AN ABSTRACT OF THE THESIS OF

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Title: Vegetation Response Following Thinning in Young Douglas-fir Forests of Western Oregon: Can Thinning Accelerate Development of Late-Successional Structure and Composition?

Abstract approved:

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Across western Oregon, Washington, and British Columbia, forest management practices over the past century reduced the amount of late-successional forest while simultaneously increasing the amount of young (less than 80 years old), managed Douglas-fir (*Pseudotsuga menziesii*) dominated forests. Recently, concerns over loss of late-successional habitat pushed management objectives on public lands away from timber production and toward maintenance and restoration of late-successional habitat. In accordance with these new objectives, The Young Stand Thinning and Diversity Study (YSTDS) was developed to test if thinning could accelerate development of late-successional habitat in young managed Douglas-fir forests. Though the YSTDS examines several components of forest ecosystems, the goal of this study was to investigate short-term (5-7 years post-treatment) responses of vegetation to thinning treatments and to evaluate this response in relation to long-term objectives of late-successional development.

The study is located on the western slope of the central Oregon Cascades. It consists of four replications of four thinning treatments (treatment areas average 30 ha each) in 30-50 year old second-growth Douglas-fir forest stands. Treatments include a control, heavy thin, light thin, and light thin with gaps. Unlike traditional thinning, the thinning treatments in this study sought to maintain and enhance overstory structural diversity by: (1) retaining species other than Douglas-fir, (2) simulating low densities that characterized development of some old-growth stands, and (3) adding canopy gaps to enhance spatial diversity. Following treatment completion, first, third, and fifth-year vegetation responses were measured

Results for overstory vegetation indicate that heavy thinning may accelerate development of large trees, one important component of old-growth structure. This was evident by faster growth of the largest trees in the heavy thin than in the control. A heavy thin may also permit more time for understory development than a lighter thin because canopies of heavy thinned stands remained open longer than canopies of light thinned stands. Variation in overstory cover, which may promote heterogeneous understory development, was higher in the treatment that included canopy gaps than in other treatments including the control. Although accelerated development of a multi-layered canopy was not evident in any treatment, retention of non-dominant tree species prevented simplification of vertical canopy structure by retaining layers that are typically removed by a low thinning prescription. In addition, mortality of non-dominant species was not greater in thinned treatments than in the control.

In the understory, results suggest that thinning can increase abundance of some vegetative layers without encouraging homogenization of the understory by clonal shrubs or exotic species. The thinnings resulted in initial declines of bryophytes, tall shrubs, and low shrubs followed by subsequent recovery and growth. While herbs displayed little initial response, a release of early-seral species was evident by 5-7 years post-treatment. Initial changes following thinning were likely due to harvesting damage and/or alteration of microclimate while subsequent changes were probably also related to increased resource availability.

It is expected that eventually similarities and differences in overstory structure among thinned treatments will be reflected in the understory. For example, variation in canopy cover created by the addition of canopy gaps was already reflected in the understory, as plant assemblages differed across the gradient from gaps to the thinned forest matrix. Hence, although understory vegetation was similar among heavy and light thins in the short-term, early closure of the canopy following a light thin could preclude continuation of late-seral understory development.

Finally, the effect of canopy gaps on the understory was more apparent at a within-stand scale than at a stand scale. Had the within-stand scale been ignored, relevant information regarding understory response would have been overlooked. This indicates that spatial scale should be considered when assessing ecological patterns.

In conclusion, it is acknowledged that there are drawbacks to thinning (e.g., certain species decline following thinning). It is also acknowledged that the short-term nature of the data permits only speculation regarding long-term succession. While these limitations are recognized, current trends indicate that a moderate to heavy thinning in combination with gap formation can hasten development of late-successional features in thinned stands relative to unthinned stands. Thus, thinning similar to that used in this study can be one useful tool in the management of young Douglas-fir forests.

Vegetation Response Following Thinning in Young Douglas-fir Forests of Western Oregon: Can Thinning Accelerate Development of Late-Successional Structure and Composition?

by
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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Liane R. Beggs, Author

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Chapter 1: Introduction to the Study

Across the landscape of western Oregon, Washington, and British Columbia, young managed forests have become a dominant feature (Bolsinger and Waddell 1993). These densely stocked forest stands are typically dominated by Douglas-fir (*Pseudotsuga menziesii*) trees less than 80 years of age (Bailey 1996). They are generally the product of replanting that followed clearcutting of late-successional forest in the mid 1900s and have historically been managed for timber production. However, increasing public concern over the loss of late-successional habitat in the early 1990s shifted the emphasis of forest management on public forest lands from timber production toward promotion of late-successional reserves (Record of Decision 1994).

The 1994 establishment of the Northwest Forest Plan called for a reduced level of harvesting in conjunction with increased emphasis on maintenance and restoration of late-successional habitat (USDA and USDI 1993, 1994). Important features of such habitat include large diameter trees, snags, and logs, as well as smaller trees of various size-class distributions, a multi-layered canopy, and a well-developed, heterogeneous understory (Franklin and Spies 1991a). Such structure may enhance habitat for a variety of flora and fauna not commonly found in dense, homogenous structures typical of many younger stands (Franklin and Spies 1991a, b, Carey 1995, Van Pelt and Franklin 2000, Franklin et al. 2002, Franklin and Van Pelt 2004).

Consequently, land managers sought management options that could promote late-successional habitat features in young forests while maintaining timber production. Although thinning was proposed as one tool that could assist in achieving these goals (McComb et al. 1993), little was known regarding the effectiveness of thinning in accelerating development of late-successional structure and composition and the long-term effects of thinning on the forest ecosystem. In response to the need for such information, the Young Stand Thinning and Diversity Study (YSTDS) was implemented in 1994. As an integrated long-term ecological study (projected to last 50 years), the YSTDS was designed to test the efficacy of various thinning treatments in accelerating development of late-successional habitat. While the YSTDS currently covers a broad realm of scientific inquiry (e.g., harvesting costs; bird, small mammal and chanterelle response), this study focuses on vegetation response to thinning during the initial post-treatment period (1 year and 5-7 years post-harvest). Documenting this initial response is necessary to provide land managers with an assessment of the potential effectiveness of thinning in promoting late-successional habitat and also to facilitate future interpretation of successional patterns and mechanisms once long-term observations have been obtained.

It is hypothesized that thinning will increase structural heterogeneity of young, managed stands, thereby hastening development of late-seral stand attributes, e.g., large trees, a multi-layered canopy, and a well-developed, heterogeneous understory (Franklin and Spies 1991a). Evidence from other studies lends support to this hypothesis. Conventional thinning has been shown to increase diameter growth of dominant trees (Staebler 1956, Miller and Williamson 1974, Oliver and Murray 1983), suggesting that thinning will accelerate development of large trees. Thinning can also promote establishment of a multi-layered canopy by encouraging crown extension and understory release and regeneration (Bailey et al. 1998). By directly impacting resource allocation, vertical and horizontal structural diversity of the overstory can also strongly influence understory composition (Berger and Puettmann 2000, Franklin et al. 2002, Franklin and Van Pelt 2004). Thinning also opens overstory canopies, at least temporarily increasing light availability on the forest floor (Thomas et al. 1999, Parker et al. 2001) and also soil moisture on drier sites (Everett and Sharrow 1985). All of these factors have been linked to increases in abundance of understory structural layers, such as herbs and shrubs, and heterogeneity of understory composition (Alaback and Herman 1988, Carey and Johnson 1995, Gilliam et al.1995, Klinka et al. 1996, Qian et al. 1997, Bailey et al. 1998, Thomas et al. 1999, Berger and Puettmann 2000, Thysell and Carey 2000, Parker et al. 2001, Thysell and Carey 2001, Muir et al. 2002, Lindh and Muir 2004).

However, in most studies cited above, vegetation response was investigated following conventional thinning treatments that were applied to enhance timber production in young stands, not to increase structural diversity (but see Thysell and Carey 2001). In the YSTDS, thinning prescriptions were developed to address the ecological objective of hastening development of late-successional stand components. Therefore, traditional low thinning prescriptions were modified to simulate natural disturbance and reflect research regarding past developmental trends of current old-growth stands. A Control (no thinning) was used as a reference for stand development without management. In all thinned treatments, tree species other than Douglas-fir were retained to maintain and potentially enhance overstory species diversity. The Light thin treatment was similar to a common commercial thin used throughout the region except for retention of non-dominant tree species. The Heavy thin treatment simulated severe disturbance and initial low density conditions that characterize development of some old-growth stands (Tappeiner et al. 1997, Poage and Tappeiner 2002). Finally, the Light thin with Gaps incorporated spatial diversity by adding canopy gaps in order to mimic small-scale mortality patterns of low intensity fire and pathogens, such as root rot.

It is uncertain, however, how these thinnings affect vegetation dynamics in young, managed stands. To address this uncertainty, this study investigates initial (1 year and 5-7 years) post-thinning vegetation response to three thinning treatments and a control in young managed Douglas-fir forests in the western Oregon Cascades. Specifically, Chapter 2 examines development of overstory structure (e.g., vertical crown structure and growth of Douglas-fir trees) and the utility of retaining non-dominant overstory species during thinning. Chapter 3 addresses development of understory vegetation structure, including herb, shrub, and forest floor bryophyte strata as well as representative clonal shrub species, and understory composition, including plant community composition, exotic species, and late-seral associated species. In addition, it also compares the impacts of structural variation in the overstory created by canopy gaps on understory vegetation structure and composition at two spatial scales.

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Chapter 2: Overstory response to alternative thinning treatments in young Douglas-fir forests of western Oregon

Abstract

An increase in land dominated by young second-growth Douglas-fir forests in the Pacific Northwest over recent decades has coincided with heightened concerns over loss of old-growth habitat. In search of options for managing young forests to provide late-successional forest structures, the Young Stand Thinning and Diversity Study was designed to test the effectiveness of modified thinning in accelerating development of late-successional structural characteristics. Thinning treatments included: a Control, a Light thin (typical of standard commercial thins), a Heavy thin (densities lower than typically prescribed), and a Light thin with Gaps (stands thinned lightly with the addition of 0.2 hectare patch cuts evenly spaced throughout the stand). Early responses (maximum of 5-7 years post-treatment) of overstory vegetation were examined. Average growth of Douglas-fir increased in all thinned stands, but growth of the largest Douglas-fir trees was accelerated only in the Heavy thin. One year after thinning, canopies of all thinned treatments were more open than the Control. Five to seven years following thinning, canopy cover of the Light thin no longer differed from the Control while canopies of other thinned treatments remained more open than the Control. As expected, the Light with Gaps thin had the highest variation in overstory canopy cover. Differentiation of vertical canopy structure among treatments was not evident at this stage. Most species had no difference in mortality among any of the treatments; those that did had highest mortality in the Control. Our results indicate that thinning can be effective in hastening development of some, but not all late-successional overstory attributes, but such acceleration is not equivalent among the different thinning treatments.

Introduction

During recent decades, young managed forest stands have become a dominant feature in the Pacific Northwest landscape. Mainly composed of planted Douglas-fir (*Pseudotsuga menziesii*) trees between the ages of 30-50 years, these stands have often replaced what was once late-successional or "old-growth" habitat (Bolsinger and Waddell 1993). These young stands often lack structural characteristics of old-growth forests such as large living trees, snags, a multi-layered canopy, and a well-developed understory (Franklin and Spies 1991a, 1991b; Spies 1991; Spies and Franklin 1991; Halpern and Spies 1995; Franklin et al. 2002). Without this suite of structural attributes, young stands may not provide the variety of habitats necessary to support a high diversity and abundance of native species (Spies 1991, Halpern and Spies 1995).

How to best manage these young stands in order to promote such late-successional habitat is a topic of considerable debate. In response to this debate, the Young Stand Thinning and Diversity Study (YSTDS) was initiated in 1994. As a comprehensive and integrated long-term ecological study, the YSTDS was designed to test the efficacy of thinning young stands in terms for accelerating development of late-successional habitat. Though retrospective studies have investigated whether thinning appears to promote late-successional habitat (e.g., Bailey et al. 1998, Thomas et al. 1999, Thysell and Carey 2000), few studies have implemented thinning with the intent of ecological enhancement (but see Thysell and Carey 2001). This paper examines short-term effectiveness of the YSTDS treatments in accelerating development of late-successional overstory characteristics.

By opening the canopy and releasing resources, thinning promotes growth of remaining overstory trees and establishment of a prominent understory layer, thereby adding complexity to these young stands and perhaps accelerating development of late-successional habitat (Muir et al. 2002). Over time, development of large trees and snags combined with a multi-layered canopy and understory may make thinned stands more similar to old-growth than unthinned stands (Muir et al. 2002). Enhanced stand complexity increases microhabitat heterogeneity and habitat suitability for many organisms (Carey and Johnson 1995, Hagar et al. 1996, Bailey and Tappeiner 1998, Rambo and Muir 1998, Carey and Harrington 2001, Hagar et al. 2004).

However, thinning traditionally has not been used to achieve ecological objectives; rather, it has mainly been a tool for enhancing timber production (for examples see the Level-of-Growing-Stock studies; Marshall and Curtis 2002). Thinning treatments implemented in this study were similar to traditional low thinnings, but were modified to address the goal of accelerating several late-successional stand attributes, including a diversity of tree species, initial low density conditions that characterized development of some old-growth stands (Tappeiner et al. 1997, Poage and Tappeiner 2002), and spatial diversity due to small-scale mortality patterns of low intensity fire and pathogens, such as root rot (Franklin and van Pelt 2004).

It is not known, however, if these thinning prescriptions will accelerate all late-successional features. For example, accelerating development of the dominant overstory component (Franklin and Spies 1991a) requires dominant trees to increase diameter and height growth following thinning (Staebler 1956, Miller and Williamson 1974, Oliver and Murray 1983). However, it is uncertain how heavily stands should be thinned to reduce competition among the largest trees to boost their growth and accelerate development of this component of “old” stand structure. It is also not known whether thinning to very low densities results in high mortality of residual trees from windthrow or other agents. While thinning may eventually promote establishment of a multi-layered canopy by encouraging crown extension and understory release and regeneration (Bailey et al. 1998), in the short-term, low thinning may simplify crown structure by removing many of the suppressed and intermediate trees (Smith et al. 1997). In addition, "alternative" conifer and hardwood species, such as those intentionally retained in this study, may be adapted to a shaded understory and experience high mortality upon canopy removal or suffer high mortality as a result of harvest damage (Tucker and Emmingham 1977, Tucker et al. 1987).

The overall objective of this study was to address these questions by characterizing early overstory response following alternative thinning treatments in young Douglas-fir stands. Specifically, the study includes a comparison among four treatments 5-7 years following thinning of the following repsonses: (1) overstory cover (2) vertical crown structure (3) growth of all Douglas-fir trees (4) growth of the largest Douglas-fir trees and (5) differences in mortality of individual tree species due to harvesting damage and competition.

Methods

Study Design and Description

The study is a randomized block design comprised of four blocks with each block containing one replication of four treatments. Study blocks are designated as: Cougar Reservoir (CR), Christy Flats (CF), Sidewalk Creek (SC), and Mill Creek (MC). Blocks were selected for homogeneity in overstory composition, stand age, management history, and size (> 56 ha). Blocks consist of Douglas-fir forests that were clearcut harvested between the mid-1940's to mid 1950's and replanted or interplanted by the late 1950's, resulting in 35-45 year old planted Douglas-fir stands at the time of study initiation. Blocks are located in the Willamette National Forest on the western slope of the Cascade Range of Oregon (400 to 900 m elevation) and are within the Western Hemlock (*Tsuga heterophylla*) zone (Franklin and Dyrness 1973). Mean annual precipitation is 230 cm, with only 5% falling between July and October. The average yearly temperature is 10.1ºC. Soils are generally well developed, ranging from thin shotty loams/clay loams to thin gravelly loams.

Within each block, each of the four treatments were assigned randomly to treatment units, resulting in a total of 16 treatment units across all blocks. Treatment units range from 15 to 53 ha in size and have varied slope and aspects (Table A1.1). Within a block, however, treatment units were selected for homogeneity in size, elevation, slope, aspect, site index, soil type, and dominant plant association (Table A1.1).

Treatment Description

The four treatments in each block are: Control, Light thin, Heavy thin, and Light with Gaps thin (hereafter abbreviated as LtGaps). Residual target densities (tph) for the thinning prescriptions were: Control = unthinned (approximately 650 tph); Light = 250-300 tph; Heavy = 125 tph; and LtGaps = 250-300 tph with additional cutting of 0.2 hectare circular gaps evenly dispersed every 2 ha (Table A2.1). Areas within the LtGaps treatment were stratified into 3 sub-treatments: (1) Gap: 0.2 acre gap; (2) Edge: a doughnut-shaped area surrounding the gap; (3) and Stand Matrix: the remainder of the treatment unit (Figure A3.1). More information on these sub-treatments is provided below, under Sampling Methods.

Treatments were applied between 1995-1997 (Table A4.1). Due to the large treatment size, buffering between treatments was not always possible, but treatments were occasionally separated by roads or other terrain barriers. At the CR and MC blocks, thinning used 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 with the added objective to leave species other than Douglas-fir. The Control provided a reference for stand development without management intervention. The Light was similar to a typical "commercial thin" commonly used throughout Oregon except for retention of species other than Douglas-fir to encourage species mix. The Heavy opened the canopy substantially more than common commercial thins and reflected recent findings that many old-growth stands initiated at very low densities (Tappeiner et al. 1997). The LtGaps treatment was intended to provide spatial diversity by simulating gap-phase mortality and created open patches within a stand matrix thinned to the same density as the Light treatment.

Baseline pre-treatment stand exam data were collected in 1993 and used to determine pre-thinning stand conditions. These data were collected differently from post-treatment data and cannot be used to make direct pre/post-treatment comparisons. However, they indicate that variation existed among blocks but pre-treatment basal areas (BA) and densities (tph) were comparable among treatment units within blocks (Table A2.1). Therefore, starting conditions within each block are assumed to be similar. Following thinning, BA was reduced in thinned treatments and stand densities were close to the prescriptions (Table A2.1).

The thinning prescriptions were successful in maintaining overstory species diversity. Post-thinning species composition was similar among treatment units, with most containing a majority of Douglas-fir along with a small component of hardwood and conifer species. An exception was the thinned treatment units in the MC block, which contained a higher proportion of hardwoods than was found in other blocks. Pre-treatment stand exams indicate this was likely due to pre-thinning species composition (data not shown) and not a result of thinning.

Sampling Methods

“First-year” post-thinning vegetation sampling occurred in the summers (June – September) of 1995-1997, depending on the time of harvest completion. In most cases, this was the first growing season following harvest (Table A4.1). Resampling was completed during the summer of 1999 and again in 2001, depicting vegetation response 3-5 growing seasons and 5-7 growing seasons post-harvest, respectively. For ease of communication, these data will be used to depict "first-year", “third-year", and "fifth-year" post-treatment vegetation responses, respectively.

Sampling was conducted using 0.1 ha (17.84 m radius) circular permanent plots (Figure A5.1). In Control, Light, and Heavy treatment units, approximately 7.5 % of the area was sampled (see Table A1.1 for total plot numbers). Transects were systematically placed through treatment units and plots were then located randomly along each transect.

Sampling for each LtGaps treatment unit used 30 plots in order to capture variation among the three sub-treatments. For each treatment unit, 10 gap plots, 10 edge plots, and 10 plots within the stand matrix were randomly selected. Gap plots were centered in the gap, including only the gap interior. Edge plots were centered 35.7 m from gap center so that each edge plot extended 7.5 m into the gap and 28.2 m into the remainder of the stand. For each gap, only one plot was placed in a random direction from the plot center in the surrounding edge. Stand Matrix plots were randomly placed throughout the remainder of the treatment unit with the criteria that plot center was located at least 71.4 m from the center of any gap, permitting sampling of any area at least 53.5 m from gap center (Figure A3.1).

Within each 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 et al. 1995). Overstory cover includes live foliage and tree bole, limbs, and snags. Diameter at breast height was also measured for all trees ≥ 5 cm dbh in each plot. Trees were tagged with a numeric tag to facilitate resampling and permit tracking of individual trees over time. Overstory cover and dbh were measured during each year of sampling. In addition, a random subsample of trees in each treatment unit that were measured for dbh was also measured for height and crown length in 1999. Another random subsample of trees in each treatment unit that were selected for height and crown measurements was cored at breast height in 1999 to determine stand age.

Overstory Cover

The five values of overstory cover within each plot were averaged to provide a plot mean. With the exception of the LtGaps treatment units, average overstory cover of each treatment unit was calculated by averaging the plot means. In the LtGaps, the number of plots in each sub-treatment (Gap, Edge, and Stand Matrix) was the same; however, each sub-treatment did not occupy an equal proportion of the total treatment unit area. To adjust for this, a weighted average of sub-treatment means was used to calculate the treatment unit means. Weights for each sub-treatment were based on the proportion of areas in each sub-treatment to total treatment unit areas (Table A6.1). The coefficient of variation (CV), an indicator of variation in overstory cover, was used to compare variation in overstory cover among treatments. The variation in overstory cover was illustrated by frequency diagrams of overstory cover.

Vertical Canopy Structure

Assessment of vertical canopy structure required height and height to crown base data for all trees within sampling plots, but these measurements were taken for only a subsample of trees. We used species-specific nonlinear equations developed by Hanus et al. (1999) and Ritchie and Hann (1987) to predict these values for unsampled trees. The equations were “localized” by using parameter estimates that were derived from regression analysis using trees whose height and crown data were measured in this study. Due to concern about small sample sizes in regression analyses, height and height to crown base of a species were predicted using parameter estimates of the species most closely resembling its growth pattern when sample size was smaller than ten. Parameter estimates for Douglas-fir were used for grand fir (*Abies grandiflora*); parameter estimates for western hemlock were used for mountain hemlock (*Tsuga mertensii*); and parameter estimates for bigleaf maple (*Acer macrophyllum*) were used for Oregon ash (*Fraxinus latifolia*), cascara buckthorn (*Rhamnus purshiana*), and willow spp. (*Salix* spp.).

Predicted values of height and crown length were then used to calculate live crown ratios (LCR) and foliage height diversity (FHD) index (MacArthur and MacArthur 1961) for each treatment unit. LCR gauges vertical length of crowns relative to tree heights and assumes continuous vegetation throughout the entirety of crowns. The FHD index assesses diversity of vertical distribution of foliage using two components: richness and evenness, similar to the Shannon-Weiner diversity index. Richness, in this case, is the number of 5-meter layers occupied by tree crowns in the stand. A 5-meter interval was selected because smaller intervals would not have compensated for the error incurred with estimations of height and crown length measures. Evenness is the relative abundance of tree crowns within these intervals. Like the Shannon-Weiner index, FHD can be strongly influenced by unbalanced dominance of richness or evenness (Hill 1973). To examine if richness or evenness was controlling FHD, both were tested separately.

Growth

Annual relative growth between first-year and fifth-year post-thinning of all Douglas-fir trees ≥ 5 cm dbh was compared among treatments. Relative growth was used because absolute growth did not account for initial differences in dbh among treatments that were an artifact of thinning (thinning removes smaller trees, inherently increasing average dbh in thinned treatments relative to the Control regardless of differences in growth). To calculate annual relative growth (expressed as % increase from first-year post-treatment dbh), absolute growth (cm/yr) was first calculated by subtracting first-year dbh from fifth-year dbh and dividing by the number of years between measurements, thus accounting for offsets in timing of first-year measurements. Annual relative growth was then calculated by dividing absolute growth by first-year dbh and multiplying by 100. To calculate average relative growth for each treatment unit, relative growth of all trees in a treatment unit was summed and divided by the total number of trees.

To specifically assess response of the largest Douglas-fir trees, i.e., trees that likely will make up the dominant stand structure, absolute growth between first-year and fifth-year post-thinning of trees with the largest dbh was compared among treatments. This was done for the largest 10, 15, 20, 25, and 30 tph in order to simulate a range of large-tree densities typical of old-growth stands (Franklin and Spies 1991a). To examine the largest 10 tph, the largest tree from each 0.1 ha plot was selected. Likewise, the 2 largest trees were selected from each 0.1 ha plot to examine 20 tph, and the largest 3 for 30 tph. For the intermediate 15 and 25 tph, half of the plots were randomly selected and the largest 2 or 3 trees, respectively, from these plots were combined with the largest 1 or 2 trees, respectively, from all plots. Absolute growth was calculated as previously described and the average for each treatment unit was then calculated by summing absolute growth of all trees in a treatment unit and dividing by the total number of trees. Absolute growth was used instead of relative growth because average initial dbh of the largest trees did not differ among treatments.

In the LtGaps treatment, no Douglas-fir were present in the gaps. Thus, growth in the LtGaps treatment represents only trees in the Stand Matrix and Edge. To evaluate potential effects of the gaps on tree development, relative growth of all Douglas-fir trees ≥ 5 cm dbh and absolute growth of the largest 10, 20, and 30 tph of Douglas-fir trees were compared between the Edge and Stand Matrix sub-treatments. Calculations were as previously described.

Mortality

Mortality of individual tree species as well as all hardwood species combined was compared among treatments. In each treatment unit, percent mortality of each species was computed by summing the number of trees of a species alive during first-year sampling but dead by fifth-year sampling, dividing by the total number of trees of that species present during first-year sampling, and then multiplying by 100. Percent mortality was calculated for all trees ≥ 5 cm dbh and for "small" trees (hereafter "small" trees refers to trees between 5 – 10 cm dbh) in order to determine (a) if species experienced differences in mortality among treatments and (b) if a difference in mortality was limited to "small" trees, e.g., competition related. Due to concerns about small sample sizes, mortality for a species was assessed only if more than 10 trees of that species were present in each treatment during first and fifth-year sampling.

For all trees ≥ 5 cm dbh, the following species were tested for differences in mortality among all treatments: bigleaf maple, golden chinquapin (*Chrysolepis chrysophylla*), Pacific dogwood (*Cornus nuttallii*), bitter cherry (*Prunus emarginata*), Douglas-fir, Pacific yew (*Taxus brevifolia*), western red cedar (*Thuja plicata*), and western hemlock. Fewer than 10 red alder (*Alnus rubra*) and incense cedar (*Calocedrus decurrens*) were observed in the Heavy treatment, so comparisons of mortality were only made among the Light, LtGaps, and Control. The following species did not have enough trees in any treatment to permit separate comparisons and were included only in the combined hardwood analysis: Pacific madrone (*Arbutus menziesii*), Oregon ash, black cottonwood (*Populus trichocarpa*), cascara buckthorn, and willow species.

In the small tree category, bitter cherry had too few trees to permit separate treatment comparisons (in addition to the species listed above) and golden chinquapin did not have enough trees in the Light treatment, so comparisons were only made among the Control, Heavy, and LtGaps treatments. These species were still included in the hardwood analysis.

Data Analysis

All analysis was done using SAS v. 8.2 statistical software (SAS Institute 2001). Comparisons among treatments and LtGaps sub-treatments were performed with ANOVA using a randomized complete block model (PROC GLM). The Tukey-Kramer adjustment was used for all multiple comparisons. Prior to ANOVA, histograms and normal probability plots were used to check all data distributions for normality. Data aggregated to the treatment unit level (n = 16 treatment units) were approximately normal; therefore, no transformations were performed. The significance level for all analyses was set at $\alpha \leq 0.05$, and $\alpha \leq 0.10$ was considered to be marginally significant.

For mortality comparisons, several species were more frequently observed in the Control than thinned treatments, resulting in more precise mortality estimates of these species in the Control treatments compared to thinned treatments. To account for decreased precision in thinned treatments, a weighted ANOVA was used to weight average mortality by total trees (for each species) in each treatment.

Time trends in overstory cover were investigated using a repeated measures analysis. A Time x Treatment interaction was used to test whether changes in overstory cover over time were equal among treatments (PROC MIXED).

Results

Overstory Cover

As expected, thinning opened up the overstory canopy. During the first and third years post-thinning, all thinned treatments had less overstory cover than the Control (Figure 2.1; Year 1: $P < 0.001$ for Heavy, Light, and LtGaps; Year 3: $P < 0.001$ for Heavy and LtGaps, $P = 0.010$ for Light). The thinning treatments differed, as the Heavy had less overstory cover than the Light (Year 1: $P = 0.004$; Year 3: $P = 0.005$). The LtGaps did not significantly differ in cover from the Light ($P > 0.100$ for both years) but was marginally higher than the Heavy (Year 1: $P = 0.076$; Year 3: $P = 0.084$). The trends in overstory canopy development differed among treatments (Time x Treatment interaction: $P = 0.021$; Figure 2.1) and five years after thinning, the Heavy and LtGaps still had less average cover than the Control (Heavy: $P < 0.001$; LtGaps: $P = 0.003$), but no longer differed from each other ($P = 0.121$). Also, the Light was no longer significantly different from the Control ($P = 0.103$; Figure 2.1). Within the LtGaps treatment, overstory cover was significantly less in the Gap than the Edge and Stand Matrix during all years of measurement ($P < 0.001$ for all years) while the Edge and Stand Matrix did not differ from each other ($P > 0.100$ for all years).

Gap creation enhanced variation in overstory cover distribution (expressed as CV). During the first year post-thinning, variation of overstory cover throughout the stand differed among all four treatments (*P* < 0.001). The Control had the least amount of variation while the LtGaps had the most. By third-year post-thinning, however, variation in the Light no longer differed from the Control (*P* = 0.214). The Heavy and LtGaps remained more variable than the Control (*P* < 0.001 for Heavy and LtGaps), and the Light (Heavy: *P* = 0.014; LtGaps: *P* < 0.001) with variation in the LtGaps being greater than variation in the Heavy (*P* = 0.006). These results did not change by the fifth-year post-thinning. The greater variation in the LtGaps treatment is primarily a result of low overstory cover in the gaps and intermediate cover through the remainder of the stand (Figures 2.2a – 2.2d).

Figure 2.1. Average overstory cover during first, third, and fifth-year post-thinning. Bars indicate 95% confidence intervals. Letters indicate significant differences among treatments (treatments with same letter do not differ at $P \leq 0.05$ level).

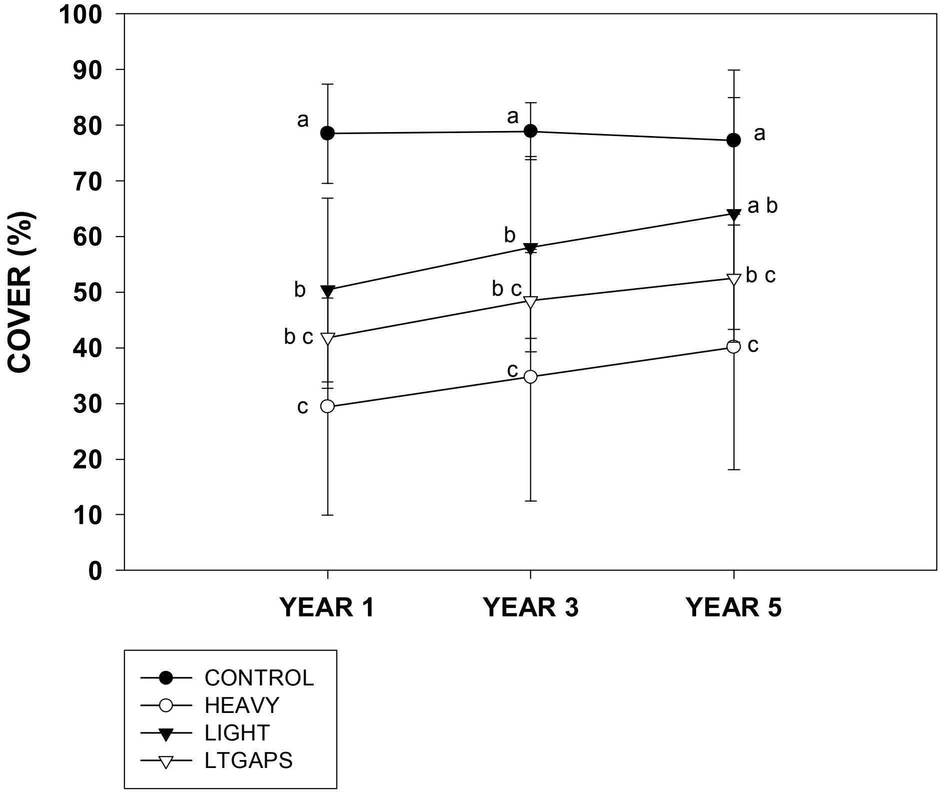


Figure 2.2a. Frequency distribution and CV ($\overline{x}$) of overstory cover for Control treatment (first-year post-thinning).

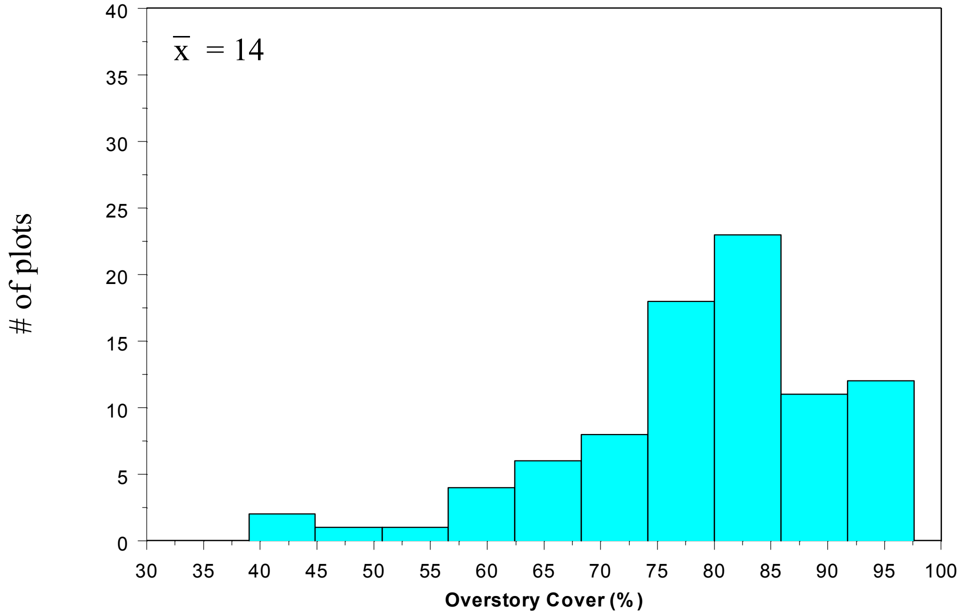


Figure 2.2b. Frequency distribution and CV ($\overline{x}$) of overstory cover for Heavy treatment (first-year post-thinning).

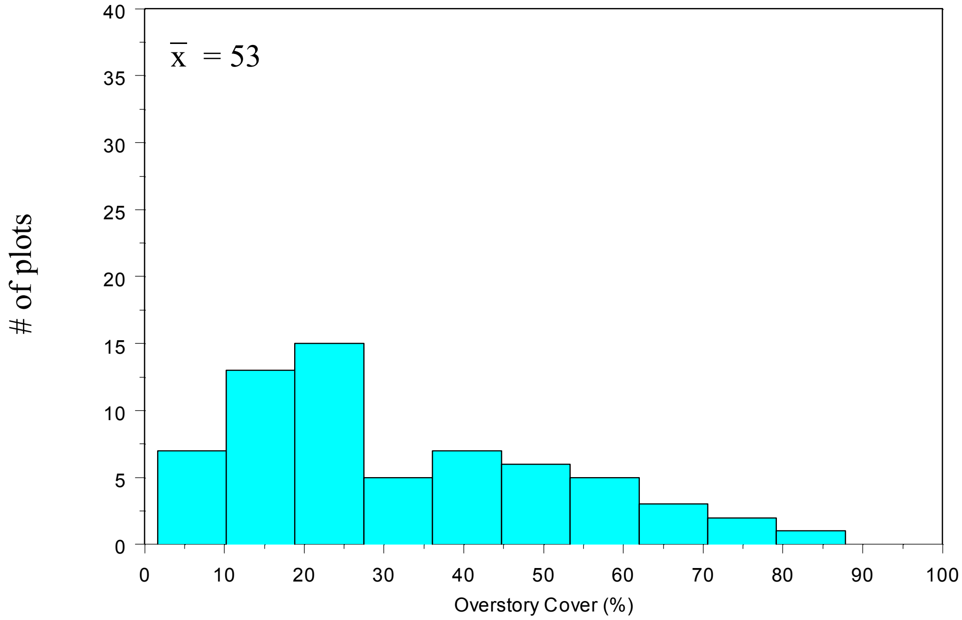


Figure 2.2c. Frequency distribution and CV ($\bar{x}$) of overstory cover for Light treatment (first-year post-thinning).

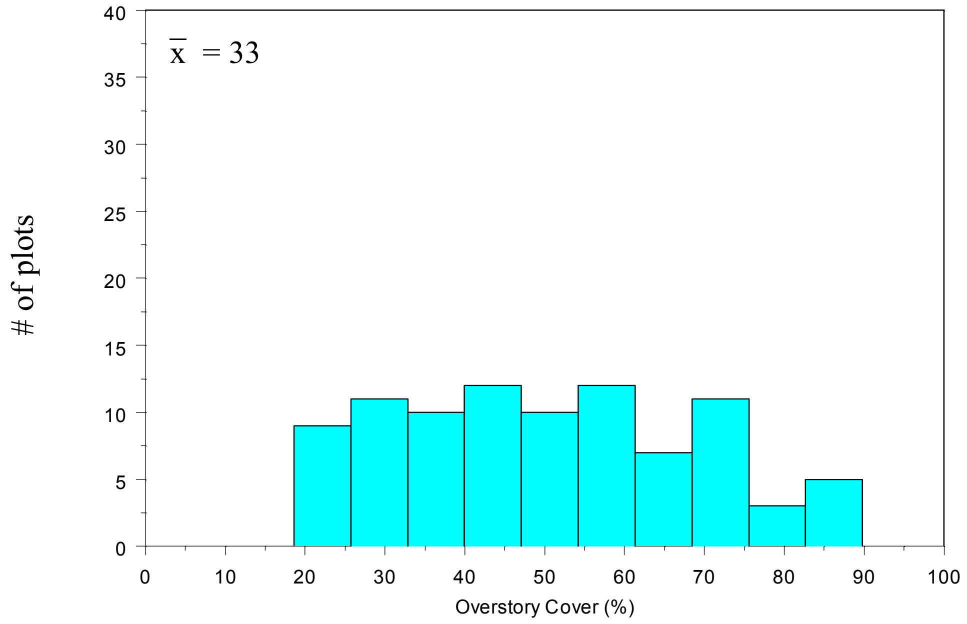
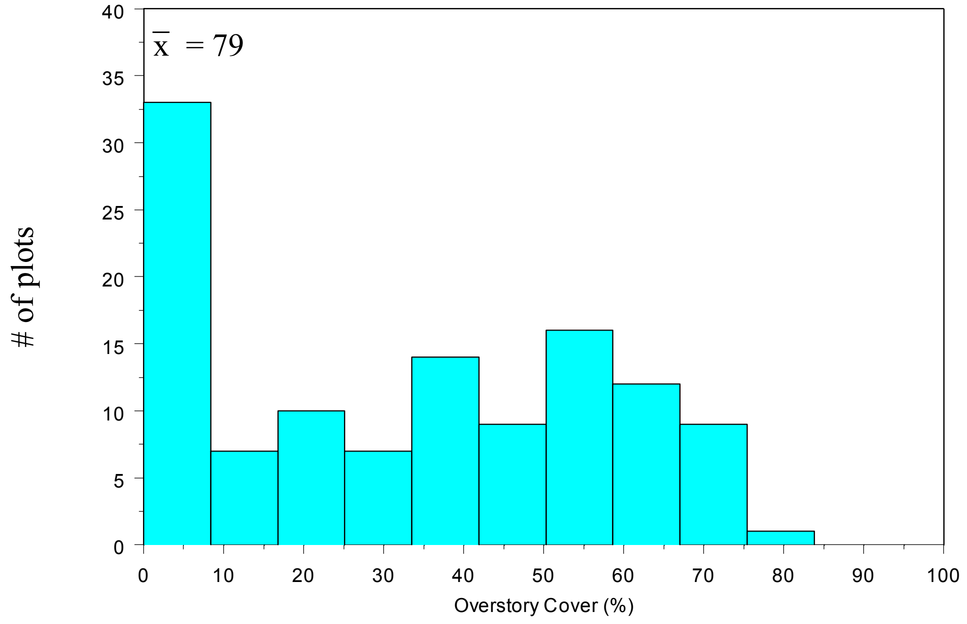


Figure 2.2d. Frequency distribution and CV ($\bar{x}$) of overstory cover for LtGaps treatment (first-year post-thinning).



Vertical Structure

Differentiation of crown layers did not seem to be significantly impacted by thinning. By third-year post thinning, FHD and LCR did not differ among treatments (*P* = 0.85 and *P* = 0.26, respectively; Table 2.1). No difference among treatments was found in richness or evenness (*P* = 0.783 and *P* = 0.473, respectively) of canopy layers.

Table 2.1. Overstory Results: (1) FHD = Foliage Height Diversity Index (third-year post-thinning); (2) LCR = Compacted Live Crown Ratio (third-year post-thinning); (3) RG = relative growth of all Douglas-fir ≥ 5 cm dbh (fifth-year post-thinning); (4) AG = absolute growth of largest 15 tph Douglas-fir trees (fifth-year post-thinning) (results did not differ for ≥ 15 tph). Numbers in parentheses provide 95% confidence intervals of estimates. Letters indicate differences among treatments; treatments with same letters do not differ at *P* ≤ 0.05 level. ANOVA *P*-value is for overall test of difference among treatments.

Treatment	**FHD**	**LCR**	**RG (% increase from initial dbh)**	**AG of Largest 15 tph (cm/yr)**
Control	1.57 *a*	0.53 *a*	1.3 *a*	0.70 *a*
	(1.51 - 1.63)	(0.50 - 0.55)	(1.0 - 1.6)	(0.61 - 0.78)
Heavy	1.58 *a*	0.55 *a*	2.4 *b*	0.94 *b*
	(1.52 - 1.64)	(0.52 - 0.58)	(2.1 - 2.7)	(0.84 - 1.0)
Light	1.57 *a*	0.51 *a*	1.8 *a*	0.78 *a*
	(1.51 - 1.63)	(0.49 - 0.54)	(1.5 - 2.1)	(0.66 - 0.84)
LtGaps	1.60 *a*	0.52 *a*	1.9 *a*	0.85 *a*
	(1.54 - 1.65)	(0.50 - 0.55)	(1.6 - 2.3)	(0.72 - 0.89)
ANOVA *P*-value	0.854	0.200	0.003	0.033

Growth

Heavy thinning enhanced average growing conditions of residual trees, as evident by the higher relative growth of Douglas-fir in the Heavy treatment. Relative growth of Douglas-fir trees ≥ 5 cm dbh differed among treatments by the time of fifth-year measurement (*P* = 0.003; Table 2.1), but only the Heavy treatment had significantly higher relative growth than the Control (*P* = 0.002). There was evidence that relative growth in the LtGaps was higher than in the Control (*P* = 0.060) and growth in the Heavy was higher than in the Light (*P* = 0.057). Within the LtGaps treatment, relative growth in the Edge was slightly, but marginally significantly higher than in the Stand Matrix (1.8 vs. 2.0, respectively; *P* = 0.064).

Large Douglas-firs also responded to improved growing conditions provided by heavy thinning. For the largest 15 tph, absolute growth was higher in the Heavy treatment than in the Control (*P* = 0.027) but did not differ between the Light and Control treatments (*P* = 0.854) or the LtGaps and Control treatments (*P* = 0.405). Results were the same for the largest 20, 25, and 30 tph. For the largest 10 tph, absolute growth of the largest Douglas-fir trees did not differ significantly among any treatments (*P* = 0.228). Within the LtGaps, absolute growth of the largest Douglas-firs did not differ between the Edge and the Stand Matrix (10 tph: *P* = 0.648; 20 tph: *P* = 0.460; 30 tph: *P* = 0.305).

Mortality

High mortality following thinning was not evident for any of the species and thinning seemed to slow mortality patterns. For trees ≥ 5 cm dbh and "small" trees, mortality of Douglas-fir and hardwoods was higher in the Control than all other treatments (Table 2.2). Within the LtGaps, neither Douglas-fir nor hardwood species differed in mortality among sub-treatments (*P* > 0.15; comparisons only between Edge and Stand Matrix for Douglas-fir; for all combined hardwoods, comparisons made with and without Gap sub-treatment). For golden chinquapin, the same pattern was true for trees ≥ 5 cm dbh except the difference between the Control and Light was not significant (Table 2.2). Within the LtGaps, mortality of golden chinquapin did not differ among sub-treatments (*P* > 0.20; comparisons made with and without Gap sub-treatment). None of the other species tested showed significant differences in mortality among treatments.

Table 2.2. Comparisons of mortality (%) among treatments (fifth-year post-thinning). Results reported only for species with significant differences among treatments. Numbers in parentheses provide 95% confidence intervals of estimates. Letters indicate differences among treatments; treatments with same letters do not differ at $P \leq 0.05$ level. ANOVA P-value is for overall test of difference among treatments.

	Treatment	**Douglas-fir**	**Golden chinquapin**	**Combined hardwoods**
All Trees (≥ 5 cm dbh)	Control	14.0 *a* (12.3 - 15.8)	27.1 *a* (19.4 - 34.9)	36.1 *a* (28.4 - 43.8)
	Heavy	4.7 *b* (0.1 - 9.3)	7.8 *b* (-1.1 - 16.7)	18.0 *b* (8.9 - 27.0)
	Light	5.9 *b* (3.1 - 8.8)	15.1 *a b* (1.5 - 28.8)	15.3 *b* (9.0 - 21.6)
	LtGaps	4.0 *b* (0.8 - 7.2)	4.4 *b* (-3.6 - 12.5)	13.4 *b* (7.0 - 19.7)
	ANOVA *P*-value	< 0.001	0.010	0.001
"Small" Trees (dbh = 5 - 10 cm)	Control	43.9 *a* (39.7 - 48.2)	27.1 *a* (-25.8 - 80.0)	43.3 *a* (33.7 - 52.8)
	Heavy	18.3 *b* (5.4 - 31.2)	14.9 *a* (-49.8 - 79.5)	22.5 *b* (11.2 - 33.8)
	Light	23.5 *b* (13.9 - 33.1)	-- --	26.7 *b* (16.4 - 36.9)
	LtGaps	14.7 *b* (6.6 - 22.8)	14.6 *a* (-48.9 - 78.0)	16.8 *b* (7.9 - 25.7)
	ANOVA *P*-value	< 0.001	0.781	0.004

Discussion

Our results indicated that some styles of thinning can place young managed stands on an accelerated trajectory to develop several late-successional stand attributes such as large diameter trees. Other attributes, such as a diversified crown structure, were not accelerated by thinning at this stage, but conditions were created that were favorable for eventual development of such structure. In addition, leaving tree species other than Douglas-fir was effective in maintaining and potentially enhancing overstory species diversity and prevented initial simplification of canopy structure.

The thinning treatments differed in terms of their impact on overstory cover and associated characteristics. Substantial reduction in stand density, like in the Heavy treatment, is necessary to ensure canopy opening is maintained for several years. Open canopy conditions permit more light to reach the forest floor (Parker et al. 2001) and, with fewer trees transpiring, generally increase soil moisture, especially on dry sites (Everett and Sharrow 1985). This can result in enhanced development of understory shrubs and herbs (Alaback and Herman 1988, Bailey et al. 1998, Thomas et al. 1999, Thysell and Carey 2000, Parker et al. 2001, Thysell and Carey 2001). The understory vegetation layer is generally desirable as it supplies wildlife forage and shelter (Carey and Johnson 1995) and contributes to forest nutrient cycling (Trofymow et al. 1991). In turn, shrub cover, especially of tall deciduous shrubs, has been positively related to abundance of many small mammal species (Carey and Johnson 1995), bird species (Hagar et al. 1996, Hagar et al. 2004), and epiphytes (Rosso 2000). Increased resource conditions under open canopies may also promote higher levels of flowering and fruiting of understory plants (Lindh 2004, Wender et al. 2004), generating additional forage for wildlife.

The pattern of canopy cover development is important as changes in understory vegetation can occur during a brief time of open canopy conditions and persist long after canopy closure (Alaback and Herman 1988, Thomas et al. 1999). However, the establishment of a prominent understory layer may require a longer duration of canopy openness (Alaback and Herman 1988, He and Barclay 2000, Thysell and Carey 2000) than is likely to occur under light thin treatments. In addition, marginal increases in resource availability under a light thin may not compensate for damage done during harvest (Thomas et al. 1999).

The uniformly open canopy typically created by evenly spaced thinnings can result in even distribution of light upon the forest floor, a condition that may encourage homogenous expansion of clonal shrubs (Tappeiner and Zasada 1993, Huffman and Tappeiner 1997, Thysell and Carey 2000, but see Thomas et al. 1999) or dense cover of understory trees such as western hemlock (Alaback and Herman 1988). These shrubs and trees provide wildlife habitat and forage. However, their uniform cover can limit understory diversity by inhibiting establishment and growth of non-clonal shrubs, many herb species, and other trees (Alaback and Herman 1988, Tappeiner and Zasada 1993, Thysell and Carey 2000, Thysell and Carey 2001). Work done by the author, however, indicates that understory vegetation is not dominated by clonal shrubs as of 5-7 years following thinning (Chapter 3). Variation in canopy cover in thinnings with gaps may prevent homogeneous dominance of clonal species by ensuring uneven distribution of resources, including scattered light (Franklin and Van Pelt 2004). This encourages more heterogeneous development of understory vegetation like that common in old-growth stands (Franklin and Spies 1991b, Van Pelt and Franklin 2000, Franklin et al. 2002, Franklin and Van Pelt 2004).

Thinning treatments differed in their ability to accelerate large tree sizes, an important component of late-successional structure in the Douglas-fir forests of the Pacific Northwest. The influence of residual density on average tree growth was as expected. The Heavy treatment, with residual densities lower than in most conventional thinnings, consistently reduced competition enough, even among the largest trees, to permit residual trees to capitalize on elevated resource availability and increase their diameter growth (Oliver and Murray 1983, Marshall and Curtis 2002). If growth trends continue, development of large diameter trees will occur faster in heavily thinned stands than unthinned stands. Because these large trees are valuable nest sites for northern spotted owls (Forsman et al. 1984), provide substrate for several epiphytic species (Clement and Shaw 1999), and may eventually become the large snags and downed logs essential to several wildlife species (Hayes et al. 1997), acceleration of their development is key in acceleration of late-successional structure.

On the other hand, our study indicates that, despite reduction in stand density, competition among the largest trees in the Light, i.e., commonly used thinning regimes, remains too high for these trees to substantially increase their growth (Staebler 1956). However, when this thinning prescription is combined with gap creation, trees bordering gaps do seem to benefit from released resources (Gray et al. 2002, McDonald and Urban 2004) and experience slightly elevated growth. It is important to note that five years may not be sufficient for trees to build up crowns and increased resource availability may not be expressed in terms of diameter growth over this time frame. Thus, it can be expected that trends detectable for edge trees may strengthen over time (Staebler 1956, Oliver and Murray 1983).

The very largest trees (10 tph) did not experience a growth release, even in the Heavy treatment, indicating that they may already have been in a dominant position with minor competition from neighbors (Staebler 1956, Oliver and Murray 1983, D'Amato and Puettmann 2004). It is important to note that, while residual densities after heavy thinning were lower than after traditional thinning, the residual density of the Heavy treatment was still higher than densities at which some old-growth stands may have initiated (Tappeiner et al. 1997, Poage and Tappeiner 2002, Winter et al. 2002). This seems to suggest that in some instances even more intensive thinnings may be necessary or desirable to accelerate growth of the largest trees.

Amplified growth of non-dominant trees and understory vegetation, however, eventually may strain resource availability, especially on drier sites (Messier and Mitchell 1994, Bennett et al. 2003). Other work, however, has shown that dominant trees in young stands tend to contribute the largest proportion of stand production up to the point of stand closure at which time dominance begins to diminish and smaller trees contribute proportionately more to stand growth (Binkley et al. 2002, Binkley 2004). It is hypothesized that when this dominance begins to relax, the trees are so large that their growth no longer balances with their greater control of resources (Binkley 2004). At this point, assuming the largest trees we investigated are dominant in our stands, the trees are likely sufficiently large to support a variety of wildlife and other species.

Despite distinctions among treatments in growth and overstory cover, vertical structure was not affected by thinning in the short term. A multi-tiered canopy capable of providing a diversified microhabitat, like that common in old-growth stands (Franklin and Spies 1991a), has not yet begun to develop in these stands. Given the early post-treatment response observed (3 to 5 growing seasons after thinning), however, significant changes in crown extension and epicormic branching were unlikely. Maybe more importantly, our results indicate that overstory crown structure in thinned stands was not simplified, as common in low thinnings (Smith et al. 1997). Leaving tree species other than Douglas-fir helped ensure that lower layers, which are removed during conventional low thinning operations, were maintained. Retention of these "alternative" species also maintained valuable ecological components, such as hardwoods (Hagar et al. 1996, Rambo and Muir 1998, Rosso 2000). A mixture of overstory species that includes hardwoods can often support a variety of species assemblages better than a forest lacking diversity in overstory composition (Hagar et al. 1996, Hayes et al. 1997, Rosso 2000). Bird species, such as the warbling vireo (*Vireo gilvus*), are positively related to hardwood presence (Hagar et al. 1996). Hardwoods also generally provide more nutrient rich leachate than conifers, making them important to forest floor bryophyte species that obtain the majority of their nutrients from leachate (Rambo and Muir 1998).

Concerns about loss of tree species other than Douglas-fir due to increased mortality in thinned stands were not warranted. Most mortality was apparently related to competition as mortality of golden chinquapin and all combined hardwood species was highest in unthinned stands. Douglas-fir mortality was also higher in unthinned stands relative to thinned stands. The dense conditions of unthinned stands probably inflicted extreme competition for resources upon suppressed and intermediate trees, resulting in high mortality (Oliver and Larson 1996, Franklin et al. 2002). By removing several intermediate and suppressed trees, thinning likely relaxed resource competition among remaining trees, thereby decreasing mortality (Oliver and Larson 1996). On the other hand, heavier thinnings did not result in instable stand conditions.

In summary, some of the thinning operations implemented in this study can be an effective way of increasing overstory complexity in young, managed stands in the western Cascades of Oregon in the long term. However, applying traditional thinning practices are not as likely to accelerate the development of late successional structures in 3-5 years following thinning. Instead, thinning practices may need to be "customized" and target specific structural components (e.g., large trees, diverse understory light conditions).

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Chapter 3: Understory vegetation response to thinning intended to accelerate development of late-seral features in young *Pseudotsuga menziesii* forests of western Oregon

Abstract

The Young Stand Thinning and Diversity Study was designed to test the efficacy of alternative thinning regimes in accelerating development of late-successional habitat. This study examined influence of those thinning treatments on understory vegetation structure and composition 5-7 years post-treatment in relation to late-seral development. It also evaluated the importance of spatial scale when assessing the impact of canopy gaps on understory vegetation. The study is located on the western slope of the central Oregon Cascades. It consists of four replications of four thinning treatments (treatment areas average 30 ha each) in 30-50 year old second-growth *Pseudotsuga menziesii* stands. Treatments included a control, heavy thin, light thin, and light thin with gaps. Following treatment completion, vegetation response was measured during the first post-treatment growing season and again 5-7 years later. The thinnings resulted in initial declines of bryophytes, tall shrubs, and low shrubs followed by subsequent recovery and growth. Of four clonal shrub species investigated, only one experienced elevated growth following thinning. While herbs displayed little initial response, a release of early-seral species was evident by 5-7 years post-treatment. Initial changes in understory vegetation following thinning were likely due to harvesting damage and/or alteration of microclimate while subsequent changes were probably more related to increased resource availability. The addition of gaps generated plant assemblages that differed across the gradient from the gap to the thinned forest matrix, but this effect was more apparent at a within-stand scale than at a stand scale. We conclude that a thinning in combination with gap formation can hasten late-successional understory development of thinned stands relative to unthinned stands, but impacts need be stratified by stand characteristics and spatial scales.

Introduction

Understory vegetation plays a key ecological role within temperate coniferous forests of the Pacific Northwest. It provides wildlife habitat (Carey 1995, 1996, Hagar et al. 1996), substrate for epiphytes (Rosso 2000, Muir et al. 2002), and contributes to nutrient cycling and forest productivity (Yarie 1980, Trofymow et al. 1991). Late-successional forests generally have a well-developed understory that provides microhabitat heterogeneity and supplies critical forage and shelter for several taxa (Franklin and Spies 1991b, Carey and Johnson 1995, Carey 1996, Hagar et al. 1996, Rosso 2000, Franklin et al. 2002). However, understory vegetation is often scarce in young (~ 30 to 80 years), managed *Pseudotsuga menziesii* (Mirbel) Franco (Douglas-fir) forests after canopy closure has commenced (Franklin et al. 2002). Consequently, young forests often lack key ecological functions provided by an understory layer and offer less suitable habitat for several species relative to late-successional forests (McComb et al. 1993, Carey and Johnson 1995, Hayes et al. 1997, Franklin et al. 2002).

The general theory of forest succession holds that young stands will undergo a period of stem exclusion during which the understory is markedly diminished after which the understory redevelops (Oliver and Larson 1996). Traditional clearcutting and planting practices have left many young forests in the Pacific Northwest with high tree densities. Until sufficient overstory mortality occurs, such conditions could prolong the closed-canopy stage, thereby depleting seedbanks and inhibiting future understory reestablishment and development (McComb et al. 1993, Tappeiner et al. 1997). Without management intervention, continued stagnation of the closed-canopy phase could greatly delay late-successional understory development (McComb et al. 1993, Tappeiner et al. 1997).

Given the increased prevalence of young managed forests on the landscape during recent decades (Bolsinger and Waddell 1993), concern over slow development of late-successional features in young managed stands spurred development of the Young Stand Thinning and Diversity Study (YSTDS) (McComb et al. 1993). This study is a long-term, integrated ecological study designed to test the efficacy of thinning in hastening development of late-successional structural attributes, including a well-developed understory, in young, managed *P. menziesii* forests. In this paper we assess the initial (5-7 years post-treatment) response of understory vegetation to thinning and evaluate whether the trajectory of this response is toward late-successional understory structure and composition.

Although understory vegetation is variable, several distinctions are apparent between understories of late-successional forests and young, managed forests. Understory biomass tends to be higher in late-successional forests than in young, closed-canopy forests (Alaback 1982, Spies and Franklin 1991, Franklin et al. 2002). In addition, structure of late-successional understories is generally complex due to patchy vegetation development (Alaback 1982, Collins et al. 1985, Franklin and Spies 1991a, Franklin et al. 2002). For example, areas of dense shrub and herb cover are often intermixed with areas of deep shade where the forest floor is covered by litter (Franklin and Spies 1991a, Franklin et al. 2002). In young forests, conversely, sparse but relatively even distribution of understory vegetation is common (Franklin and Spies 1991a, Spies and Franklin 1991, Bailey 1996). In addition, although most understory species are not restricted to any single stage of forest development (Spies 1991, Halpern and Spies 1995), many species (e.g., several orchid and ericaceous species) are closely associated with late-successional habitat (Spies 1991, Halpern and Spies 1995).

Opening of the canopy in young forests by traditional thinning has been shown to increase resource availability (Thomas et al. 1999, Parker et al. 2001), thereby encouraging growth of understory vegetation (Bailey et al. 1998, Thomas et al. 1999, Thysell and Carey 2000). However, thinning can also encourage invasion by exotic species (Bailey et al. 1998, Mack et al. 2000, Thysell and Carey 2000) and unimpeded growth of clonal shrubs (Tappeiner and Zasada 1993, Messier and Mitchell 1994, Huffman and Tappeiner 1997, Thomas et al. 1999, He and Barclay 2000). While increased cover of these shrubs can benefit some taxa, uniform cover of them may limit understory development by hampering growth of non-clonal shrubs, herbaceous species, or trees (Alaback and Herman 1988, Thysell and Carey 2000, Thysell and Carey 2001). Therefore, if thinning promotes a homogenous understory of clonal shrubs or exotic species, it could undermine the goal of creating a heterogeneous, late-seral understory.

In most studies that have investigated the impact of thinning on understory vegetation (e.g., Alaback and Herman 1988, Bailey and Tappeiner 1998, Lindh and Muir 2004), thinning prescriptions were developed solely to optimize timber production (but see Thysell and Carey 2001). In the YSTDS, thinning prescriptions were developed to address the influence of heterogeneity in overstory structure on late-seral understory development (Anderson et al. 1969, Franklin and Spies 1991a, Berger and Puettmann 2000, Franklin and Van Pelt 2004). Therefore, traditional low thinning prescriptions were modified at the stand-level to maintain a diversity of tree species and simulate initial low density conditions of old-growth stand development (Tappeiner et al. 1997, Poage and Tappeiner 2002).

In addition to stand-level modifications, the YSTDS also attempted to incorporate within-stand spatial diversity through the formation of canopy gaps. Because individual plants respond most to their immediate environment (e.g., neighboring species and stand structure) (Goldberg 1987, Wagner and Radosevich 1998, D'Amato and Puettmann 2004), gaps are likely to impart a localized effect on understory structure and composition that diminishes as distance from the gap increases (Chen et al. 1992, Brandeis et al. 2001a). Hence, the influence of gaps may be diluted at a stand-level scale, whereas their effects may be more evident at a within-stand scale.

To test whether thinning like that applied in the YSTDS will encourage late-successional understory development in young, managed *P. menziesii* forests, we compared first-year and 5-7 years post-treatment understory vegetation response among three thinning treatments and an unthinned control. Specifically, we examined the impact of thinning on: (a) understory vegetation structure, including the herb, low shrub, tall shrub, and forest floor bryophyte strata as well as specific clonal shrub species and (b) plant community composition, including exotic species and late-seral associated species. In addition to stand-level responses for each treatment, we also investigated the same components at a finer spatial resolution for one treatment that included creation of canopy gaps. This provides a comparison of the influence of spatial variation in canopy structure on understory vegetation at large and small spatial scales. We conclude by relating short-term vegetation responses following thinning to long-term late-seral development of understories.

Methods

Study Description and Design

The study is located in the Willamette National Forest, on the western slope of the Cascade Range in central Oregon. This area falls within the *Tsuga heterophylla* (Raf.) Sarg. (Western Hemlock) zone (Franklin and Dyrness 1973). Mean annual precipitation is 230 cm, with only 5% falling between July and October. The average yearly temperature is 10.1ºC. Soils are generally well developed, ranging from thin shotty loams/clay loams to thin gravelly loams.

The study used a randomized block design comprised of four blocks. Each block contains one replication of four treatments, providing a total of 16 treatment units in the study. Blocks consist of *P. menziesii* forests that were clearcut harvested between the mid-1940's to mid 1950's and replanted or interplanted by the late 1950's. Criteria for block selection included similarity in overstory composition, stand age, management history, and size (> 56 ha). Study block designations that will be used throughout the paper are: CR (Cougar Reservoir); MC (Mill Creek); CF (Christy Flats); and SC (Sidewalk Creek). Within blocks, treatment units were similar in size, elevation, slope, aspect, site index, soil type, and dominant plant association (Table A1.1). Across all blocks, treatment units range in size from 15 to 53 hectares (ha), are mid-elevation, and have varied slope and aspects (Table A1.1).

Pre-thinning stand conditions were assessed using stand exam data collected prior to harvest in 1993. Direct pre- / post-treatment comparisons cannot be made because stand exam and post-treatment sampling were conducted differently. However these pre-treatment data indicate that while variation existed among blocks, initial basal area (BA) and density (tph) were comparable among treatment units within blocks

(Table A3.1). Therefore, pre-treatment conditions within each block are assumed to be similar.

Treatment Description

Each block contains four treatments: Control, Light thin, Heavy thin, and Light with Gaps thin (hereafter abbreviated as LtGaps). Treatments were applied between 1995-1997 (Table A4.1). Within blocks, treatments were randomly assigned and were implemented in close proximity to each other but were occasionally separated due to roads or other terrain barriers. 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 low-thinning prescriptions (Smith et al. 1997) with the added objective to maintain diversity by leaving species other than *P. menziesii*. The Control provided a reference for stand development without management intervention (Table A3.1). The Light was similar to a typical "commercial thin" that is commonly used throughout the region except for the retention of species other than *P. menziesii* to encourage species mix (Table A3.1). The Heavy opened the canopy substantially more than common commercial thins and reflected recent findings that many old-growth stands may have initiated at very low densities (Tappeiner et al. 1997) (Table A3.1). The LtGaps treatment was intended to provide spatial diversity by simulating gap-phase mortality. It created open patches (0.2 ha circular gaps evenly dispersed every 2 ha) within a stand matrix thinned to the same density as the Light treatment (Table A3.1). Areas within the LtGaps treatment are stratified into 3 sub-treatments: (a) Gap, (b) Edge, (c) and Stand Matrix (Figure A2.1). More information on theses sub-treatments is provided under Sampling Methods.

Post-thinning species composition in most treatment units consisted mostly of *P. menziesii* along with small components of mixed hardwood and conifer species. An exception to this was the thinned treatment units in the MC block, all of which contained a higher proportion of hardwoods than was found in other blocks. Pre-treatment stand exams indicate this was likely due to pre-thinning species composition (data not shown) and not a result of thinning.

Sampling Methods

Vegetation sampling occurred in the summer of 1995, 1996, or 1997, depending on time of harvest completion. In most cases, sampling was done during the first post-treatment growing season. However, all of SC Heavy, ¾ of SC LtGaps, and approximately ¼ of MC Light and CF LtGaps were sampled during the second growing season post-treatment (Table A4.1). For ease of communication, these data will collectively be referred to as 1997. Resampling was completed during the summer of 2001, depicting vegetation response 5-7 growing seasons post-harvest. Hereafter, these data will be referred to as 2001.

In Control, Light, and Heavy treatment units, approximately 7.5 % of the area was sampled. Transects were systematically placed through treatment units and sampling plots were located randomly along each transect. In each LtGaps treatment unit, 10 gaps, 10 edges, and 10 areas within the stand matrix were randomly selected and sampled with one plot each (30 total plots) in order to capture variation among the three sub-treatments. Gap plots were centered in the gap, allowing only the gap interior to be sampled by these plots (Figure A2.1). Edge plots were centered in a random direction 35.7 m from gap center so that each edge plot extended 7.5 m into the gap and 28.2 m into the remainder of the stand (Figure A2.1). For each gap, only one plot was placed in the surrounding edge. Stand Matrix plots were randomly placed throughout the remainder of the treatment unit with the criteria that plot center was located at least 71.4 m from the center of any gap, permitting sampling of all area at least 53.5 m from gap center (Figure A2.1).

Permanent 0.1 ha (17.8 m radius) circular plots were used for sampling. Within each 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 et al. 1995). Presence of all understory species was also recorded in each plot. Two parallel 14.5 m transects were nested within each plot (Figure A5.1). Eight 0.1 m^2 subplots were evenly spaced along each transect, providing a total of 16 subplots per plot (Figure A5.1). 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 not to species. 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 follows Hitchcock and Cronquist (1973).

Understory Structure

Understory structure was characterized by two components: vegetative layers (forest floor bryophytes, herbs, low shrubs, and tall shrubs/small trees) and representative clonal shrub species. 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 2004). Because clonal shrubs can dominate understory structure following thinning (Tappeiner and Alaback 1989, Tappeiner and Zasada 1993, Huffman and Tappeiner 1997, Bailey et al. 1998, Brandeis et al. 1999, Brandeis et al. 2001b), clonal shrub expansion was investigated by comparing abundance of four clonal species: *Gaultheria shallon* Pursh, *Mahonia nervosa* (Pursh) Nutt., *P. munitum*, and *P. aquilinum* among treatments. These species were chosen because they are often a dominant understory species in this region, they utilize varying degrees of vegetative reproduction, and they often inhibit development of other understory species (Tappeiner and Alaback 1989, Tappeiner and Zasada 1993, Huffman and Tappeiner 1997, Bailey et al. 1998, Brandeis et al. 1999, Brandeis et al. 2001b).

Understory Composition

Understory composition was described by three components: overall plant community composition, exotic species abunance, and frequency of late-seral 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 and Cronquist 1973). Abundance of exotic species was assessed collectively rather than by individual species. Species identified in previous studies as late-seral associates (Halpern 1989, Spies 1991, Lindh and Muir 2004) were used as representatives of late-seral species composition.

Data Analysis

Data aggregation – Large-scale

Prior to statistical analysis, data were aggregated to the treatment unit level. Cover of each species and ground surface features (e.g., exposed mineral soil, coarse litter, and fine litter) and overstory cover were averaged across subplots or transects for each plot. With the exception of LtGaps treatment units, treatment unit means were calculated by averaging plot means. In LtGaps treatment units, sub-treatments (Gap, Edge, and Stand Matrix) 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 sub-treatment means. Weights for each sub-treatment were based on the proportion of each sub-treatment in the total treatment unit area (Table A6.1).

Impacts of thinnings on abundances of late-seral associated species were difficult to assess because all these species had cover values below 1% in all treatment units; therefore, frequency, defined as the percentage of plots in each treatment unit where the species was present, was used as an indicator of occurrence. Only 2001 data were used because this represented time of maximum recovery from harvest disturbance available in the dataset. Because frequency can be influenced by sampling size (Gleason 1925, Palmer and White 1994), frequency in the LtGaps treatment could be overestimated due to relatively intensive sampling in this treatment. To address this, the LtGaps treatment was excluded and analyses were rerun; results did not change and therefore only results that included the LtGaps treatment are reported.

Statistical analysis – Large-scale

Treatment comparisons of vegetation layers, clonal species, exotic species, and 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). Changes in abundance of vegetation layers, clonal species, and exotic species over time were also compared among treatments. Using a repeated measures analysis, a Time x Treatment interaction tested whether changes in cover were equal among treatments over time (PROC MIXED). Data aggregated to the treatment unit level (n = 16 treatment units) were approximately normal; therefore, no transformations were performed.

To examine plant community composition, multivariate community analysis was conducted using PC-ORD v. 4.0 (McCune and Medford 1999). Differences in community composition among treatments and between years (1997 vs. 2001) were tested using multi-response blocked permutation procedure (MRBP) (Mielke 1979). MRBP does not require distributional assumptions, making it well-suited for community data that is usually non-normal and non-linear (McCune and Grace 2002). In addition to testing for differences among groups, MRBP also provides an effect size, A, that measures within-group agreement. Values of A generally range from 0 to 1, with 0 denoting as much within-group homogeneity as expected by chance and 1 denoting complete homogeneity within groups (McCune and Grace 2002). A can also be less than 0, indicating there is less within group homogeneity than expected by chance (McCune and Grace 2002). Tests for differences in composition among treatments were segmented into two analyses: (1) a test of difference among all treatments and (2) a test of difference among only thinned treatments, excluding Controls. The tests were performed separately for 1997 and 2001 data because changes in treatments between years could mask differences among treatments. The change of composition in treatments over time (1997 vs. 2001) was examined by separately testing each treatment for differences. Although the probability of type-I error ($\alpha \leq$

0.05) was conservative given the small sample size, probability of type-I error was probably higher than 0.05 due to the multiple tests.

To illustrate plant community patterns, an ordination was conducted with non-metric multi-dimensional scaling (NMS) (Kruskal 1964, Mather 1976). Ordination was performed using the Sørensen distance measure on the "slow and thorough" autopilot setting (maximum iterations = 400; runs with real data = 40; stability criterion = 0.00001). To adjust for skewness in the data, rare species (species occurring in less than 2 treatment units) were deleted and data were log transformed (McCune and Grace 2002). To retain all zero values, 0.001 (derived from McCune and Grace (2002)) was added to cover values of all species prior to transformation. One outlier (CF Heavy 1997) remained following transformation. The outlier had extremely low cover of several species that were relatively common in many other treatment units (e.g., *M. nervosa*) and a high amount of exposed mineral soil (Table 3.1), indicating it may have experienced a high degree of harvesting disturbance. Inclusion of the outlier, however, did not change overall configuration of points in the ordination or final interpretations. Therefore, the outlier was included in the final ordination. Environmental variables (i.e., overstory cover and exposed mineral soil) were not compared statistically but were used to aid interpretation of the ordination (Table 3.1).

Indicator species analysis (Dufrêne and Legendre 1997) was used to identify species indicative of treatments and also of years (1997 vs. 2001). This method calculates an indicator value (IV) from relative abundance and relative frequency of each species in each group. Due to lack of strong differentiation among thinned treatments (see Results), comparisons were made only between "thinned" (i.e., all thinned treatments were lumped into one group) and "control." Indicator species for the Control and thinned stands were identified separately for 1997 and 2001. Likewise, indicator species for 1997 and 2001 were identified separately for the Control and thinned stands. Results permitted contrasts between Controls and thinned stands as well as assessment of change in the treatments between years.

Table 3.1. Environmental variables (overstory cover and exposed mineral soil) used in interpretation of ordinations. Table provides average 1997 cover (%) for each Treatment/Block (large-scale) and each LtGaps Sub-treatment/Block (small-scale). Standard deviation is in parentheses. Values for 2001 (not shown) followed similar patterns. (CR = Cougar Reservoir block; MC = Mill Creek block; CF = Christy Flats block; SC = Sidewalk Creek block).

			Block			
		Treatment	**CR**	**MC**	**CF**	**SC**
Large-scale	**Overstory Cover (%)**	Control	82 (6)	82 (10)	80 (14)	70 (14)
		Heavy	25 (25)	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 (9)	2 (5)	9 (8)	2 (6)
		LtGaps	5 (2)	2 (1)	4 (1)	5 (3)
Small-scale	**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 (3)
	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)

Data aggregation – Small-scale

Stratified sampling of sub-treatments within the LtGaps treatment units also permitted within-stand small-scale examination of the impact of spatial variation in the overstory on understory structure and composition. For this analysis, other treatments units (i.e., Control, Heavy, and Light) were excluded and each LtGap sub-treatment unit (Gap, Edge, and Matrix) was treated as a separate treatment unit (n = 12; 3 sub-treatments in each of 4 blocks). Sub-treatment means for overstory cover, ground surface features, individual species, vegetative layers, clonal shrub species, and late-seral associated species were calculated by averaging plot means within each sub-treatment.

Statistical analysis – Small-scale

For investigating differences between gaps, edges, and forest matrices, statistical analysis of vegetative layers, clonal shrub species, late-seral associated species, and plant community composition (including MRBP and indicator species analysis) employed the same techniques as described for large-scale analysis. In place of treatment unit means, sub-treatment unit means were used for the small-scale analyses. For univariate analyses, data aggregated to the sub-treatment unit level were approximately normal (n = 12 sub-treatments); therefore no transformations were performed.

Ordination was also used to illustrate compositional variation among sub-treatments. Methods and data were identical to those described for the large-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 (derived from McCune and Grace (2002)) in order to retain zero values. Following transformation, one outlier (CF Gap 2001) remained. This sub-treatment unit had relatively high cover of *Sencecio sylvaticus* L., an invasive, exotic plant typical of disturbed soil. Because exclusion of the outlier in the analysis did not change final interpretations, this site was included in the final ordination. Values for environmental variables that facilitated interpretation of the ordination are displayed in Table 3.1.

Results

Structure – Large-Scale

Understory vegetation layers

Five to seven years following thinning, most understory layers have recovered from initial decline after harvest (Table 3.2). 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 pre-harvest levels (simulated by 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 within treatments. 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 it did in the Control (Time x Treatment interaction: $p = 0.008$; Treatment vs. Control comparisons: Heavy: $p = 0.010$; Light: $p = 0.032$; LtGaps: $p = 0.011$). The same was true for low shrub cover (Time x Treatment interaction: $p < 0.001$; Treatment vs. Control comparisons: Heavy: $p = 0.012$; Light: $p = 0.020$; LtGaps: $p = 0.024$).

Clonal shrubs

Elevated growth of some clonal shrub species was evident following thinning, but the increase in low shrub cover was not entirely attributable to these species (Table 3.3). Abundance of *M. nervosa* initially declined following thinning, but recovered by 2001. *G. shallon* also had less cover in the Light than the Control in 1997, but no differences were detectable by 2001. Increase in cover between 1997 and 2001 was greater in the Light treatment than the Control for *M. nervosa* ($p = 0.034$; Time x Treatment interaction: $p = 0.003$) and was greater in the Heavy treatment than the Control for *P. aquilinum* ($p = 0.029$; Time x Treatment interaction: $p = 0.028$).

Composition – Large-Scale

Plant communities

Understory plant communities showed significant differentiation among all treatments but no differences among only thinned treatments (MRBP; All treatments: 1997: $p = 0.002$; 2001: $p = 0.008$; Only thinned treatments: 1997: $p = 0.165$; 2001: $p = 0.709$), indicating that the major compositional distinction was between all thinned treatments and the Control. The compositional differences among all treatments was similar in 1997 ($A = 0.06$) and 2001 ($A = 0.06$). In contrast, compositional differences among thinned treatments were less in 1997 ($A = 0.01$) than in 2001 ($A = -0.06$). Over time, plant communities did not change in the Control (A < 0.01, $p = 0.473$), while composition changed significantly in all thinned treatments (Light: $A = 0.12$, $p = 0.030$; Heavy: $A = 0.14$, $p = 0.031$; LtGaps: $A = 0.14$, $p = 0.031$).

Ordination of treatment units on abundance of all species produced a final three-dimensional solution ($p = 0.0196$, final stress = 13.521, final instability = 0.00001, 67 iterations). The ordination was rotated to maximize treatment differences along the first axis, thereby facilitating interpretation. A vector overlay connecting treatment units within the same year and block was also used to highlight differences among treatment units within blocks. The three axes accounted for 84.6% of the total variation in the raw data (Axis 1 = 41.7%; Axis 2 = 25.8%; Axis 3 = 17.1%) and represented patterns in species composition between thinned treatments and controls, between years, and among blocks. Axis 3, which was mostly related to differences in composition among blocks, explained the least amount of variation; therefore only the major patterns represented by Axis 1 and Axis 2 are discussed.

The first axis represented compositional patterns related mostly to treatment differences between controls and 1997 thinned treatment units (Figure 3.1). Within blocks, 1997 thinned treatment units were located more toward the positive end of Axis 1 while controls aligned more along the negative end of Axis 1 (Figure 3.1). This separation was related to differences in canopy conditions (overstory cover: r = -0.5; Table 3.1) and harvest disturbance (exposed mineral soil: r = 0.73; Table 3.1), with 1997 thinned treatment units having open canopies and high harvest disturbance relative to controls. Accordingly, species composition in 1997 thinned treatment units was dominated by early-seral herbaceous species and species indicative of disturbed environments (e.g., *S. sylvaticus*) while the controls harbored more shade-tolerant bryophytes and a few late-seral associated herbs (Table 3.4). In addition several low shrub species (e.g., *G. shallon, M. nervosa*) were more common in controls than they were in most 1997 thinned treatments (Table 3.4). The shift between 1997 and 2001 thinned treatments toward controls along Axis 1 (Figure 3.1) was primarily due to recovery of several low shrub species and bryophytes in thinned treatment units.

Table 3.2. 1997 and 2001 post-treatment cover (%) of understory vegetation layers and exotic species in each treatment (large-scale) and in each LtGaps sub-treatment (small-scale). Numbers in parentheses provide 95% confidence intervals. Letters indicate differences among treatments; treatments with same letters do not differ at $p \leq 0.05$ level. ANOVA *P*-value is for overall test of difference among treatments.

	Year	Treatment	Bryo.	Herbs	Low Shrubs	Tall Shrubs / Small Trees	Exotic Species
Large-scale	1997	Control	24 *a* (17 - 32)	19 *a* (14 - 25)	32 *a* (18 - 46)	44 *a* (33 - 54)	0 *a* (-0.03 - 0.07)
		Heavy	4 *b* (0 - 9)	18 *a* (14 - 23)	14 *b* (1 - 26)	19 *b* (-1 - 38)	0 *a* (-0.04 - 0.24)
		Light	12 *a b* (3 - 21)	16 *a* (10 - 22)	14 *b* (3 - 26)	13 *b* (4 - 22)	0 *a* (-0.03 - 0.21)
		LtGaps	11 a *b* (-9 - 31)	18 *a* (12 - 25)	19 *b* (3 - 35)	16 *b* (6 - 26)	0 *a* (-0.03 - 0.31)
		ANOVA P-value	0.014	0.457	< 0.001	0.002	0.062
	2001	Control	28 *a* (8 - 49)	17 *a* (12 - 21)	27 *a* (5 - 49)	44 *a* (25 - 62)	0 *a* (-0.25 - 0.70)
		Heavy	24 *a* (0 - 48)	24 *a* (11 - 37)	37 *a* (16 - 58)	25 *a* (1 - 49)	0 *a* (-0.05 - 0.26)
		Light	34 *a* (6 - 62)	22 *a* (14 - 29)	35 *a* (21 - 49)	19 *a* (7 - 31)	0 *a* (-0.11 - 0.35)
		LtGaps	26 *a* (-4 - 57)	23 *a* (11 - 34)	39 *a* (26 - 53)	22 *a* (6 - 39)	1 *a* (-1.71 - 3.67)
		ANOVA P-value	0.750	0.229	0.383	0.064	0.515
Small-scale	1997	Matrix	12 *a* (7 - 18)	20 *a* (16 - 23)	24 *a* (18 - 30)	16 *a* (11 - 21)	*0 a* (-0.03 - 0.08)
		Edge	12 *a* (7 - 17)	17 *a* (14 - 20)	19 *a b* (15 - 23)	17 *a* (11 - 23)	0 *a* (-0.03 - 0.24)
		Gap	4 *a* (2 - 5)	22 *a* (17 - 27)	13 *b* (9 - 17)	8 *a* (5 - 10)	1 *a* (-0.29 - 1.66)
		ANOVA P-value	0.100	0.518	0.026	0.052	0.064
	2001	Matrix	32 *a* (23 - 39)	26 *a* (21 - 30)	44 *a* (37 - 51)	25 *a* (18 - 30)	0 *a* (-0.24 - 0.50)
		Edge	26 *a* (19 - 34)	22 *a* (19 - 26)	38 *a* (32 - 44)	23 *a* (16 - 29)	1 *a* (-1.78 - 3.70)
		Gap	8 *a* (5 - 11)	19 *a* (15 - 22)	44 *a* (39 - 50)	17 *a* (11 - 22)	5 *a* (-7.69 - 16.68)
		ANOVA P-value	0.057	0.211	0.359	0.073	0.319

Table 3.3. 1997 and 2001 post-treatment cover (%) of four clonal shrub species in each treatment (large-scale) and LtGaps sub-treatment (small-scale). Numbers in parentheses provide 95% confidence intervals. Letters indicate differences among treatments; treatments with same letters do not differ at $p \leq 0.05$ level. ANOVA *P*-value is for overall test of difference among treatments.

	Year	**Treatment**	***M. nervosa***	***G. shallon***	***P. munitum***	***P. aquilinum***
Large-scale	**1997**	Control	14 *a* (6 - 21)	7 *a* (1 - 13)	4 *a* (-2 - 11)	2 *a* (0 - 4)
		Heavy	5 *b* (1 - 9)	3 *a b* (-3 - 10)	2 *a* (-1 - 4)	1 *a* (0 - 2)
		Light	5 *b* (3 - 8)	2 *b* (-3 - 7)	3 *a* (0 - 6)	1 *a* (-1 - 4)
		LtGaps	6 *b* (2 - 10)	6 *a b* (-6 - 17)	3 *a* (-1 - 6)	1 *a* (0 - 1)
		ANOVA P-value	< 0.001	0.032	0.176	0.173
	2001	Control	13 *a* (2 - 25)	6 *a* (-3 - 16)	4 *a* (-1 - 9)	1 *a* (-1 - 2)
		Heavy	11 *a* (6 - 15)	6 *a* (-1 - 13)	5 *a* (-3 - 13)	6 *a* (-1 - 13)
		Light	12 *a* (7 - 18)	5 *a* (-3 - 12)	7 *a* (-2 - 16)	3 *a* (0 - 7)
		LtGaps	11 *a* (6 - 16)	8 *a* (-2 - 19)	7 *a* (-3 - 18)	2 *a* (-1 - 5)
		ANOVA P-value	0.849	0.180	0.133	0.134
Small-scale	**1997**	Matrix	7 *a* (1 - 13)	7 *a* (-16 - 34)	4 *b* (0 - 9)	1 *a* (-1 - 3)
		Edge	6 *a* (2 - 11)	6 *a* (-6 - 17)	3 *a b* (-1 - 6)	1 *a* (0 - 1)
		Gap	4 *a* (-2 - 9)	1 *a* (-8 - 15)	1 *a* (0 - 2)	1 *a* (-1 - 3)
		ANOVA P-value	0.177	0.141	0.038	0.734
	2001	Matrix	13 *b* (4 - 21)	10 *a* (-11 - 34)	12 *a* (-9 - 32)	1 *a* (-1 - 5)
		Edge	11 *a b* (7 - 15)	9 *a* (-2 - 19)	6 *a* (-2 - 15)	2 *a* (-1 - 5)
		Gap	8 *a* (3 - 12)	4 *a* (-6 - 15)	3 *a* (-3 - 9)	6 *b* (0 - 12)
		ANOVA P-value	0.054	0.081	0.139	0.023

Figure 3.1. 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).

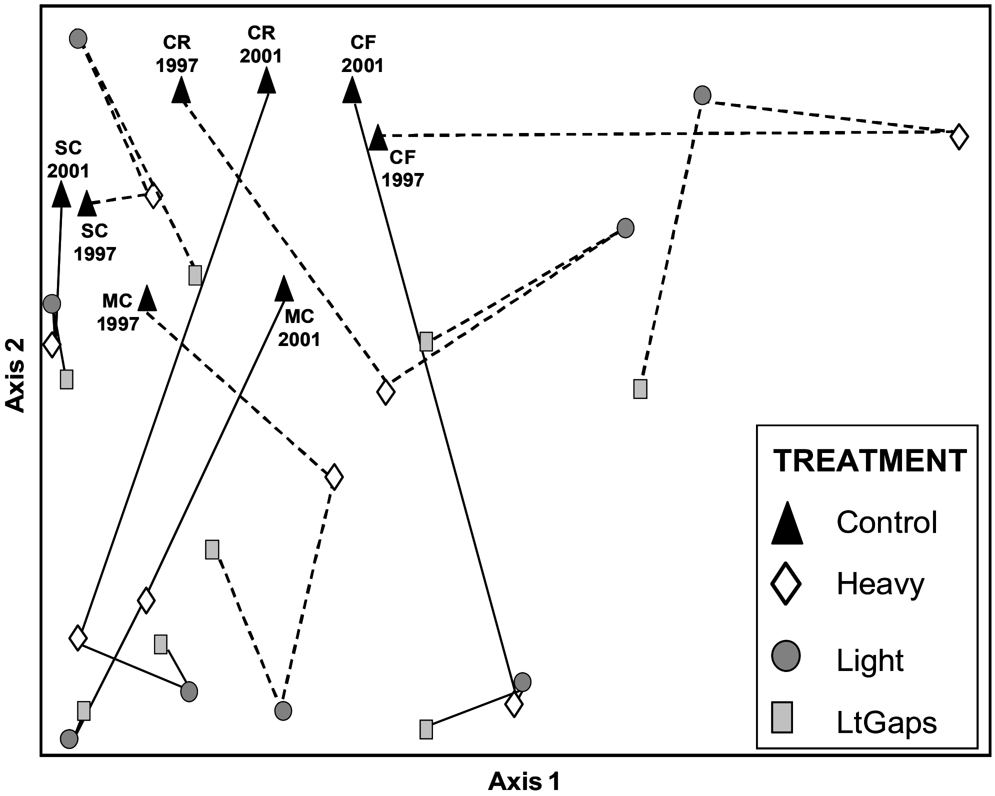


Table 3.4. Correlations (Correl.; - = negative correlation; + = positive correlation) of species with axes for large-scale ordination (Figure 3.1) and small-scale ordination (Figure 3.2). Axis 3 correlations not shown. Except where noted, positive correlations of all species are: r > 0.50 and negative correlations of all species are: r < - 0.50 ([1]: r = 0.40; [2] r = 0.30; [3] r = 0.20; [4] r = -0.40; [5] r = -0.30).

	Correl.	Axis 1	Axis 2
Large Scale	–	Bryophytes	*Anaphalis margaritacea* (L.) Benth.
		Chimaphila umbellata	*Campanula scouleri* Hook. ex A. DC.
		Corylus cornuta Marsh.	*Epilobium angustifolium* L.
		Gaultheria shallon	*Galium triflorum* Michx.
		Mahonia nervosa	*Hypericum perforatum* L.
		Rhododendron macrophyllum D. Don ex G. Don	*Rubus parviflorus* Nutt.
		Vaccinium parvifolium Sm.	*Rubus ursinus* Cham & Schlecht.
		Vancouveria hexandra (Hook.)	*Trientalis latifolia* Hook.
	+	*Cirsium* spp. [2]	*Chimaphila menziesii* [2]
		Epilobium watsonii Barbey [1]	*Chimaphila umbellata*
		Gnaphalium microcephalum Nutt.	*Rubus nivalis* Dougl. ex Hook. [3]
		Lactuca serriola L. [3]	*Taxus brevifolia* Nutt.
		Ribes lobbii Gray [3]	*Trillium ovatum* [2]
		Senecio sylvaticus	*Xerophylum tenex* (Pursh) Nutt. [2]
Small Scale	–	*Gaultheria shallon*	*Epilobium minutum* [4]
		Mahonia nervosa	*Gnaphalium* spp. [5]
		Trillium ovatum	*Lactuca serriola* [4]
		Vaccinium parvifolium	*Luzula* spp. D.C. [5]
		Vancouveria hexandra Hook.	*Senecio sylvaticus*
	+	*Cirsium* spp.	*Hypericum perforatum*
		Epilobium watsonii	*Rubus leucodermis*
		Gnaphalium microcephalum	*Rubus parviflorus*
		Lotus purshianus F.E. & E.G. Clem.	*Rubus ursinus*
		Rubus leucodermis Doulg. ex Torr. & Gray	*Trientalis latifolia*
		Senecio sylvaticus	*Whipplea modesta* Torr.

Axis 2 also represented compositional differences between controls and thinned treatment units but was also related to changes in composition in thinned treatment units between 1997 and 2001 (Figure 3.1). Within blocks, most thinned treatments were associated more with the negative end of Axis 2 than controls, but the negative association was stronger for the 2001 thinned treatment units than for the 1997 thinned treatment units. Species composition in 2001 thinned treatment units was characterized by the release of several early-seral herbs and sub-shrubs (i.e., generally perennial herbaceous species with a woody base; e.g., *Chimaphila umbellata* (L.) W. Bart.) (Table 3.4). This release occurred in all thinned treatments and resulted in species composition of thinned treatment units (within blocks) being more similar to each other in 2001 post-treatment than it had been in 1997 post-treatment (see magnitude of separation among thinned treatments in 1997 vs. 2001; Figure 3.1). It also differentiated species composition of thinned treatment units from that of the controls (see magnitude of separation between thinned treatments and controls along Axis 2, Figure 3.1). This effect was more pronounced in some blocks (e.g., CF) than others (e.g., SC), and was likely associated, at least in part, with differences in harvest disturbance (Table 3.1). Proximity of most 1997 thinned treatment units to controls along the second axis was more related to lower abundances of species that were common in 2001 thinned treatment units than the presence of species associated with controls.

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., *Epilobium angustifolium* L.) (Table 3.5). Many species were also indicative of 2001 thinned treatment units but not 1997 thinned treatment units or controls (Table 3.5, Table 3.6), confirming the release of early-seral species and recovery of low-shrubs in 2001 thinned treatment units.

Exotic species

Thinning did not significantly promote establishment or growth of exotic species (Table 3.2). Overall, cover of exotic species was very low in all treatments. Although not statistically different, the LtGaps was most impacted by exotic species, mostly due to one localized invasion of *Cytisus scoparius* (L.) Link (see also section about Exotic species – small scale).

Late-seral associated species

Most late-seral species were unaffected by thinning. However, frequency of two species declined following thinning (Table 3.7). *C. umbellata* had lower frequency in all thinned treatments relative to the Control (Heavy: $p = 0.005$; Light: $p = 0.001$; LtGaps: $p = 0.001$). The same was true for *Goodyera oblongifolia* Raf. (Heavy: $p < 0.001$; Light: $p = 0.001$; LtGaps: $p < 0.001$). *Chimaphila menziesii* (R. Br. ex D. Don)

Spreng. also had marginally lower frequency in the LtGaps treatment than the Control ($p = 0.089$).

Structure – Small Scale

Overall the comparison of conditions in gaps, edges, and forest matrices confirmed trends found on the stand level. However, several important distinctions pointed out that the spatial scale of treatment assessment is an important factor influencing the interpretation of study results.

Understory vegetative layers

At a small scale, thinning affected minor differentiation of vegetation layers among sub-treatments (Table 3.2). Low shrub cover in the Gap was less than that of the Edge and Stand Matrix in 1997, but recovery of this layer occurred by 2001. Similarly, tall shrub cover was marginally less in the Gap than the Edge ($p = 0.07$) in 1997, but recovery was evident by 2001. Bryophyte cover did not differ among sub-treatments in 1997 but was marginally less in the Gap than the Stand Matrix by 2001 ($p = 0.06$).

Clonal shrubs

Similar to the large-scale, thinning imparted variation among sub-treatments in cover of clonal shrub species (Table 3.3). Abundance of *P. munitum* was less in the Gap than the Stand Matrix during the first-year post-treatment but no longer differed among sub-treatments by 2001 due to increased cover in the Gap. Cover of *M. nervosa* was higher in the Stand Matrix than in the Gap and cover of *P. aquilinum* was higher in the Gap than in the Edge and the Stand Matrix by 2001. From 1997 to 2001, cover of *P. aquilinum* increased more in the Gap than it did in the Edge or Stand Matrix (Time x Treatment interaction: $p = 0.052$; Gap vs. Edge: $p = 0.023$; Gap vs. Stand Matrix: $p = 0.001$).

Table 3.5. 1997 and 2001 post-treatment indicator species of large-scale treatments (Control / Thinned) and small-scale LtGaps sub-treatments (Edge / Gap / Matrix). (IV = Indicator value; $p \leq 0.05$ for all species).

	Year	Species	Group	IV
Large-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 elata* (Nutt.) Greene	Control	63
		Chimaphila umbellata	Control	69
		Holodiscus discolor (Pursh) Maxim	Control	73
		Taxus brevifolia	Control	76
		Trillium ovatum	Control	70
		Campanula scouleri	Thinned	75
		Cirsium spp.	Thinned	83
		Epilobium angustifolium	Thinned	84
		Galium triflorum	Thinned	59
		Graminoids	Thinned	65
		Pteridium aquilinum	Thinned	56
		Rubus leucodermis	Thinned	92
		Rubus ursinus	Thinned	55
		Trientalis latifolia	Thinned	70
		Whipplea modesta	Thinned	55
Small-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 gymnocarpum Nutt.	Edge	69
		Epilobium watsonii	Gap	91
		Cirsium spp.	Gap	74
		Rubus leucodermis	Gap	61
		Rubus parviflorus	Gap	69

Table 3.6. 1997 and 2001 indicator species for each treatment (Control / Thinned) and LtGaps sub-treatments (Edge / Gap / Matrix). (IV = Indicator value; $p \leq 0.05$ for all species).

	Treatment	Species	Group	IV
Large-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
		Epilobium angustifolium	2001	61
		Fragaria virginiana Duchesne	2001	63
		Graminoids	2001	62
		Hieracium albiflorum	2001	69
		Lactuca murealis (L.) Fresen.	2001	59
		Linnea 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 mollis Nutt.	2001	83
		Trientalis latifolia	2001	64
		Viola sempervirens	2001	54
		Whipplea modesta	2001	61
Small-scale	**Matrix**	--	1997	--
		--	2001	--
	Edge	--	1997	--
		Whipplea modesta	2001	65
	Gap	*Senecio sylvaticus*	1997	100
		Gnaphallium microcephallum	2001	100
		Graminoids	2001	64
		Rubus leucodermis	2001	100
		Rubus parviflorus	2001	85
		Rubus ursinus	2001	56
		Trientalis latifolia	2001	74

Table 3.7. ANOVA tests for overall differences in frequency (2001 data) of late-seral species among thinning treatments and control (large-scale) and among LtGaps sub-treatments (small-scale).

Species	**Large-scale p-value**	**Small-scale p-value**
Achyls tryphylla	0.696	0.020
Adenocaulon bicolor	0.911	0.023
Anemone deltoidea Hook.	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 lanciniata Gray	0.299	0.770
Dicentra formosa	0.489	0.086
Goodyera oblongifolia	< 0.001	0.126
Linnea borealis	0.396	0.144
Maianthemum racemosum (L.) Link	0.802	0.140
Syntheris reiniformis (Dougl. ex Benth.) Benth.	0.451	0.125
Tiarella trifoliata L.	0.209	0.126
Vancouveria hexandra	0.915	0.367

Composition – Small Scale

Plant communities

Understory plant communities showed significant differentiation in composition among sub-treatments (MRBP; 1997: $p = 0.014$; 2001: $p = 0.005$). The distinction in composition among sub-treatments was larger in 2001 ($A = 0.11$) than in 1997 ($A = 0.05$) post-treatment data. A significant change of plant communities over time was also evident in all sub-treatments (Stand Matrix: $A = 0.11$, $p = 0.041$; Edge: $A = 0.13$, $p = 0.033$; Gap: $A = 0.19$, $p = 0.031$).

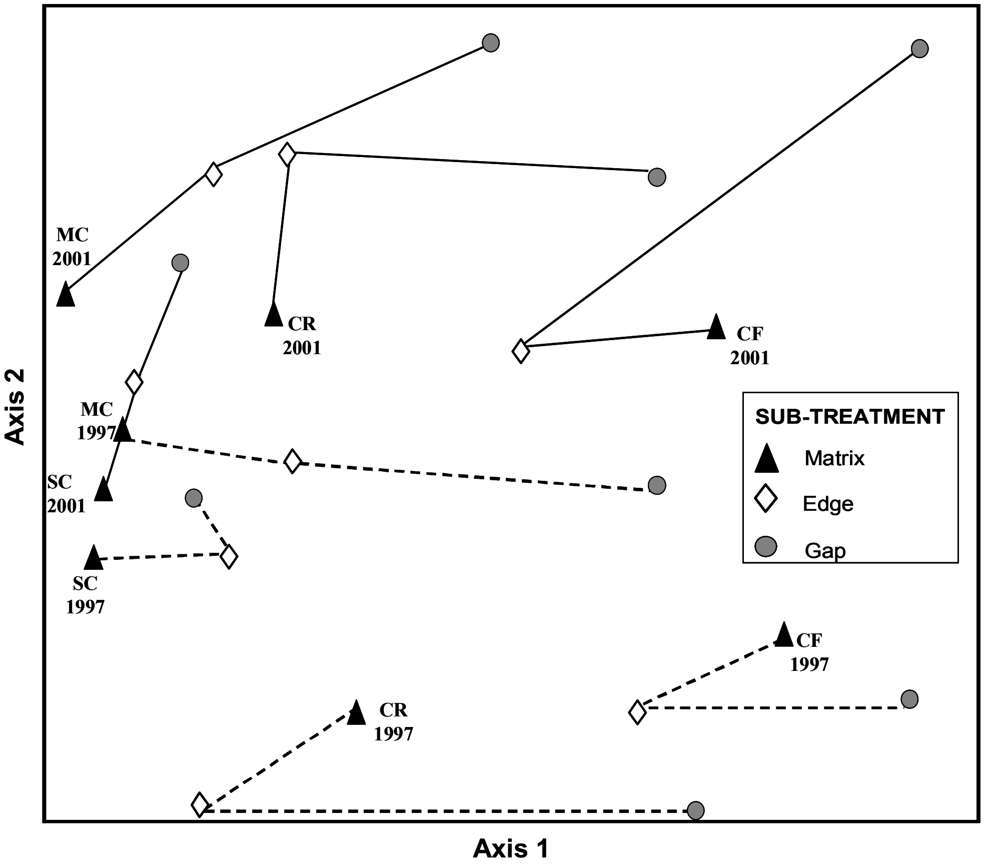
Ordination of sub-treatment units on abundance of all species yielded a final three-dimensional solution ($p = 0.0196$, final stress = 12.6, final instability = 0.00001, 68 iterations). Rotation of the ordination and a vector overlay, as described for the large-scale ordination, were used to aid in interpretation of the small-scale ordination. The three axes accounted for 83.3% of the total variation in the raw data (Axis 1 =

37.5%; Axis 2 = 30.5%; Axis 3 = 15.3%) and represented patterns in plant community composition among sub-treatments, among blocks, and between years. Axis 3, which was mostly related to differences in composition among blocks, explained the least amount of variation; therefore only the major patterns represented by Axis 1 and Axis 2 are presented.

Axis 1, which explained the most variation, represented compositional differences among sub-treatments (Figure 3.2). Within blocks, Gaps were associated with the positive end of Axis 1 while the Edge and Stand Matrix were associated with the negative end of the second axis (Figure 3.2). Like at the large-scale, this differentiation of plant communities among sub-treatments was closely related to canopy cover (overstory cover: r = -0.57; Table 3.1) and harvest disturbance (exposed mineral soil: r = 0.68; Table 3.1). Open conditions near the gap center favored plant assemblages consisting mostly of light-demanding early-seral herbs and shrubs (e.g., *S. sylvaticus* and *Cirsium* spp.; Table 3.4), while the Stand Matrix and Edge contained more shade-tolerant shrubs and herbs (Table 3.4). Differentiation of plant communities among sub-treatments was most pronounced in the CF block where cover of exposed mineral soil in the Gap was high after harvest (Table 3.1) and was weakest in the SC block where cover of exposed mineral soil in the Gap was low in 1997 (Table 3.1).

Axis 2 represented a change of plant communities in sub-treatments over time (Figure 3.2). Within blocks, 2001 sub-treatment units were positively associated with the second axis while 1997 sub-treatment units were negatively associated with Axis 2 (Figure 3.2). Similar to the large-scale, this was mostly due to release of several early-seral species by 2001, especially in the Gaps (Table 3.4). However, unlike at the large-scale where thinned treatment units became more similar over time (Figure 3.1), at the small-scale, sub-treatment units became more distinct over time (see magnitude of separation among sub-treatments within each year, Figure 3.2).

Figure 3.2. Ordination of LtGaps sub-treatment units on abundance of all species (Axis 1 and Axis 2; Axis 3 not shown). Vectors connect 1997 (dashed line) and 2001 (solid line) sub-treatment units within each block. Labels next to Matrix sub-treatments 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 3.5). In addition, annuals and biennials indicative of Gaps in 1997 were replaced by herbaceous and woody perennials by 2001 (Table 3.5). A release of early-seral species was also evident between 1997 and 2001, but was most apparent in the Gap (Table 3.6).

Exotic species

Except for one localized occurrence, thinning yielded little differentiation in exotic cover among sub-treatments (Table 3.2). Though the Gap consistently had the highest cover by exotics, the difference among sub-treatments was only marginally significant in 1997 and was insignificant in 2001. This was mostly because exotic species invasion was generally limited to invasion by *C. scoparius* in the Gap of the MC block and was not a common trend across blocks (Cover of *C. scoparius* in the MC block: S. Matrix = 0%; Edge = 3%; Gap = 14%; Not present in LtGaps treatment units of other blocks).

Late-seral associated species

Habitat differentiation among sub-treatments influenced occurrence of several late-seral species. Of species that differed in occurrence among sub-treatments (Table 3.7), most responded unfavorably to gaps. Frequencies of *Adenocaulon bicolor* Hook., *C. menziesii*, and *Achyls triphylla* (Sm.) DC. were lower in the Gap than in the Edge (*A. bicolor*: $p = 0.059$; *C. menziesii*: Edge: $p = 0.053$; *A. triphylla*: $p = 0.017$). *Adenocaulon bicolor* also occurred less frequently in the Gap than the Stand Matrix ($p = 0.024$). There was also suggestive evidence that frequency of *C. menziesii* was less in the Gap and Stand Matrix ($p = 0.087$) and that frequency of *C. umbellata* was lower in the Gap than the Edge ($p = 0.088$). *Dicentra formosa* (Haw.) Walp. never occurred in the Gap and was present in the Edge and Stand Matrix, but comparisons among sub-treatments were insignificant.

Discussion

Before discussing implications of our results, it is important to acknowledge the limitations. First, we did not have specific pre-treatment data on species composition. Without this, it is difficult to attribute species occurrences and abundances solely to treatment effects. Therefore, though our discussion often focuses on specific species, these species are used to describe ecological and successional patterns rather than to predict how thinning will impact individual species. Second, inferences for canopy gaps are restricted to those of the size and density applied in this study. While this provides valuable ecological insight into the potential influence of canopy gaps on vegetation, gaps of other sizes and densities could produce effects different from those discussed in this study. Finally, our conclusions are limited by the short-term nature (5-7 years) of our data; hence, interpretations of future conditions are tentative at this time. Nonetheless, documentation and understanding of initial response is critical to comprehension of long-term successional patterns and mechanisms.

Structure

Understory structure differed most between thinned and unthinned stands, with minor discrepancies among thinning intensities. Over time, vegetative structure in thinned stands recovered to pre-treatment levels, simulated by the Control. 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 to tall and low shrubs.

In addition to ground disturbance, it is likely that initial decline of forest floor bryophytes following heavy thinning was attributable to desiccation resulting from 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 (Cheo 1946, Green et al. 1995, Hannerz and Hanell 1997). Ground layer bryophytes are more sensitive to such surface level drying factors than vascular plants because their lack of conductive tissue prevents them from benefiting from increases in sub-surface soil moisture in thinned stands (Thomas et al. 2001).

Despite initial declines, recovery of most vegetation layers to pre-thinning levels was evident within 5-7 years of harvest. In fact, the linear increase in abundance of herbs and low shrubs in thinned treatment units over time relative to controls indicate that abundance of herbs and low shrubs in thinned stands may soon exceed those of unthinned stands. These strata have increased elsewhere following disturbance and overstory removal (Alaback 1982, Tappeiner and Zasada 1993, Bailey et al. 1998, Harrington and Edwards 1999, Thomas et al. 1999). Enhanced resource levels following thinning are likely linked to this phenomenon (Cheo 1946, Everett and

Sharrow 1985, Harrington and Edwards 1999, Thomas et al. 1999, Parker et al. 2001, Beggs et al. *Submitted*). Elevated resources boost plant vigor, spurring increases in growth as well as sexual and vegetative reproduction (Thompson and Wilson 1978, Tappeiner and Zasada 1993, Huffman and Tappeiner 1997, Wender et al. 2004).

While low shrub abundance increased over time in thinned stands, concerns over homogenization of the understory by rapid growth of few clonal shrub species (Tappeiner and Zasada 1993, Thysell and Carey 2000) were not warranted at this time. Increases over time in thinned stands were apparent only for *M. nervosa* and *P. aquilinum*, with that of *M. nervosa* appearing to be more related to recovery from harvest damage than release (Table 3.3). However, because recovery is still occurring for these species (Table 3.3), longer time may be needed to assess their true impact on the understory composition. As canopies begin to close and light levels drop, vegetative reproduction and relatively high allocation to belowground structures may confer competitive advantage to clonal species (Alaback 1982, Tappeiner and Alaback 1989, Tappeiner and Zasada 1993, Antos and Halpern 1997).

In comparison to low shrubs, tall shrubs seem to be recovering more slowly in thinned stands. Due to their elevated position in the forest canopy, they probably experienced the most damage from harvest. Consequently, most recovery is likely resprouting and growth from smaller stems rather than expansion of larger plants. This is a significant distinction because the ecological role of 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 and Tappeiner 1997). In addition, old, large shrub branches host several bryophytic communities (Rosso 2000). Therefore, although abundance of tall shrubs may be nearing that of pre-thinning levels, plant size may be insufficient to provide valuable food and substrate.

Composition

Overall, composition of thinned stands was quite distinct from unthinned stands but was relatively unaffected by thinning intensity (Figure 3.1). Unlike findings of other studies (Bailey et al. 1998, Thysell and Carey 2000), this shift in composition following thinning was not largely influenced by the presence of exotic species (Table 3.2, Table 3.5, Table 3.6). Rather, it was more related to the release of several early-seral subordinate forest herbs and sub-shrubs (e.g., *C. umbellata*) in thinned stands (Table 3.5, Table 3.6) (Halpern 1989).

Unthinned stands harbored shade-tolerant species such as *C. menziesii*, *C. umbellata*, and *T. ovatum* while species typical of high light environments and disturbed soil such as *E. angustifolium*, and *Cirsium* spp. P. Mill, dominated thinned stands. *C. menziesii* and *C. umbellata* along with *G. oblongifolia*, all obligate mycotrophs (Castellano and Trappe 1985), were also the only three late-seral associates to display a negative response to thinning (Table 3.7). It is important to note, however, that all late-seral species were relatively uncommon; therefore, absolute values of decline are small. Nonetheless, mycotrophic species have been identified in other studies as being sensitive to disturbance (Halpern 1989, Halpern and Spies 1995, Lindh and Muir 2004). In addition to mycorrhizal symbionts, other specific microhabitat features such as deep litter layers may be critical for the survival of these species (Castellano and Trappe 1985, Lindh and Muir 2004). Changes in moisture and light levels at the forest floor following thinning (Green et al. 1995, Parker et al. 2001) as well as soil disturbance (Buckley et al. 2003) could potentially disrupt these microhabitat components and may be responsible for the decline of such species in thinned stands. Displacement by other generalist species may also be a contributing factor (Grime 1979, Meier et al. 1995).

In thinned stands, patches of exposed mineral soil (Table 3.1) and an open canopy (Beggs et al. *Submitted*) likely increased resource availability (Everett and Sharrow 1985, Harrington and Edwards 1999, Parker et al. 2001) and facilitated seed dispersal, germination, and establishment (Thompson and Wilson 1978, Alaback and Herman 1988), thereby permitting opportunistic annual and biennial species such as *S. sylvaticus* to quickly colonize and potentially displace less competitive species (Grime 1979, Meier et al. 1995). A rapid post-disturbance peak in annuals and biennials has been noted elsewhere (West and Chilcote 1968, Dyrness 1973, Schoonmaker and

McKee 1988, Halpern 1989) and may also be linked in part to rooting systems adapted to capitalize upon post-disturbance nutrient flushes (West and Chilcote 1968, Antos and Zobel 1984, Antos and Halpern 1997).

The dominance of annuals and biennials was short-lived, however, with understory dominance shifting toward early-seral perennial forest herbs and sub-shrubs by 5-7 years after thinning (Halpern 1989). This suite of species (e.g., *E. angustifolium* and *Trientalis latifolia* Hook.) are more efficient at nutrient uptake than annuals (Halpern 1989, Antos and 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 and Zobel 1984, Meier et al. 1995).

While thinning encouraged recruitment and growth of several species, most late-seral associates exhibited no response to thinning. Although resiliency to disturbance is not uncommon for these species (Spies 1991, Halpern and Spies 1995), the lack of response also indicates 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 structure (Beggs et al. *Submitted*) and lag-times between changes in structure and vegetation response can exist (Thomas et al. 1999), lack of response is not unexpected.

Vegetation composition of thinned stands was not greatly influenced by invasion of exotic species, contrasting with results of other studies (Alaback and Herman 1988, Bailey et al. 1998, Thysell and Carey 2000, Parker et al. 2001). It must be noted, that some studies that found increases in exotic species following thinning (Bailey et al. 1998, Thysell and Carey 2000) also examined the impact of exotic grass species. While exotic grasses did not visually appear to be a major component of the vegetation at any of our sites (personal observation), we did not identify grasses to species and therefore may have slightly underestimated the influence of exotic species. Of the exotic species identified in our study, most had minimal influence on understory composition (Table 3.2). During the first year post-treatment, most were transient species (e.g., *S. sylvaticus*) (Schoonmaker and McKee 1988, Antos and Halpern 1997).

However, invasion by the noxious weed, *C. scoparius*, was problematic in one LtGaps treatment unit that was located near a major highway and a community refuse center, two sources of abundant seed. This restricted occurrence suggests that increased resource availability and soil disturbance can make thinned stands vulnerable to exotic species (Mack et al. 2000, Thysell and Carey 2000, Sakai et al. 2001), but invasion of exotic species is primarily dependent upon the proximity of local seed sources (Mack et al. 2000, Thysell and Carey 2000).

Thinning was likely not the only factor influencing post-treatment species composition. The degree of harvest disturbance, an indirect effect of thinning, also probably impacted composition (Buckley et al. 2003, Berger et al. 2004). This is demonstrated mostly by the differentiation in composition of the CF and SC blocks (Figure 3.1). At the CF block, the mechanical harvesting system and thinning operations resulted in heavy site disturbance whereas the skyline system used at the SC block confined most disturbance to skyline corridors (James Mayo, USDA Forest Service, *personal communication*). Consequently, thinned stands of the CF block had low abundance of several species (e.g., *M. nervosa*, *Acer circinatum* Pursh.) relative to other thinned and unthinned stands and the release of several species such as *E. angustifolium* and *R. ursinus* were delayed. Conversely, at the SC block, there were relatively slight changes in abundance of most species following thinning and the release of species that was common in other blocks was minimal in the SC block (Figure 3.1)

Post-thinning understory composition was also probably strongly influenced by pre-treatment conditions (Hughes and Fahey 1991). Though few specifics are known on pre-treatment understory composition of treatment units, the SC block was distinguished from other blocks by its more xeric plant associations (Table A1.1) and high abundance of *G. shallon* (data not shown). Following thinning in the SC block, vegetation composition of thinned stands was somewhat differentiated from that in the unthinned stand, but the divergence was not nearly as prominent as in other blocks (Figure 3.1). Other studies on relatively dry sites also found limited understory vegetation response following thinning (He and Barclay 2000). These results reinforce previous findings that while overstory cover strongly influences abundance of vegetation, composition may be driven more by other factors such as soil moisture, site quality, and site history (McCune 1982, Moore and Vankat 1986, Klinka et al. 1996, He and Barclay 2000).

Small-scale spatial variation

At a small-scale, within-stand overstory structural variation imparted subtle influence on understory vegetation structure (Table 3.2, Table 3.3). Forest floor bryophytes were more common under canopy cover of the Stand Matrix relative to the open Gap, likely because of disturbance and dessication as previously discussed. Conversely, the high light environment of the Gap likely promoted rapid spread of some clonal species characterized by shallow lateral root systems such as *P. aquilinum* (Halpern 1989) (Table 3.3). Although not all vegetative strata displayed preference for specific sub-treatments (Table 3.2, Table 3.3), associations of some vegetative layers and clonal species with different areas of the stand suggest responses to different environmental conditions in sub-treatments (Whittaker and Simon 1975).

Small-scale compositional trends were also apparent, with several species exhibiting specific microhabitat affinities. Habitat in the Gap likely offered high levels of light and soil resources (Moore and Vankat 1986, Gray et al. 2002), encouraging recruitment and growth of several early-seral herbs and shrubs such as *Epilobium watsonii* Barbey and *Rubus leucodermis* Dougl. ex Torr. & Gray (Table 3.5). Open conditions probably also facilitated seed dispersal (Thompson and Wilson 1978) and spurred vegetative reproduction via stolons and shallow rhizomes common for several of these species (Moore and Vankat 1986, Halpern 1989, Antos and Halpern 1997). Conversely, lower light availability in the Stand Matrix and Edge relative to the Gap favored species such as *M. nervosa* and *Vaccinium parvifolium* Sm. that can tolerate shade and allocate more resources to below-ground development (Tappeiner and Alaback 1989, Huffman and Tappeiner 1997).

Interestingly, several late-seral associated species along with *Whipplea modesta* Torr. exhibited high affinity for the microhabitat found in the Edge. Many of these species are relatively small in stature but can spread via vegetative or sexual reproduction. However, they probably cannot compete strongly compete with the vigorous vegetative spread of more robust species like *M. nervosa* in the Stand Matrix nor the rapid seed dispersal of species such as *Cirsium* spp. in the Gap (Grime 1979). Success in the edge environment, therefore, is likely a complex interaction of morphological and reproductive adaptations (Moore and Vankat 1986, Matlack 1994). In the edge environment where risk of dessication is lower than in a gap, species with large leaves (e.g., *A. tryphylla*) may be more efficient light gatherers than herbaceous species typical of canopy gaps (Givinish 1987, Bailey et al. 1998). In addition, reproductive plasticity may make these species well-suited for the transitional edge environment where microclimate can change dramatically over short distances (Brothers and Spingarn 1992, Chen et al. 1995, José et al. 1996).

Structural and compositional distinctions among sub-treatments suggest that canopy gaps are important in promoting understory heterogeneity (Collins et al. 1985). This heterogeneity was especially apparent with the increasing divergence of composition among sub-treatments over time (Figure 3.2). However, this contrasts with large-scale trends where composition of the LtGaps treatment became more similar to other thinned treatments over time (Figure 3.1). Hence, time trends suggest that at a large-scale, the addition of gaps appeared to do little to alter the understory structure and composition relative to a more traditional thin. Had we limited our analysis to the large-scale, key 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 at only a single spatial scale may limit our understanding of small-scale ecological mechanisms. Conversely, this also suggests that for landscape-level phenomena, gaps like those implemented in this study are likely to have little impact. However, more research on gap size and spacing in late-successional forests and the effect of gaps in young managed forests is necessary to better understand the contribution of canopy gaps to landscape-level processes.

Late-seral development

Post-treatment trends indicate that thinning that includes gap creation may hasten development of late-seral understories in young, managed *P. menziesii* forests, but that timing of this development is likely to differ for structure and composition. For structure, if linear trends of increased abundance continue, some vegetative layers (i.e., herbs and low shrubs) may soon be more abundant than they are in unthinned stands. This increase in abundance is an important component of late-seral development for young, closed-canopy stands (Alaback 1982, Franklin et al. 2002). In addition, gap creation generated within-stand heterogeneity in understory structure and composition, another important element of late-seral understories (Franklin and Spies 1991a). Thinning also did not yet encourage dominance of clonal shrub species that could homogenize the understory and discourage late-seral development.

On the other hand, thinning did not appear to readily hasten establishment of late-seral composition. Instead, thinning appeared to create niches for several early-seral species (Dyrness 1973, Schoonmaker and McKee 1988, Halpern 1989). The prevalence of early-seral species in thinned stands relative to unthinned stands could be counterproductive to the goal of accelerating a late-seral understory. Alternatively, many early-seral species are maintained in late-seral understories, but at low abundances (Halpern 1989, Spies 1991). Reestablishment of these species in young stands replenishes seedbanks for future development and did not negatively affect most late-seral associated species. Hence, it is possible that thinning will hasten late-seral composition in a thinned stand relative to an unthinned stand by replenishing seedbanks and accelerating development of late-seral overstory (Beggs et al. *Submitted*) and understory structure.

Therefore, if we consider a directional pattern of succession, it is not likely that thinning immediately accelerates succession nor is it likely to set understories of thinned stands back to an early-seral stage identical to that following stand initiation. Rather, we see two hypotheses concerning mechanisms by which thinnings with gap creation alter successional trajectories. First, while undertories of thinned stands undergo another early-seral phase, the more rapid structural changes in thinned stands relative to unthinned stands may accelerate the transition between early-seral and late-seral stages with gaps lagging behind during the transition to provide centers of early successional plant associations in late-seral forests. Second, gaps may close in and eventually provide centers of late successional plant composition. More long-term observations are necessary to fully evaluate these processes.

Management implications

While our data indicate that thinning with gap creation can hasten development of certain aspects of late-seral understories, intensity of thinning (i.e., heavy versus light) had little short-term effect on understory vegetation. However, thinning intensity may eventually influence the understory through its effect on overstory structure. Following light thinning, overstory canopy closure occurs more quickly (5-7 years after thinning) than in heavily thinned stands (Beggs et al. *Submitted*). Because recovery of understory vegetation is still occurring in these stands, rapid canopy closure may preclude continued development of the understory in lightly thinned stands. In addition, development of late-successional overstory structure (e.g., large trees) appears to be accelerated more by heavy thinning than light thinning (Beggs et al. *Submitted*). Due to the strong influence that overstory structure imparts on understory vegetation (Franklin et al. 2002), a heavy thin may therefore be more successful in hastening development of late-successional understory structure and composition.

In addition, the degree to which thinning impacted understory vegetation varied among blocks. This was likely a product of differences in harvesting systems, pre-thinning vegetation composition, and site conditions (e.g., soil moisture). Furthermore, influence of clonal shrubs is expected to be greater on relatively dry, nutrient poor sites that have a high abundance of clonal shrubs prior to treatment (He and Barclay 2000) than on most of our sites. Such factors, therefore, must be considered in order to fully assess potential impacts of thinning on understory vegetation.

Finally, while thinning can enhance structure and composition of understory vegetation, it does have drawbacks under certain conditions. Increased resources and soil disturbance can make thinned stands susceptible to invasion by exotic species if an abundant local seed source is present. In addition, some species decline following thinning and tend to favor the closed and undisturbed habitat of unthinned stands. Thinning can also damage some structural components such as old, tall shrubs that may take considerable time to recover. These findings suggest that thinning that minimizes impacts on the ground and/or includes retention of unthinned residual patches (Thysell and Carey 2001, Bradbury 2003) may aid in preserving important structural features and providing refugia for species that exhibit sensitivity to thinning. These patches should be specifically selected to preserve desirable overstory and/or understory conditions. Future study, however, will be necessary to determine the effectiveness of such approaches (Thysell and Carey 2001, Bradbury 2003).

In conclusion, thinning, especially a thinning of moderate to heavy intensity that incorporates gap formation, can be effective in accelerating development of some features of a late-seral understory in young, managed stands. However, we reiterate that our conclusions are based only on short-term observations and therefore are somewhat tentative. Furthermore, important factors that influence understory vegetation dynamics must be considered, including pre-thinning composition and site conditions, type of harvesting system, and the local presence of exotic species prior to implementing any type of thinning. With these factors accounted for, thinning similar to that implemented in this study, can be one useful tool in management of young *P. menziesii* forests.

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Chapter 4: Conclusion and Recommendations

Conclusion

This study examined overstory and understory vegetation response following experimental thinning in young (40-50 years of age), managed Douglas-fir forests of the western Oregon Cascades. While the focus of this inquiry was on short-term (5-7 years post-treatment) outcomes, the implications of initial effects on long-term late-successional development were also assessed. As part of the larger Young Stand Thinning and Diversity Study (YSTDS), this research contributes to the understanding of long-term forest ecosystem dynamics in Douglas-fir systems. It also provides forest managers with new information regarding the effectiveness of thinning in hastening development of late-successional habitat in young Douglas-fir plantations.

While this research presents evidence that development of certain late-successional habitat components can be accelerated by moderate to heavy thinning that incorporates canopy gaps, it also indicates that such treatments do not influence all characteristics in the same manner and do not create "instant old-growth." In the overstory, growth of the largest trees, which are likely to eventually become the dominant structural components of late-seral forests (Franklin and Spies 1991a, b), was accelerated only by heavy thinning (i.e., 125 trees per hectare (tph)). Evidence of a multi-layered canopy, however, was not present in any treatment by 5-7 years after thinning. Most understory vegetation layers (e.g, low shrubs) appeared to be undergoing recovery from damage incurred during harvest, but trends indicated that some (i.e., low shrubs and herbs) may soon be more abundant in thinned stands than unthinned stands. This increase in abundance of understory vegetation is thought to be important in the understory transition from a closed-canopy young forest to a late-successional forest (Alaback 1982, Franklin et al. 2002). The addition of canopy gaps also imparted within-stand spatial heterogeneity in understory composition, another important component of late-seral understory development. However, understory composition of thinned stands was characterized by greater presence of early-seral species rather than of late-seral species.

Although the strongest distinctions in vegetation response were between thinned and unthinned stands, there were also subtle distinctions among thinning treatments. In the overstory, growth of the largest trees increased only following heavy thinning. In addition, a heavy thin permits more time for late-seral understory development than a light thin, as indicated by the earlier canopy closure of lightly thinned (i.e., 250 to 300 tph) stands. Therefore, although understory vegetation displayed little initial response to thinning intensity (i.e., heavy vs. light), this may change if differences in overstory structure continue to develop in these treatments over time. In addition, canopies of thinned stands are prone to return to levels similar to controls, as evident by trends in canopy closure; hence, retaining open canopies following thinning is likely to require future management intervention.

The addition of canopy gaps imparted the greatest variation in within-stand overstory canopy cover, completely opening canopies in gaps while leaving more cover in the thinned forest matrix. The variation in overstory cover created by canopy gaps corresponded to variation of understory composition, as a mosaic of species assemblages was generated across the gradient from the gap interior to the thinned forest matrix. This indicated that effects of overstory structure are already reflected in understory development (Berger and Puettmann 2000, Franklin and Van Pelt 2004). Thus, as future thinning prescriptions are developed, incorporation of canopy gaps can be one important component in achieving ecological objectives.

Finally, spatial scale can influence ecological interpretations, as evident by the more obvious effect of canopy gaps on understory vegetation at the within-stand scale that at the stand-scale. Understanding stand-level (and even landscape level) effects are critical when assessing successional patterns and large-scale phenomena, such as visual quality. However, this study points out that ignoring more localized effects may limit our understanding of underlying ecological mechanisms. Hence, as studies become larger in scope and size, the influence of scale should not be overlooked.

Limitations and Future Research

The thinning treatments applied in this study were a "first-attempt" to modify thinning in order to meet ecological objectives. The results of this study demonstrate that the type of thinning used in this study can accelerate development of some late-seral features, but they also suggest modifications that may potentially improve the efficacy of thinning in meeting ecological goals.

The heaviest thinning in this study was once considered "extreme," but fears of opening the stands too much seem unfounded. Instead, the heavy thinning was the only treatment to accelerate growth of the largest trees and it did not result in high mortality (i.e., windthrow) in the overstory. Future study that evaluates ecological tradeoffs of even more intensive thinning would aid in determining thinning intensity thresholds that are most effective in promoting late-seral attributes. In addition, the impact of using canopy gaps to create heterogeneity in understory composition was demonstrated. However, inferences about effects of gaps, especially in terms of large-scale assessments, are restricted to gap sizes and densities applied in this study. Future research that examines different gap sizes and densities at various spatial scales will help to clarify the role of gaps in stand structure and late-seral development. Also, thinning had many positive effects on vegetation components, but certain structures (e.g., tall shrubs) and species (e.g., some ericaceous species) were negatively impacted by harvest operations or subsequent changes in microsite. This suggests that retaining residual patches or designing harvests to minimize impacts on desirable understory patches may help to maintain these component in thinned stands (Thysell and Carey 2001, Bradbury 2003). Future work should evaluate the feasibility and utility of such options.

Finally, this study examined vegetation response only during the first 5-7 years following thinning. While interpreting this initial response is critical for understanding successional pathways and providing land managers with a timely evaluation of the early effects of these treatments, assessment of future conditions is speculative. Furthermore, it is recognized that conclusions drawn from this research could change as future study elucidates successional trends. This underscores the need to continue with future observations to better understand long-term forest successional pathways. This will not only enhance our understanding of forest ecosystem dynamics, but will also assist with development of future management options.

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APPENDICES

Appendix 1

Table A1.1. Site characteristics for each treatment unit. (CR = Cougar Reservoir Block; MC = Mill Creek Block; CF = Christy Flats Block; SC = Sidewalk Creek Block).

Block	Treatment	Area (Ha)	Age	Elev. (m)	Slope (%)	Aspect	Site Index[1]	Dominant Plant Association[2]	Total # of Plots
CR	Control	30.0	40	805	18.8	E	107	Tshe/Gash	23
CR	Heavy	19.4	40	792	24	E	105	Tshe/Mane	13
CR	Light	37.2	38	610	17.1	E	107	Tshe/Mane	26
CR	LtGaps	14.6	40	792	16	ENE	105	Tshe/Mane	29[3]
MC	Control	52.6	42	902	21.1	SSEE	105	Tshe/Mane	25
MC	Heavy	34.8	42	658	22.9	SE	105	Tshe/Mane	23
MC	Light	37.2	43	524	20	S	105	Tshe/Mane	30
MC	LtGaps	19.8	42	439	8.9	SSW	106	Tshe/Mane	29[3]
CF	Control	30.8	39	878	6.2	SE	117	Tshe/Mane	23
CF	Heavy	20.2	36	905	0	SE	120	Tshe/Mane	15
CF	Light	32.0	39	902	5.3	SE	117	Tshe/Mane	24
CF	LtGaps	38.9	40	905	5.3	SSEE	118	Tshe/Mane	30
SC	Control	51.0	37	634	11.4	N	114	Tshe/Rhma-Gash	17
SC	Heavy	19.0	35	652	16	NW	115	Tshe/Rhma-Gash	13
SC	Light	22.3	33	646	21.8	NNE	122	Tshe/Rhma-Gash	15
SC	LtGaps	30.4	39	671	14.5	N	111	Tshe/Rhma-Gash	30

[1] Dominant tree height at 50 years, King's Site Index Tables

[2] Plant associations based on McCain and Diaz (2002) [updated version]; Tshe = western hemlock; Mane = Oregon grape (*Mahonia nervosa*); Rhma = western rhododendron (*Rhododendron macrophyllum*); Gash = salal (*Gaultheria shallon*)

[3] One matrix plot was removed

Appendix 2

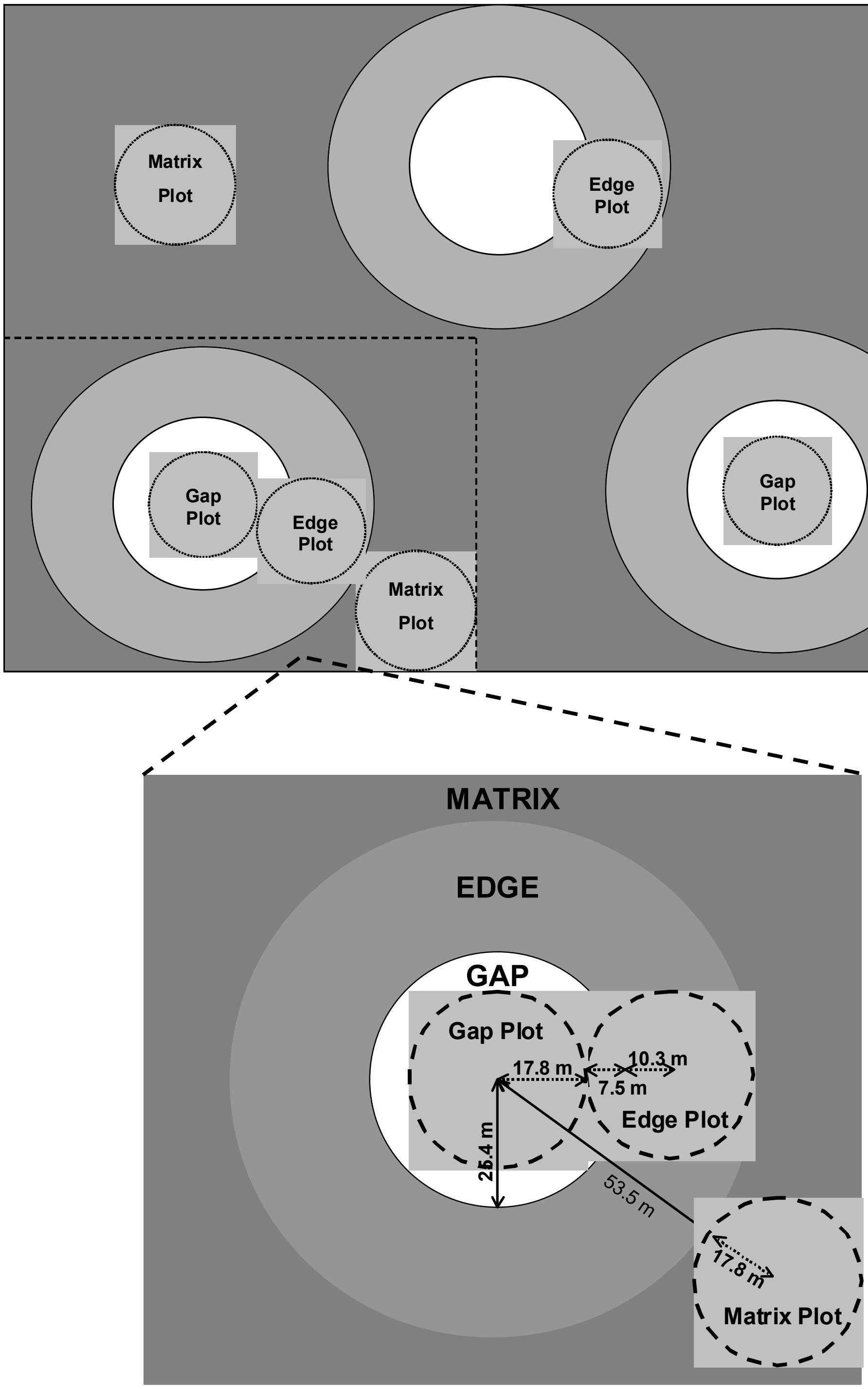
Table A2.1. Description of thinning treatments.

Block	Treatment	Target Density (tph)	Pre-treatment Density [1] (tph)	Pre-treatment BA [1] (m^2 / ha)	Post-treatment Density [1] (tph)	Post-treatment BA [1] (m^2 / ha)
CR	Control	Unthinned	929	30	753	53
CR	Heavy	125	800	27	151	14
CR	Light	250-300	865	39	312	21
CR	LtGaps	250-300 + Gaps	891	36	221	19
MC	Control	Unthinned	402	35	655	40
MC	Heavy	125	466	36	283	13
MC	Light	250-300	339	40	415	25
MC	LtGaps	250-300 + Gaps	335	36	346	18
CF	Control	Unthinned	737	42	869	47
CF	Heavy	125	880	48	133	21
CF	Light	250-300	871	39	207	32
CF	LtGaps	250-300 + Gaps	855	40	198	27
SC	Control	Unthinned	756	28	792	39
SC	Heavy	125	820	25	165	12
SC	Light	250-300	800	26	277	20
SC	LtGaps	250-300 + Gaps	743	30	225	15

[1] Pre-treatment measures include all trees ≥ 5 cm dbh. Post-treatment measures include all trees ≥ 8 cm dbh. Pre-treatment data were also sampled differently from post-treatment data. Therefore, these numbers are not presented in order to make direct pre- / post-treatment comparisons, but to illustrate similarities of pre-treatment conditions within each block.

Appendix 3

Figure A3.1. Schematic of sampling design and plot layout in LtGaps treatment. Not drawn to scale.



Appendix 4

Table A4.1. Type of harvest system, year of harvest completion, and year of first sampling for each treatment unit. The "% plots in harvest area" is the percentage of the total sampling plots in each treatment unit that were located in the area harvested by each specific harvest method.

Block	Treatment	Harvest Method	Harvest Completion	First Year of Sampling	% of Plots in Harvest Area	Post-harvest Growing Season Sampled During 1995-1997, 1999, and 2001		
						1995-1997	**1999**	**2001**
CR	Control	--	--	1995	--	--	--	--
CR	Heavy	Tractor	September 1995	1996	46	First	Fourth	Sixth
		Skyline	November 1995	1996	54	First	Fourth	Sixth
CR	Light	N/A	April 1995	1995	23	First	Fifth	Seventh
		N/A	April 1995	1996	15	Second	Fifth	Seventh
		Tractor	September 1995	1996	54	First	Fourth	Sixth
		Skyline	September 1995	1996	8	First	Fourth	Sixth
CR	LtGaps	Tractor	September 1995	1996	31	First	Fourth	Sixth
		Skyline	October 1995	1996	69	First	Fourth	Sixth
MC	Control	--	--	1995	--	--	--	--
MC	Heavy	Tractor	September 1996	1997	30	First	Third	Fifth
		Skyline	February 1996	1996	52	First	Fourth	Sixth
		Skyline	February 1997	1997	17	Second	Fourth	Sixth
MC	Light	Tractor	September 1995	1996	63	First	Fourth	Sixth
		Tractor	September 1996	1997	23	Second	Fourth	Sixth
		Skyline	March 1995	1996	13	Second	Fifth	Seventh
MC	LtGaps	Tractor	September 1996	1997	100	First	Third	Fifth

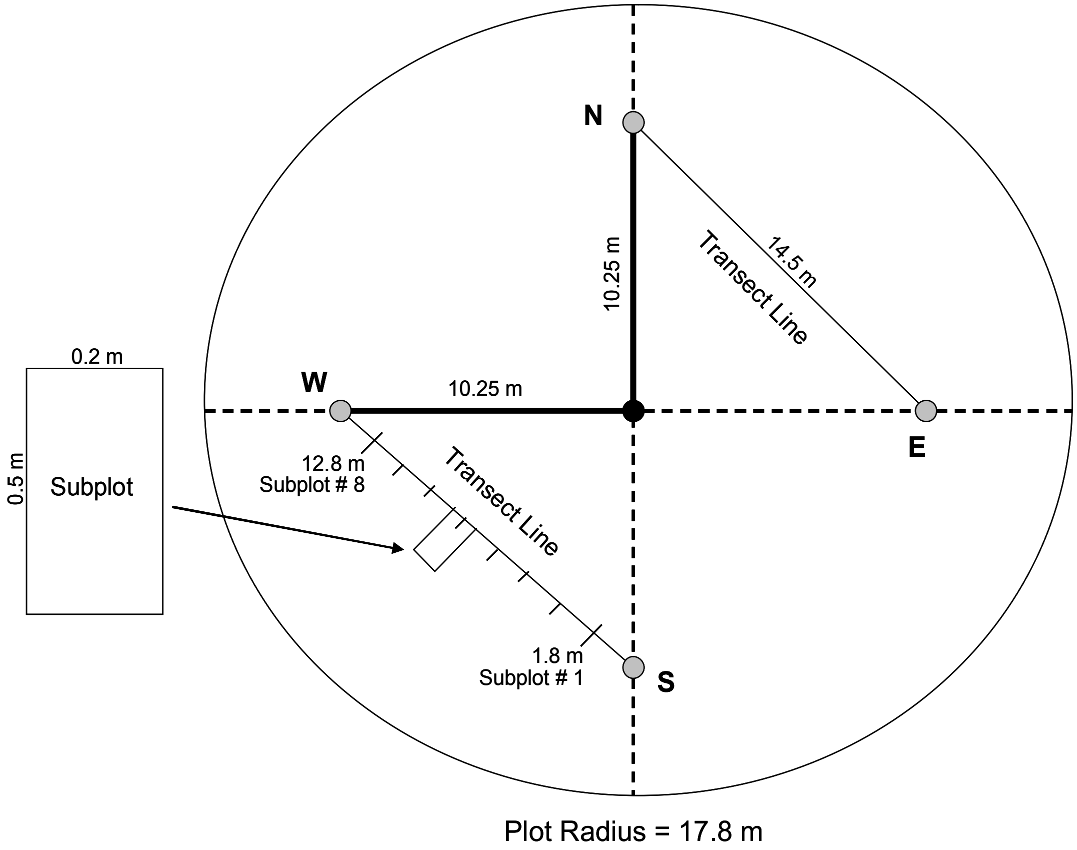
Table A4.1 (Continued)

Block	Treatment	Harvest Method	Harvest Completion	First Year of Sampling	% of Plots in Harvest Area	Post-harvest Growing Season Sampled During 1995-1997, 1999, and 2001		
						1995-1997	**1999**	**2001**
CF	Control	--	--	1996	--	--	--	--
CF	Heavy	H-F [1]	February 1997	1997	100	First	Third	Fifth
CF	Light	H-F	February 1997	1997	100	First	Third	Fifth
CF	LtGaps	H-F	October 1995	1997	27	Second	Fourth	Sixth
		H-F	August 1996	1997	73	First	Third	Fifth
SC	Control	--	--	1997	--	--	--	--
SC	Heavy	Skyline	April 1995	1996	100	Second	Fifth	Seventh
SC	Light	Skyline	November 1995	1996	100	First	Fourth	Sixth
SC	LtGaps	Skyline	January 1995	1996	73	Second	Fifth	Seventh
		Skyline	August 1995	1996	27	First	Fourth	Seventh

[1] H-F = Harvester/Forwarder

Appendix 5

Figure A5.1. Schematic of 0.1 ha permanent vegetation sampling plot (subplot only used for understory vegetation sampling). Not drawn to scale.



Appendix 6

Table A6.1. Proportional area of sub-treatments in each LtGaps treatment unit used for the weighted averaging calculations

Block	**Sub-treatment**	**Percentage of area in treatment unit**
CR	Matrix	20.2
CR	Edge[1]	70.1
CR	Gap[1]	8.8
MC	Matrix	31.7
MC	Edge[1]	60.7
MC	Gap[1]	7.6
CF	Matrix	19.2
CF	Edge[1]	71.8
CF	Gap[1]	9.0
SC	Matrix	11.2
SC	Edge[1]	78.9
SC	Gap[1]	9.9

[1] Gaps covered approximately 20% of each treatment unit, but only the interior of the gap was sampled by Gap plots (the exterior of the gap was sampled by Edge plots); therefore, the proportion of total gap area represented by Gap sampling is less than the area actually covered by gap.