control by 2001. Tall shrub cover in thinned treatments still appeared much lower than in the Control by 2001 but was not statistically different due to high variability among blocks. Unlike other vegetation layers, herbs did not undergo initial decline following harvest. In fact, herbaceous cover in all thinned treatments increased more between 1997 and 2001 than in the Control (Time × Treatment interaction: $p = .008$; Treatment versus Control comparisons of change over time—Heavy: $p = .010$; Light: $p = .032$; LtGaps: $p = .011$). The same was true for low shrub cover (Time × Treatment interaction: $p < .001$; Treatment versus Control comparisons of change over time—Heavy: $p = .012$; Light: $p = .020$; LtGaps: $p = .024$). Following thinning, variation in abundance of most vegetation layers was similar among all treatments with a few exceptions. In 1997, there was suggestive evidence that variation of bryophytes was higher in the Heavy thinned than the Control ($p = .072$). By 2001, bryophytes were more variable in the LtGaps than the Control ($p = .018$) and there was suggestive evidence that low shrubs were more variable in the Control than the LtGaps ($p = .061$).

The sensitivity analysis that explored impacts of increasing the number of gaps within LtGaps suggested that doubling or tripling the number of gaps would not have resulted in different patterns in understory structural

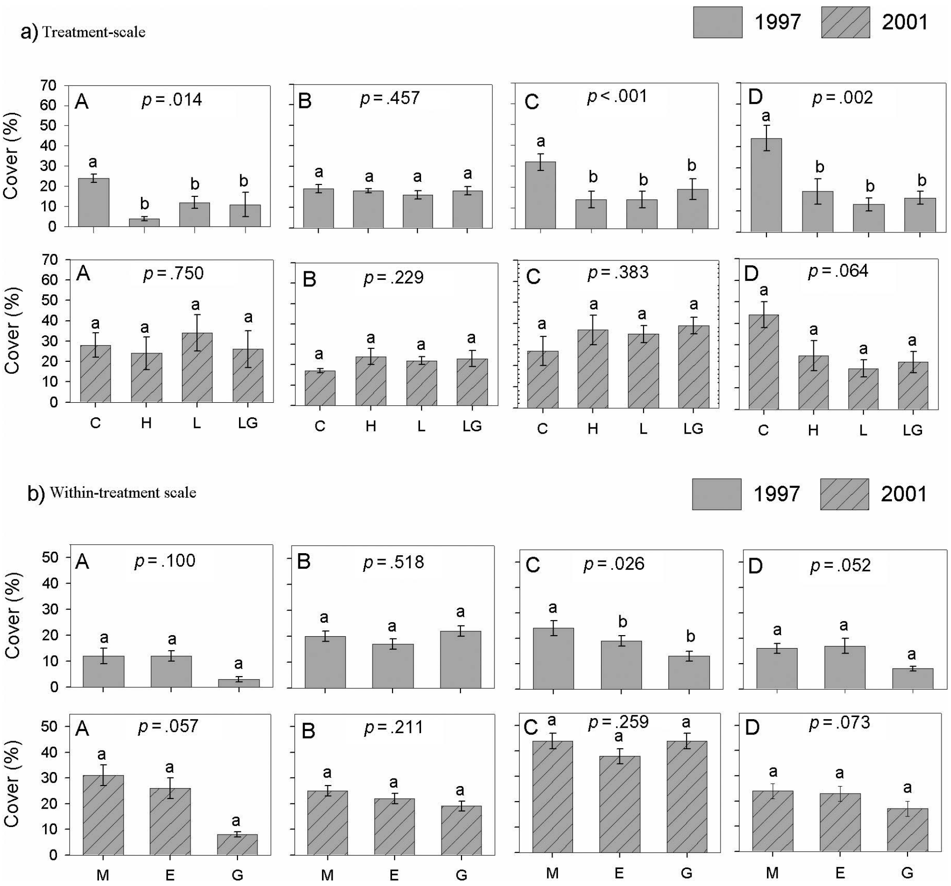

FIGURE 2a–2b 1997 and 2001 post-treatment cover (%) of (A) bryophytes, (B) herbs, (C) low shrubs, and (D) tall shrubs for (a) all treatments (treatment-scale) and (b) LtGaps habitats (within-treatment scale). Error bars represent 1 standard error. Letters indicate differences among treatments; treatments with same letters do not differ at $p \leq .05$ level. ANOVA p-value is for overall test of difference among treatments. (C = Control, H = Heavy, L = Light, LG = LtGaps; M = Matrix, E = Edge, G = Gap).

response. However, it must be cautioned that these simulation results were only exploratory and rely on the assumption that gaps act independently and don't influence each other, even at higher densities.

Composition—Treatment-Scale

PLANT COMMUNITIES

Understory plant communities showed significant differentiation among all treatments but no differences among thinned treatments (MRBP; All treatments—1997: p = .002; 2001: p = .008; thinned treatments only—1997: p = .165; 2001: p = .709), indicating that the major compositional distinction was between thinned treatments and the Control. The compositional differentiation among all treatments was similar in 1997 (A = .06) and 2001 (A = .06). Similarly, there was little difference in compositional differentiation among only thinned treatments (excluding Control) in 1997 (A = .01) and 2001 (A = −.01). Over time, plant communities did not change in the Control ($A < .01$, $p = .473$), while composition changed significantly in all thinned treatments (Light: A = .12, p = .030; Heavy: A = .14, p = .031; LtGaps: A = .14, p = .031).

The final three-dimensional ordination (p = .0196, final stress = 13.521, final instability = .00001, 67 iterations) illustrated complex patterns of understory composition that were related to block, treatment, and time. Three axes accounted for 84.6% of the total variation in the raw data. Axis 3, which was weakly related to differences in composition among blocks, explained the least amount of variation; therefore, only Axis 1 and Axis 2 are discussed.

The ordination displayed a separation of blocks, indicating that overall species composition was dependent upon conditions specific to each block (Figure 3). In addition, the magnitude of compositional response among

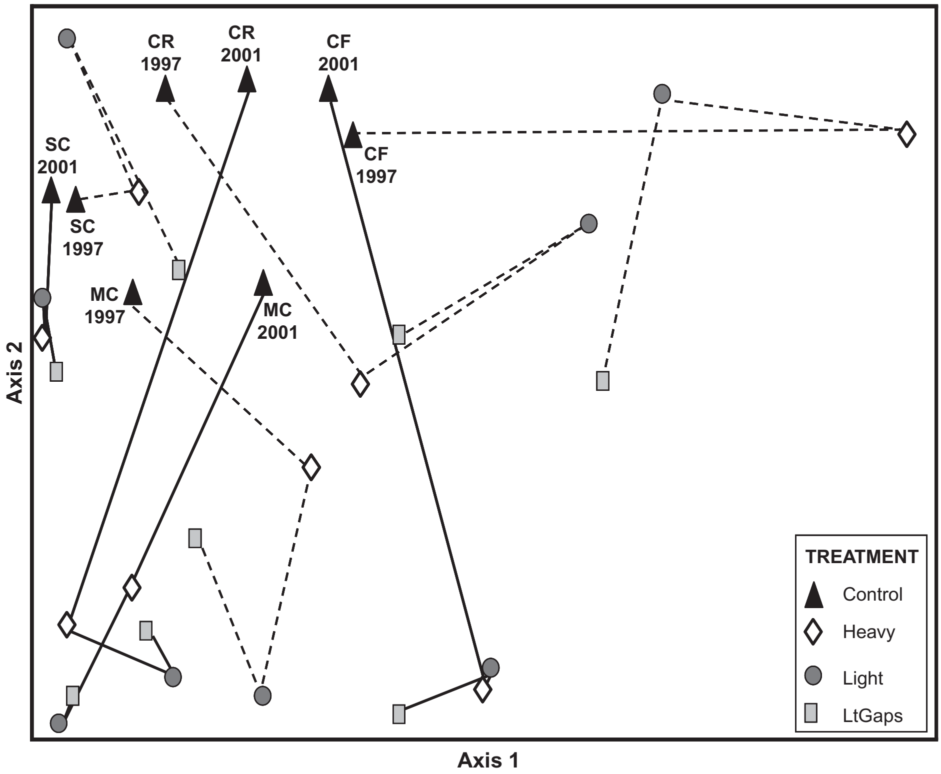

FIGURE 3 Ordination of treatment units on abundance of all species (Axis 1 and Axis 2; Axis 3 not shown). Vectors connect treatment units within each block for 1997 (dashed line) and 2001 (solid line). Labels next to Control treatments designate groups by block/year. (CR = Cougar Reservoir block; MC = Mill Creek block; CF = Christy Flats block; SC = Sidewalk Creek block).

thinned treatment units varied by block and was likely associated, at least in part, with differences in harvest disturbance (Table 1). Within each block, however, the direction and magnitude of compositional response was similar among 1997 thinned treatment units and among 2001 thinned treatment units. While clear patterns of differentiation among thinning treatments were not readily apparent, separation of all thinned treatment units from Controls was evident. For 1997 treatment units, the separation of thinned treatments and Controls was related to differences in canopy conditions (overstory cover: $r = -.5$; Table 1) and harvest disturbance (exposed mineral soil: $r = .73$; Table 1), with 1997 thinned treatment units having open canopies and more exposed mineral soil relative to Controls. Accordingly, species composition in 1997 thinned treatment units was dominated by early-seral annual and biennial herbaceous species and species indicative of disturbed environments while Controls harbored more shade-tolerant bryophytes and a few late-seral associated herbs (Table 2). A shift in the directional response was apparent between 1997 and 2001 thinned treatments units. This was due mostly to a release of several early-seral herbs (Table 2). Although not statistically significant (see above), 2001 thinned treatment units tended to cluster closer together than 1997 thinned treatment units, within blocks, suggesting an increasing similarity of composition among thinned stands over time.

Indicator species analysis further clarified patterns apparent in the ordination. Species indicative of Controls denoted shade and undisturbed soil (e.g., *Trillium ovatum* Pursh) while species indicative of thinned treatments suggested relatively high light levels and disturbed soil (e.g., *Chamerion angustifolium* L. Holub ssp. *Angustifolium*; Table 3). Many early-seral perennial species were also indicative of 2001 thinned treatment units but not 1997 thinned treatment units or controls (Table 3, Table 4), confirming the release of early-seral perennial species and recovery of low-shrubs in 2001 thinned treatment units.

EXOTIC SPECIES

Thinning did not significantly promote establishment or growth of exotic species (1997: $p = .10$; 2001: $p = .51$). Overall, cover of exotic species was very low in all treatments (all treatments averaged close to 0% in 1997 and 2001, except for the 2001 LtGaps, which averaged 1%). Although not statistically different, the LtGaps had the highest average abundance of exotic species, mostly due to one localized invasion of *Cytisus scoparius* (L.) Link.

LATE-SERAL SPECIES

Late-seral species cover was generally very low and was unaffected by thinning. The only exceptions were obligate mycotrophs, of which two

TABLE 2 Correlations (− = Negative Correlations; + = Positive Correlations) of Species With Axes for Treatment-Scale Ordination (Figure 3) and Within-Treatment Scale Ordination (Figure 4)

Correlation	Axis 1	Axis 2
Treatment-scale		
−	Bryophytes (−.63)	Anaphalis margaritacea (L.) Benth. (−.51)
	Chimaphila umbellata (−.46)	Campanula scouleri Hook. ex A. DC. (−.81)
	Corylus cornuta Marsh. (−.44)	Chamerion angustifolium (−.73)
	Gaultheria shallon (−.91)	Galium triflorum Michx. (−.65)
	Mahonia nervosa (Pursh) Nutt. (−.70)	Hypericum perforatum L. (−.58)
	Rhododendron macrophyllum D. Don ex G. Don (−.53)	Rubus parviflorus Nutt. (−.81)
	Vaccinium parvifolium Sm. (−.59)	Rubus ursinus Cham. & Schlecht (−.68)
	Vancouveria hexandra (Hook.) Morr. & Dcne. (−.66)	Trientalis borealis Raf. (−.73)
+	Cirsium spp. P. Mill (.30)	Chimaphila menziesii (.23)
	Epilobium watsonii Barbey (.38)	Chimaphila umbellata (.52)
	Gnaphalium microcephalum Nutt. (.46)	Rubus nivalis Dougl. ex. Hook. (.20)
	Lactuca serriola L. (.25)	Taxus brevifolia Nutt. (.46)
	Ribes lobbii Gray (.24)	Trillium ovatum (.25)
	Senecio sylvaticus (.58)	Xerophyllum tenax (Pursh) Nutt. (.31)
Within-treatment scale		
−	Gaultheria shallon (−.90)	Epilobium minutum Lindl. ex Lehm. (−.38)
	Mahonia nervosa (−.73)	Gnaphalium spp. L. (−.33)
	Trillium ovatum (−.41)	Lactuca serriola (−.41)
	Vaccinium parvifolium (−.78)	Luzula spp. DC. (−.35)
	Vancouveria hexandra (−.67)	Senecio sylvaticus (−.69)
+	Cirsium spp. (.64)	Hypericum perforatum (.71)
	Epilobium watsonii (.61)	Rubus leucodermis Dougl. ex Torr. & Gray (.69)
	Gnaphalium microcephalum (.54)	Rubus parviflorus (.64)
	Lotus purshianus F.E. & E.G. Clem. (.48)	Rubus ursinus (.68)
	Rubus leucodermis (.41)	Trientalis borealis (.76)
	Senecio sylvaticus (.36)	Whipplea modesta Torr. (.70)

Note. Axis 3 correlations not shown.

out of three species that were evaluated declined following thinning (Table 5). For example, *Chimaphila umbellata* (L.) W. Bart. had lower frequency in all thinned treatments relative to the Control (Heavy: $p = .005$; Light: $p = .001$; LtGaps: $p = .001$). The same was true for *Goodyera oblongifolia* Raf. (Heavy: $p < .001$; Light: $p = .001$; LtGaps: $p < .001$). *Chimaphila menziesii* (R. Br. ex D. Don) Spreng. also had marginally, but not significantly, lower frequency in the LtGaps treatment than the Control ($p = .089$).

TABLE 3 Indicator Species of Treatments/Habitats for Control and Thinned (All Combined) Treatments (Treatment-Scale) and Edge/Gap /Matrix Habitats (Within-Treatment Scale) From 1997 and 2001

	Year	Species	Group	IV
Treatment-scale	1997	Bryophytes	Control	54
		Chimaphila menziesii	Control	82
		Chimaphila umbellata	Control	80
		Mahonia nervosa	Control	53
		Rubus nivalis	Control	79
		Thuja plicata Donn ex. D. Don	Control	64
		Trillium ovatum	Control	71
		Viola sempervirens Greene	Control	56
		Cirsium spp.	Thinned	78
		Galium triflorum	Thinned	68
		Senecio sylvaticus	Thinned	92
	2001	*Boykinia occidentalis* Torr. & Gray	Control	63
		Chimaphila umbellata	Control	69
		Holodiscus discolor (Pursh) Maxim.	Control	73
		Taxus brevifolia	Control	76
		Trillium ovatum	Control	70
		Campanula scouleri Hook. ex A. DC.	Thinned	75
		Cirsium spp.	Thinned	83
		Chamerion angustifolium	Thinned	84
		Galium triflorum	Thinned	59
		Graminoids	Thinned	65
		Pteridium aquilinum	Thinned	56
		Rubus leucodermis	Thinned	92
		Rubus ursinus	Thinned	55
		Trientalis borealis	Thinned	70
		Whipplea modesta	Thinned	55
Within-treatment scale	1997	–	Matrix	–
		Chrysolepis chrysophylla (Dougl. ex. Hook.) Hjelmqvist	Edge	68
		Cirsium spp.	Gap	69
		Epilobium parviflorum Schreb.	Gap	69
		Senecio sylvaticus	Gap	58
	2001	*Maianthemum stellatum* (L.) Link	Matrix	67
		Rosa gymnocarpa Nutt.	Edge	69
		Epilobium watsonii	Gap	91
		Cirsium spp.	Gap	74
		Rubus leucodermis	Gap	61
		Rubus parviflorus	Gap	69

Note. IV = Indicator value; $p \leq .05$ for all species.

Structure—Within-Treatment Scale (LtGaps Only)

Overall, the comparison of conditions in gaps, edges, and forest matrices paralleled treatment-scale trends. However, several important distinctions indicated that the assessment of the smaller spatial scale for the LtGaps

TABLE 4 Indicator Species of 1997 and 2001 for Control and Thinned (All Combined) Treatments (Treatment-Scale) and Edge/Gap/Matrix Habitats (Within-Treatment Scale)

	Treatment/ Habitat	Species	Group	IV
Treatment-scale	Control	–	1997	–
		–	2001	–
	Thinned	*Senecio sylvaticus*	1997	87
		Achyls tryphylla	2001	53
		Alnus rubra Bong.	2001	50
		Bryophytes	2001	54
		Campanula scouleri	2001	73
		Chamerion angustifolium	2001	61
		Fragaria virginiana Duchesne	2001	63
		Graminoids	2001	62
		Hieracium albiflorum Hook.	2001	69
		Mycelis muralis (L.) Dumort.	2001	59
		Linnaea borealis L.	2001	54
		Mahonia nervosa	2001	52
		Polystichum munitum	2001	53
		Pteridium aquilinum	2001	57
		Rubus leucodermis	2001	92
		Rubus parviflorus	2001	59
		Rubus ursinus	2001	54
		Symphoricarpos hesperius G.N. Jones	2001	83
		Trientalis borealis	2001	64
		Viola sempervirens	2001	54
		Whipplea modesta	2001	61
Within-treatment scale	Matrix	–	1997	–
		–	2001	–
	Edge	–	1997	–
		Whipplea modesta	2001	65
	Gap	*Senecio sylvaticus*	1997	100
		Gnaphalium microcephallum	2001	100
		Graminoids	2001	64
		Rubus leucodermis	2001	100
		Rubus parviflorus	2001	85
		Rubus ursinus	2001	56
		Trientalis borealis	2001	74

Note. IV = Indicator value; $p \leq .05$ for all species.

treatment is an important factor influencing the interpretation of the study results.

At a within-treatment scale, thinning resulted in short-term differentiation of vegetation layers (Figure 2b). Low shrub cover in the Gap was less than that of the Edge and Stand Matrix in 1997, but this difference was not apparent by 2001. Similarly, tall shrub cover was marginally less in the Gap than the Edge (p = .07) in 1997, but was comparable in both habitats by 2001. Bryophyte cover did not differ in 1997 but was marginally less in the Gap than the Stand Matrix by 2001 (p = .06).

TABLE 5 ANOVA Tests for Overall Differences in Frequency (2001 Data) of Late-Seral Species Among Thinning Treatments and Control (Treatment-Scale) and Among LtGaps Habitats (Within-Treatment Scale)

Species	Treatment-scale *p*-value	Within-treatment scale *p*-value
Achyls tryphylla	0.696	0.020
Adenocaulon bicolor	0.911	0.023
Anemone deltoidea	0.169	0.043
Blechnum spicant (L.) Sm.	0.573	0.150
Chimaphila menziesii	0.099	0.046
Chimaphila umbellata	0.001	0.010
Cornus canadensis L.	0.421	0.371
Coptis laciniata Gray	0.299	0.770
Dicentra formosa	0.489	0.086
Goodyera oblongifolia	< 0.001	0.126
Linnaea borealis	0.396	0.144
Maianthemum racemosum (L.) Link	0.802	0.140
Synthyris reniformis (Dougl. ex. Benth). Benth	0.451	0.125
Tiarella trifoliata L.	0.209	0.126
Vancouveria hexandra	0.915	0.367

Composition—Within-Treatment Scale (LtGaps Only)

PLANT COMMUNITIES

Understory plant communities showed significant differentiation in composition among habitats (MRBP; 1997: $p = .014$; 2001: $p = .005$). Compositional differentiation among habitats was larger in 2001 ($A = .11$) than in 1997 ($A = .05$) data. A significant change of plant communities over time was also evident in all habitats (Stand Matrix: $A = .11$, $p = .041$; Edge: $A = .13$, $p = .033$; Gap: $A = .19$, $p = .031$).

The final three-dimensional ordination ($p = .0196$, final stress = 12.6, final instability = .00001, 68 iterations) illustrated patterns in plant community composition related to differences among the post-treatment habitats, blocks, and time. The three axes accounted for 83.3% of the total variation in the raw data. Axis 3, which was weakly related to differences in composition among blocks, explained the least amount of variation; therefore, only Axis 1 and Axis 2 are presented.

Similar to the treatment-scale ordination, a separation of blocks indicated that plant community composition was strongly related to conditions specific to each block (Figure 4). In addition, the magnitude of compositional response among habitat units varied among blocks and was probably related, at least in part, to the degree of harvest disturbance (exposed mineral soil: $r = .68$; Table 3). Within each block, however, the magnitude and direction of compositional response was similar in 1997 and 2001, with Gaps differentiating from the Edge and Stand Matrix. This separation was closely related to canopy cover (overstory cover: $r = -.57$; Table 1) and harvest disturbance (exposed mineral soil: $r = .68$; Table 1). Open conditions near the gap center favored plant assemblages consisting mostly of light-demanding early-seral herbs and shrubs (Table 2), while the Stand Matrix and Edge contained more shade-tolerant shrubs and herbs (Table 2). A strong separation of 1997 and 2001 habitat units also illustrated the dynamic change in plant communities at small scales. Similar to the treatment-scale, this distinction was mostly due to release of several early-seral species by 2001, especially in the Gaps (Table 2). Unlike at the treatment-scale, however, where composition of thinned treatments did not differentiate over time (Figure 3), at the within-treatment scale, the differences between gap, edges, and stand matrix became more distinct over time (Figure 4).

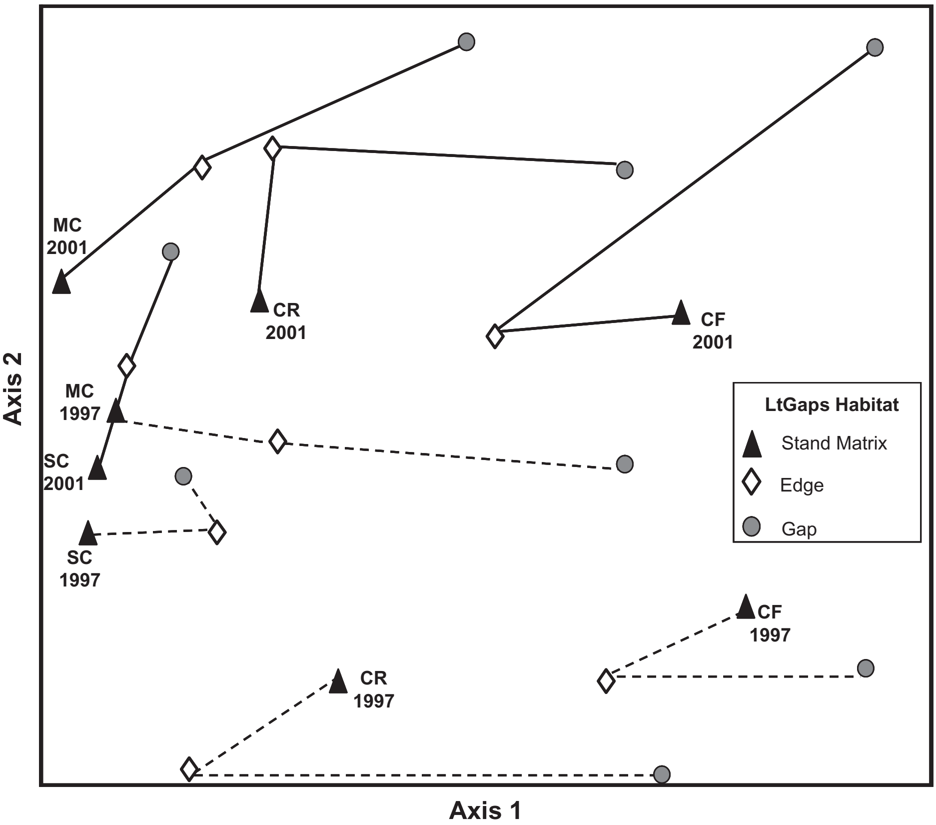

FIGURE 4 Ordination of LtGaps habitats on abundance of all species (Axis 1 and Axis 2; Axis 3 not shown). Vectors connect 1997 (dashed line) and 2001 (solid line) habitat units within each block. Labels next to Matrix habitats designate groups by block/year. (CR = Cougar Reservoir block; MC = Mill Creek block; CF = Christy Flats block; SC = Sidewalk Creek block).

Patterns in the ordination were supported by indicator species analysis. Early-seral species indicative of high light levels favored the Gap while more shade tolerant species favored the Stand Matrix and Edge (Table 3). In addition, two annual species indicative of Gaps in 1997 were replaced by herbaceous and woody perennials by 2001 (Table 3). A release of early-seral species was also evident between 1997 and 2001 and was most apparent in the Gap (Table 4).

EXOTIC SPECIES

Except for one localized occurrence, thinning yielded little differentiation in exotic cover among habitats (1997 average cover was 0%, 0%, and 1% for Matrix, Edge, and Gap, respectively; 2001 average cover was 0%, 1%, and 5% for Matrix, Edge and Gap, respectively). Though the Gap consistently had the highest abundance of exotic species, the difference among habitats was only marginally significant in 1997 (p = .06) and was insignificant in 2001 (p = .31). Exotic species invasions were generally limited to species that did not contribute large amounts of cover (e.g., *Senecio sylvaticus* L.) and the results were skewed by a single invasion of *C. scoparius* in the Gap of the MC block (Cover of *C. scoparius* in the MC block: S. Matrix = 0%; Edge = 3%; Gap = 14%; Not present in LtGaps treatment of other blocks).

LATE-SERAL SPECIES

Differentiation among habitats influenced occurrence of several late-seral species. Of species that differed in occurrence among habitats (Table 5), most responded unfavorably to gaps. For example, frequencies of *Adenocaulon bicolor* Hook., *C. menziesii*, and *Achyls triphylla* (Sm.) DC. were higher in the Edge than in the Gap (*A. bicolor*: p = .059; *C. menziesii*—Edge: p = .053; *A. triphylla*: p = .017). There was also suggestive evidence that frequencies of *C. umbellata* and *Anemone deltoidea* Hook. were higher in the Edge than the Gap (p = .088 and p = .095, respectively). *A. bicolor* and *A. deltoidea* also occurred more frequently in the Stand Matrix than the Gap (p = .024 and p = .046, respectively) and there was suggestive evidence that frequency of *C. menziesii* was higher in the Stand Matrix than the Gap (p = .087). *Dicentra formosa* (Haw.) Walp. never occurred in the Gap and was present in the Edge and Stand Matrix, but comparisons among habitats were insignificant.

DISCUSSION

Understory vegetation of thinned stands appeared to still be affected by harvesting disturbance, limiting our assessment of alternative thinning treatments as effective tools to spur development of late-seral conditions in young forests to the initial recovery phases. However, several trends appeared that likely influence long-term development of understory vegetation. Overall, understory vegetation did not respond drastically different to any of the three thinning prescriptions, but all types of thinning significantly altered understory vegetation of young, managed forests relative to unthinned forests by influencing canopy openness and ground disturbance. Furthermore, the influence of canopy gaps on vegetation patterns was evident at a within-treatment scale. These results will likely have long-term implications for understory development and are, therefore, critical to understanding the role of thinning intensity and patterns in forest management.

Structure

As suggested by the correlation of vegetation patterns with ground disturbance, initial reductions in most vegetation layers were likely a product of harvest disturbance, with falling trees and heavy equipment probably causing considerable stem breakage and mortality of tall and low shrubs. In addition to the harvesting disturbance, it was likely that the initial decline of forest floor bryophytes following heavy thinning was attributable to desiccation resulting from the sudden extreme opening of the overstory canopy and loss of shrub cover. Reduction of canopy cover can result in higher air temperatures, lower humidity, and elevated evaporative moisture loss on the forest floor (Green, Grace, & Hutchings, 1995; Hannerz & Hanell, 1997).

The initial response of vegetation structure to thinning was very dynamic. Despite initial declines, abundance of most vegetation layers in thinned stands was similar to the Control within 5–7 years of harvest. Evidence from other studies suggests that most strata may continue to increase due to enhanced resource levels following thinning, but long-term data will be necessary to evaluate this assumption (Alaback, 1982; Tappeiner & Zasada, 1993; Small & McCarthy, 2002).

Recovery of tall shrubs appeared at this time to be slower than that of other strata. Tall shrubs generally occupy an elevated position in the forest canopy, consequently increasing their susceptibility to harvest damage. Thus, most recovery was likely resprouting and growth from smaller stems rather than expansion of larger plants. This is an important distinction because the ecological role of many tall shrubs is strongly tied to their size. Tall shrubs of differing heights enhance connectivity through the forest canopy, thereby supplying wildlife nest and forage sites (Carey, 1996; Hagar et al., 1996). Fruit production is also generally greater for larger plants (Huffman & Tappeiner, 1997) and old, large shrub branches host several bryophytic communities (Rosso, 2000). Therefore, although cover of tall shrubs may be nearing that of unthinned stands, smaller plant sizes may limit their value as structure and habitat.

Composition

Overall, composition of thinned stands was quite distinct from unthinned stands and, when assessed for the whole treatment area, was relatively unaffected by thinning intensity or canopy gaps (Figure 3). The compositional shift following thinning was mostly related to the release of several early-seral subordinate forest herbs in thinned stands (Halpern, 1989). Unthinned stands harbored shade-tolerant species while species indicative of high light environments and disturbed soil dominated thinned stands.

In thinned stands, patches of exposed mineral soil and an open canopy (Davis, Puettmann, & Tucker, 2007) likely increased resource availability and facilitated seed dispersal, germination, and establishment, thereby permitting opportunistic annual species to quickly colonize and potentially displace less competitive species (Grime, 1979; Alaback & Herman, 1988; Meier, Bratton, & Duffy, 1995; Harrington & Edwards, 1999). A rapid post-disturbance peak in annuals has been noted in similar ecosystems and may also be linked in part to rooting systems adapted to capitalize upon post-disturbance nutrient flushes (West & Chilcote, 1968; Schoonmaker & McKee, 1988; Halpern, 1989; Antos & Halpern, 1997).

The dominance of annuals was short-lived, however, with understory dominance shifting toward early-seral perennial forest species by 5–7 years after thinning (Halpern, 1989). This suite of species is more efficient at nutrient uptake than annuals (Antos & Halpern, 1997). In addition, rapid seed dispersal, early development of horizontal roots, and clonal growth allow many early-seral perennials to quickly occupy a disturbed site and exclude other species possessing slower reproductive mechanisms (Antos & Zobel, 1984; Meier, Bratton, & Duffy, 1995).

While thinning encouraged recruitment and growth of several species, most late-seral associated species exhibited no response to thinning. Only three late-seral species—all obligate mycotrophs (Castellano & Trappe, 1985)—declined in frequency following thinning. It must be noted, though, that all late-seral species were relatively uncommon and thus absolute values of treatment differences are small. Because of the rarity of these species, pre-treatment data would have been most helpful for this aspect of the study. Thus, analysis of these species should be viewed cautiously. However, our results agree with the general understanding that mycotrophic species are sensitive to disturbances, as has been shown in a variety of studies (Halpern, 1989; Halpern & Spies, 1995; Roberts & Zhu, 2002; Lindh & Muir, 2004). Specific microhabitat features, such as deep litter layers, may be critical for survival of these species (Castellano & Trappe, 1985; Lindh & Muir, 2004). Changes in moisture and light levels (Green, Grace, & Hutchings, 1995; Parker, Elliott, Dey et al., 2001), as well as soil disturbance (Buckley, Crow, Nauertz et al., 2003), could disrupt microhabitat components, resulting in the reduced presence of such species in thinned stands. Displacement by other generalist species may also be a contributing factor (Grime, 1979; Meier, Bratton, & Duffy, 1995). The lack of positive response by late-seral associated species also suggests that conditions in thinned stands are not favorable enough to encourage their expansion. Given that most thinned stands are only beginning to display elements of late-successional overstory structure (Davis, Puettman, & Tucker, 2007) and lag-times between changes in structure and vegetation response can exist (Thomas, Halpern, Falk et al., 1999), a lack of positive response was not unexpected at this early stage.

Vegetation composition of thinned stands was not greatly influenced by invasion of exotic species, with the exotic species that were present being mostly transient species (Schoonmaker & McKee, 1988). This contrasts with results of other studies (e.g., Bailey, Mayrsohn, Doescher et al., 1998; Thysell & Carey, 2000; Parker et al., 2001), but many studies that found increases in exotic species examined the impact of exotic grass species (Bailey, Mayrsohn, Doescher et al., 1998; Thysell & Carey, 2000). While exotic grasses did not appear to be a major component of the vegetation at our sites (personal observation), we did not identify grasses to species and, therefore, may have slightly underestimated the influence of exotic species. A sole exception to the minimal impact of exotic species was the invasion by the noxious weed, *C. scoparius*, in a single LtGaps treatment unit. This unit was located near a major highway and a community refuse center, both of them sources of abundant seed. Our results lead to the hypothesis that while increased resource availability and soil disturbance may provide favorable conditions in thinned stands favorable for exotic species (Mack et al., 2000; Sakai et al., 2001), invasion of exotic species is primarily dependent upon availability of propagules and local seed source (Perendes & Jones, 2000; Thysell & Carey, 2000).

Reduced overstory density was likely not the only factor influencing post-treatment species composition. Pre-treatment conditions also impacted current composition (Hughes & Fahey, 1991, Fahey & Puettmann, 2007). Though comprehensive pre-treatment data on understory composition was not available, inventory data indicated that the SC block was distinguished from other blocks by its more xeric plant associations (Beggs, 2005) and high abundance of *Gaultheria shallon* Pursh (data not shown). At this site, vegetation composition of thinned stands was differentiated from the unthinned stand, but the divergence was not nearly as prominent as in other blocks. These results reinforce previous findings that overstory cover strongly influences abundance of vegetation, but composition is also strongly driven by factors such as soil moisture, site quality, and site history (McCune, 1982; Moore & Vankat, 1986; He & Barclay, 2000). In addition, the degree of ground disturbance likely differed among harvest systems and was helpful in understanding vegetation response (Buckley, Crow, Nauertz et al., 2003; Berger, Puettmann, & Host, 2004). However, direct comparisons of harvesting systems were not possible in this study as documentation was insufficient to assign specific plots to harvesting systems.

Influence of Gaps

The interpretation of the role of gaps on vegetation development varied with the spatial scale of the analysis. At a treatment-scale, impacts of canopy gaps on understory vegetation were not statistically detectable. However, examining the impact of gaps at a smaller spatial scale (within-treatment) revealed that gaps impart significant, but apparently localized influence on understory vegetation (Fahey & Puettmann, 2008).

Associations of vegetative layers and species with different habitat areas in the LtGaps suggest responses to differing resource and environmental conditions (Whittaker, 1975; Fahey & Puettmann, 2007). This was likely due to variation in ground disturbance and resource availability (Fahey & Puettmann, 2008). Habitat in gaps likely offered high levels of light and soil resources (Moore & Vankat, 1986; Gray, Spies, & Easter, 2002), encouraging recruitment and growth of several early-seral herbs. Open conditions probably also facilitated seed dispersal (Thompson & Wilson, 1978) and spurred vigorous vegetative reproduction via stolons and rhizomes common for several of these species (Antos & Zobel, 1984; Moore & Vankat). Conversely, lower light availability in the Stand Matrix and Edge relative to the Gap favored species that may be susceptible to dessication (e.g., bryophytes), can tolerate shade, and can allocate more resources to below-ground development (Tappeiner & Zasada, 1993; Huffman & Tappeiner, 1997).

A few late-seral associated species exhibited high affinity for the microhabitat at the edge of gaps. Success in the edge environment is likely a complex interaction of morphological and reproductive adaptations (Moore & Vankat, 1986; Matlack, 1994, Fahey & Puettmann, 2008). Most of species that exhibited an affinity for edges are relatively small in stature but can spread via vegetative or sexual reproduction. In the edge environment where risk of desiccation is lower than in gaps, species with large leaves may be more efficient light gatherers than herbaceous species typical of canopy gaps (Givinish, 1987; Bailey, Mayrsohn, Doescher et al., 1998). In addition, reproductive plasticity may make these species well-suited for transitional edge environments where microclimate can change dramatically over short distances (Brothers & Spingarn, 1992; Chen, Franklin, & Spies, 1995; José, Gillespie, George et al., 1996). More research on edge effects as well as the life-histories of these species is needed to more clearly understand these patterns (Nelson & Halpern, 2005; Fahey & Puettmann, 2007).

Structural and compositional distinctions among habitats suggest that canopy gaps are important in promoting small-scale understory heterogeneity (Collins, Dunne, & Pickett, 1985), which was especially apparent with the increasing divergence of composition among habitats over time. However, at the larger treatment-scale, the addition of gaps (with the size, frequency, and layout applied in this study) appeared to do little to alter the understory structure and composition relative to a more traditional thinning. Had we limited our analysis to treatment-scale averages for this treatment, key small-scale patterns in understory heterogeneity that may greatly influence future conditions would have been undetected. This underscores the importance of considering appropriate scales when interpreting ecological trends; examining responses that act at various spatial scales using only a single spatial scale—most commonly the treatment scale—may limit our understanding of ecological mechanisms (Ganio & Puettmann, 2008). Conversely, the lack of differentiation among thinning treatments, even when gap area was increased in the simulation study, also suggests that for operational-level or landscape-level phenomena that integrate across stands, gaps of the size implemented in this study may have limited impacts.

Finally, the within-treatment scale analysis of the LtGaps also highlights the need for new data analysis techniques better suited for treatments intended to increase within-stand heterogeneity. By increasing heterogeneity, the higher variation around the mean makes differences among treatments difficult to detect when comparing "average treatment" conditions.

MANAGEMENT IMPLICATIONS

Thinning influenced structural and compositional development of stands, but the complex patterns in development of understory vegetation need to be considered when applying thinning treatments with the goal to spur development of late-seral understory characteristics. First, if desirable understory vegetation—especially if concentrations of tall shrubs exist—they should be protected to avoid damage during the harvesting operations. Second, thinning intensity seems to be of lesser importance in determining understory vegetation development than the decision whether to thin or not. Third, the addition of canopy gaps has limited short-term impacts on understory vegetation for features and considerations that act at stand scales. However, gaps may provide for a greater diversity in vegetation at smaller spatial scales, which may be important for wildlife taxa, such as some small mammals that are less mobile and respond to localized habitat features. Our exploratory results suggest that increasing the number of gaps may not alter these patterns, but Fahey and Puettmann (2008) suggest that increasing the gap size would.

Finally, the harvesting disturbance in conjunction with increased resources can make thinned stands more susceptible to invasion by exotic species if an abundant local seed source is present. In addition, a few species appear to decline following thinning and, if present in stands, may warrant protection during the thinning operation. Lastly, it should be noted, that our recommendations are based on conditions during the initial recovery phase after thinning. Assessment of the influence of these initial differences on long-term trends requires further study.

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