AN ABSTRACT OF THE DISSERTATION OF

Briana C. Lindh for the degree of Doctor of Philosophy in Botany and Plant Pathology presented on May 23, 2003.
Title: Understory Herb and Shrub Responses to Root Trenching, Pre-commercial Thinning, and Canopy Closure in Douglas-fir Forests of the Western Cascades, Oregon.

Abstract approved: Patricia S. Muir
Patricia S. Muir

This thesis examines factors limiting understory herb presence and flowering in young second-growth Douglas-fir (*Pseudotsuga menziesii*) forests on the west side of the Cascade Mountains, Oregon, USA. I studied the belowground effects of canopy trees on understory herbs and shrubs in old-growth forests using trenched plots from which tree roots were excluded. Effects of tree density and stand age were tested by comparing the understory community composition of old-growth stands and pre-commercially thinned and unthinned young second-growth stands. I also examined the effect of conifer basal area on understory herb presence and flowering within one young second-growth watershed. In young stands, I focused on three groups of understory herb species: disturbance-responsive (release), forest generalist and old-growth associated.

The effects of root trenching on vegetation and soil moisture were tested in closed-canopy and gap locations in two old-growth Douglas-fir (*Pseudotsuga menziesii*) forests. Ten years after installation, trenched plots averaged 92% total understory cover while untrenched plots averaged 47% cover. Trenched plots under closed canopies were moister than control plots throughout the growing season; the trenching effect on soil moisture became apparent in the generally wetter gaps only at the end of the growing season. Vegetation responses to trenching were concomitantly larger under closed canopies than in gaps.

*Stands that had been pre-commercially thinned 20 years earlier exhibited understory composition more similar to old growth than did unthinned stands. Thinned stands exhibited higher frequencies, abundances and density of flowering of old-growth associated herbs than did unthinned stands, but lower than did old-growth stands. Forest generalist and release species showed mixed responses to thinning.

I used both general linear models and classification and regression tree models to explore the association of herb species presence and flowering with conifer basal area and abiotic variables. Both modeling approaches yielded similar biological insights. Flowering was more sensitive than presence to current stand basal area. *Flowering of old-growth associated and release species was negatively correlated with conifer basal area. Linear models allowed clearer hypothesis tests, while tree-based models had greater explanatory power and provided information about interactions between variables.

Understory Herb and Shrub Responses to Root Trenching, Pre-commercial Thinning, and Canopy Closure in Douglas-fir Forests of the Western Cascades, Oregon.

by
Briana C. Lindh

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APPROVED:

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

Briana C. Lindh

Briana C. Lindh, Author

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CONTRIBUTION OF AUTHORS

Dr. Thomas Spies initiated the trenching experiment (Chapter 2), and Dr. Andrew Gray installed the experiment and collected the soil moisture data. Both assisted with the writing of Chapter 2.

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UNDERSTORY HERB AND SHRUB RESPONSES TO ROOT TRENCHING, PRE-COMMERCIAL THINNING, AND CANOPY CLOSURE IN DOUGLAS-FIR FORESTS OF THE WESTERN CASCADES, OREGON

CHAPTER 1: INTRODUCTION

The first twenty years of plant succession after logging is relatively well studied in the Pacific Northwest. Removal of the overstory is followed by a period of herb and shrub dominance, which later gives way to tree dominance (Alaback 1982, Halpern 1988, Schoonmaker and McKee 1988, Halpern 1989, Halpern and Franklin 1991). The period after canopy closure in young second-growth forests is less well understood. One widely cited study from southeast Alaska provides an overview of understory dynamics in young and mature forests (Alaback 1982). Herb biomass dropped sharply after canopy closure and only gradually recovered as stands passed 150 yrs of age. It is not clear, however, how widely Alaback's work should be applied. Coastal Sitka spruce forests regenerate much more densely than do forests in drier areas. Further, Alaback sampled stands that were well stocked with conifers and did not include a significant hardwood component; poorly stocked and mixed composition stands may show different dynamics over time (Hanley and Barnard 1998). Studies of successional dynamics in young forests in Oregon and Washington have shown declines in understory herb cover following canopy closure, but these studies have been hampered by small sample sizes and the large variation in species composition among stands of a given age (Long and Turner 1975, Schoonmaker and McKee 1988).

While the period following canopy closure is poorly understood, it may be pivotal in understanding the dynamics of understory herbs in managed landscapes. Meier *et al.* (1995) suggested five mechanisms that might lead to reduced understory herb abundance and diversity in second-growth forests of the eastern US; they apply equally well in the West.

I. Mechanical damage from logging disturbance.

II. Physiological stress and/or competition with weedy or exotic plant species soon after logging and during succession.

III. Low rates of reproduction and slow growth of understory herbs.

IV. Limited spread and slow dispersal of understory herbs due to clonal reproduction and ant-mediated dispersal of seeds.

V. Loss of suitable habitat and disruption of gap-phase succession.

While the first two mechanisms pertain primarily to the period before the canopy closes in second-growth forests, the latter three apply to the period after canopy closure. In the Pacific Northwest, we know that most species survive clearcutting, although sometimes with greatly reduced abundance (Dyrness 1973, Halpern 1988, Halpern 1989, Schoonmaker and McKee 1988). While physiological stress during the open-canopy period may contribute to further declines in abundance for some species (Halpern 1989), competition from early seral species has not been shown to reduce abundance of forest herbs (Halpern unpublished data). Some subordinate forest herbs ("release" herbs *sensu* Halpern 1989) increase in abundance as a result of canopy removal. As the second-growth forest canopy closes, most members of the understory herb community are present but not in the abundances typical of the pre-disturbance forest. Their dynamics in the young forest will determine how quickly the forest will return to old-growth composition.

While the chapters of this thesis address several topics, they can all be seen as attempts to understand the factors limiting understory herb abundance in the forest environment. I used flowering, in addition to presence and abundance, as a measure of plant performance because it should be more responsive to current habitat suitability than are the other two measures. Flowering also serves as a potential measure of the capacity of a population to expand and colonize vacant portions of a stand.

Patterns of herb species presence, and even abundance, may not reflect current stand conditions well. For long-lived clonal plants, lifetime fitness is determined largely by survival through unfavorable conditions (Eriksson 1993). As a result, presence and abundance reflect the history of stand conditions and chance dispersal events as well as the current stand environment. While little work has been done on flowering in Pacific Northwest understory herbs (but see Jules 1996, St. Pierre 2000), research on other forest species suggests that flowering should be more responsive than presence or abundance to current stand conditions.

In perennial forest understory herbs, allocation of energy to flowering is dependent on the availability of adequate resources and is correlated with plant size

(Sohn and Policansky 1977, Winn and Pitelka 1981, Pitelka et al. 1985, Cain and Damman 1997, Cunningham 1997, Geber et al. 1997, Jules 1996, St. Pierre 2000, Ehrlen and van Groenendael 2001). Because larger individuals tend to occur in areas with higher resource levels, flowering is tied to resource availability. Flowering of some species is more likely to occur at higher light levels (Pitelka et al. 1980, Lubbers and Christiansen 1986, Cunningham 1997); belowground resources may also limit flowering for some (St. Pierre 2000). Individuals that flower in one year tend to continue flowering in subsequent years (but see Inghe and Tamm 1988), rarely showing an observable cost of reproduction (Pitelka et al. 1985, Horvitz and Schemske 1988, Cain and Damman 1997, Ehrlen and van Groenendael 2001). A lack of observable cost of reproduction may result from the ability of plants to rapidly replenish stored reserves (Cunningham 1997). Asexual reproduction can be less costly than sexual reproduction (Muir 1995) and may in fact represent a form of storage rather than energy expenditure (Chazdon 1991).

The goal of this thesis is to elucidate some of the factors that control the distribution and flowering of understory herbs in young forests. By examining flowering in young forests, I focused on the suitability of young forest habitat for understory herbs and on the potential for sexual reproduction in these stands. My primary focus was on the effects of stand basal area, which is directly affected by forest management. In addition to stand conditions, understory herb populations also respond to abiotic factors such as insolation, temperature and soil moisture availability. I explored the relationship of herb presence and flowering to slope, aspect, and watershed position, surrogates for these underlying variables, as well as interactions between stand basal area and environment. Particular herb species were selected to represent a variety of responses to harvest disturbance (Halpern 1989) and associations with stand age (Spies 1991). Species were characterized as old-growth associated, forest generalist, or release.

Each chapter explores a different facet of the response of understory herbs to the forest environment. Chapter 2 focuses on the belowground effects of trees on the understory, exploring how tree roots may affect herb and shrub cover and flowering. The effect of belowground competition was examined using a root trenching experiment that had been established 10 yrs earlier. Chapter 3 addresses the differences in community composition between young and old forests. I tested the hypothesis that thinning of young stands would encourage old-growth associated herb species by expediting the development of old-growth stand structure. Chapter 4 examines the effects of abiotic variables and conifer basal area on the distribution of presence and flowering of individual herb species. I contrast insights obtained from generalized linear models and tree-based models, two fundamentally different modeling approaches. I conclude with an overview of my findings in Chapter 5.

RESPONSES OF HERBS AND SHRUBS TO REDUCED ROOT COMPETITION UNDER CANOPIES AND IN GAPS: A TRENCHING EXPERIMENT IN OLD-GROWTH DOUGLAS-FIR FORESTS.

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CHAPTER 2: RESPONSES OF HERBS AND SHRUBS TO REDUCED ROOT COMPETITION UNDER CANOPIES AND IN GAPS: A TRENCHING EXPERIMENT IN OLD-GROWTH DOUGLAS-FIR FORESTS

Abstract

We tested the effect of root trenching on vegetation in closed-canopy and gap locations in Douglas-fir (*Pseudotsuga menziesii* (Mirb) Franco) forests. Based on theory, we expected belowground competition to be intense in a region with low summer rainfall, and trench responses to be greater in the high light environment of the gaps. We installed 1 m deep trenches around study plots and lined the trenches to prevent re-invasion by tree roots. Soil moisture was measured monthly during the growing season for the first three years after trench installation. Vegetation in these trenched plots was compared to control plots 10 years after installation of the plots. Trenched plots with no vegetation manipulation averaged 92% total understory cover while untrenched plots averaged 47% cover. Contrary to our expectation, both vegetation and soil moisture responses to trenching were greater in areas of high tree canopy cover than in gaps. Trenched plots under closed canopies were moister than control plots throughout the growing season while the trenching effect became apparent in the overall wetter gaps only at the end of the growing season. We conclude that at these sites, understory plants were limited at least as much by belowground competition as by aboveground competition.

Introduction

The relative importance of aboveground and belowground controls on understory responses to disturbances of the tree canopy is not well understood. While the response of vegetation to canopy gaps has largely been discussed in terms of light (Whigham *et al.* 1993, Pascarella and Horvitz 1998), the death of canopy trees also influences soil moisture (Gray *et al.* 2002) and nutrient availability (Matson and Boone 1984). Root trenching studies have frequently demonstrated that growth and establishment of herbs, shrubs and tree seedlings is strongly influenced by belowground competition for moisture and nutrients. In a recent review of root trenching studies, Coomes and Grubb (2000) cite situations in which understory response to gaps was controlled more by light than by water or nutrients and others in which the reverse was true. They propose a conceptual framework that predicts the relative importance of root competition as a function of summer rainfall, soil fertility and the density of shade cast by the dominant tree species. Where soils are nutrient rich and moist throughout the year, vegetation responses to gaps will be controlled more by aboveground competition than by belowground competition. Where soils are nutrient poor and dry in summer, they predict a large response to root trenching (release from belowground competition). Coomes and Grubb (2000) further propose that trenching effects should be larger in gaps than under dense closed canopies; they argue that the lack of light under the closed canopy should prevent a large response to an increase in belowground resource availability.

Few studies have examined responses of understory vegetation to reduced root competition and canopy openness in the dense *Pseudotsuga menziesii* forests of the Pacific Northwest. The climate in this region is characterized by abundant winter precipitation with summer drought and soils that are relatively nutrient poor. According to the conceptual framework of Coomes and Grubb (2000), we should expect root trenching in this region to increase vegetation establishment and growth *via* an increase in soil moisture and nutrient levels. The dense shade of the tree canopies would be expected to prevent large trench responses under closed canopies, while canopy gaps should show large trench responses. Only two studies have evaluated root competition in Douglas-fir forests (Christy 1986, Simard *et al.* 1997), and their results are only partly consistent with each other and with the predictions of Coomes and Grubb (2000). In Oregon, Christy (1986) found that trenching to reduce root competition had a greater effect on growth of juvenile *Tsuga heterophylla* (Raf.) Sarg. than did creation of canopy gaps. However, Simard *et al.* (1997) did not find any effects of trenching on growth of *Pseudotsuga menziesii* seedlings in British Columbia. Neither study found that growing season soil moisture increased in trench plots as would be predicted by Coomes and Grubb (2000). Simard *et al.* (1997), along with Hart and Sollins (1998), found increases in soil moisture in trench plots in relation to controls only in early fall, after plant growth has ceased. The failure of these studies to find a soil moisture response is surprising given the summer drought that is characteristic of *Pseudotsuga menziesii* forests. In contrast, Gray *et al.* (2002) did find that growing season soil moisture was higher in gaps and in trench plots than in controls in conifer forests in Washington and Oregon. None of these studies reported how differences in soil moisture between trench and control plots varied over the growing season or between years. Given the variation observed in vegetative and soil moisture response to release from root competition and canopy shading in this region, and the inconsistency of some of the results with predictive models, it is clear that our understanding of these processes is incomplete.

No studies have examined the response of the herb and shrub layer to reduced root competition in Pacific Northwest *Pseudotsuga menziesii* forests. In contrast to tropical forest understories, Pacific Northwest forest understories have relatively few tree seedlings; herbs and shrubs make up most of the diversity and biomass. McCune (1986), in a grand fir (*Abies grandis* (Dougl.) Lindl.) forest in Montana, showed striking increases in herb cover (a jump from 7 to 55%) as a result of trenching. In white pine (*Pinus strobus* L.) forest in New Hampshire, Tuomey and Keinholz (1931) found an eight-fold increase in the number of understory herb and shrub individuals eight years after trenching. Differences persisted 20 years after establishment, with particularly striking establishment and growth of eastern hemlock (*Tsuga canadensis* (L.) Carr.) individuals in the trenched plot (Lutz 1945). Walters and Breckle (1985) review the results of several studies published in Russia and Germany. Trenching in boreal spruce (*Picea* spp.) or Siberian fir (*Abies sibirica* Ledeb.) forest transformed sparse understories into lush carpets dominated by *Oxalis acetosella* L. (Karpov 1961, 1962, 1969; Slavikova, 1958, 1965, 1966 in Walter and Breckle 1985). Trenching studies generally examine vegetative rather than reproductive responses, perhaps because it is widely held that light is the primary resource that limits flowering of understory vegetation (Chazdon 1991, Niesenbaum 1993, Cunningham 1997). The one study that has examined the effect of killing tree roots on flowering in an understory herb found no treatment effect (Hughes *et al.* 1988). Using observational data, however, St. Pierre (2000) found that soil moisture and light levels helped explain flowering of two understory herb species in experimental canopy gaps.

In this study we extend research into root competition and gap effects by examining the response of cover and flowering of forest herbs and shrubs to trenching in old-growth *Pseudotsuga menziesii* forests in the Pacific Northwest. Our objectives are: 1) to compare the cover of herbs and shrubs in trenched and untrenched plots in canopy gaps and beneath closed canopies; 2) to compare the number of flowering ramets in these treatments; 3) to evaluate changes in soil moisture over the growing season and among years in relation to the treatments.

Methods

Our two study sites were in mid-elevation old-growth forests on the west side of the Cascade Mountains in northern Oregon and southern Washington. Both were mixed-species stands with a dominant canopy of *Pseudotsuga menziesii* and a sub-canopy of *Tsuga heterophylla*. Recent (last 25 years) average annual precipitation at the H.J. Andrews Experimental Forest site (44°15'N, 122°15'W) and at the Wind River Experimental Forest (45°50'N, 122°00'W) is about 220 cm, with less than 10% of that falling during the months June-September.

Trenched plots (belowground gaps) were installed to complement an experimental canopy gap study at the H. J. Andrews and Wind River (Gray and Spies 1996). These plots were installed in 1990 and monitored for four years for soil moisture response (Gray *et al.* 2002). Vegetation in the plots had never been quantified until the present study.

Our experimental design was a split-plot, with two whole plots (closed-canopy or naturally occurring gap) at each of the two sites (H. J. Andrews and Wind River). Within each whole plot, four factorial combinations of trenching (trenched or control) and clipping (clipped or not) were assigned randomly to four adjacent (separated by 2-5 m) sub-plots. While we did not measure initial plant cover, sub-plots were selected to be visually homogeneous. Treatment effects could potentially be confounded with differences in initial cover; however, random assignment of treatments to plots sought to avoid this problem. Trenched plots were created by severing tree roots to a depth of 1 m around the perimeter of a 3 m x 3 m area. Plots did not include sapling or adult trees but did include occasional tree seedlings less than 30 cm tall. The trenches were lined with 0.5 mm stainless steel mesh on up- and down-slope sides and black plastic on other sides to prevent the re-invasion of tree roots. The clipping treatment was applied during the first three years of the experiment and then discontinued; the objective of the treatment was to estimate understory vegetation effects on soil moisture. All plants (herbs, shrubs and tree seedlings) were clipped to ground level. After clipping was discontinued, some existing plants recovered and many new plants seeded in. Although the clipping treatment *per se* is not the focus of this paper, clipped plots were included in this analysis to increase the sample size over which trenching effects could be estimated.

We sampled the plant communities in these plots in the summer of 2000, 10 years after installation. Sampling was carried out in a 2x2 m plot set within the 3x3 m treatment plot to avoid edge effects. Cover of each plant species was estimated visually and added to yield a total cover value, which for some plots exceeded 100%. We also counted the number of flowering ramets for each species; because different species flowered in each plot, numbers for each species were added to give total number of flowering ramets. Growing season soil moisture in the plots was sampled monthly in May-October of 1991, 1992, and 1993. Volumetric soil moisture was determined using time domain reflectometry (TDR; model 1502C, Tektronix Inc., Beaverton, Oregon, USA; Gray and Spies 1995, Gray *et al.* 2002). Two parallel probes extended vertically 45 cm into the soil in each plot; the value reported for each plot is the average from two sets of probes. In this paper we present the monthly trends in soil moisture and relationship between vegetation and soil moisture response; a previous analysis provided a test of significance of the effect of trenching on soil moisture (Gray *et al.*, 2002).

Cover and flowering response variables were analyzed in a split plot ANOVA with canopy cover as the whole plot factor and trenching and clipping as subplot factors. The analysis was carried out using PROC MIXED in SAS (version 8, SAS Institute Inc. 1999) with trenching, clipping and canopy openness as fixed effects, and site as a random block effect. The approximate normality of the cover data supported a parametric analysis. Number of flowering ramets was log-transformed to improve normality.

Results

Plots were dominated by herbs and low shrubs, with occasional tall shrubs and tree seedlings present. Trenched plots had higher vegetation cover than controls in both the intact vegetation (unclipped plots) and recovering vegetation (clipped plots) (Fig 1, $F_{1,6} = 64.74$, $p= 0.0002$). Trenched plots (unclipped) had 92% cover while control plots had 47% cover. Trench plots in gaps had about 30 percentage points higher plant cover than trenched plots under closed canopy, providing an estimate of response to aboveground gaps.

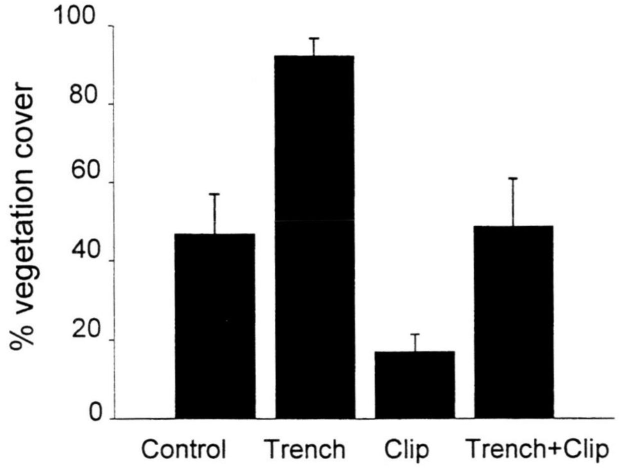

Figure 1. Response of understory vegetation to trenching and clipping (averaged over canopy openness). Sample size for each bar is four (an open and closed canopy plot at each of two sites). Error bars are one standard error.

Cover in the trenched plots was comprised of the fern *Polystichum munitum* (Kaulf.) Presl (Polypodiaceae) and the low shrub *Berberis nervosa* Pursh (Berberidaceae) at the H. J. Andrews gap area, the herb *Coptis laciniata* Gray

(Ranunculaceae) at the Andrews closed-canopy area, and the herb *Achlys triphylla* (Smith) DC. (Berberidaceae) at both canopy densities at Wind River. These species were also present in the control plots, but at lower abundance. The total number of flowering ramets (of all species) tended to be higher in trenched than control plots (26 vs. 16; $F_{1,6}$=4.40, p=0.08). At the H. J. Andrews, most flowering ramets belonged to the herb *Tiarella trifoliata* L. (Saxifragaceae), and at Wind River to the herb *Achlys triphylla*.

The effect of trenching on soil moisture was evident throughout the growing season and in all three years (Fig. 2). Each year varied in the initial soil moisture measurement, but the pattern of drying over the summer and the relative position of the treatments were the same in all years. The trenched plots exhibited the highest soil moisture; trenched plots had high and similar soil moisture regardless of canopy density. In the gap areas, the control plots started at the same soil moisture as the trenched, but dried down faster to end the season four percentage points drier. In the closed canopy areas, the control plots were much drier than the trenched plots (eight percentage points), and that difference was already present in May at the time of the first measurement. Statistical evidence for an effect of clipping on soil moisture was weak but suggestive ($F_{1,1}$=5.32, p=0.06). Considering only untrenched plots, clipped plots had four percentage points higher soil moisture than unclipped; however, in trenched plots, clipping had no effect.

Like soil moisture, the vegetation responded much more to trenching in the closed canopy area. The average difference in plant cover between trenched and

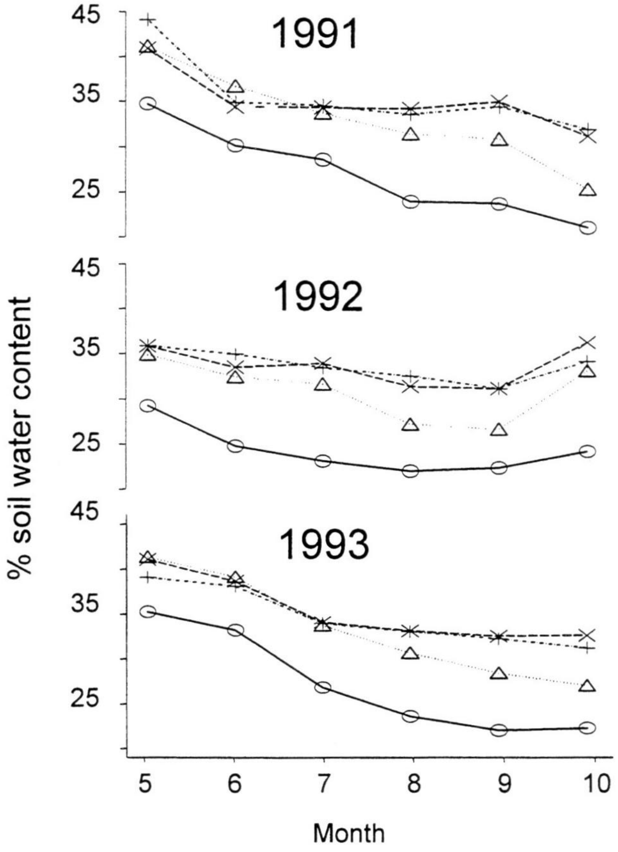

Figure 2. Soil moisture measured throughout the growing season in unclipped plots. Each point is the average of two values (one from each site). Circles (o) are closed canopy control plots, triangles (Δ) are gap control plots, pluses (+) are closed canopy trench plots and crossed lines (×) are gap trenched plots.

control plots was much greater in closed-canopy than gap areas (64 percentage points *versus* 27 percentage points, considering only those plots with unclipped vegetation; see Fig 3). The plot pairs that show the largest difference in plant cover associated with trenching also show the largest differences in soil moisture (Figure 3).

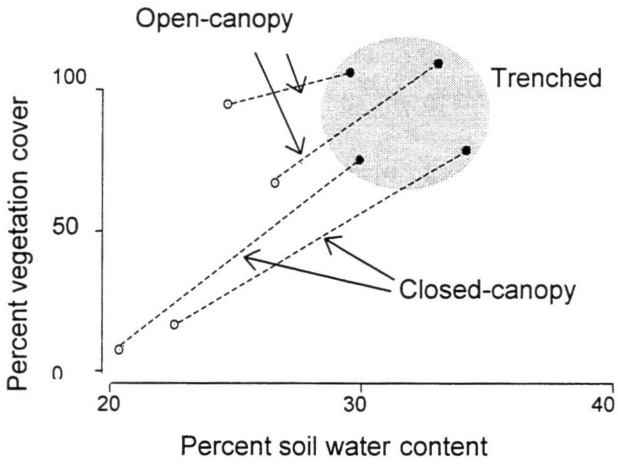

Figure 3. Vegetation cover and soil moisture in control and trenched plots. Each point is the value from one sample plot; open symbols correspond to control plots, filled symbols to trenched plots, lines connect adjacent pairs of control and trenched plots. Soil moisture values are from October 1991, the driest month in the first year following trenching.

Discussion

Our data show clear differences in understory vegetation cover, flowering and growing season soil moisture associated with the removal of competition by tree roots. This finding matches our expectation that belowground competition should be important in summer-dry regions. Our results clarify that even in a closed-canopy old-growth coniferous forest, belowground competition may be more important than light limitation. At our sites, the difference in plant cover moving from control to trench under a closed canopy (45 percentage points) was larger than that associated with moving from closed canopy to gap areas, where light levels should be optimal for understory plants (30 percentage points).

Both vegetation and soil moisture responses to trenching were much higher in the closed canopy areas than in the gaps. Our finding contrasts with the prediction of

Coomes and Grubb (2000) that trench responses would be greater in gaps. In our sites, the gaps probably had lower root densities than the closed canopy sites. Experimental gaps nearby had much lower fine root densities in mineral soil than did control plots (Vogt *et al.* 1995). Severing the less-numerous roots in our gap areas would have had less effect on belowground resources than severing the dense carpet of roots in the closed-canopy area. Further evidence for lower root densities in the gap is provided by the fact that the difference in soil moisture between control and trenched plots was already present in May in the closed canopy area while it developed gradually over the summer in the gaps. The dependence of the trenching effect on canopy environment (and by extension root density) may explain why other researchers found trenching effects on soil moisture only at the end of the growing season (Simard *et al.* 1997, Hart and Sollins 1998) if their sites had lower root densities than ours.

The magnitude of vegetation response that we observed correlated well with the magnitude of effect that trenching has on soil moisture (see Figure 3). Our vegetation response may be due to soil moisture alone, or to a concomitant increase in the availability of nutrients, which we did not measure. However, in a nearby site Hart and Sollins (1998) found that trenched plots had total nitrogen amounts indistinguishable from control plots, although trenched plots did have higher rates of nitrogen mineralization. Since increased water availability can increase both the supply of available nitrogen and the ability of the plant to take it up (Chapin *et al.* 1987, Riegel *et al.* 1992), it is not easy to separate the effects of water and nutrients.

Findings from trench studies carried out in temperate and tropical regions suggest responses to both soil moisture and nutrients (Coomes and Grubb 2000). Studies from wet conifer forests in Europe have suggested that nutrients mediate the trenching response (reviewed in Walter and Breckle 1985). Walter and Breckle (1985) suggest that at the aridity limit of European tree species, understories tend to be depauperate because on these sites the trees are using all the available water and leaving none for the understory. In the open, dry *Pinus ponderosa* Laws. forests of eastern Oregon, Riegel and coworkers (1992) showed that understories were limited by belowground resources rather than light. They found increases in both water and nitrogen levels as a result of trenching and concluded that plants were responding to both. In fact, we should expect plants in forest understories to be simultaneously limited by water, nutrients, and light and to be able to respond to increased abundance of any of these resources (Chapin *et al.* 1987). Studies in tropical forests have produced comparable results, with trenching having zero or negative effects on plant performance in nutrient rich wet sites (Denslow 1991, Ostertag 1998) and positive effects in nutrient poor (Coomes and Grubb 1998) or dry sites (Gerhard 1996).

Understory plants in summer-dry coniferous forests face limiting levels of several resources because the trees whose canopies shade the understory also bear roots that deplete levels of water and nutrients in the soil. Smith and Huston (1989) hypothesize that plants cannot develop strategies to simultaneously efficiently use low levels of water and light. Shade tolerant plants should develop large thin leaves at the expense of a limited root system, while drought tolerant plants should have large below-ground allocation and thick evaporation-resistant leaves. Coomes and Grubb

(2000) suggest that plants that do tolerate both stresses have the small leaves of a drought adapted plant and grow extremely slowly as a result of their very limited light capture. Of the herbs that responded most vigorously to trenching in the closed canopy sites in our study, one appears tolerant of both drought and shade while the other is a shade tolerator that evades drought through early senescence in the summer. *Coptis laciniata*, the dominant species in the shade plots at the H. J. Andrews, exhibits small, thick, evergreen leaves that probably resist evaporation well. It is highly clonal, slow growing, and able to occupy even the densest forest. *Achlys triphylla*, which dominated the trenched plots at Wind River, has large thin leaves more typical of a shade adapted plant. Perhaps as a result, it appears very vulnerable to drought. It occupies the wettest sites within coniferous forests and uses a "spring ephemeral" strategy otherwise rare in western coniferous forests to evade the dry late-summer period.

We found suggestive evidence that the number of flowering ramets was higher in trenched plots than in controls; this effect was stronger in the closed-canopy areas than in gaps. This result suggests that for the species flowering in our plots (primarily *Tiarella trifoliata* L. and *Achlys triphylla*), not only vegetative growth but sexual reproduction is limited by belowground resources. This experimental result supports the observational work of St. Pierre (2000) who found that *Tiarella trifoliata* fecundity was explained better by soil moisture than by light levels in gaps.

As mentioned above, previous work on effects of trenching in *Pseudotsuga menziesii* forests has focused on understory trees rather than shrubs and herbs (Christy 1986, Simard *et al.* 1997) and has found mixed results. Working only a few kilometers away from one of our study sites, Christy (1986) found that root trenching around suppressed *Tsuga heterophylla* juveniles increased their growth. Simard *et al.* (1997) transplanted *Pseudotsuga menziesii* seedlings into trenched and control plots, and found that trenching had no significant effect on total growth; reduced height (vs. stem diameter) growth in the trenched seedlings suggested a negative effect of root trenching. Simard *et al.* (1997) attributed this lack of positive response to two factors: one, that soil moisture may not have been limiting in her system because of significant summer rainfall and two, that trenching lowered mycorrhizal diversity on the roots of the seedlings and precluded mycorrhizal connections between the seedlings and overstory trees. Since the understory herbs and shrubs that responded to trenching in our study are probably mostly vesicular-arbuscular mycorrhizal (Brundrett and Kendrick 1988), they are unlikely to share mycorrhizal species or direct hyphal connections with the overstory; trenching would thus not have any deleterious effect. Interestingly, tree seedlings established and grew fairly well in our trenches, suggesting either that these species (primarily *Abies* species and *Tsuga heterophylla*) do not rely on mycorrhizal innoculum or hyphal connections from the canopy trees or that the benefit provided by trenching outweighed the loss of mycorrhizae.

Our results suggest that in the summer-dry *Pseudotsuga menziesii* forests that we studied, belowground competition may play a large role in explaining the patterns of understory-overstory interactions. Even under dense shade, root trenching produced dramatic increases in understory plant cover. Densely stocked young coniferous forests, referred to as “closed canopy” or “dark” often have depauperate herb layers. Although light limitation probably plays a role, young forests have the highest root densities of any stand age (Vogt *et al.* 1983) and the even spacing of these forests will result in few belowground "gaps". The characteristic patchiness of old-growth forest understories (Franklin *et al.* 1981) may also be better explained by patchiness of belowground rather than aboveground resources. Above and belowground gaps will be correlated but not necessarily totally overlapping in space or time; this lack of overlap may help explain observed disjunctions between canopy cover and understory vegetation response.

CHAPTER 3: EFFECTS OF PRE-COMMERCIAL THINNING ON UNDERSTORY HERB AND SHRUB COMMUNITY COMPOSITION

Abstract

In the U.S. Pacific Northwest, young forests under 100 years of age comprise 70% of the forested landscape. Because they are dominated by dense and evenly spaced trees and support little structural or species diversity, there is interest in management of young stands to increase diversity, particularly of late-successional species. One hypothesis holds that because young stands that are thinned are more likely to develop large, widely spaced trees, they may develop ecological communities more similar to old-growth. I tested this hypothesis by comparing the understory herb and shrub communities of pre-commercially thinned and unthinned young stands and old-growth stands. Sites were located in Douglas-fir (*Pseudotsuga menziesii*) forests in the H. J. Andrews Experimental forest in the Cascade Mountains of western Oregon. Young stands were approximately 40 yr old at the time of sampling; thinning occurred 20 yr earlier. Ordination of sample plots in terms of their species composition identified a strong gradient in community composition from young to old-growth stands; thinned stands exhibited composition more similar to old growth than did unthinned stands. Thinned stands had higher frequency, abundance (cover or density) and density of flowering of old-growth associated herbs than did unthinned stands but lagged behind old-growth sites. Forest generalist and release species showed mixed responses to thinning. Low shrub cover was moderately higher in thinned than unthinned or old-growth stands. I conclude that pre-commercial thinning may be a useful management tool to encourage old-growth associated understory

herbs without precipitating dominance of the understory by low shrubs and weedy species.

Introduction

The replacement of native forests with plantations is a significant conservation issue (Ehrlich 1996). The structure and composition of the second-growth forest is often substantially different from that of the native forest. There is global interest in the restoration of native biodiversity in these planted forests (Keenan *et al.* 1997, Ashton *et al.* 1998, Moles and Drake 1999, Stanturf and Madsen 2002, Zerbe 2002). Many approaches focus on restoration of native forest tree composition and structure, with the expectation that other components of biodiversity will follow (Allen *et al.* 2002, Poage and Tappeiner 2002, Schuler *et al.* 2002, Vallauri *et al.* 2002).

Stands less than 100 years old comprise 70% of the forested landscape in the Pacific Northwest (USFS 2000), and close to 95% of privately owned timberland in western Oregon (Oregon Board of Forestry 1995, Azuma *et al.* 2002). Management practices in these young forests will determine future levels and patterns of biodiversity in the Pacific Northwest landscape. Young managed stands exhibit very different structure than the old-growth forests they replaced, with higher tree densities and lower variation in tree size and canopy height than old-growth stands (Spies and Franklin 1991). In addition, current young forests may be more densely stocked than the young stands that developed into today's old growth (Poage and Tappeiner 2002). These observations have led some to suggest that thinning, by fostering development of old-growth stand structure, may accelerate development of ecological communities more similar to those found in old-growth (*e.g.* Poage and Tappeiner 2002). I tested this hypothesis for understory herb and shrub communities of 40-yr-old managed forests that had been pre-commercially thinned approximately 20 yr prior to my sampling. No previous study has examined whether pre-commercial thinning of young stands accelerates development of understory composition toward that characteristic of old-growth forests.

Studies of thinning (commercial and pre-commercial) to date provide an inconsistent picture of long-term (*circa* 20 yr) understory response. Bailey *et al.* (1998) found significant increases in understory cover. Similarly, Thysell and Carey (2001) showed that repeatedly thinned sites may have much lusher and more diverse understories than unthinned sites. Heavy thinning can have a positive effect while light thinning may have a negative effect on understory cover (Thomas *et al.* 1999). Some studies have found no evidence for a long-term positive effect of thinning on understory herbs (He and Barclay 2000), or herbs and shrubs (Alaback and Herman 1988).

Although many argue that young managed stands may require silvicultural manipulation to encourage development of old-growth characteristics (Thysell and Carey 2001, Poage and Tappeiner 2002), few present empirical data on the differences in understory composition between young managed and older forests (but see Bailey *et al.* 1998). The magnitude and nature of these differences should determine the urgency of restoration-oriented action, as well as the kind of intervention that may be needed. Spies (1991) showed that while no herb or shrub species were found exclusively in old-growth, many showed higher frequency or cover in old growth than in mature or young forests that had regenerated naturally after fire. No survey of similar breadth has been conducted for planted forests, and it is unclear how different the results would be if it were. In a smaller but still spatially extensive study, Bailey *et al.* (1998) found that, although abundance of disturbance-sensitive species, nitrogen-fixing species, grasses and exotic species were all increased by commercial thinning, there was wide and largely overlapping variation in composition among thinned, unthinned, and old-growth forest plots.

In my analysis of compositional differences between old and thinned and unthinned young forests, I contrast the use of three different measures of community composition. I examine the use of total species composition (presence/absence) because these data are easy to collect and integrate the responses of many species to environmental and management variables. I was particularly interested in contrasting the responses of herb species that were known to be old-growth associated, forest-habitat generalists, and release species. For these focal species, I contrasted two measures of performance: vegetative abundance (cover or ramet density) and flowering effort (density of flowering stems or inflorescences). I hypothesized that flowering would be more responsive to management than the other two measures because flowering in understory herbs occurs only when resource levels are relatively high (Pitelka *et al.* 1980 and cited references, Winn and Pitelka 1981, Lubbers and Christiansen 1986, Hughes *et al.* 1988, Cunningham 1997, Geber *et al.* 1997). In contrast, I expected presence/absence data to be relatively insensitive to management, but correlated with environmental factors such as aspect and elevation.

The objectives of this study were to:

1. Determine whether pre-commercial thinning accelerates development of old-growth composition in the herb and shrub understories of young managed stands.

2. Identify species that are indicators for young and old-growth stands.

3. Contrast the use of total species composition (presence/absence) with the use of abundance or flowering of focal species in addressing the first two objectives.

Methods

Study sites and sampling design

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

Young stands originated between 1956 and 1970 after clearcut harvest and broadcast burning of old-growth stands and were seeded or planted with *Pseudotsuga menziesii*. Pre-commercial thinning was carried out 15-22 yr after planting. Trees averaged approximately 10 to 15 cm in diameter at breast height at the time of

Table 1. Characteristics of study sites. Unit numbers are H. J. Andrews designations for clearcut harvest units. Design descriptions are as follows. Velasquez Martinez: control and two levels of thinning applied randomly to three adjacent subunits. Checkerboard: randomized application of control and levels of thinning to checkerboard of 0.4 ha subunits. Haphazard: Haphazard placement of one or more control subunits within a thinned unit. Degrees south was defined as degrees south from north, "TPH" designates trees per hectare, and "NA" indicates not available.

Block	Unit	Size (ha)	Elevation (m)	Slope (%)	Degrees south	Year planted	Year thinned	Design	Pre-thin total tph	Thin spacing (m)	Post-thin total tph
1	L107	11	657	38	29	1959	1981	Velasquez Martinez	5515	1.8 3.0	2224 1112
	OG		673	45	37						
2	L111	9	750	28	76	1966	1981	Velasquez Martinez	2282	2.7 3.7	1127 618
	L112	13	757	35	58	1967	1984	Checkerboard	2550	3.4 3.7 4.6	NA
	L112A	15	775	35	62	1969	1984	Haphazard	1297	3.7	NA
	L113	6	775	35	62	1967	1984	Checkerboard	4476	3.0 3.7 5.2	NA
	OG		758	29	100						
3	L231	15	669	71	38	1956	1977	All thin	7380	NA	721
	L104	11	578	35	66	1956		Control	9524		
	OG		603	51	64						

Table 1 (Continued).

Block	Unit	Size (ha)	Elevation (m)	Slope (%)	Degrees south	Year planted	Year thinned	Design	Pre-thin total tph	Thin spacing (m)	Post-thin total tph
4	L405	13	860	15	148	1963	1981	Velasquez Martinez	1698	3 5.5	754 329
	L405A	10	847	25	93	1963	1983	Haphazard	NA	3.7	NA
	OG		855	34	129						
5	L601	17	720	55	95	1961	1980	Haphazard	6279	3.7 4.6	840 580
	L602	16	785	46	20	1961	1983	Haphazard	4991	3.0 3.7 4.9	NA
	OG		720	34	60						
6	L701	12	822	42	151	1960	1981	Velasquez Martinez	1623	3.0 5.5	NA NA
	L701A	15	820	42	155	1962		Control	1144		
	OG		845	29	134						

thinning; they were cut with chainsaws and left to decompose where they fell. Prescribed spacing of residual trees ranged from 1.8 to 5.5 m (Table 1).

Sampling was carried out in six locations (blocks) within the Lookout Creek Watershed of the HJA, at elevations ranging from 578 to 860 m and on a variety of aspects (Table 1). Blocks were made up of one or more adjacent harvest units (defined by one clearcut harvest event) and a nearby old-growth area with similar slope and elevation. I sampled in all HJA units for which records of thinning treatments were available. Some blocks contained multiple harvest units in which different thinning designs had been used. Multiple occurrences of a treatment within a block were averaged to yield one thinned, unthinned and old-growth "treatment area" per block.

Several experimental designs had been used in the thinning studies that I sampled within (Table 1). In most blocks, thinning and control (unthinned) treatments were imposed within single clearcut harvest units. Four of the six blocks contained units that had been established to study tree growth response to intensities of thinning (Velasquez Martinez *et al.* 1992). In this experiment each unit was split in three parts along lines parallel to the dominant direction of slope; control (unthinned), light thinning and heavy thinning treatments were randomized among these three subunits. Within each of the subunits four permanent study areas were marked. Other thinned units included two designs: first, checkerboards of 0.4 ha subunits to which control and thinning treatments were applied in a randomized pattern; and second, thinned units with one or more 0.4 ha control subunits placed haphazardly within them. One block (number 3) did not contain thinning and control treatments interspersed within a block; I sampled in adjacent thinned and unthinned units that had undergone clearcut harvest in one year but as separate sales. This block was dropped from most analyses once I determined that the thinned and unthinned units differed in environmental as well as treatment variables.

In blocks with permanently marked study areas I established 9 m radius plots at the center of each marked study area. In all units without permanent study areas, I established 9 m radius plots at random points 50-100 m apart along transects spaced uniformly and spanning the unit. Numbers of plots per unit were selected with a goal of one plot per hectare. In total, I sampled 178 plots in 6 blocks, approximately 10 plots per treatment per block.

Data collection

In each plot I recorded the presence of all herb and shrub species and estimated abundance and flowering of eleven focal herb species (Table 2). I also estimated total cover of low shrubs, which included only the two dominant species *Berberis nervosa* and *Gaultheria shallon.* Scientific names follow Hitchcock and Cronquist (1973). The 11 focal herb species were chosen because they were abundant, included a mix of old-growth associated species (Spies 1991), forest generalists (not associated with old growth according to Spies 1991), and release species (subordinate forest species that are released by canopy disturbance; see Halpern 1989), and had phenologies such that flowering was evident throughout the study period. Sampling was conducted in June and July 2002. *Anemone deltoidea* and *Anemone lyallii* were considered as one taxon

Table 2. Focal species, with groups based on stand age association (Spies 1991) and disturbance response (Halpern 1989). Measures of abundance (number of ramets or percent cover) and flowering (number of flowering ramets or number of inflorescences) are given for each species.

Species	Family	Species group	Abundance	Flowering
Achlys triphylla	Berberidaceae	Old growth	ramets	ramets
Coptis laciniata	Ranunculaceae	Old growth	cover	ramets
Linnaea borealis	Caprifoliaceae	Old growth	cover	inflorescences
Tiarella trifoliata	Saxifragaceae	Old growth	ramets	ramets
Vancouveria hexandra	Berberidaceae	Old growth	cover	ramets
Anemone deltoidea/ lyallii	Ranunculaceae	Forest generalist	ramets	ramets
Trillium ovatum	Liliaceae	Forest generalist	ramets	ramets
Hieracium albiflorum	Asteraceae	Release	ramets	ramets
Osmorhiza chilensis	Apiaceae	Release	ramets	ramets
Trientalis latifolia	Primulaceae	Release	ramets	ramets
Whipplea modesta	Hydrangeaceae	Release	cover	inflorescences

because it was not possible to tell non-flowering individuals of the two species apart. Abundance was estimated visually: for species with easily distinguishable ramets I counted the number of ramets in the 9 m radius plot; for other species I estimated percent cover. Number of flowering events per 9 m radius plot was estimated similarly: number of flowering ramets where possible, and number of inflorescences for species without distinct ramets. In each plot I also recorded environmental and stand structural variables including slope, aspect, and basal area of *Pseudotsuga menziesii*, hardwoods (*Alnus rubra*, *Acer macrophyllum* and *Castanopsis chrysophylla*), and shade-tolerant conifers (*Tsuga heterophylla, Thuja plicata* and *Taxus brevifolia*). Basal area (BA) was estimated using a BAF-10 (English) prism in young stands and a BAF-20 prism in old growth. Aspect was re-coded as degrees south from true north (east and west coded the same) to emphasize north-south variation.

Statistical methods

Data structure: Analyses were conducted for all three measures of community composition (frequency of all shrub and herb species and abundance and flowering of the 11 focal species), except where specified otherwise. Frequency data included only the 61 species that occurred in 10 or more plots; rare species were omitted because they can obscure multivariate patterns (McCune and Grace 2002). All 61 species occurred in at least 3 treatment areas. For multivariate analyses, abundance and flowering values were re-expressed as a fraction of the total for each species (relativized by species total) to remove differential weighting of species due to natural differences in abundances and to the variety of measures used for abundance (number of ramets for some species, cover for others). Exploratory analysis of factors that varied at the plot level was carried out using all 178 plots. For all other analyses, plots from the same treatment area were averaged to produce a dataset (*n*=18) suitable for hypothesis tests on the effects of treatment. For all analyses except the ordination, Block 3 was omitted, leaving a sample size of 15 treatment areas. Presence/absence data aggregated to the treatment area level became frequency, the percentge of plots in a treatment area occupied by a species.

Multivariate analyses: I used non-metric multidimensional scaling ordination (NMS; McCune and Grace 2002) in PC-ORD version 4.10 (McCune and Mefford 1999) to examine patterns in community composition within and between treatments. Ordination was carried out both at the treatment area level (*n*=18) and at the plot level (*n*=178), with Sorensen distance as the measure of compositional distance between plots. NMS provides a good low-dimensional representation of the major patterns in a multivariate community dataset (McCune and Grace 2002). "Stress" measures the lack of fit between distances in the full-dimension dataset and the reduced-dimension solution. For each dataset, an optimal dimensionality was chosen based on (1) the absolute stress of the solution, (2) the stress of the solution compared to those for randomized data and (3) biological interpretability. After choosing dimensionality based on a smaller number of runs, I ran 40 different random starting configurations (step length=0.2, stability criterion=0.000001, 400 iterations maximum) and picked the lowest stress solution to interpret.

Multivariate tests for differences between treatments were conducted using blocked multi-response permutation procedure (MRPP) a non-parametric randomization-based alternative to multivariate ANOVA (PCORD version 4.10; McCune and Grace 2002). MRPP generated a probability that the treatment groups had smaller within-group distance than groups based on random re-assortment of the data. It also gave an effect size "A", the chance-corrected within-group agreement. "A" ranges from 0 to 1, with 0 denoting as much within-group heterogeneity as expected by chance and larger values denoting less within-group heterogeneity (McCune and Grace 2002). I used blocked MRPP to test the overall effect of treatment as well as to test pairwise differences between individual treatments; tests were carried out for all three measures of community composition (frequency and abundance and flowering of focal species). An 0.05 probability of type-I error was used for all tests, which is a conservative criterion given the small sample size. Because no adjustments were made for multiple comparisons, the actual probability of type-I error is somewhat higher than 0.05. Based on ordination results, Block 3, in which thinning and control (unthinned) treatments did not occur in one harvest unit (see Table 1), was excluded from this and all subsequent analyses, leaving a sample size of 15.

Univariate analyses:

Indicator Species Analysis (ISA; Dufrene and Legendre 1997; PC-ORD version 4.10) was used to compare old and young (unthinned) stands and identify species with concentrations of frequency in one or the other. I dropped thinned stands because their composition was so similar to unthinned stands that ISA yielded very few indicators for either treatment with both in the analysis. In a given treatment area, each species was either present or absent and occupied some percent of the sample plots. ISA generated indicator values based on the combination of both measures of prevalence. The probability of obtaining as strong or stronger an indicator value by chance was evaluated using a randomization test that re-assigned plots to treatments. No blocking option is available for ISA. I report only those indicator values with p-values less than 0.05.

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

Results

Stand structure

Treatments had significant effects on basal area of shade-tolerant conifers and hardwoods, as well as on low shrub cover (p 0.05, Table 3). Thinned, unthinned, and old-growth stands did not differ in basal area of the dominant conifer, *Pseudotsuga menziesii*. Thinned stands, along with old-growth stands, had significantly lower basal area of hardwoods than did unthinned stands (p<0.05 for pairwise comparisons, see Table 3).

Table 3: Treatment means for tree and shrub variables, Block 3 excluded (*n*=15). Overall significance from blocked analysis of variance; treatments with different letter superscripts were significantly different in *post hoc* paired t-tests (*p* 0.05). Tolerant BA = basal area of shade-tolerant conifers

	Unthinned	Thinned	Old-growth	F	P
P. menziesii BA (m^2/ha)	31.88	31.69	26.04	2.05	0.20
Tolerant BA (m^2/ha)	2.28^{a}	1.84^{a}	31.6^{b}	61.35	<0.001
Hardwood BA (m^2/ha)	2.79^{a}	0.443^{b}	0.19^{b}	8.28	0.01
Low shrub cover (%)	23.46^{ab}	31.26^{a}	10.45^{b}	4.41	0.05

Note: P-value for *post-hoc* test for treatment differences for Tolerant BA <0.002, others <0.05.

Because of the decline in hardwood basal area with thinning, total basal area declined slightly with thinning intensity (Figure 1). Basal area varied widely within thinning intensities. Old-growth stands had higher basal area of shade-tolerant conifers than did either thinned or unthinned stands; low shrub (*Gaultheria shallon* and *Berberis nervosa*) cover was lower in old growth than in thinned stands ($p<0.05$ for pairwise comparisons, see Table 3).

Community composition

Flowering and abundance were positively correlated for all focal species, with coefficients of determination (r^2) ranging from 0.4 to 0.9 (Figure 2). Overall, the relationship between flowering and abundance for release species showed higher coefficients of determination than did that for forest generalist or old-growth associated species.

The three treatments (thinned, unthinned and old-growth) differed significantly from each other in community composition whether the analysis was based on

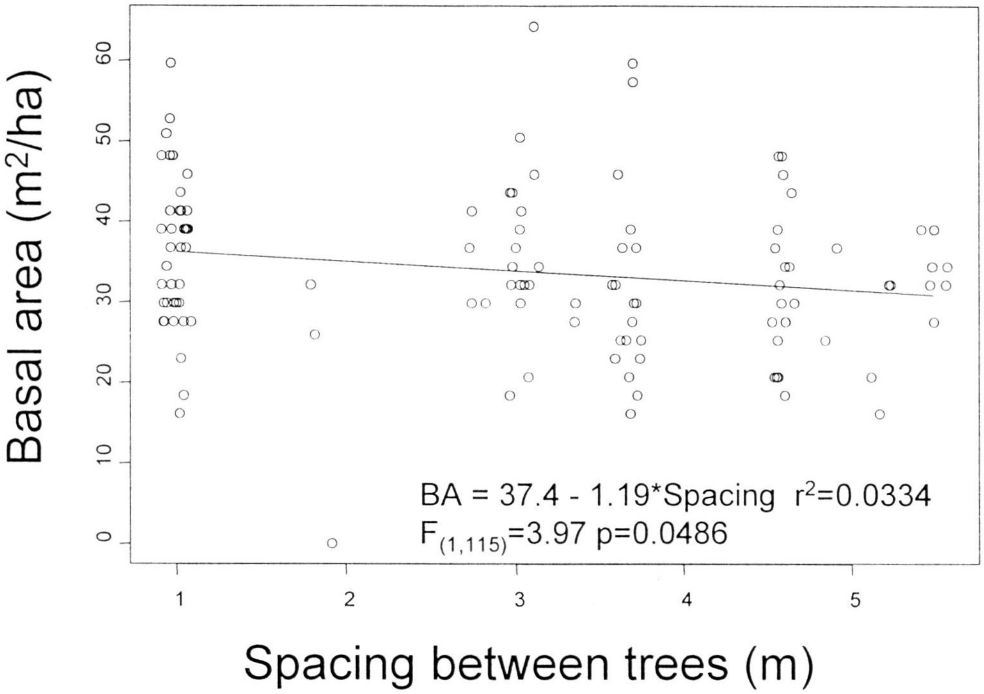

Figure 1: Relationship between thinning intensity (spacing between trees in meters) and total basal area (m^2/ha) 20 yrs after pre-commercial thinning. Unthinned stands were arbitrarily assigned a spacing of one. Points were jittered for better resolution.

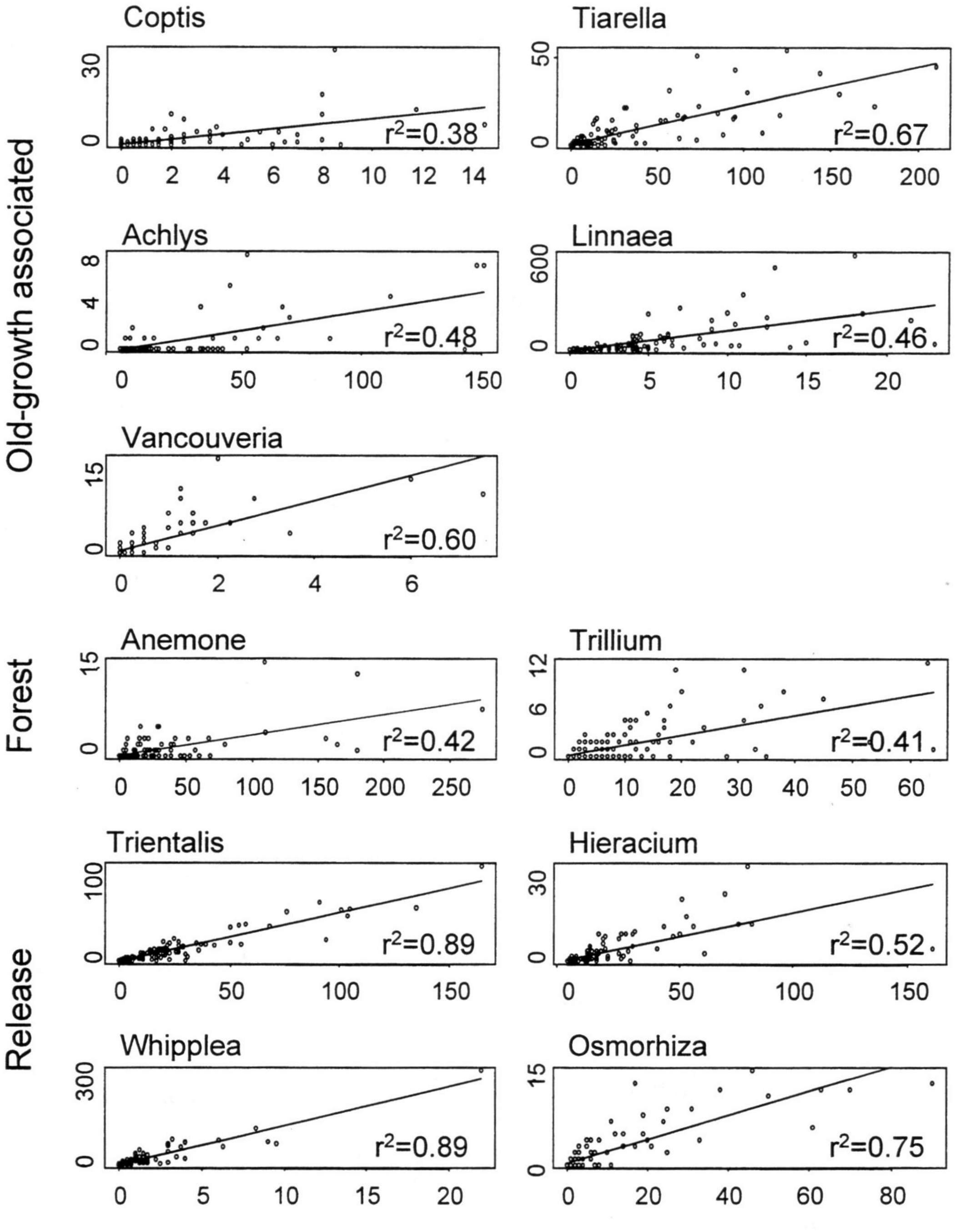

Figure 2. Flowering *versus* abundance for focal species. Y-axis is number of flowering ramets for most species (number of inflorescences for *Linnaea borealis* and *Whipplea modesta*). Units on x-axis are number of ramets for most species (percent cover for *Coptis laciniata*, *Linnaea borealis*, *Vancouveria hexandra* and *Whipplea modesta)*.

frequency of all species, or abundance or flowering of focal species (Blocked MRPP *p*-value <0.02; Table 4). Unthinned and thinned stands each differed significantly from old-growth for all three measures of community composition in comparisons paired by block ($p \leq 0.02$). Unthinned stands differed from thinned stands only in terms of frequency ($p=0.02$), and the within-group agreement for this comparison was six-fold smaller than that from the contrasts that included old stands. There was suggestive statistical evidence for an effect of thinning on flowering of focal species ($p=0.11$); a larger sample size would be needed to adequately test this effect.

Table 4: Blocked MRPP of differences in understory community composition among treatments, Block 3 excluded, $n=15$. A = chance corrected within-group agreement (effect size), *p* = probability of randomized groups having as large a within-group agreement.

	Overall		Unthinned vs. Old growth		Thinned vs. Old growth		Unthinned vs. Thinned	
	A	*p*	A	*p*	A	*p*	A	*p*
Frequency	0.12	0.002	0.12	0.02	0.13	0.02	0.02	0.02
Abundance	0.08	0.01	0.08	0.02	0.10	0.02	-0.02	0.90
Flowering	0.12	0.002	0.12	0.02	0.12	0.012	0.02	0.11

Ordination of frequency data aggregated to the treatment area level ($n=18$) yielded a two-dimensional solution that explained 83% of the variation in the raw data (NMS ordination, final stress=14.3). Most of the variation (63%) was explained by Axis 1, which separated young unthinned stands from old-growth stands (Fig. 3). In five of the six blocks, thinned treatment areas were closer to old-growth composition than were unthinned areas. The one exception was Block 3 (see Table 1) in which

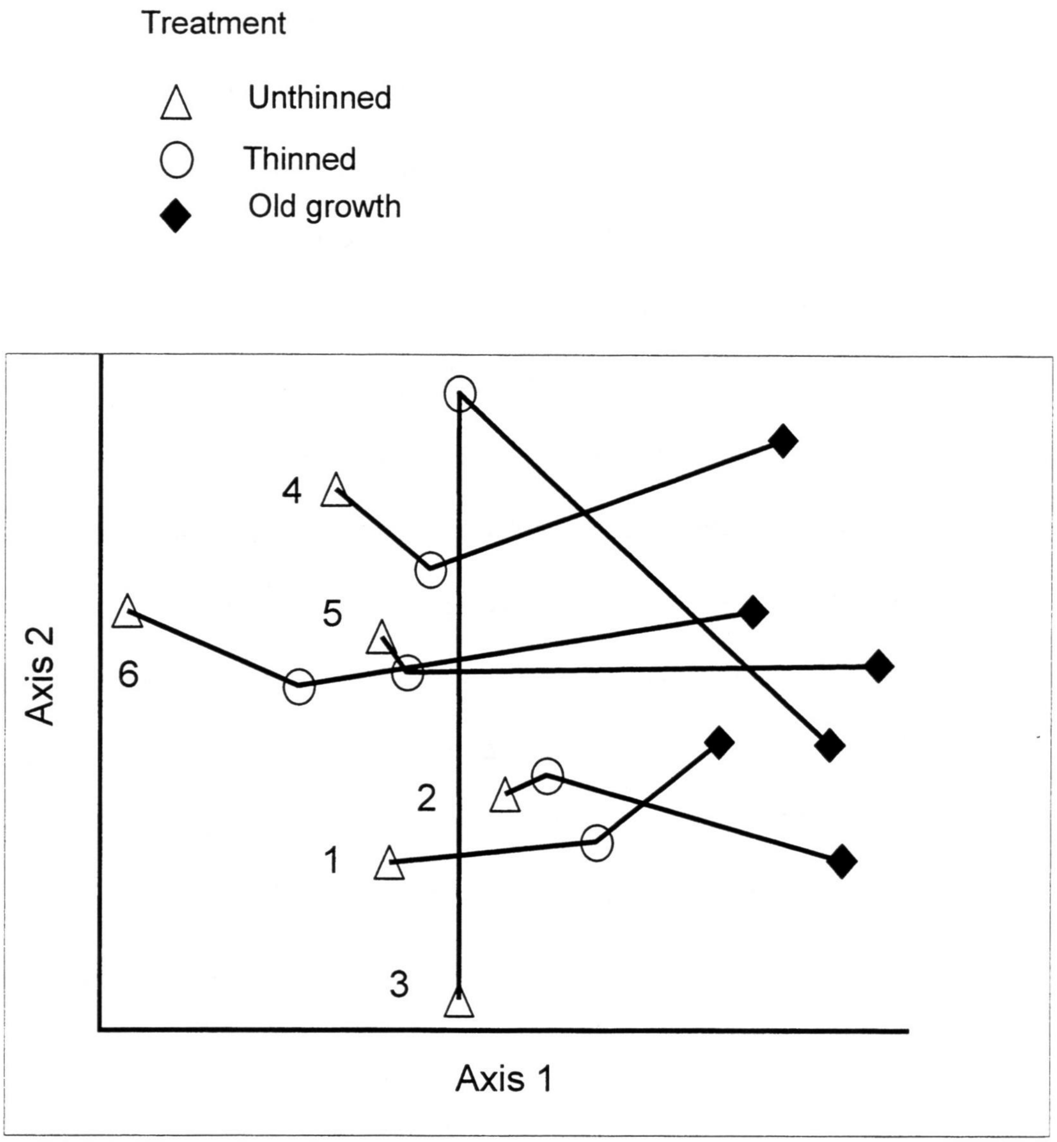

Figure 3. NMS ordination of species frequency data aggregated to treatment area level (n=18). Lines connect treatment areas in a block; block numbers correspond to Table 1.

thinned and unthinned treatments occurred in separate clearcut harvest units rather than interspersed within one harvest unit. The magnitude of difference in species composition between thinned and unthinned treatments varied among blocks (Fig. 3), as did the difference between unthinned and old-growth treatments.

Taxa with strong ($|r| \geq 0.5$) negative correlations with Axis 1, and therefore higher frequency in young (unthinned and thinned) treatment areas, included release herbs and vines such as *Galium triflorum*, *Osmorhiza chilensis*, *Trientalis latifolia*, *Whipplea modesta*, *Campanula scouleri*, *Stachys* spp., and *Rubus ursinus* (Table 5). Shrubs whose frequency was negatively correlated with Axis 1 included *Holodiscus discolor* and *Symphoricarpos mollis*. Species positively correlated with Axis 1, and therefore reaching higher frequencies in older stands, included herbs found by Spies (1991) to be old-growth associated: *Linnaea borealis*, *Vancouveria hexandra*, *Achlys triphylla*, *Coptis laciniata* and *Tiarella trifoliata* (Table 5). Other species positively correlated with Axis 1 included the forest generalist *Trillium ovatum*, the ericaceous herb *Pyrola asarifolia*, the orchid *Goodyera oblongifolia* and the ericaceous shrub *Rhododendron macrophyllum*.

The second axis, which explained 20% of the variation in the data, represented a gradient from mesic sites at lower elevations (low scores) to drier sites at higher elevations (high scores; correlation of scores with elevation equal to +0.59). Taxa with strong ($|r|>0.5$) negative correlations with this axis were the herbs *Listera* spp., *Vancouveria hexandra*, and *Achlys triphylla*, the fern *Blechnum spicant* and the deciduous tree *Alnus rubra*, while species with strong positive correlations included

Table 5. Correlations of species frequency with axes in NMS ordination of treatment areas ($n = 18$). R^2 = proportion of variation in the species data accounted for by position on the axis. All species with correlations greater than or equal to 0.5 are shown.

	R^2	Species	Correlation
Axis 1: Young (-) to old (+)	0.63	*Galium triflorum*	-0.9
		Rubus ursinus	-0.8
		Hieracium albiflorum	-0.8
		Whipplea modesta	-0.8
		Lactuca muralis	-0.6
		Holodiscus discolor	-0.6
		Boykinia elata	-0.6
		Symphoricarpos mollis	-0.6
		Campanula scouleri	-0.6
		Stachys spp.	-0.6
		Trientalis latifolia	-0.5
		Osmorhiza chilensis	-0.5
		Chimaphila menziesii	-0.5
		Vancouveria hexandra	+0.5
		Pyrola asarifolia	+0.5
		Trillium ovatum	+0.6
		Achlys triphylla	+0.7
		Rhododendron macrophyllum	+0.7
		Goodyera oblongifolia	+0.7
		Tiarella trifoliata	+0.8
		Coptis laciniata	+0.8
		Linnaea borealis	+0.9
Axis 2: Wet (-) to dry (+)	0.20	*Alnus rubra*	-0.7
		Blechnum spicant	-0.6
		Vancouveria hexandra	-0.6
		Listera spp.	-0.5
		Achlys triphylla	-0.5
		Corallorhiza spp.	+0.5
		Xerophyllum tenax	+0.5
		Synthyris reniformis	+0.7
		Trientalis latifolia	+0.7

the herbs *Trientalis latifolia*, *Corallorhiza* spp., *Synthyris reniformis* and *Xerophyllum tenax* (Table 5).

In Block 3, thinned and unthinned units fell equally far from old-growth composition on Axis 1 but were widely separated on Axis 2. Because the environment of the thinned and unthinned treatment areas clearly differed, this block was omitted from hypothesis tests of treatment effects. The thinned unit was steeper and at slightly higher elevation than the unthinned unit (Table 1). In other blocks, all three treatment areasfell in similar positions on Axis 2, suggesting that there were few pre-treatment differences between the treatment areas within each block.

Ordination of plot level data (*n*=178) allowed exploration of the factors that are correlated with small-scale variation in plant community composition within treatment areas. In the ordination based on presence-absence data, three gradients captured 70% of the variation in the data (NMS ordination, stress = 20.5; Fig. 4). Plots along Axis 1 varied from young to old growth (with little separation of thinned and unthinned plots); this axis explained 30% of the variation in the full-dimensional data (Table 6). Basal area of shade-tolerant conifers was positively correlated with this axis.

Positions on Axis 2 varied from from mesic sites at lower elevations (low scores) to drier sites at higher elevations (high scores); this axis explained another 26% of the variation in the data. Hardwood basal area was negatively correlated with this axis, while degrees south, elevation, and *Pseudotsuga menziesii* basal area were positively correlated. Plots on Axis 3 (not shown) varied from shallow to steep slopes, explaining 14% of the variation in the data (Table 6). Percent slope was positively correlated with this axis, while elevation was negatively correlated. The ordination

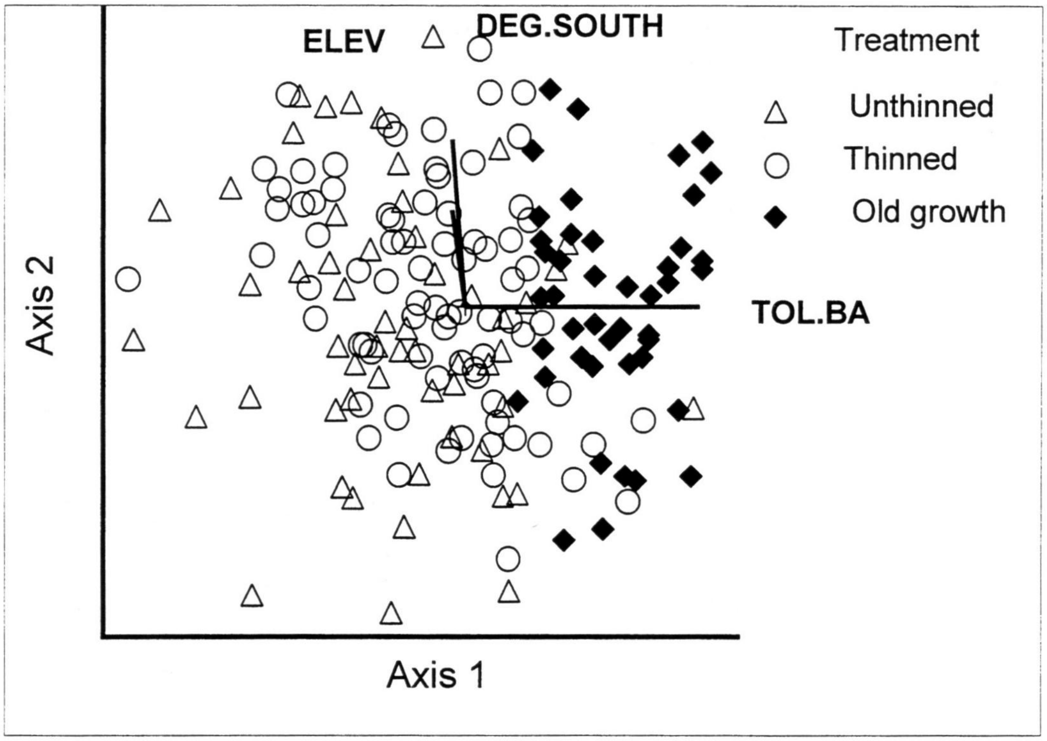

Figure 4. NMS ordination of species presence-absence data at plot level (*n*=178). Vectors represent strength of correlations of environmental and stand structure variables with the ordination axes. TOL.BA = basal area of shade-tolerant conifers. DEG.SOUTH = Degrees south from magnetic north. ELEV = Elevation.

Table 6. Correlations of environmental variables and species presence with axes in NMS ordination of plot-level (*n*=178) presence/absence data. All environmental variables with correlations greater than or equal to 0.3 and all species with correlations greater than or equal to 0.4 are shown. TOL.BA = basal area of shade-tolerant conifers, PSME.BA = basal area of *Pseudotsuga menziesii*, HW.BA = basal area of hardwoods, DEG.SOUTH = degrees south from magnetic north. ELEV = elevation, SLOPE = percent slope.

	R^2	Env. variable	Correlation	Species	Correlation
Axis 1: Young (-) to old (+)	0.30	TOL.BA	+0.64	*Galium triflorum*	-0.6
				Whipplea modesta	-0.6
				Trientalis latifolia	-0.5
				Hieracium albiflorum	-0.5
				Rubus ursinus	-0.4
				Stachys spp.	-0.4
				Goodyera oblongifolia	+0.4
				Coptis laciniata	+0.4
				Tiarella trifoliata	+0.5
				Linnaea borealis	+0.5
Axis 2: Wet (-) to dry (+)	0.26	HW.BA	-0.31	*Trillium ovatum*	-0.5
		PSME.BA	+0.30	*Vancouveria hexandra*	-0.5
		DEG.SOUTH	+0.41	*Achlys triphylla*	-0.5
		ELEV	+0.53	*Athyrium filix-femina*	-0.4
				Oxalis oregana	-0.4
				Blechnum spicant	-0.4
				Tiarella trifoliata	-0.4
				Trientalis latifolia	+0.4
				Chimaphila umbellata	+0.5
				Whipplea modesta	+0.5
Axis 3: Shallow(-) to steep (+)	0.14	ELEV	-0.30	*Hieracium albiflorum*	-0.4
		SLOPE	+0.25	*Smilacina spp.*	-0.4
				Chimaphila umbellata	-0.4
				Tiarella trifoliata	-0.4
				Pachistima myrsinites	-0.4
				Gaultheria shallon	+0.4
				Xerophyllum tenax	+0.4

diagram (Figure 4) shows clear separation of old from young stands but does not distinguish between thinned and unthinned young stands; other sources of variation apparently masked the effects of thinning at this level of aggregation. Spacing of thinning also was not correlated with position in the ordination diagram. Ordinations using abundance or flowering (not shown) were similar to the presence/absence ordination. All three ordinations explained approximately 70% of the variation in the data, with approximately 30% explained by the stand-age axis.

Indicator species for old and young stands (Table 7) included many of the same species that were correlated with the stand age gradient (Tables 5 and 6). Indicator species for old growth (Table 7) included the focal herbs *Linnaea borealis*, *Coptis laciniata* and *Tiarella trifoliata*. The forest orchid *Goodyera oblongifolia* provided the strongest indicator value for old growth, with the ericaceous shrubs *Rhododendron macrophyllum* and *Chimaphila umbellata* also serving as significant indicators. Significant indicators for young stands included the release herbs *Osmorhiza chilensis*, *Whipplea modesta* and *Hieracium albiflorum*, the forest

Table 7: Indicator Species Analysis for differences between young (thinned and unthinned) and old-growth treatment areas based on frequency of all species (*n*=15). Values following species names are indicator values (IV), out of a maximum possible of 100.

Young	IV	p-value	Old growth	IV	p-value
Osmorhiza chilensis	100	0.008	*Goodyera oblongifolia*	83	0.008
Symphoricarpos mollis	93	0.021	*Tiarella trifoliata*	71	0.020
Galium triflorum	86	0.008	*Rhododendron macrophyllum*	73	0.033
Whipplea modesta	76	0.036			
Hieracium albiflorum	70	0.020	*Coptis laciniata*	73	0.017
Asarum caudatum	66	0.034	*Linnaea borealis*	64	0.008
Rubus ursinus	61	0.042	*Chimaphila umbellata*	63	0.008

understory shrub *Symphoricarpos mollis*, the ubiquitous trailing vine *Rubus ursinus*, and the mesic-sites species *Asarum caudatum*.

All 11 focal species were present in at least 20% of plots, regardless of treatment, with the exception of *Osmorhiza chilensis,* which was absent in old growth (Table 8a). Old-growth species and forest generalist species were more frequent, generally more abundant, and flowered more in old-growth than young stands (Figure 5); the differences were statistically significant for at least one metric for all species except *Vancouveria hexandra* (Table 8). Variation in abundance and flowering of forest (old-growth associated and generalist) herbs also tended to be higher in old-growth than young stands (Table 8); in plot-level data (not shown) this effect was stronger (two-to-ten fold higher standard errors in old growth).

Old-growth associated species generally increased in response to thinning (Fig. 6); however, individual species differences between unthinned and thinned stands were statistically significant only for frequency (Table 8). Although abundance and flowering of old-growth species tended to show larger responses to treatments than did frequency (Figs. 5, 6), individual species responses were not significant because abundance and flowering were highly variable between blocks (Table 8). Forest generalists showed mixed responses to thinning, with *Anemone* spp. responding positively and *Trillium ovatum* negatively (Figure 6).

In contrast to the old-growth species, release herbs showed lower measures of performance in old-growth than in unthinned stands (Fig. 5). Differences in frequency were significant for all species except *Trientalis latifolia*; differences in flowering and abundance were not statistically significant (Table 8). Release herbs showed mixed

Table 8. Frequency, abundance, and flowering of focal species in treatments. Values are followed by standard errors. Block 3 omitted, $n=15$. P-values are from blocked ANOVA. Treatments with different letter superscripts were significantly different ($p \leq 0.05$) in post-hoc paired t-tests.

a. Frequency

	Species	Unthinned	Thinned	Old growth	P
Old growth	*Coptis laciniata*	33 ± 12^{a}	49 ± 10^{b}	88 ± 6^{c}	0.00004
	Tiarella trifoliata	34 ± 13^{a}	41 ± 13^{a}	83 ± 9^{b}	0.005
	Achlys triphylla	37 ± 12^{a}	50 ± 10^{b}	72 ± 13^{c}	0.0007
	Linnaea borealis	54 ± 6^{a}	74 ± 6^{b}	97 ± 3^{c}	0.001
	Vancouveria hexandra	45 ± 8	57 ± 4	69 ± 11	0.2
Forest generalist	*Anemone deltoidea /lyallii*	53 ± 15	54 ± 12	79 ± 12	0.3
	Trillium ovatum	72 ± 7	71 ± 12	86 ± 4	0.3
Release	*Trientalis latifolia*	76 ± 15	85 ± 8	58 ± 12	0.12
	Hieracium albiflorum	66 ± 8^{a}	70 ± 11^{a}	29 ± 9^{b}	0.04
	Whipplea modesta	71 ± 14^{a}	64 ± 17^{a}	22 ± 9^{b}	0.01
	Osmorhiza chilensis	19 ± 5^{a}	58 ± 9^{b}	0 ± 0^{c}	0.0006

Note: P-values for *post-hoc* tests for the following contrasts were less than or equal to 0.005: *Coptis* unthinned *vs*. old-growth, *Linnaea* unthinned *vs*. old-growth and unthinned *vs*. thinned, and *Osmorhiza* thinned *vs*. unthinned.

Table 8 (Continued).
b. Abundance (Letters in parentheses denote abundance estimation method: *n* for number of ramets in a 250 m^{2} circle, *c* for percent cover).

	Species	Unthinned	Thinned	Old growth	P
Old growth associated	*Coptis laciniata* (*c*)	0.46 ± 0.24^{a}	0.41 ± 0.15^{a}	3.98 ± 0.58^{b}	0.0001
	Tiarella trifoliata (*n*)	8.86 ± 6.63	14.85 ± 4.91	33.26 ± 13.68	0.2
	Achlys triphylla (*n*)	4.81 ± 3.42	9.17 ± 3.68	17.96 ± 10.47	0.4
	Linnaea borealis (*c*)	1.46 ± 0.59^{a}	2.42 ± 0.56^{a}	5.29 ± 0.68^{b}	0.004
	Vancouveria hexandra (*c*)	0.52 ± 0.41	0.31 ± 0.12	0.40 ± 0.16	0.9
Forest generalist	*Anemone deltoidea/ lyallii* (*n*)	6.45 ± 2.36	19.72 ± 11.62	26.55 ± 11.02	0.13
	Trillium ovatum (*n*)	6.24 ± 1.61	5.92 ± 1.93	8.87 ± 2.45	0.6
Release	*Trientalis latifolia* (*n*)	23.04 ± 11.35	20.92 ± 7.91	8.31 ± 3.97	0.13
	Hieracium albiflorum (*n*)	13.66 ± 4.02	10.04 ± 2.29	1.84 ± 0.79	0.08
	Whipplea modesta (*c*)	1.28 ± 0.77	1.58 ± 0.96	0.03 ± 0.01	0.3
	Osmorhiza chilensis (*n*)	3.42 ± 1.67^{ab}	8.47 ± 2.69^{a}	0.00 ± 0.00^{b}	0.03

Note: P-values for *post-hoc* tests for the following contrasts were less than or equal to 0.005: *Coptis* unthinned *vs.*old-growth and thinned *vs.* old-growth.

Table 8 (Continued).
c. Flowering (Letters in parentheses indicate flowering parameter estimated: *n* for number of flowering ramets in a 250 m^2 circle, *f* for number of inflorescences)

	Species	Unthinned	Thinned	Old-growth	P
Old growth associated	*Coptis laciniata* (*n*)	0.73 ± 0.42^{a}	0.21 ± 0.09^{a}	4.12 ± 1.25^{b}	0.009
	Tiarella trifoliata (*n*)	2.74 ± 1.37^{a}	3.62 ± 1.45^{ab}	8.68 ± 2.91^{c}	0.10
	Achlys triphylla (*n*)	0.07 ± 0.07	0.25 ± 0.20	0.68 ± 0.42	0.3
	Linnaea borealis (*f*)	16.5 ± 7.64^{a}	17.43 ± 5.31^{a}	114.75 ± 20.49^{b}	0.00009
	Vancouveria hexandra (*n*)	0.59 ± 0.34	1.21 ± 0.49	1.60 ± 0.54	0.2
Forest generalist	*Anemone deltoidea/ lyallii* (*n*)	0.55 ± 0.37	0.67 ± 0.42	1.35 ± 0.68	0.03
	Trillium ovatum (*n*)	1.25 ± 0.44	0.54 ± 0.23	1.68 ± 0.24	0.07
Release	*Trientalis latifolia* (*n*)	10.51 ± 5.45	10.29 ± 4.37	4.92 ± 2.63	0.15
	Hieracium albiflorum (*n*)	2.83 ± 1.00	2.96 ± 0.82	0.74 ± 0.34	0.2
	Whipplea modesta (*f*)	15.45 ± 8.79	28.35 ± 16.79	0.96 ± 0.44	0.2
	Osmorhiza chilensis (*n*)	0.49 ± 0.19^{a}	2.20 ± 0.63^{b}	0 .00 ± 0.00^{a}	0.007

Note: P-values for *post-hoc* tests for the following contrasts were less than or equal to 0.005: *Linnaea* unthinned *vs.*old-growth and thinned *vs.* old-growth.

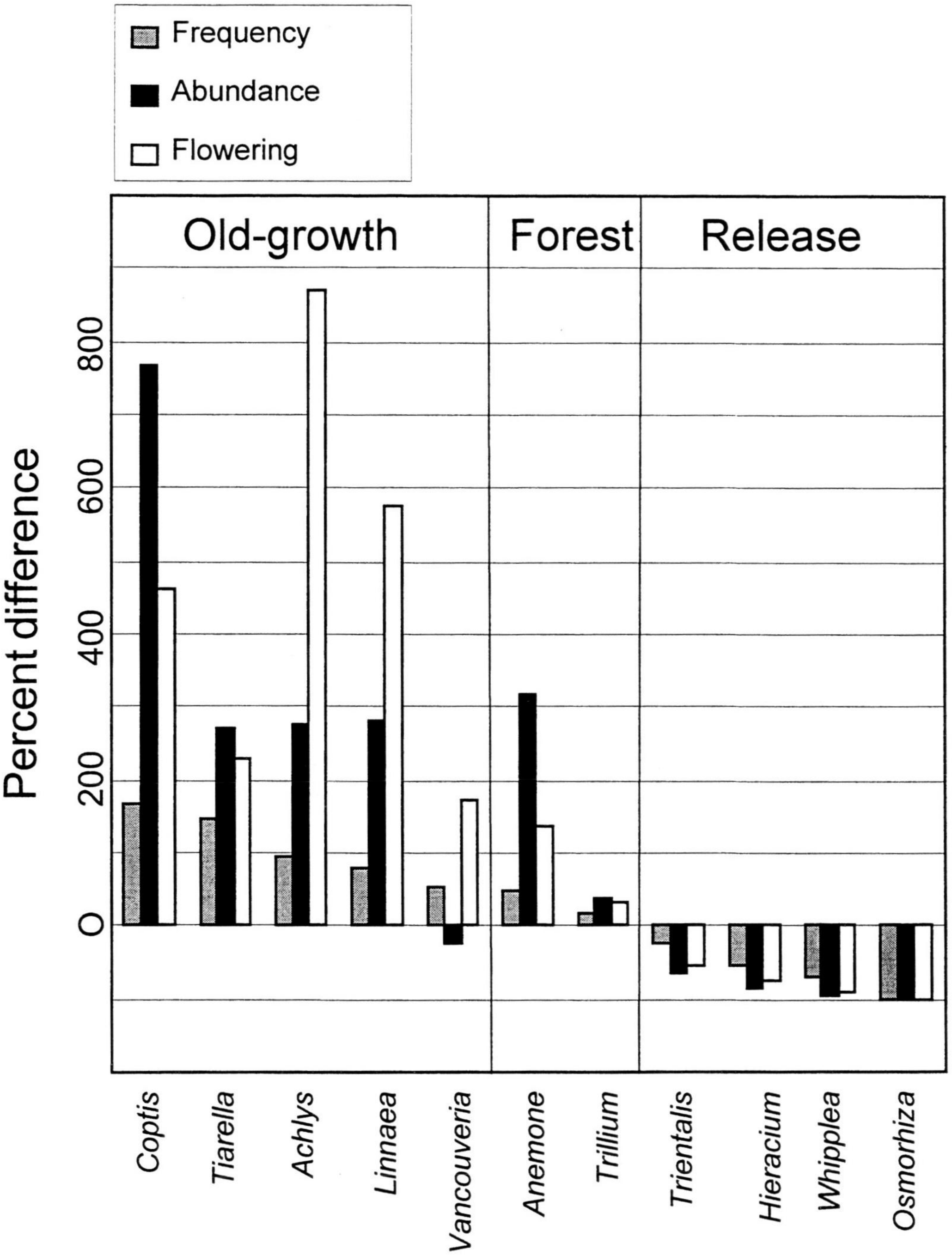

Figure 5. Percent difference between old growth and unthinned treatment areas in frequency, abundance and flowering of focal species. Difference = (Old-growth average – unthinned average)/(unthinned average). Block 3 excluded, *n* =15.

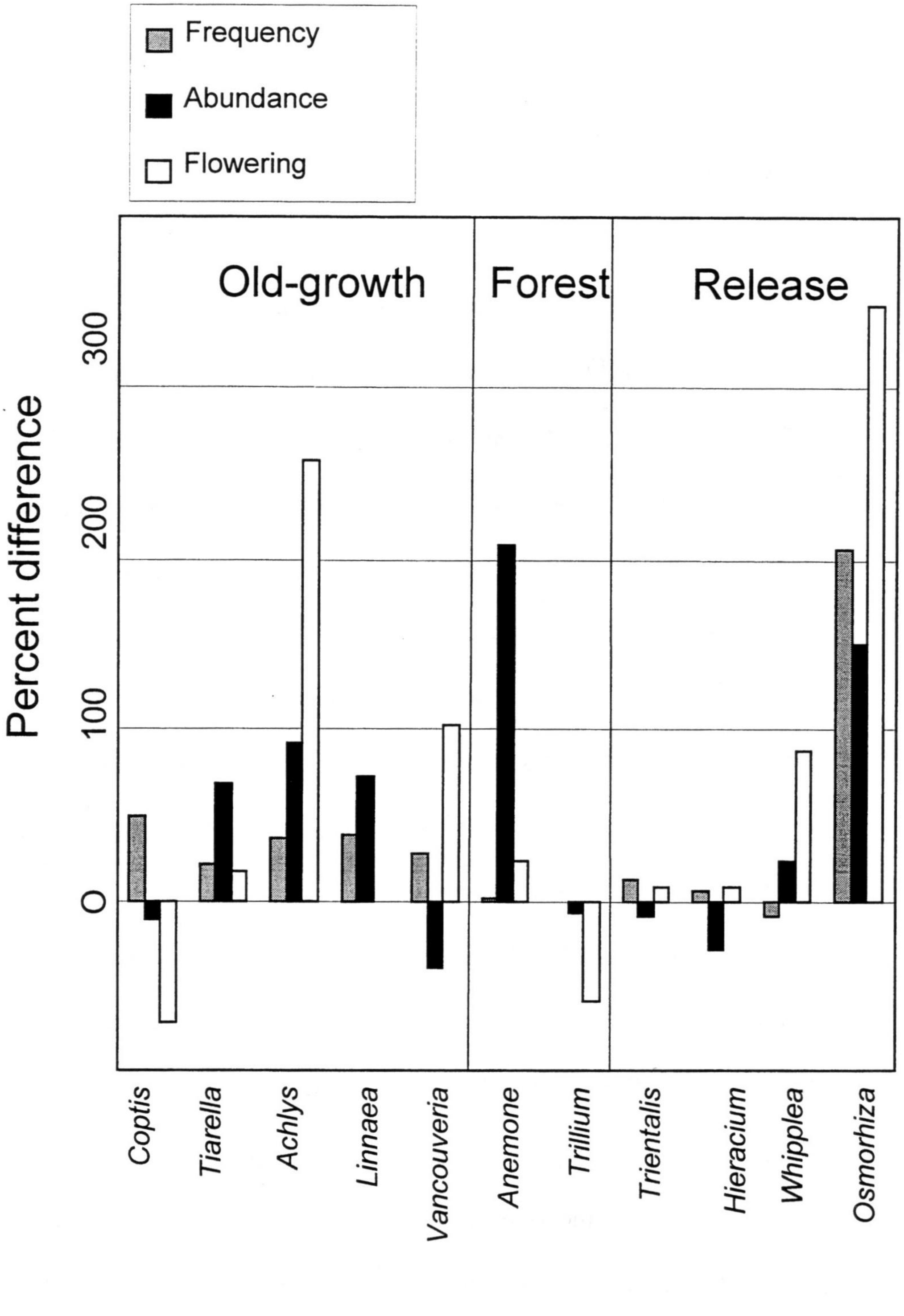

Figure 5. Percent difference between thinned and unthinned treatment areas in frequency, abundance and flowering of focal species. Percent difference = (Thinned average – unthinned average)/(unthinned average). Block 3 excluded, *n*=15.

responses to thinning, with the exception of *Osmorhiza chilensis*, which responded very positively to thinning for all measures (Fig. 6).

Discussion

Effects of thinning

Thinning has been proposed as a tool to increase biodiversity in young managed stands (Franklin 2001, Thysell and Carey 2001). In the young forests examined in this study, effects of pre-commercial thinning were evident in the understory herb and shrub community 20 yr later. Ordination analysis revealed a compositional gradient from old to young stands, with thinned stands falling closer to old growth than did unthinned stands. While old-growth associated species generally performed better in thinned than unthinned stands, the relatively high abundance of release herbs in thinned stands differentiated their composition from that of old growth. Levels of old-growth species performance in thinned stands remained well below those found in old-growth stands.

Differences in the herb and shrub community observed 20 yr after pre-commercial thinning are probably legacies of large differences in stand structure immediately following thinning. Thinning treatments removed up to three-quarters of the trees, likely leaving the canopy significantly more open than in unthinned stands. Thinning may also increase below-ground resource availability (Brix and Mitchell 1986), which can limit understory plant growth (Chapter 2). Thinning led to increased rates of tree growth, however, with the heaviest thins exhibitg the highest rates of growth (Velasquez Martinez *et al.* 1992). The thinned stands had fewer trees, but these trees grew faster and achieved larger diameters than the trees in the unthinned stands. Twenty years after harvest, I found that the unthinned stands had higher basal area of hardwoods, while thinned and unthinned stands exhibited indistinguishable basal areas of *Pseudotsuga menziesii*, the dominant conifer. While I did not measure canopy closure, summed tree diameter (and thus basal area) correlates well with fisheye photography based estimates of canopy closure ($r^2 = 0.94$; Ronnie and Lertzman 2003). Thomas *et al.* (1999) found that canopy cover did not differ between controls and plots with different levels of thinning 20 yr after thinning. In my sites 20 yr after thinning, both thinned and unthinned stands appeared to exhibit relatively uniform closed canopies.

The lack of difference in *Pseudotsuga menziesii* basal area between thinned and unthinned stands may also be explained by the fact that not only did trees in thinned sites grow faster, but they were able to withstand snow and wind damage better. In my sites, significant numbers of trees in steep unthinned areas toppled as a result of snow loads in the winter of 1996 (Dave Perry, unpublished data). That thinned trees can be more stable in the face of storm damage has been observed elsewhere (Nykanen *et al.* 1997, Wilson and Baker 2001). Areas of toppled trees formed treefall gaps in unthinned but not thinned sites; these gaps were added to a smaller number of disease pockets that occurred in both thinned and unthinned stands. Conventional wisdom holds that competition is the dominant mortality process operating in young stands, with disease and other gap-creating processes not becoming important until stands are older (Franklin 2001). In the stands studied here, gap-formation processes were operating in dense young stands and were at least partially inhibited by thinning. Thysell and Carey (2001) also observed that natural gap-formation processes had begun in unthinned but not thinned young stands. Formation of gaps in my unthinned study sites may have diminished differences in overstory basal area and understory composition between thinned and unthinned stands.

The effects of thinning on the understory may depend on the timing and intensity of the thinning event. Pre-commercial thins are carried out before or soon after canopy closure, while commercial thins can occur in stands that are much older. Canopy closure is known to cause declines in most understory species, both forest-associated and release (Halpern 1989, Lindh 1994). Thinning implemented before canopy closure should allow species that have done well in the clearcut environment to retain high population levels. Effects of thinning after canopy closure will be limited by the declines (and local extinctions) that have already occurred. Moreover, young trees will quickly grow to capture resources that are made available by thinning. Older trees in commercial thins may not be capable of resuming rapid growth, leaving more resources available for the understory. Recent evidence suggests that all but the lightest commercial thins may reduce timber volume over the long term, freeing up resources for understory vegetation (Marshall and Curtis 2001).

In my sites, pre-commercial thinning was conducted after canopy closure had occurred but while the trees were still young (~20 yr). Responses of some release species (*Trientalis latifolia* and *Hieracium albiflorum*) to thinning may have been limited because these species may already have declined in the young stand before thinning was imposed (*e.g.* Halpern 1989). One release species, *Osmorhiza chilensis*, responded very positively to thinning, perhaps because its seed is easily dispersed by animals or because it requires only moderate canopy openness. Old-growth associated species showed consistent increases in frequency, but inconsistent responses in abundance and flowering. These species may have colonized plots when resource levels were relatively high following thinning; declining resource availability may be limiting performance in those plots 20 yr later.

Thomas *et al.* (1999) found that heavy pre-commercial thins had small but lasting (~20 yr) positive effects on understory cover despite the absence of a lasting effect on overstory cover, while light thins actually had persistent negative effects. In their sites, old-growth and wet-site species responded more positively to intensity of thinning than did open-site species. In contrast, pre-commercial thinning may not lead to increases in understory herb and shrub cover in wet coastal sites where shade-tolerant trees regenerate rapidly, filling available space and outcompeting understory herbs and shrubs (Alaback and Herman 1988).

Commercial thins carried out later in stand development can have larger effects on understory cover and composition than pre-commercial thins (Bailey *et al.* 1998, Thysell and Carey 2001). Release species seem to respond more positively to commercial than to pre-commercial thinning, perhaps reflecting the more persistent canopy openness (Bailey *et al.* 1998, Thysell and Carey 2001). Bailey *et al.* (1998) found significant increases in nitrogen-fixing species, grasses and sedges, matted vines and exotic species in response to thinning, while unthinned sites had levels of these species indistinguishable from old-growth. In stands with little initial understory cover, Thysell and Carey (2001) found a 7% increase in herb cover associated with two rounds of commercial thinning, 20 and 5 yr earlier, with large increases by many ruderal and release species, and a doubling of *Gaultheria shallon* cover. While the positive response of *Gaultheria shallon* appears to be a universal response to commercial thinning, other understory herbs and shrubs may fail to respond to commercial thinning in some situations (He and Barclay 2000).

There is concern that thinning will lead to dominance by low shrubs, particularly *Gaultheria shallon*, which may exclude more diverse herb communities (Thysell and Carey 2001, Franklin 2001). Both *Gaultheria shallon* and *Berberis nervosa* have higher rates of vegetative spread in thinned *versus* unthinned stands; *Gaultheria* more strikingly than *Berberis* (Huffman *et al.* 1994, Huffman and Tappeiner 1997). Populations of *Gautheria shallon* in thinned sites also have higher biomass, greater vigor of vegetative growth, and a lower root:shoot ratio than do populations in unthinned stands (Huffman *et al.* 1994, Messier and Mitchell 1994). In my sites, pre-commercial thinning increased cover of low shrubs from 23 to 30% but the increases were not large or consistent enough to be statistically significant. Thomas *et al.* (1999) report a moderate positive slope of *Gaultheria shallon* abundance with intensity of pre-commercial thinning. *Gaultheria shallon* responds more positively to commercial thinning, showing increases of 12-40 percentage points in cover compared to control stands (Bailey *et al.* 1998, He and Barclay 2000, Thysell and Carey 2001). Thus, pre-commercial thinning may offer an opportunity to manipulate structure without precipitating dominance of the understory by low shrubs.

Differences between old and young stands

Old growth stands in my study sites exhibited composition distinct from that of young managed stands. Old-growth forest understories had lower cover of low shrubs, higher basal area of shade-tolerant conifers, and exhibited different patterns of herb species abundance than did young stands. My results contrast with those of Bailey *et al.* (1998), who, in stands 50-120 yr old, found that unthinned and old-growth low shrub and herb communities showed largely overlapping patterns of variation in composition, even after accounting for the large differences in composition among geographically distinct study sites. The only strong differentiation in composition found by Bailey *et al.* (1998) was between young stands dominated by *Gaultheria shallon* and all other stands. Bailey *et al.* (1998) may not have found consistent differences between young and old stands because their young stands were considerably older than mine and through natural stand development should have moved towards old-growth composition. The lack of differentiation of young and old stands in their results may also be explained in part by the spatial heterogeneity of cover and composition in the understory layer of old growth forests. Old-growth forest understories are made up of a mosaic of lush patches under canopy gaps interspersed with depauperate areas under *Tsuga heterophylla* (Franklin *et al.* 1981). In my sites, however, variation within old growth was not enough to mask clear distinctions between the composition of young and old stands.

Several of my analyses identified species with affiliation for old or young stands: species correlations with ordination axes, indicator species analysis, and analysis of variance of treatment effects on individual focal species. The results of all three approaches were generally consistent. I focus below on analysis of variance results for focal species and indicator species analysis results for other species, and on the contrast between old growth and unthinned stands.

Four old-growth associated focal species achieved significantly higher frequencies in old-growth than young stands: *Coptis laciniata*, *Tiarella trifoliata, Achlys triphylla* and *Linnaea borealis*. *Coptis laciniata* and *Linnaea borealis* also had significantly higher cover and flowered significantly more in old-growth than in unthinned stands. Although they are more prevalent in old growth, these species are not old-growth obligate (Spies 1991). *Linnaea borealis* can tolerate and even capitalize on overstory removal (Halpern 1989), and it responds well to the formation of canopy gaps in old-growth forests (St. Pierre 2000). In gaps it can form large patches of continuous cover that are rarely seen in more homogeneous stands. *Tiarella trifoliata* and *Coptis laciniata* are more sensitive to canopy removal but survive at reduced levels following clearcutting (Dyrness 1973, Halpern 1989).

Other indicators for old growth included ericaceous and orchid species whose old-growth association may reflect reliance on a well-developed forest floor litter layer and/or the availability of mycorrhizal symbionts. Ericaceous species such as *Chimaphila umbellata* rely heavily on mycorrhizal associations specialized for the decomposition of litter (Read 1983). Orchids such as *Goodyera oblongifolia* are known to require mycorrhizae to extract carbon from decomposing litter at least early in development (Alexander and Hadley 1985).

Indicators for young forests were mostly opportunistic species that do well in clearcut and other open environments. Although they emerged as indicators for young closed-canopy forests, their abundance may actually have declined since canopy closure. The very high abundances reached by these species in the clearcut environment provides a legacy that inflates their abundance in the otherwise marginally suitable young forest environment (McKenzie *et al.* 2000a). These species persist mostly in areas of low tree density, for example treefall gaps, stream channels and rocky outcroppings.

Differences between measures of community composition

All three metrics revealed similar gradients in community composition, suggesting that flowering and abundance of focal species are responding to the same set of habitat variables that drive patterns of species presence/absence. Flowering and abundance should yield similar results because the two measures are themselves positively, although not tightly, correlated for all species.

For individual species, abundance and flowering generally revealed larger magnitudes of differences among treatments than did frequency, as expected. Perennial forest herbs tolerate marginal habitat conditions and tend to remain present regardless of stand conditions; abundance and flowering should be more responsive to current resource availability for all species (Pitelka *et al.* 1985, Eriksson 1993, Damman and Cain 1998). However, because abundance and flowering were more variable than presence, the larger effect sizes associated with these metrics yielded fewer statistically significant differences. All three metrics should show some noise because species may be absent from currently suitable sites due to slow colonization rates. Presence is the least variable measure of plant performance, however, because variation in abundance and flowering are imposed on top of that in the presence data.

The inclusion of many more species (61 vs. 11), made frequency data a stronger multivariate indicator of differences between treatments. While abundance and flowering data are useful for studying within-stand patterns of response to environmental or stand structure variables (Chapter 4), presence/absence data may provide a more efficient test of differences between treatments.

Conclusion

Poage and Tappeiner (2002) suggest that thinning may accelerate the development of old-growth species composition in young stands by creating stand structure more like old growth. However, two lines of evidence suggest that this may be a simplistic view of stand development. Although precommercial thinning did accelerate the growth of larger trees in my study, it probably reduced the formation of treefall gaps, which characterize natural stand development. In addition, thinning did not increase basal area of shade-tolerant understory trees, an important component of old-growth structure. Thinning did move the composition of the understory closer to that of old-growth, but the formation of old-growth stand structure may not have been the mechanism for this change. Instead, thinning probably affected understory composition by slowing the decline of understory species that would otherwise occur following canopy closure.

It is important to examine the patterns and mechanisms of response of different groups of organisms to thinning rather than assuming that larger trees will favor all groups. Different thinning prescriptions may be important for different taxa (Muir *et al.* 2002). Commercial thinning yields merchantable timber and may have large and lasting positive effects on canopy openness and total understory biomass. Commercial thinning can also encourage the development of understory tree and shrub layers that may be important for many taxa, but may also facilitate invasion by exotic species, at least temporarily (Bailey *et al.* 1998, Muir *et al.* 2002). Pre-commercial thins, on the other hand, may encourage old-growth associated understory herbs without precipitating the dominance of understories by low shrubs and weedy species, at least in part because canopies may re-close more quickly. There is likely to be a tradeoff between the development of shade-tolerant understory trees (mostly *Tsuga heterophylla*), favored by species such as the northern spotted owl which require canopy heterogeneity, and the development of a lush understory of typical old-growth species. Natural old-growth understories consist of a mosaic of lush patches in treefall gaps and depauperate areas under *Tsuga* canopies (Franklin et al. 1981). This structure may be hard to replicate without allowing the growth of large trees and their death to form treefall gaps.

Thinning of young managed stands may not be necessary for the development of old-growth stand structure because old-growth tree sizes and canopy heterogeneity may develop successfully in stands as dense as 800 tree per ha (tree-to-tree spacing of 3.5 m; Winter *et al.* 2002). The question that remains is whether old-growth conditions develop more quickly in thinned than in unthinned stands. Unthinned stands may have more treefall gaps in the short to medium term, but will probably be slower to develop larger trees. The resulting depauperate understory with occasional lush patches in gaps may be closer to old-growth compostion than the evenly distributed understory of more resource-demanding species of a commercially thinned stand. On a longer timescale, however, thinning may speed the growth of large trees that can create old-growth sized treefall gaps when they fall. Pre-commercial thins are a promising tool because they appear to accelerate tree growth while simultaneously moving understory composition closer to that of old growth.

CHAPTER 4: MODELING UNDERSTORY HERB PRESENCE AND FLOWERING: EFFECTS OF CONIFER BASAL AREA AND ABIOTIC VARIABLES

Abstract

This chapter examines the distribution of understory herb presence and flowering within one 100 ha second-growth forest watershed. I focus on the relationship between herb performance and conifer basal area. While the literature on understory herbs in young forests assumes a negative relationship between herb performance and tree density, analysis of this relationship has not always provided a clear answer. I used both general linear models and classification and regression tree (CART) models to explore the association of herb species performance with conifer basal area and abiotic variables. Both modeling approaches yielded similar biological insights. Flowering was more sensitive to conifer basal area than was species presence. Flowering for old-growth associated and disturbance-responsive species was negatively associated with conifer basal area; there was some evidence for a positive association of forest-generalist herb flowering with conifer basal area. Linear models allowed for clearer hypothesis tests, while CART models had greater explanatory power and provided information about interactions between variables.

Introduction

Young forests undergo rapid changes in the understory environment. The canopy closes, stays closed for a period, then opens again as the gap dynamics of the mature forest begin. The competitive effect of trees on the understory is thought to be most intense in young forests, when, at least in densely-stocked stands, an "understory exclusion" phase of stand development occurs (Oliver and Larson 1990). While "understory exclusion" refers primarily to understory trees, this can be a period of decline for herbs as well (Long and Turner 1975, Alaback 1982, Schoonmaker and McKee 1988, Lindh 1994). The overstory may affect the understory *via* shading (Stewart 1988, St. Pierre 2000) or belowground competition (McCune 1986, Lindh 1994, Coomes and Grubb 2000), or both.

If herbs decline in young forests as a result of competitive effects of trees, one would expect herb distributions to be negatively correlated with tree density, canopy cover, or basal area. While some studies have demonstrated this pattern (Stewart 1988, St. Pierre 2000), others have shown positive associations between herb abundance and measures of tree abundance. In the period around canopy closure, forest herb cover can be positively correlated with canopy cover; this positive correlation declines to zero in the early years after canopy closure (Lindh 1994). Positive correlations may result from facilitation of one group by the other in the clearcut environment, or by coincident survival or establishment in favorable microsites. In a large-scale study of mature (100-200 year old) forests, McKenzie and coworkers (2000a) found that cover of "release herbs", subordinate forest herbs that expand following overstory removal (Halpern 1989), was positively correlated with stand density. They hypothesized that the younger forests (with greater stem density) retained the highest residual populations of disturbance-responsive species, a legacy of earlier stages of stand development.

This chapter seeks to clarify the relationship between herb performance, conifer basal area and abiotic factors in a 35-year-old forest in western Oregon. Species performance was measured in terms of both presence and flowering. While patterns of presence change slowly and may therefore be asynchronous with overstory conditions, density of flowering should reflect current stand conditions. Clonal perennial herbs can often survive for long periods of time under adverse conditions; survival involves limited growth and vegetative reproduction (or even slow shrinkage) and no sexual reproduction (Pitelka *et al.* 1985, Eriksson 1993, Damman and Cain 1998). Sexual reproduction occurs only when resource levels are high (Pitelka *et al.* 1980 and references cited therein, Winn and Pitelka 1981, Lubbers and Christiansen 1986, Hughes *et al.* 1988, Cunningham 1997, Geber *et al.* 1997).

I focus on species representing three groups with different associations with stand age (Spies 1991) and responses to clearcutting (Dyrness 1973, Halpern 1989). Few species specialize in the young-forest environment, so most of the herbs found in these forests reach their highest abundances in other stages of stand development (Spies 1991). I tested the hypothesis that these species groups would show different responses to conifer basal area. Species groups were defined as follows:

1. <u>Release species</u> are subordinate forest herbs and shrubs that are released by overstory removal (Halpern 1989, McKenzie *et al.* 2000). They are associated with young or mature rather than old-growth forests, or show no stand-age affiliation (Spies 1991). In the watershed where my work took place, they showed a ~75% decline in abundance in response to canopy closure (Halpern

1989, Lindh 1994). Frequency fell more slowly but still declines by about 25% in the period following canopy closure (Halpern unpublished data).

2. Forest generalists are also associated with young or mature rather than old-growth forests, or show no stand-age affiliation (Spies 1991). These species decline as a result of clearcut harvest and recover slowly thereafter (Dyrness 1973). In the watershed I studied, they occupied few plots at the time of canopy closure and colonized 1-2% of plots per year thereafter (Halpern unpublished data).

3. Old-growth associated species (Spies 1991) are generally shade tolerant but respond positively to canopy gaps (Stewart 1988, St. Pierre 2000). They decline in abundance after clearcutting but are not eliminated (Dyrness 1973, Halpern 1989). Although their abundances declined in my study watershed following canopy closure, their frequency increased slightly during this period (Halpern unpublished data).

Plant presence and flowering data are often difficult to model because they contain many zeroes. This property precludes application of statistical methods that require normality. I tested two approaches that are appropriate for such data: classification and regression trees, which are non-parametric; and generalized linear models, *e.g.* logistic regression, which allow specifications of response distributions other than Gaussian. Although both methods build models that include only those variables with the strongest effects, the resulting models are very different in form. Generalized linear models fit linear relationships between explanatory and response variables, while classification and regression tree (CART) models consist of sequential bifurcations of the data based on threshold values in explanatory variables. Generalized linear models are widely used in ecology, while CART methods are gaining popularity. Comparisons of the two modeling approaches have tended to focus on large datasets and predictive goals (Franklin 1998, Vaysierres *et al.* 2000; but see McKenzie *et al.* 2000a). This paper compares the performance of the two approaches on a small dataset more typical of many ecological studies. I compare model results in terms of the insights they yield rather than their predictive utility alone.

Methods

Data collection

Data were collected in Watershed 1 at the H. J. Andrews Experimental Forest, which is located on the west slope of the Cascade Range in Oregon, USA (44°N, 122°30'W). This region experiences summer drought, with less than 10% of the total rainfall of 220 cm falling during the summer months (Bierlmaier and McKee 1989). Watershed 1 is deeply dissected, with a central stream channel and steep north and south facing slopes. The headwall faces west, with a saddle at the top. Soil parent materials are volcanic in origin, including ash flows, brecchias, basalts and andesites (Stephens 1964). Steep valley slopes intermix colluvial deposits with occasional exposed bedrock. Soil surface horizons are poorly developed loams with high porosity (Rothatcher *et al.*1967, Dyrness 1969).

Old-growth forest in Watershed 1, *Pseudotsuga menziesii* with a subcanopy of *Tsuga heterophylla*, was clearcut logged between1963 and 1966 using high lead cables, and broadcast burned in fall 1967. Planting and seeding with *Pseudotsuga menziesii* carried out over the next four years (Halpern 1988, Halpern 1989). Prior to harvest, 131 permanent plots were established on 6 transects spaced regularly perpendicular to the stream channel. Plots were placed every 30 m along transects, with 12 to 27 plots per transect (Halpern 1988, 1989). The limited size of the study area, as well as its long history of ecological studies (Rothatcher *et al.* 1967; Halpern 1988, 1989; Halpern and Spies 1995), facilitated model interpretation. The small size of the dataset is typical of many ecological studies, allowing wide extrapolation of my methodological findings.

Understory herb data were collected in June and July of 2000 and 2001 in 9 m radius (250 m^2) permanent plots. Presence/absence was recorded for all focal species (see Table 1). Nomenclature follows Hitchcock and Cronquist (1973). Density of flowering ramets was recorded for focal species with distinct ramets; number of inflorescences was recorded for species with stolons (*Whipplea* and *Linnaea*). Data for *Anemone deltoidea* and *Anemone lyallii* were combined because I could not tell these two species apart in their vegetative state. Data for *Achlys triphylla* and *Vancouveria hexandra* (both Berberidaceae) were also combined because these two species showed similar habitat associations and occurred in numbers too small to model individually. Flowering in *Anemone*, *Hieracium* and *Osmorhiza* was

Table 1: Focal species with stand-age and disturbance-response group designations.

Group	Species	Family
Old-growth	*Coptis lacinata*	Ranunculaceae
	Tiarella trifoliata	Saxifragaceae
	Linnaea borealis	Caprifoliaceae
	Achlys triphylla and *Vancouveria hexandra*	Berberidaceae
Forest generalist	*Trillium ovatum*	Liliaceae
	Anemone lyallii/deltoidea	Ranunculaceae
	Chimaphila menziesii	Ericaceae
Release	*Trientalis latifolia*	Primulaceae
	Whipplea modesta	Hydrangeaceae
	Hieracium albiflorum	Asteraceae
	Osmorhiza chilensis	Apiaceae

sampled in 2001 only. I modeled numbers of flowering ramets or inflorescences rather than percent of plants flowering because percentages can be misleading. For example, populations that are growing may show low percent flowering because many individuals are pre-reproductive.

Tree diameters were measured in 2001 in the 9 m radius circular plots by an H.J. Andrews Experimental forest vegetation sampling crew. Within each plot all trees ≥1.37 m in height were tagged and measured for diameter (dbh). I used data for all conifers ≥5 cm in dbh. *Pseudotsuga menziesii* was the dominant conifer, with a significant presence of *Tsuga heterophylla* and some representation of *Thuja plicata* and *Taxus brevifolia*. Data for trees <5 cm dbh were excluded because small trees were associated with openings in the dominant canopy. For each plot, conifer diameters were converted to basal areas, summed, and expressed on a per ha basis (not slope corrected). Because hardwood species were found in limited areas within the watershed (stream banks, rocky slopes, ridgetops), hardwood basal area behaved poorly in models and was omitted. GPS locations for plots were derived from GPS locations of transect endpoints. Vertical distances of plots from streams and ridges were derived from a 10 m DEM. Slope (percent) and aspect were measured in the field. Aspect, measured as N, NE, E, SE etc. was re-coded to emphasize north-south variation as a measure of exaposure to solar radiation (North=1, NE and NW both 2, E and W both 3, SE and SW both 4, South=5.). Table 2 gives definitions of explanatory variable definitions and summary statistics. Data on plot-level soil types were defined by Rothatcher 1967; however, soil types tended to occur in patches in the watershed and were thus confounded with aspect and distance from stream and ridge. I converted the soil type variable to stony (stony and talus soil types)/not stony, which was less confounded with position in the watershed.

Table 2: Explanatory variable definitions, units and quartiles of values.

Variable name	Units	1st Q	Median	3rd Q	Definition
CONIFER	m^2/ha	15	24	32	Summed area at breast height of all conifers over 5 cm diameter .
OFFSTREAM	m	18	58	92	Elevation in meters above the stream channel, based on 10 m DEM.
OFFRIDGE	m	25	63	94	Elevation in meters below the ridgeline, based on 10 m DEM.
SLOPE	%	25	46	70	Percent slope measured in the field.
STONY					Indicator variable, 0 for non-stony soil types, 1 for stony and talus types.
DEGSOUTH					Aspect measured in the field; re-coded as N=1; E, W=3, S=5.

Plots with extreme values of response or explanatory values were dropped. One plot was dropped because it bordered old-growth and contained twice the conifer basal area of any other plot. Plots with more than twice as many inflorescences (or flowering ramets) as any other plot distorted model results and were dropped; one plot was dropped for *Linnaea borealis* and one for *Achlys* and *Vancouveria.*

Fisheye photos of the tree canopy were used to estimate the light environment of individual flowering and non-flowering patches of *Chimaphila menziesii* and *Linnaea borealis*. Patches were located in a relatively flat area at the top of Watershed 1. Flowering patches were selected randomly with paired non-flowering patches located randomly at least 20 m away. Patches were defined as areas with no more than a 1 m break between ramets; no flowering ramet could be within 5 m of a non-flowering patch. Photos were taken above flowering and non-flowering patches when there was no direct light on the canopy – before sunrise, after sunset, or on overcast days. Photos for paired flowering and non-flowering patches were taken sequentially under the same light conditions. Photos were taken with a Sigma 8 mm hemispherical lens on a Nikon FM2 camera body using TMAX 100 black and white print film. The camera body was held ~1 m above the ground surface using a tripod. Analysis of fisheye photographs was carried out using the CANOPY software package (Rich 1989), which generates separate estimates of the percent of incident direct (DSF) and indirect (ISF) radiation reaching a point.

Statistical methods

Separate models were fit for presence and flowering of each focal species. Presence was modeled for all sample plots, while flowering was modeled in only those plots where the species was present. Numbers of flowering ramets (or inflorescences) were strongly non-normal (right skewed); inclusion of only those plots where the species was present made the data approximately Poisson. Overdispersion occurred because some plots had very large numbers of flowers, likely belonging to one clone. I interpret models based on the data from 2001 because the observers were more experienced in the second year of data collection. General linear models were also fit to 2000 data for comparison. All analysis was carried out in S-PLUS 2000 (MathSoft 1999a).

General linear models: General linear models (GLMs) fit linear relationships between explanatory and response variables, with the user specifying the distribution of response. For analysis of presence/absence data (logistic regression) I specified a binomial distribution for the response (since the binomial sample size is one the data are actually Bernoulli trials). For flowering (Poisson regression) I specified that the response was Poisson distributed, but included a term that allowed for overdispersion (quasi-likelihood approach; Schabenberger and Pierce 2002). The value of the dispersion parameter estimates the degree of overdispersion, with a value of one indicating no overdispersion. Full models contained main effects of all variables with no interaction terms. Inclusion of interaction terms in addition to main effects was tried but abandoned because interactions were never significant. The small size of this dataset probably precluded finding significant interaction terms (Vaysierres *et al.* 2000). The function `step.glm` was used to carry out backwards stepwise model selection; terms were dropped from the model until no improvement in the Akaike information criterion (AIC) was observed. The AIC reflects the log likelihood of the model (a measure of how well the data fit the model) as well as the number of terms in the model, leading to the creation of the most parsimonious model with good fit to the data (MathSoft 1999b). Forward selection yielded identical results. Relative significance of variables within a model for one species was evaluated using t-statistics from the S-PLUS output. Relative significance of terms based on t-statistics matched that obtained from more robust (and time consuming) drop-in-deviance tests.

In GLMs, model parameters were estimated using maximum likelihood rather than least-squares estimation. Parameter estimates were chosen to maximize the likelihood of the model given the observed data and the specified distribution. The fit of the model to the data was expressed as the deviance, which is twice the likelihood of a saturated model (one variable for every data point) minus twice the likelihood of the fitted model (Neter *et al.* 1996). The deviance for a Bernoulli (0/1 response) logistic regression model is defined as:

$$Dev = 2\left[\sum_{i=1}^{n} y_i \log\left(\frac{\hat{\mu}_i}{1-\hat{\mu}_i}\right) - \sum_{i=1}^{n} \ln(1-\hat{\mu}_i)\right]$$

Where *i* indexes the observations (plots), y_i is zero for absences and one for presences, and $\hat{u}_i$ is the predicted value for each observation (Schabenberger and Pierce 2002).

The deviance for a Poisson regression model is defined as:

$$Dev = 2\left[\sum_{i=1}^{n} y_i \log\left(\frac{y_i}{\hat{\mu}_i}\right) - \sum_{i=1}^{n}(y_i - \hat{\mu}_i)\right]$$

Where *i* indexes the observations (plots), y_i is the observed number of events (flowering ramets) for each observation and $\hat{u}_i$ is the predicted number of events per observation (Schabenberger and Pierce 2002). When a Gaussian distribution is specified the formula for deviance reduces to the more familiar sums of squares (Schabenberger and Pierce 2002). Model deviance was compared to that of a null model, which fit one overall mean to the data. Models fit better, and approached the likelihood of the saturated model, as more variables were added. Improvement in model fit can be expressed as percent reduction in deviance (PRD) from the null model to the current fitted value. PRD is analogous to the more familiar coefficient of determination (R^2). Use of PRD with GLMs is debated in the literature because PRD does not scale the same as R^2; direct comparison of the two measures may not be appropriate (Schabenberger and Pierce 2002).

The fit of logistic regression models was also evaluated based on reduction in error rate. Probabilities of presence from logistic regression were converted into 0/1 predictions using a cutoff of 0.5; all plots with probabilities greater than or equal to 0.5 were predicted to be presences while all plots with probabilities of presence less than 0.5 were predicted to be absences. The choice of 0.5 as the threshold value was supported by the fact that, for most species, errors of omission (presences predicted to be absences) and commission (absences predicted to be presences) occurred with approximately equal frequency (data not shown). Changing the cutoff changed the ratio of errors of omission and commission but did not reduce (and often increased) the overall error rate. Predictions from logistic regression were compared to a null model in which all plots were predicted to be presences if at least 50% were presences, absences if more than 50% were absences.

Classification and regression tree (CART) models: CART models were carried out using the contributed library rpart (Therneau and Atkinson 1997; available at http://www.stats.ox.ac.uk/pub/SWin) in SPLUS-2000. Classification tree models were used for presence/absence data. Poisson regression tree models were used for flowering data. The Poisson option for regression is available only in rpart, not in the native SPLUS function tree; Poisson regression trees gave results more similar to Poisson GLMs than did the default Gaussian option.

CART models are based on binary recursive partitioning of the response data rather than on fitting linear relationships between explanatory and response variables (Breiman *et al.* 1984). The data are repeatedly split into two groups (nodes) based values of an explanatory variable. The algorithm tries all threshold points in all explanatory variables and picks the one that provides daughter nodes with the most homogeneous response values. Each split is defined by a threshold value in an explanatory variable; the number of splits can be referred to as the number of variables in the tree.

For classification tree models, the response data are presence/absence and the

Gini coefficient, *f(p)*, is the measure of homogeneity of a node:

$$f(p) = p(1-p)$$

Where *p* is the proportion of presences in that node (Therneau and Atkinson 1997). A terminal node is predicted to contain either presences or absences. For regression tree models on Poisson data, deviance is the measure of the homogeneity of the nodes. The formula for deviance is the same as that given above for GLMs, with a slight modification in the calculation of $\hat{u}_i$ (the predicted number of flowering events; Therneau and Atkinson 1997). The model generates a predicted number of flowers per plot for each terminal node. Termination of the branching process is controlled by the value of the complexity parameter (Cp). This process optimizes the error rate penalized for the number of terminal nodes in the tree. I used the default complexity parameter setting of 0.01.

The error rate for classification tree models is simply the number of misclassified cases (`rpart` does not give deviances for classification tree models). A percent drop in error rate can be calculated by comparing the number of misclassified cases in the terminal nodes to the number of misclassifications under the null model. The null model predicts the observations to be all presences or all absences, whichever predominate in the data; the null number of misclassifications is simply the smaller of total presences and total absences. For example, *Tiarella* was present in 114 plots and absent in 16, so the null error rate is 16/130.

Model size was investigated using 10-fold cross-validation: The dataset was split into 10 parts; for each partition a model was fit on 9 parts and tested on the tenth.

For each model, drop-in-deviance or error rate is calculated for the full fitted model and all smaller subset models. Optimal model size is defined as the one that produces smallest residual deviances or error rates; each of the 10 runs produces an estimate of optimal model size. I report the mean estimate of optimal model size.

Comparison of model types: For model comparisons I "pruned" the CART models to contain the same number of variables (splits) as the linear models. I also report model performance for full CART models, generated under default settings, to illustrate where adding additional terms can improve explanatory power. Poisson regression and Poisson regression tree models were compared based on percent reduction in deviance. Logistic regression and classification tree models were compared based on reduction in error rate. The relative performance of linear and threshold fits were also compared by including only conifer basal area in models of flowering and comparing GLM and CART reductions in deviance.

Light levels for flowering and non-flowering patches: Differences in light levels between flowering and nonflowering patches were tested using paired t-tests.

Results and Discussion

Biological findings

Most individual species occurred in 50-75% of the sample plots, and flowered in 25-60% of the plots they occupied (Table 3). Old-growth associated species were generally present in fewer plots and flowered in a smaller percent of occupied plots than release species; forest-generalist species showed intermediate frequencies and numbers of flowering events.

Table 3. Number of plots occupied (out of 130) in 2001, number of plots with flowering events, and average number of flowering ramets or inflorescences in occupied plots.

Group	Species	Occupied	Flowering	Mean No. Flowers
Old-growth	*Coptis lacinata*	65	13	0.29
	Tiarella trifoliata	16	9	1.06
	Linnaea borealis	54	19	5.05
	Achlys triphylla and *Vancouveria hexandra*	84	23	1.71
Forest	*Trillium ovatum*	87	44	1.18
	Anemone lyallii/deltoidea	99	31	1.36
	Chimaphila menziesii	83	67	4.75
Release	*Trientalis latifolia*	116	94	15.9
	Whipplea modesta	91	60	20.6
	Hieracium albiflorum	97	47	1.63
	Osmorhiza chilensis	61	24	1.11

Trientalis, a release species, was the most common species, present in 116 of the 130 plots and flowering in 94. No CART model for presence is presented for this species because too few plots were unoccupied to allow successful model fitting. In contrast, *Tiarella*, an old-growth associated species, was the least frequent focal species, present in 16 plots and flowering in 9. Flowering could not be modeled for *Tiarella* because flowering events were too rare.

Old-growth species: Old-growth species were more likely to be present on north facing aspects (Tables 4a, 5a). Distance from a stream also had a negative effect for most, while other variables had species-specific effects. Percent reductions in deviance for logistic regression models were generally higher than those for release species but were still relatively low (<50%), emphasizing the influence of historical events, including stochastic processes of dispersal and establishment.

Current patterns of old-growth species presence may reflect both long-term occupancy of some sites and differential survival in plots during the clearcut phase. Plots on south-facing aspects would have experienced high soil surface temperatures following logging (Jones 1995). Tree regeneration was also slow on steep and rocky sections of the south-facing half of the study watershed, leaving some sections without tree cover 40 yr after harvest. High temperatures and/or a lack of tree cover may have diminished survival of old-growth associated species on south-facing slopes. The negative effect of distance from stream suggests an association of old-growth associated understory species with mesic microsites. A similar confounding of stand age and moisture associations has been observed for some old-growth associated lichen species (McCune 1993).

While old-growth species were generally present without regard for conifer basal area, flowering was negatively correlated with conifer basal area within occupied plots (Tables 4b, 5b). This plot-level effect of conifer basal area on flowering was corroborated at the micro-site-level by contrasting transmittance of light by the canopy above flowering and non-flowering patches of *Linnaea*. Indirect light levels were significantly higher for flowering than non-flowering patches ($p<0.01$; Table 6). This sensitivity to canopy environment is not surprising given that flowering of both *Tiarella* and *Linnaea* are higher in gap than non-gap areas (St. Pierre

Table 4. Coefficients for generalized linear models, 2001 data. For species groups, OG = old-growth and Forest = forest generalist. For each species, letter suffixes indicate relative significance of terms (*a* most significant, *e* least) based on t-statistics. PRD=percent reduction in deviance. DP=dispersion parameter (flowering models only). Bold indicates variables (and relative importance) that were the same in models based on 2000 data. See Table 2 for variable definitions. Note that coefficients for logistic regression models cannot be interpreted without transformation.

a. Presence

Group	Species	ASPECT	CONIFER	OFFSTREAM	OFFRIDGE	SLOPE	STONY	PRD
OG	*Coptis*	**-1.05 a**		**-0.0170 c**	+0.0092 d		**-1.34 b**	31
	Tiarella	**-0.791 d**	**+0.137c**	**-0.0327 b**	**-0.0369 a**	**+0.0279 e**		45
	Linnaea	**-0.841 a**		**-0.0097 d**	**-0.0123 b**	**-0.0204 c**		23
	Achlys and Vancouveria	**-0.441 a**		+0.0095 c	**+0.0138 b**			11
Forest	*Trillium*	**-0.690a**		**-0.0089** c			**-1.52 b**	21
	Anemone		**+0.0532** b	-0.0224 a	-0.0054 c			19
	Chimaphila	**-1.07** a	**+0.129** b	**+0.0154 c**		**-0.0350 d**	**1.03 e**	45
Release	*Trientalis*	**+0.338 a**						03
	Whipplea	**-0.522a**			**-0.0098** c	**-0.0259 b**		19
	Hieracium (2001 only)			*-0.0166 a*				10
	Osmorhiza (2001 only)	*-0.210d*	*-0.0415c*	*-0.0133 a*			*-1.16 b*	11

b. Flowering

Group	Species	ASPECT	CONIFER	OFFSTREAM	OFFRIDGE	SLOPE	STONY	PRD	DP
OG	*Coptis*		**-0.0518 a**			**-0.0175 b**		12	1.40
	Linnaea		**-0.0410 b**			**-0.0205 a**		13	10.4
	Achlys and Vancouveria	+0.407 c	**-0.0605** b	**-0.0147** a	**-0.0045** e		+0.880 d	58	4.39
Forest	*Trillium*	-0.225a						05	2.35
	Anemone	*-0.273c*	*-0.0270d*		*+0.0144b*	*-0.0301a*		17	6.99
	Chimaphila	-0.202c	**+0.0842a**			-0.0101d	**+1.24b**	49	3.85
Release	*Trientalis*	+0.169 d	**-0.0501 a**	**-0.0081 b**	-0.0040 e		+0.492 c	37	22
	Whipplea	+0.311b	**-0.0582 a**		-0.0044 d		+0.791 c	47	51
	Hieracium (2001 only)	*+0.166c*	*-0.0288b*	*-0.0172a*				22	3.22
	Osmorhiza (2001 only)	*+0.290c*		*-0.0136a*	*-0.00859b*			18	3.00

Table 5. CART models based on 2001 data. VAR1 is the first split at the base of the tree, VAR2 first split in the left branch, VAR3 is the first in the right branch, if present; otherwise the second split in the left branch. Inequalities represent the direction associated with a more positive response; values following inequalities are the threshold values on which splits were based.

a. Presence

Group	Species	VAR1	VAR2	VAR3
Old-growth	*Coptis*	DEGSOUTH <2.5	OFFSTREAM<48	CONIFER>18
	Tiarella	DEGSOUTH <2.5	OFFRIDGE<41	OFFSTREAM<30
	Linnaea	DEGSOUTH <2.5	SLOPE<8	OFFRIDGE<22
	Achlys and Vancouveria	DEGSOUTH <2.5	SLOPE>11	OFFRIDGE>32
Forest	*Trillium*	CONIFER>13	OFFRIDGE<63	DEGSOUTH <4.5
	Anemone	OFFSTREAM<143	OFFRIDGE<157	OFFSTREAM<70
	Chimaphila	CONIFER>23	DEGSOUTH <2.5	DEGSOUTH <4.5
Release	*Trientalis*	OFFSTREAM<93	OFFSTREAM>110	
	Whipplea	SLOPE<58	DEGSOUTH >2.5	OFFSTREAM>17
	Hieracium	OFFSTREAM<60	OFFRIDGE<73	CONIFER>11
	Osmorhiza	OFFSTREAM<17	CONIFER<23	OFFSTREAM<28

b. Flowering

Group	Species	VAR1	VAR2	VAR3
Old-growth	*Coptis*	SLOPE<53	STONY<0.5	CONIFER<31
	Linnaea	SLOPE<35	OFFRIDGE<24	CONIFER<32
	Achlys and Vancouveria	CONIFER<9.0	OFFSTREAM<59	CONIFER<17
Forest	*Trillium*	SLOPE >38	CONIFER>20	DEGSOUTH <1.5
	Anemone	OFFSTREAM<13	CONIFER<10	OFFRIDGE>45
	Chimaphila	CONIFER>29	STONY>0.5	OFFRIDGE>84
Release	*Trientalis*	CONIFER <13	CONIFER <23	OFFSTREAM<53
	Whipplea	CONIFER<10	CONIFER<32	SLOPE<33
	Hieracium	OFFSTREAM<19	CONIFER<19	OFFRIDGE<96
	Osmorhiza	OFFSTREAM<14	CONIFER<18	OFFRIDGE<92

2000). Steeper slopes supported fewer flowers for two of the three species (Tables 4b, 5b); the mechanism for this reduction may be lower light availability on steeper slopes.

Table 6. Differences in direct (DSF) and indirect (ISF) light levels (expressed as percent of incident radiation) between paired flowering and non-flowering patches. Differences calculated as flowering – non-flowering light levels. Probability values from paired t-tests.

Species	Index	Difference	T	df	P
Linnaea borealis	DSF	0.99	1.57	20	0.13
	ISF	1.66	3.35	20	0.003
Chimaphila menziesii	DSF	1.76	2.23	20	0.04
	ISF	0.54	1.30	20	0.20

Models for flowering of most old-growth species showed smaller reductions in deviance than did models for old-growth presence. Since flowering was modeled for occupied plots only, I did not expect the drops in deviance to be directly comparable. The poor explanatory power of these models indicates that flowering in occupied plots is occurring stochastically or in response to variables that I did not measure. Overall, models for flowering of old-growth species also showed smaller reductions than models for flowering of release species. While flowering for all species should be tied to current resource levels, old-growth species flower much less consistently than do release species (Lindh unpublished data; see also Table 3). Most old-growth species can reproduce vegetatively and often forgo sexual reproduction in favor of vegetative reproduction or mere persistence (Bierzychudek 1982, Eriksson 1996).

The highest percent reduction in deviance in a linear flowering model was for *Achlys* and *Vancouveria* (the two species were modeled together; Table 4b). Coording to the linear model, these species flowered more often in plots with low basal area, in plots on south-facing aspects, in plots close to streams or ridges and in plots with stony soils. The CART model (Fig. 1) emphasizes the importance of conifer basal area and distance from stream and omits aspect and distance from ridge (perhaps because they are correlated with the first two variables). In the field, I observed these species flowering at edges of talus slopes or streambeds with very open canopies and presumably high water availability. This specific flowering microhabitat in second-growth is quite distinct from the widespread locations throughout old-growth where these species flower (Lindh personal observation).

Forest generalists: Presence of forest generalist herb species was most often associated with north-facing aspects and with higher conifer basal area (Tables 4a, 5a). Surprisingly, conifer basal area also had a positive effect on flowering for two of these species: a linear (GLM) effect for *Chimaphila* and a threshold (Poisson regression tree) effect for *Trillium*. Both species flower and establish well in young stands. Flowering in *Trillium* has been tied to plant size rather than to resource levels *per se* (St. Pierre 2000). *Trillium* individuals in higher basal area plots may be older than those in more open plots or may have accumulated more stored resources. The success of *Trillium* in young stands in my study area contrasts with the near-absence of *Trillium* adults and juveniles in young second-growth forests in southern Oregon (Jules 1996). In my study area, frequency, density, and flowering of *Trillium* are

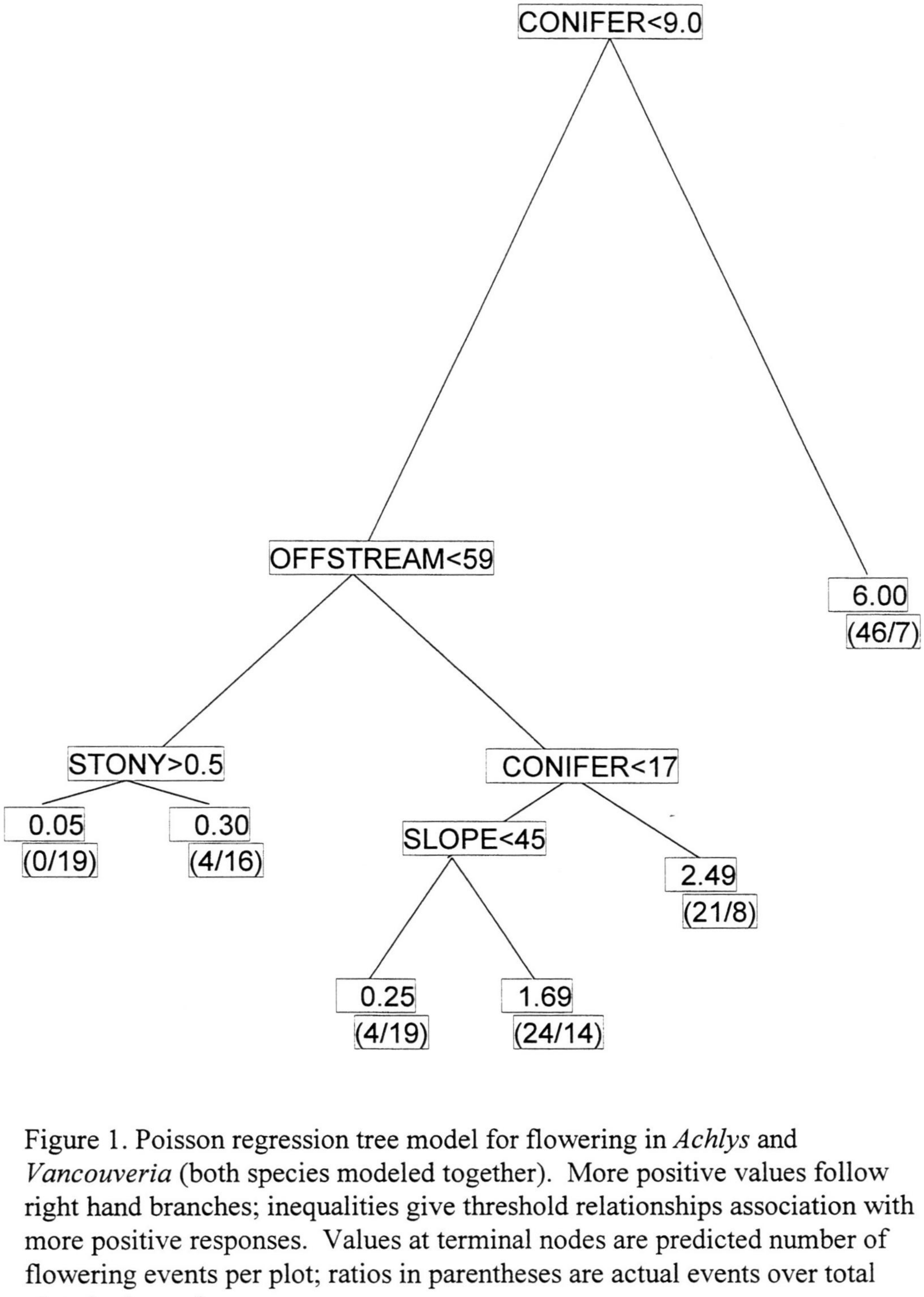

Figure 1. Poisson regression tree model for flowering in *Achlys* and *Vancouveria* (both species modeled together). More positive values follow right hand branches; inequalities give threshold relationships association with more positive responses. Values at terminal nodes are predicted number of flowering events per plot; ratios in parentheses are actual events over total plots in the node.

higher in old than young forests, but only by about 30% (Chapter 4).

While *Chimaphila menziesii* flowered more in plots with higher basal area of conifers, patches with flowering plants experience significantly higher direct light levels than did non-flowering patches ($p<0.05$; Table 6). These results are not necessarily contradictory: *Chimaphila's* ability to capitalize on the young forest environment suggests that it may, like some *Pyrola* species, have mycorrhizal connections with overstory trees. The fact that achlorophyllous clones (or parts of clones) are observed in nature (Lindh, personal observation) is suggestive of a partly parasitic habit (Leake 1994). If the species receives carbon *via* both photosynthesis and mycorrhizal connections it should be expected to flower in the highest-light microsites within stands with high densities of vigorous Douglas-fir growth.

Release species: Linear models for presence of release species showed no consistent patterns among species (Table 4a), while three of four CART models showed a negative effect of distance from stream (Table 5a). Percent reductions in deviance were small for the presence models, suggesting the influence of unmeasured factors or random events in the distribution patterns. Because these species are ubiquitous in the landscape, propagule density may be relatively high. While old-growth species may be present only in habitats that have been consistently favorable, release species will be present wherever suitable conditions arise briefly, and will persist for some time after suitability declines.

In contrast, flowering of release species was strongly negatively related to conifer basal area in both model types (Tables 4b, 5b). South facing aspects and plots close to ridges, streams, or both (which occur high in the central portion of the watershed) also supported larger numbers of flowers (Tables 4b, 5b). Percent reductions in deviance were much higher for flowering than for presence, suggesting that flowering responds more strongly to stand basal area and abiotic variables than does presence. Release herb abundances are lower in old-growth than young forests (Chapter 3); young forests represent a period of decline between maximum abundance in the clearcut and relative rarity in the old growth forest. The strong negative relationship between conifer basal area and flowering betrays the resource-sensitivity of these species. Aspect and proximity to ridges probably also influence light availability, while proximity to streams should influence water availability. McKenzie *et al.* (2000a) found that percent cover of release herbs, which may respond to canopy closure more slowly than does flowering, was positively correlated with stand density. My results support their explanation of this observation: the positive correlation between release herb abundance and tree density resulted from the confounding of age and density in their sample rather than from an ability of these species to thrive in dense stands.

Year-to-year variation in model results

GLMs for flowering based on 2000 and 2001 data generally agreed on the first two variables and often did not agree on the inclusion of any further variables (Table 4b). Flowering data are noisy because some species flower in only some years (Lindh unpublished data; see also Inghe and Tamm 1988, Tyler 2001), while other flowering events may have occurred were overlooked. These results suggest that testing of the flowering models on an independent dataset would probably support the inclusion of only the first two variables. Models for presence were, not surprisingly, more similar between the two years (Table 4a), often containing three or four of the same variables. Presence should be relatively stable from year to year, and should be harder for an observer to miss.

Comparison of model types

Inclusion of explanatory variables: CART models for presence and flowering identified the same first variable and direction of effect as GLMs in 12 of 21 cases, with the most important GLM variable occurring second or third in the CART model in 7 more cases (compare Table 4b and Table 5b). Of 63 variables in the first three splits of the CART presence and flowering models, only about one-third were not among the selected variables in the corresponding GLM. The two modeling approaches agreed best when the overall explanatory power of the models was high.

The similarity in variable selection between the two methods was remarkably high given the differences in their variable selection procedures. GLMs report the effect of a variable after accounting for all other variables in the model. As a result, a variable may be omitted if it is correlated with a variable that has a stronger effect. CART models choose variables one at a time, with the variable with the strongest effect chosen first. Variables enter lower in the tree only if their effect is strong in a subset of the data defined by earlier splits. A variable may have a relatively weak effect across the whole dataset and yet appear in only one branch or not at all. Furthermore, the effect of a variable low in the tree is estimated after accounting for variables above it in the tree, while the effect of a variable high in the tree is not corrected for the effects of any of the variables below it.

Estimation of interaction effects: Because the CART models in my study included many of the same variables as the GLMs, the CART models could be used to identify potentially important interactions between explanatory variables. Many of the interactions suggested by CART models were species-specific, but some patterns emerged.

For three taxa (*Anemone*, *Hieracium*, *Osmorhiza*), conifer basal area's negative effect on flowering manifested only in plots far from streams, perhaps where competition for water was more intense. Figure 2 shows this interaction in the model for *Hieracium* flowering. This interaction was also evident for two other species (*Achlys*, *Chimaphila*) for which distance from stream had negative effects only on plots with high conifer basal area. This interaction may reflect the fact that abundance and flowering of understory herbs can be controlled by below- as well as above-ground resources (Chapter 1; Pitelka *et al.* 1980, St. Pierre 2000). If soil moisture is less available far from streams, conifer depletion of soil moisture (see Chapter 1) should have a greater effect there. This hypothesis is supported by the observation that stands at the lower moisture limit for the dominant tree species have more depauperate understories than one would expect based on canopy closure (Walter and Breckle 1985).

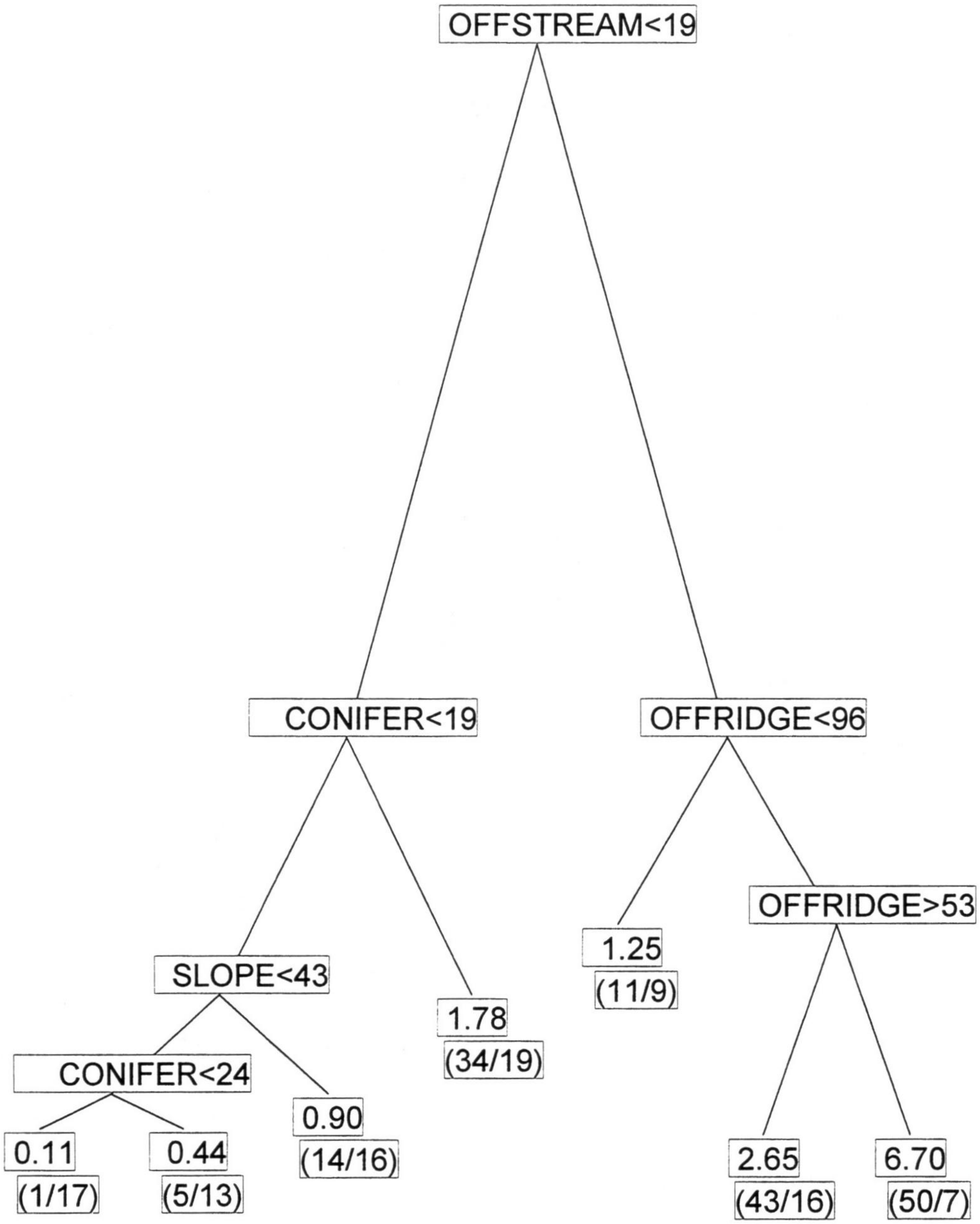

Figure 2. Interaction of distance from stream and conifer cover in the Poisson regression tree model for *Hieracium albiflorum* flowering. Direction of inequalities refer to the right hand branch, which contains the higher response values. Values at terminal nodes are predicted number of flowering events per plot; ratios in parentheses are actual events over total plots in the node.

Model size: Different modeling approaches and testing procedures supported the inclusion of different numbers of variables in each model. Default CART models generally contained the most parameters, usually to a degree that was not interpretable, and cross-validated CART models the fewest. Full CART models for presence ranged in size from three to seven splits, while cross-validation of these trees suggested many fewer splits – often zero (Table 7a). The full tree size was supported by cross-validation only in the case of *Chimaphila* presence. Cross-validation of CART models for flowering was even more conservative, most often rejecting all splits (Table 7b). While cross-validation of Poisson regression tree models (used here for flowering) is known to be overly conservative (Therneau and Atkinson 1997), cross-validation of classification tree models (used here for presence) is usually recommended (Urban 2002).

Linear models based on stepwise selection included a biologically interpretable intermediate number of variables. Comparison of GLMs based on two years of data, however, supported inclusion of only one or two variables per model for flowering and removal of some variables from most presence models. Linear models pruned to reflect year-to-year variation still included more variables than were supported by cross-validation of CART models, suggesting that cross-validation removes biologically meaningful variables in datasets of this size. CART models identified many of the same variables as linear models, but perhaps because most variables' effects were estimated in small subsets of the data many variables did not survive cross-validation.

Table 7. Comparison of model performance and size for GLMs and CART models of presence and flowering. Model performance is presented as percent reduction in deviance (PRD) or percent reduction in error rate or both. Numbers of variables are given for GLMs (and reduced tree-based models) and for full CART models, as well as the number of variables supported by cross-validation of CART models (CV).

a. Presence

			% Reduction in error rate			Number of variables		
Group	Species	GLM PRD	GLM	CART Reduced	CART full	GLM and CART Reduced	CART Full	CART CV
Old-growth	*Coptis*	31	38	68	74	4	7	6
	Tiarella	45	-6	0	0	5	3	0
	Linnaea	23	19	50	59	3	7	2
	Achlys and *Vancouveria*	11	9	34	34	3	4	0
Forest	*Trillium*	21	23	30	40	3	7	0
	Anemone	19	-3	39	39	3	4	1
	Chimaphila	45	15	62	62	5	5	5
Release	*Trientalis*	03	-7	NA	NA	1	NA	NA
	Whipplea	19	31	36	36	3	3	0
	Hieracium	10	0	0	30	1	4	0
	Osmorhiza	11	26	49	56	4	7	1

Table 7 (Continued).
b. Flowering

		Percent reduction in deviance (PRD)			Number of variables		
Group	Species	GLM	CART Reduced	CART Full	GLM & CART Reduced	CART Full	CART CV
Old-growth	*Coptis*	11	30	41	2	4	0
	Linnaea	13	31	36	2	3	0
	Achlys and Vancouveria	48	56	56	5	5	1
Forest	*Trillium*	5	5	27	1	6	0
	Anemone	17	42	44	4	6	0
	Chimaphila	49	46	46	4	4	3
Release	*Trientalis*	37	47	54	5	9	2
	Whipplea	47	49	50	4	5	1
	Hieracium	22	35	54	3	6	1
	Osmorhiza	18	36	38	3	4	0

Explanatory power of models: GLMs for presence contained one to five variables and decreased error rates by a mean of 15% (range -6 to 38%; Table 7a). Classification trees pruned to include the same number of parameters performed better, decreasing error rates by a mean of 37% (range 0-68%); full CART models performed even better, with a mean reduction of 43% (range 0-74%). Differences between model types were less striking for models of flowering (Table 7b). GLMs for flowering also contained one to five variables and produced a mean reduction in deviance of 27% (range 5-49%). Regression tree models with the same number of parameters as the corresponding GLM' s produced a mean reduction in deviance of 38% (range 5-56%), with full CART models producing a 45% reduction in deviance on average (range 27-56%).

Overall, CART models performed better than GLMs. CART models have been found to perform better than linear models in terms of predictive accuracy or deviance explained in predicting understory cover (McKenzie *et al.* 2000a), landscape-level shrub distribution (Franklin 1998), fire return intervals (Mckenzie *et al.* 2000b) and vegetation recovery after volcanic eruption (Lawrence and Ripple 2000). This superior performance of CART models holds true even when the models are tested against independent datasets, and can even when linear models are optimized to include interactions and polynomial effects suggested by CART models (Vaysierres *et al.* 2000). All of the researchers mentioned above compared the explanatory power of linear models to that of CART models which contained many more splits than the linear models included parameters. I calculated error rates for both full CART models and those pruned to have the same number of splits as the number of parameters in linear models. While full CART models performed somewhat better than reduced CART models, the differences were usually small; addition of splits to CART models did not change the relative explanatory power of CART and linear models. Because much of the reduction in deviance occurs with the first few splits, inclusion of extra splits low in CART models does little to improve their explanatory power.

Linear vs. threshold effects of explanatory variables: CART models generate threshold values in explanatory variables rather than linear coefficients. These thresholds can be more intuitive than regression coefficients. The old-growth species *Coptis* and *Linnaea*, for example, flower less in stands with over 30 m^2/ha conifer basal area, while the release species are more intolerant of conifer basal area and have a threshold of 20 m^2/ha. In small datasets where complicated response shapes cannot be estimated (Vaysierres 2000), threshold values may provide a better approximation of explanatory variable effects than would linear fits.

For conifer basal area as the sole explanatory variable and flowering as the response, threshold fits outperformed linear fits whenever linear fits produced small reductions in deviance (Table 8, Fig. 3a). Poor linear fits occurred when there were many zeroes in the data and/or when the relationship was nonlinear. For some of these species, a linear fit to the maximum response values for each value of basal area (Cade *et al.* 1999, McKenzie *et al.* 2000a) would have been better than a linear fit to the whole dataset. Even when linear relationships were strong, threshold fits still produced as much reduction in deviance as did linear fits (Figure 3b).

Table 8. Coefficients and percent reductions in deviance (PRDs) for linear (GLM) and CART models of the effect of conifer basal area (modeled alone) on flowering. Threshold values are given for CART models; inequalities indicate the direction of a more positive response.

Group	Species	Lin. coef.	Threshold	GLM PRD	Tree PRD
Old-growth	*Coptis*	-0.0477	<28	6	14
	Linnaea	-0.0332	<34	3	12
	Achlys and *Vancouveria*	-0.101	<9.1	31	31
Forest	*Trillium*	-0.00539	<37	0	3
	Anemone	0	>35.2	0	3
	Chimaphila	+0.0678	>29	24	24
Release	*Trientalis*	-0.0642	<13	28	29
	Whipplea	-0.0937	<9.6	38	32
	Hieracium	-0.0351	<8.7	6	13
	Osmorhiza	-0.0205	<17	2	9

Biological Conclusions

For many focal species, flowering was tied to stand basal area while presence was largely decoupled from it, reflecting instead the abiotic environment, stand history and random dispersal events. Abundance (models not shown) showed intermediate responsiveness to current stand basal area. Patterns of presence of old-growth species, which can remain stable over long periods, were tied more strongly to abiotic variables than were those of more transitory release herbs. Flowering of old-growth species, which are gap exploiters, and of release species generally responded negatively to increasing conifer basal area. Most models reduced null deviance or error rates by less than 50%, suggesting a strong role of chance events or unmeasured

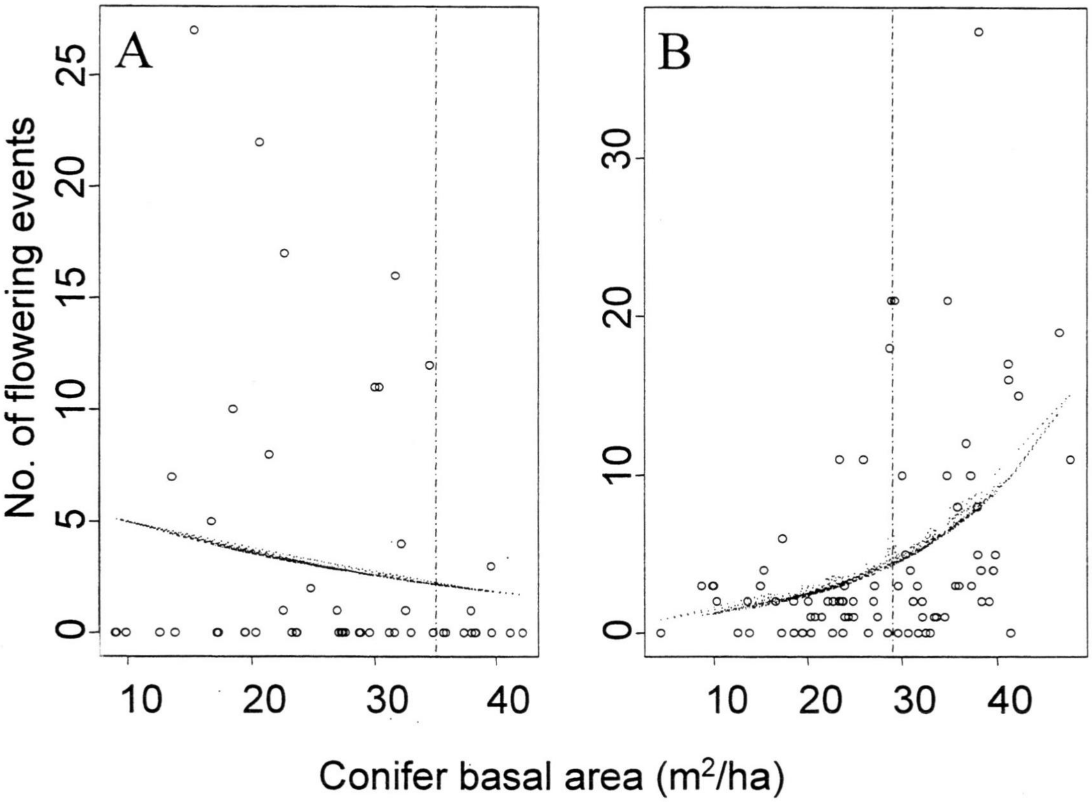

Figure 3. Linear (Poisson GLM) and threshold (Poisson regression tree) fits to the relationship between conifer basal area and number of flowering events (inflorescences or flowering ramets per 9 m radius plot) for *Linnaea borealis* (A) and *Chimaphila menziesii* (B). Vertical lines indicate threshold value from CART models.

variables in determining the distribution and flowering of understory herbs. It is important to note that my models should not be extrapolated beyond the watershed where they were developed. While the biological insights that they offer may be more general, the particular relationship of presence and flowering to variables such as aspect and distance above stream are certainly specific to the striking relief and simple topography of my study watershed. In a more spatially extensive dataset, effects of variables would be likely to differ in different portions of the dataset. In such a dataset, CART models might be more useful in identifying different effects of variables in different portions of the landscape. My study site also had low abundance of tree species other than *Pseudotsuga menziesii*. Given that different canopy species can have different effects on the understory (Stewart 1988, Hanley and Barnard 1998), sites with different canopy composition might show different understory/overstory relationships.

Statistical conclusions

While overall results were similar, CART models provided greater reductions in error rates (or deviance for flowering models) than GLMs. Threshold fits to the relationship between explanatory and response variables were clearly as good or better than linear fits. Despite the superior performance of the CART models, the GLMs allowed for clearer tests of hypotheses. Linear models provided a simpler answer to the question of whether a variable was important or not, and had the advantage of estimating effects across the entire dataset. Although neither method handles intercorrelation of variables very well, linear models had the advantage of correcting a variable's effect for all other variables in the model, rather than just those appearing above it in the tree. Linear models also provided more reasonable model sizes; default CART models included too many variables while cross-validation eliminated meaningful variables. CART models did provide insight into interactions between variables, insight that would otherwise have been impossible to obtain with a dataset of this size. I suggest the use of the two methods in tandem, with CART models being used heuristically to enhance understanding of variable effects and interactions or to suggest terms to include in refinements of linear models.

CHAPTER 5: CONCLUSION

This thesis explored the relationship between overstory trees and understory herbs and shrubs. While most of my work took place in young forests, Chapter 2 examined the effects of tree roots on the understory in two old-growth forests. We found increases in understory vegetation cover, flowering and growing season soil moisture associated with the removal of competition by tree roots. Even under dense shade, root trenching produced dramatic increases in understory plant cover. Our results suggest that in the summer-dry *Pseudotsuga menziesii* forests that we studied, belowground competition may play a large role in explaining the suppression of understory herbs and shrubs by trees in young, as well as old, forests. Densely stocked young coniferous forests, referred to as “closed canopy” or “dark” often have depauperate herb layers. Although light limitation probably plays a role in herb suppression, young forests have the highest root densities of any stand age (Vogt *et al.* 1983) and the even spacing of these forests will result in few belowground “gaps”. If belowground competition is as important as aboveground competition in limiting understory development, basal area may provide a better measure of tree competitive effects than does canopy cover alone.

Chapter 3 explored the long-term (~20 yr) effects of pre-commercial thinning on the understory herb community in second-growth forests. The understories of thinned stands were more similar to old-growth composition than were the understories of unthinned stands. However, the formation of old-growth stand structure may not have been the mechanism for this change. Instead, thinning probably affected understory composition by slowing the understory herb losses that would otherwise occur following canopy closure. Pre-commercial thinning is promising as a management tool because it may increase abundance of old-growth associated understory herbs without precipitating the dominance of understories by low shrubs and weedy species.

Chapter 4 explored the distribution of presence and flowering of selected understory herbs within one second-growth watershed. Flowering was negatively associated with current conifer basal area; in contrast, presence was largely decoupled from conifer basal area and responded instead to the abiotic environment and to random dispersal events. Presence of old-growth associated herbs species was tied more strongly to abiotic variables such as aspect and elevation than was release herb presence. Flowering of both old-growth species and release species responded negatively to increasing tree basal area. Models for presence and flowering showed only moderate explanatory power, suggesting a strong role of chance events and unmeasured variables in determining distribution and flowering of understory herbs.

Overall, flowering of focal species did not prove to be a superior measure for gauging understory herb responses to management. Presence of all understory herb and shrub species, a measure that is relatively stable over time and incorporates information from many species, provided better separation of treatments. Within one second-growth watershed, however, flowering was more sensitive than presence to tree basal area (abundance showed intermediate sensitivity). In my study sites, variation in tree basal area occurred mostly within sites rather than among sites, making flowering a better measure of within- than among-site variation. This lack of variation among treatments reflected the fact that 20 yrs of tree growth had all but erased differences in basal area between treatments. If I had sampled sooner after thinning, when there were still clear differences in basal area between treatments, flowering might have been a more useful measure of treatment effects.

Although young forests host a diverse flora comprised of release, forest generalist and old-growth associated herbs, young forest understory communities are still far from old-growth composition. Several lines of evidence suggest that old-growth associated species are limited by young forest habitat quality rather than by intrinsically slow population growth rates. Flowering of old-growth species is much less abundant in young than old forests, probably as a result of high tree density. As a result, rates of seed production are probably very low in young forests. Interestingly, when seeds are experimentally added to young forests, germination and establishment of old-growth species can take place (Lindh unpublished data). Where canopy gaps do occur in young forests, lush populations of these species may develop in ~5 years (Lindh personal observation). In addition, the fact that thinning can increase populations, to a degree detectable even 20 yrs later, suggests that recovery to old-growth population levels is possible when appropriate habitat conditions are present.

Pre-commercial thinning probably provided a brief amelioration of the understory environment, ending when the young trees grew enough to return resource levels to their pre-thinning levels. Higher resource levels should have allowed population increases for all forest herbs, old-growth associated and not. Pre-commercial thinning appeared to provide a narrow enough window of resource availability, however, that the thinning event did not precipitate dominance of the understory by low shrubs or non-forest species. Abundances of old-growth species were still well below their old-growth levels, however, and abundances of release species were somewhat elevated. Heterogeneity of the canopy in old-growth forests keeps overall resource levels low enough to suppress low shrubs, weeds, and even resource-demanding (release) forest herbs, while allowing development of old-growth associated species in gaps. Thinning does nothing to promote gaps, and may even inhibit the formation of windthrow gaps.

Managers face the choice of intervening in stand development to accelerate the development of old-growth levels of structural heterogeneity or allowing natural stand dynamics to play out. Some planted forests may be more dense than historical young forests (Poage and Tappeiner 2002), and may therefore be on trajectories that will not achieve old-growth structure in acceptable periods of time. However, some of today's old-growth stands developed despite initially high stand densities (Winter *et al.* 2002). Thinning increases spacing between trees and accelerates tree growth. Larger trees are an important component of old-growth structure (Spies and Franklin 1991). However, uniformly thinned stands may be very homogeneous, and heterogeneity of tree sizes is more indicative of old-growth structure than is tree size *per se* (Spies and Franklin 1991). Dense unthinned stands may undergo more mortality events than thinned stands and therefore develop more canopy heterogeneity. Variable density thinning has been proposed as a mechanism to achieve larger tree sizes and heterogeneous stand structure (Thysell and Carey 2001, Muir *et al.* 2002, Poage and Tappeiner 2002). The success of variable density thinning in restoring old-growth understory herb and shrub composition has yet to be demonstrated, however. The choice between intensive manipulation and hands off management of young second-growth stands may hinge on the outcome of variable density thinning experiments currently taking place around the Pacific Northwest.

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APPENDIX

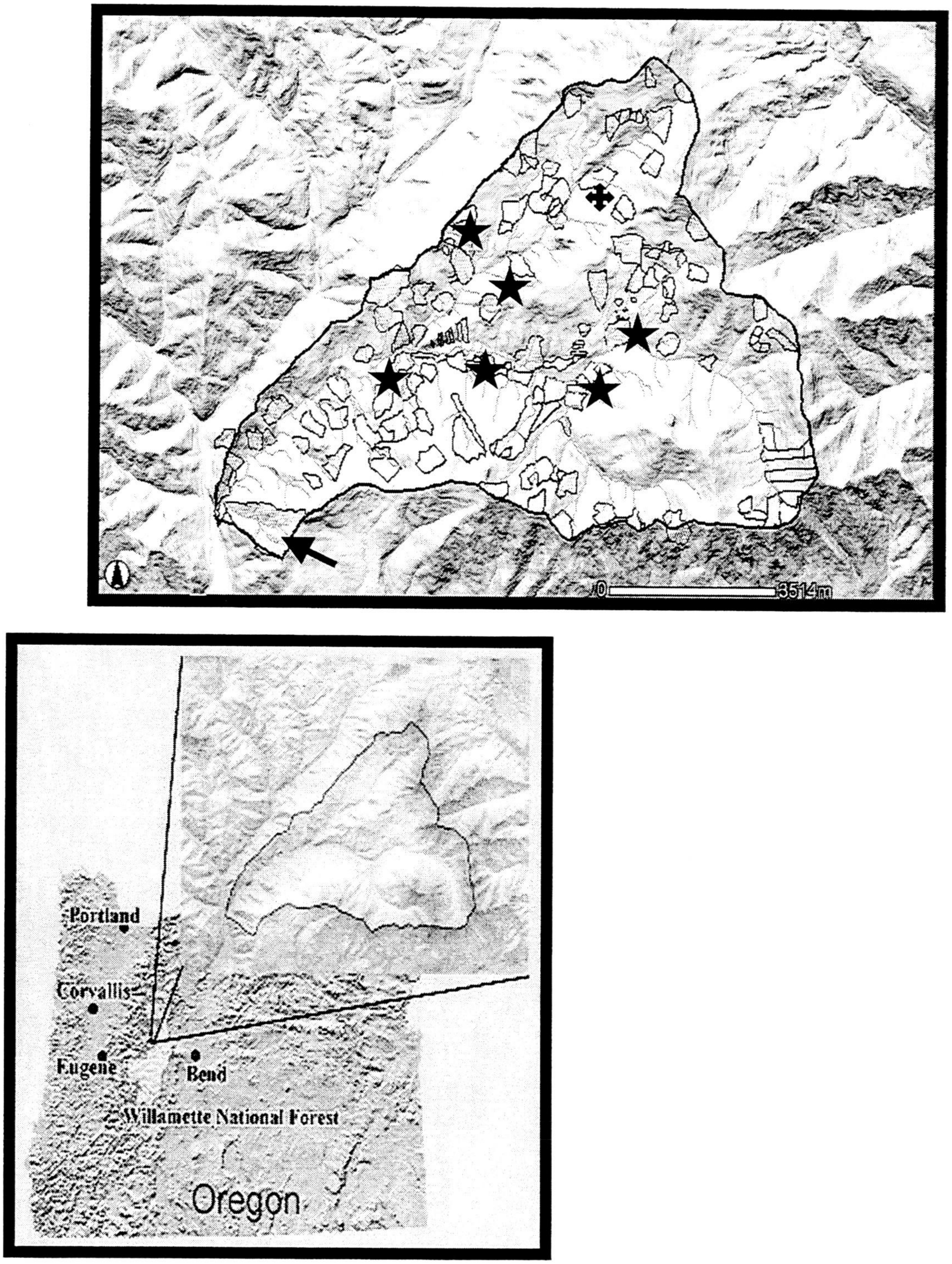

Figure 1. Map of H.J. Andrews Experimental Forest with harvest units outlined. Stars mark sampling blocks for thinning study (Chapter 3), the arrow marks Watershed 1 (Chapter 4), and the cross marks trenching study site (Chapter 2).

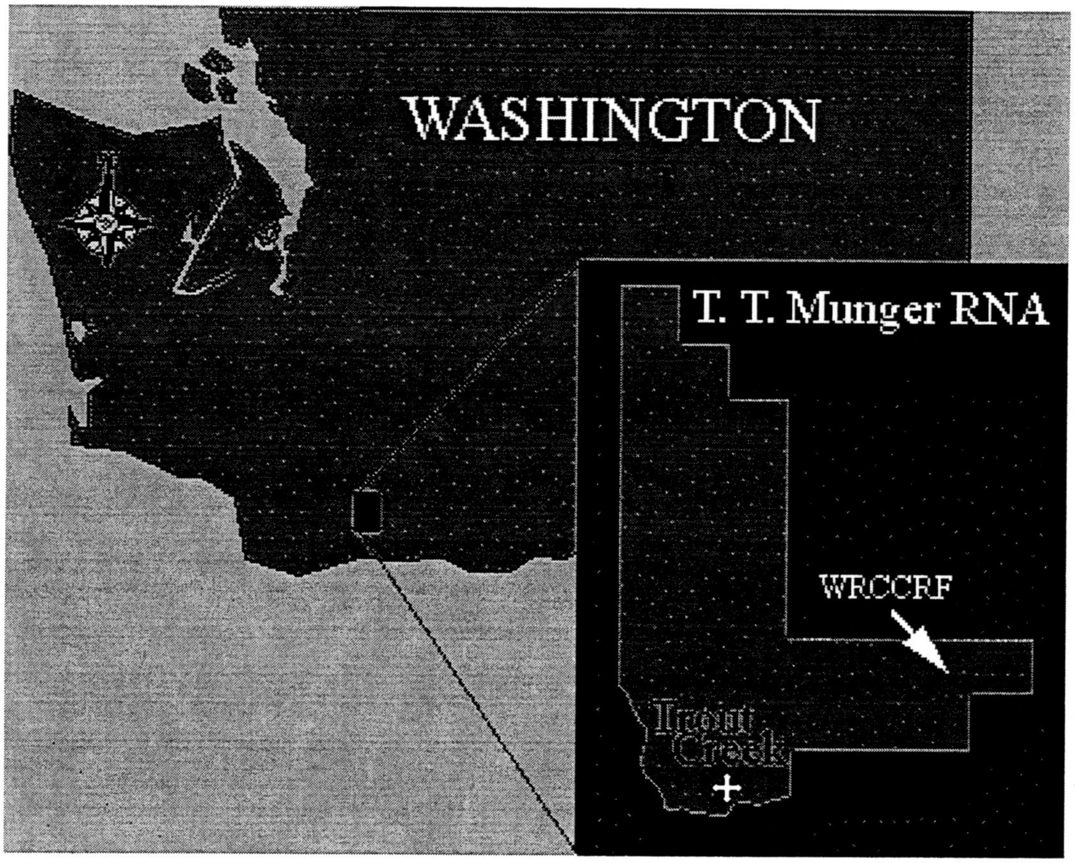

Figure 2. Map of Wind River Experimental Forest (T. T. Munger RNA and Wind River Canopy Crane Research Forest). Cross marks trenching study site (Chapter 2).