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The Response of Understory Plants to Canopy Closure in a Second-growth Forest in the Oregon Cascades

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Table of Contents

List of Tables

List of Figures

Abstract

Management of Pacific Northwest forest lands for timber has increased the frequency of disturbance in the landscape and thereby increased the percent of young forest in the landscape. Young forests typically have less understory plant cover than any other forest successional stage. High cover and diversity of understory plants, however, are desirable for a variety of management objectives. This thesis examines the changes in understory plant cover around canopy closure in a second-growth forest. The data examined in this thesis are part of a long term study of succession after clearcut logging in the Oregon Cascades. This study is the first attempt to monitor long-term successional changes after logging on a single site. Invading and residual herb cover declined by 30 and 60% respectively in the period leading up to and just after canopy closure. Invading shrub cover declined by almost 80% during the period examined. The only group of species that increased in cover after tree canopy closure were the shade-tolerant woody species that had been present in the watershed before logging. Trends in species abundance are examined in terms of their shade-tolerance. Failure of understory plant regeneration is examined as an alternative hypothesis for plant declines. Hypotheses about the composition of the flora of a managed landscape are examined in light of the results of the present study.

Introduction

Dominance of Douglas-fir in the Pacific Northwest

Coniferous forests dominate the region between the Cascade mountains and the Pacific ocean in Oregon and Washington. Conifer dominance in this region is explained by a combination of climatic factors. Winters in the Pacific Northwest are mild and wet while summers are hot and dry. Retaining their needles in the winter, conifers are able to photosynthesize and grow during the fall and winter when water is available. Conifers dominate in size as well as numbers. Trees may reach 200 cm in diameter and 80 m in height, living for 1,000 or more years (Waring and Franklin, 1979). In the *Tsuga heterophylla* zone, between 150 and 1000 meters in elevation, Douglas-fir (*Psuedotsuga menziesii*) and Western hemlock (*Tsuga heterophylla*) are the primary species. Trees making minor contributions to the forest canopy or understory are Western redcedar (*Thuja plicata*), red alder (*Alnus rubra*), bigleaf maple (*Acer macrophyllum*), and golden chinquapin (*Castanopsis chrysophylla*) (Franklin and Dyrness, 1973).

Historically, fire provided the dynamic force in this landscape of giants. One estimate of the historic average fire return interval for the region is 230 years (Agee, 1991). Fire has determined the composition of almost all of the natural forests in the Pacific Northwest. Of the conifers, Douglas-fir best exploits fire. Large Douglas-firs are able to survive fire, unlike Western hemlock, their main competitor. After an intense fire has destroyed most of the trees in a stand, Douglas-fir germinates on the exposed soil and grows well in the high-light environment. Hemlock prefers litter mats or nurse logs, excelling in the dim understory of an intact stand (Minore, 1979).

Douglas-fir fails to regenerate in a closed canopy stand of its own species. As a result, Western Hemlock is considered the true climax species of the region (Franklin and Dyrness, 1973). So pervasive is the influence of fire in the landscape, however, that few if any stands are dominated by hemlock.

Four stages of succession

Forest succession is often divided into four stages: stand initiation, stem exclusion, understory re-initiation, and old-growth (Alaback, 1982; Norse, 1990; Oliver and Larson, 1990; Oliver et al., 1985; Spies and Franklin, 1991). The successional sequence begins with the destruction of the old stand. Stand replacement, usually initiated by forest fire, can also occur after windthrow or a catastrophic incidence of pathogens. All these agents of disturbance are patchy and incomplete in their effects, clearing some areas while leaving most of the original trees in others. Even if no live trees are left, coarse woody debris from the previous stand remain to modify the environment of the new stand. The high levels of woody debris present in old-growth stands remain in young post-disturbance stands, declining to a low point in the middle of the successional sequence (Agee, 1991; Spies and Franklin, 1991).

Stand initiation begins with the germination of tree seeds, primarily Douglas-fir, on the nutrient rich ash of the burn. Sites with remnant adult trees or nearby intact stands re-seed relatively quickly and completely. Large burns that lack adequate seed rain may take 50 or more years to re-seed naturally (Norse, 1990). After a wildfire, the vegetation is composed of both opportunistic, weedy species not present in the undisturbed forest (invaders) and remaining forest species (residuals). The coexistence of residual and invading species creates a much higher diversity of plant species than is present in undisturbed stands (Nieland, 1958).

Dominance of the burned site passes from herbs to shrubs to trees. Tree canopy closure occurs 15-30 years after tree initiation (Long and Turner, 1975). Canopy closure is marked by the transition to competition between trees. After this point, tree growth will be primarily vertical, with each tree developing a mono-layer crown that moves upward, limited to one fixed horizontal area by its encroaching neighbors (Oliver and Larson, 1990). Tree canopy closure heralds the beginning of the stem-exclusion phase of succession. Young stands have the highest density of trees and lowest understory herb cover in the successional sequence. Mean tree diameter and total basal area of trees is lowest, however, in young stands (Spies and Franklin, 1991). The dense canopy that excludes tree initiation also excludes most understory herbs and shrubs. A forest is usually referred to as young until it is about 100 years old.

As the trees continue to grow, some die and canopy gaps are formed. The formation of a more heterogeneous canopy structure during the understory re-initiation phase allows the growth of some understory herbs and shrubs, as well as regeneration of trees. Understory re-initiation occurs when the forest is mature, about 100-200 years after stand initiation. As the process of tree death and understory tree and herb re-initiation continues, the forest enters the old-growth phase. Diversity of canopy structure, tree size, and tree species characterizes the old-growth stage. Herbs and shrubs flourish under the canopy gaps of the old-growth forest (Oliver and Larson, 1990). The old growth stage may last 1,000 years or more (Norse, 1990).

In the Oregon Cascades, understory species diversity is highest in old-growth forests, lowest in mature stands, and intermediate in young stands.

Only 35 of 171 Oregon Cascade Range understory species showed significant differences in frequency of occurrence between age classes (Spies, 1991). Rather than being limited to one age class, understory species show different levels of abundance in stands of each age class.

The Understory of a Young Forest

> "The shaded forest floor becomes devoid of living plants and consists of brown, dead leaves, twigs, and stems." (Oliver and Larson, 1990, p. 147)

The traditional view of forest succession holds that young forests have closed canopies while old forests have more heterogeneous canopies with some openings (Oliver and Larson, 1990). As a result, it is held, understory species are scarce until the canopy has diversified, 150- 200 years after disturbance (Norse, 1990). Franklin and Dyrness (1973) note, however, that some young Douglas-fir stands have relatively open canopies and well-developed understories. These two pictures of what happens in succession have led to two pictures of what determines plant diversity and abundance. Both models agree that understory species diversity is low in young forests. The more traditional model holds that light levels determine plant cover and that light levels are low in the young forest and higher in the old growth (Oliver and Larson, 1990). This model supports the picture of a young forest floor devoid of plant life.

The second model focuses instead on the micro-habitat diversity of the forest floor, especially the diversity of light levels. The widely spaced trees of the young forest create an understory environment with relatively high but uniform light levels (Spies, 1991). This uniform light environment is exploited by woody species which form single-species mono-layers and exclude herb species. In this view, old-growth forests support higher diversity of understory species not because of higher light levels but higher micro-site heterogeneity. As the forest enters the old-growth stage, large trees begin to die, creating some large canopy openings. Simultaneously, however, the presence of Western hemlock in the sub-canopy and understory of stand increases. The shade tolerant canopy of the hemlock is denser than that of the Douglas-fir, and allows less light to penetrate to the forest floor. This mosaic of sunlit gaps and deep hemlock shade supports plant species with a wide range of ecological requirements (Spies, 1991).

These two models reflect the existence of relatively open and very densely stocked young stands. Light is probably the key factor determining understory biomass, while microsite heterogeneity determines diversity. Young forests generally have lower understory plant diversity than older forests. Some young forests have extremely dense canopies and low understory plant cover. Young stands with open canopies may have a flourishing understory made up of relatively few species. Support for the variety of understory patterns in different age classes comes from Tom Spies' study of a large sample of stands in the Oregon Cascades. He found that mean understory species cover was highest in the old-growth site 37 times, highest in the mature site 30 times, and highest in the young forest 22 times (Spies, 1991).

Structure of managed forests

Traditional clearcut logging removes all large trees in their entirety. The remaining woody material is burned to reduce the danger of wildfire and to facilitate planting. Clearcuts can be re-seeded or replanted. Both methods differ from natural regeneration in that they supply a greater density of seedlings, that these seedlings are all approximately the same age, and that they are all Douglas-firs. The suppression of competing vegetation, traditionally accomplished using herbicides, further increases the homogeneity of the growth of the Douglas-fir seedlings (Norse, 1990; Raphael, 1984). The young Douglas-firs form a relatively evenly closed canopy, usually within 20 years (Long and Turner, 1975). The high density of even-aged Douglas-fir, the lack of tree species diversity, and the paucity of coarse woody debris create an understory environment lacking heterogeneity.

Managed forests differ from natural forests at the landscape as well as the stand level. Landscapes managed for timber currently reflect the dispersed cutting pattern popular in the 1970's and '80's. The landscape is made up of a checkerboard of patches of clearcut, young, and, occasionally, mature forest. Old-growth forests are largely absent from the landscape. The patches of different ages of forest are much more even in their size and distribution than would be found in a natural landscape (Norse, 1990). The face of the forest landscape depends strongly on the length of the logging rotation in use. Most managed stands are currently logged every 50-80 years. Longer rotations would increase the percent of mature and old-growth forests in the landscape.

Summary of early successional trends in managed forests

To predict the fate of understory species in managed stands, a clear picture of patterns of understory response to canopy change is required. Succession can be studied by monitoring one site through time or by sampling a variety of sites that are at different stages of succession (a chronosequence). Although it is impossible to control for all between-site variation, the chronosequence approach is more commonly used because the sampling can be accomplished within a limited period of time. Several studies have used chronosequences to examine the effects of canopy closure on understory cover, biomass, and diversity in the coniferous forests of the Pacific Northwest. Schoonmaker and McKee (1988) and Long and Turner (1975) examined Douglas-fir forests in the Oregon and Washington Cascades, while Alaback (1982) sampled a similar chronosequence in the Sitka spruce/Western hemlock forests of Southeast Alaska. The study that I analyze in this thesis represents the first attempt to monitor long-term succession on one site. This study, which is located in the H. J. Andrews Experimental Forest in the Oregon Cascades, has followed succession after clearcut logging for 30 years (Dyrness, 1973; Halpern, 1987, 1988, 1989; Halpern and Franklin, 1990; Halpern and Spies, in press).

To provide a context for the later successional events analyzed in this thesis, I have summarized the results obtained in the H. J. Andrews study to date. Immediately following logging and burning, plant species cover and diversity plummeted to near zero. Species not found in the undisturbed forest (invaders) exploited the favorable light environment after canopy removal. In the first two years after logging, the sites were dominated by invading species, primarily perennial *Epilobiums* and the exotic annual *Senecio sylvaticus*. Most of the forest understory species survived logging or regenerated from seed in the first few years after disturbance (Halpern, 1989). Most residual species had returned to cover values similar to or higher than those in old-growth within the first five years (Dyrness, 1973). Residual and invading herbs showed similar cover values for the first ten years after logging. Ten to 20 years after logging, invading herbs declined strikingly while residual herbs declined only slightly (Halpern and Spies, in press). The herb dominated phase is normally followed by a shrub dominated phase (Franklin and Dyrness, 1973). In the H. J. Andrews study, residual shrubs played a minor role in the clearcut environment. Plots that had undergone extensive soil disturbance during logging and burning passed through a transitional stage of dominance by invading shrubs. Undisturbed plots were more likely to make the transition directly from herb to tree dominance (Halpern and Franklin, 1990).

The effect of tree canopy closure on understory species

Growth of overstory trees has myriad effects on the understory environment. A closed tree canopy intercepts most of the light that would have reached the forest floor. The understory environment is moister and cooler than the clearcut environment; the tree canopy buffers the understory against environmental extremes. Trees extract the nutrients and water required for growth from the soil, possibly at the expense of understory species. Conifer fine-root biomass peaks at canopy closure, suggesting that competition for below-ground nutrients is probably strongest at this time (Vogt et al., 1987). Increased litterfall may prevent establishment of understory species by covering mineral soil or through allelopathic interactions (Alaback, 1982; Del Moral and Cates, 1971).

The chronosequence studies of succession provide a relatively consistent picture of events at canopy closure (Schoonmaker and McKee, 1988; Long and Turner, 1975; Alaback 1982, 1984) In managed forests of the Pacific Northwest, understory diversity, total and residual, drops at canopy closure; species that had invaded the clearcut are lost, and understory cover/biomass tends to decrease. Response to canopy closure differs among groups of understory species, however. While invading species appear to decrease after canopy closure, post-canopy closure demographic patterns for residual species are unclear. Undoubtedly, some forest species, probably those adapted to forest gaps, will decline after canopy closure. Shade-tolerant forest herbs, on the other hand, may persist under a closed canopy.

Objectives of this thesis

Increasing species diversity in young stands has become a management objective on public lands (Cascade Center for Ecosystem Research, 1993). Understory plants play a key role in forest diversity by providing cover and forage for a variety of birds and mammals (Norse, 1990). The transition from the clearcut to the young closed-canopy forest is accompanied by the loss of understory biomass and diversity. Understanding the patterns of understory species decline at canopy closure is crucial to attempts to manage for understory diversity.

This thesis examines the response of understory species to tree canopy closure on two watersheds in the Oregon Cascades. The watersheds were logged 31 years ago; I have examined the data from 16 years after logging to the present. The second-growth forest present on the watersheds is intermediate in terms of canopy uniformity between naturally regenerated forests and highly managed plantations. Aside from slash-burning and artificial regeneration of Douglas-fir, the watersheds were not subjected to extensive vegetation management.

The changes in the understory environment that accompany tree canopy closure suggest several hypotheses regarding the patterns of shrub and herb responses to canopy closure. The most basic is that herb and shrub cover decline in response to canopy closure. I tested this hypothesis by examining herb and shrub cover values in the years just before and after canopy closure. I predicted that invading species would decline more quickly than residual species; this hypothesis was addressed by splitting herb and shrub cover into residual and invading groups. If understory cover declines as tree cover increases, I hypothesized that understory cover would be negatively correlated with tree cover in each year of the study. I examined data on individual understory species to test the hypothesis that their reaction to canopy closure would depend on their degree of shade-tolerance.

Methods

Design of field experiment

The data analyzed in this thesis come from a study of succession initiated by Ted Dyrness in 1962. This study was located on the 117 ha H.J. Andrews Experimental Forest in the Blue River ranger district of the Willamette National Forest, 50 miles east of Eugene, Oregon. The Experimental Forest ranges in elevation from 442-1082 m and slopes are typically greater than 50%. The vegetation of experimental Watersheds 1 and 3 is classified in the Western hemlock (*Tsuga heterophylla*) zone. The pre-logging overstory was composed of old-growth (300-500 year old) and mature (125 year old) Douglas-fir. Western hemlock was the primary understory tree, with golden chinquapin in the understory of dry sites and Western redcedar in wet sites (Dyrness, 1973).

Watersheds 1 and 3 were cable-logged beginning in 1962; Watershed 2, which lies between them, was not logged. All 96 ha of Watershed 1 was harvested between the fall of 1962 and the summer of 1966 and the slash was burned in fall of 1966. Watershed 3 was cut in three dispersed patches, 5, 9, and 11 ha in area, during the winter of 1962-63; slash was burned in the fall of 1963.

Restocking of Douglas-fir proceeded differently on the two watersheds. Watershed 1 was seeded in its entirety in 1967, and 10 ha were re-seeded in 1968. Because regeneration was poor, Watershed 1 was then planted with two-year old trees in 1969 and 40 ha were replanted with two- and three-year-old trees in 1971. All three units of Watershed 3 were planted with three-year-old trees in 1964.

Before harvesting occurred, six randomly located and evenly spaced transects were laid out in Watershed 1 and ten in Watershed 3. A total of 193 sample plots two meters to a side (4 m^2) were located 30.5 m apart along the transects. Crown cover of all species present on the plots was recorded before logging in 1962 and has been resampled every 1-5 years since then. In this thesis, I examine data that were collected in 1979, 1980-81, 1983, 1987, 1990, and 1994. The sampling in each year was performed by a different crew. Small changes between successive samples may result from differences between crew's cover estimations.

Data Analysis

Watersheds

Although logging was initiated on the two watersheds in the same year, slash burning was completed 3 years earlier on Watershed 3. In the analysis of the earlier stages of succession, Dyrness (1973) and Halpern (1987, 1988, 1989) referred to time since slash burning rather than time since logging was initiated; in any given calendar year, the events on Watershed 3 were three years ahead of Watershed 1. Although tree cover was higher on Watershed 3 throughout this study, canopy closure occurred in the same year on both watersheds. Because my focus is on the effects of canopy closure, I chose to consider the data from the two watersheds together, and did not correct for the different timing of early events on the watersheds. My analysis begins with the year 1979, which is 16 years after logging was initiated. This year was the 12th growing season after slash burning on Watershed 1 and the 15th on Watershed 3. I refer to the years between logging and 1983 as the clearcut or open-canopy phase.

Community-level

My analysis of plant cover is divided in several ways. The first division is of plants into growth form: herbs, shrubs, and trees. I have used Ted Dyrness's and Charlie Halpern's classification of species by growth form, in which species were classified according to height (Dyrness, 1973; Halpern, 1987). The 'herb' category includes all species <0.6 m tall at maturity, 'shrubs' are those species above 0.6 m in height but not a part of the canopy or sub-canopy, and 'trees' are those species reaching canopy or sub-canopy height at some point in succession.

The percent of each plot covered by each species was recorded. The cover value for a given growth form is the sum of the covers of all species belonging to that growth form. This additive value can exceed 100% due to overlap between species. Although overall estimates were also made for each growth form, the additive estimate has three advantages: the individual species estimates that it is composed of are more accurate than the overall estimates, it gives a more accurate picture of the biomass of plants on a plot because it encompasses overlap, and it can be calculated for any grouping of species. The additive cover value for trees includes all tree heights, not just tree cover at the canopy level. All cover values reported represent the average over all the plots.

Within growth form, species were classified as residual or invading. I used Ted Dyrness and Charlie Halpern's classification for Watersheds 1 and 3 of species as residual or invading (Dyrness, 1973; Halpern, 1987). Residual species are those that were present on undisturbed sites in the watersheds prior to logging. This classification is unique to these two watersheds, although some information for it was drawn from other studies. A complete list of species classified by growth form and residual or invading status appears in Appendix B. Because residual conifers made up the vast majority of the tree cover, and because my focus is on the understory, tree cover is not divided into residual and invading species.

Most analyses were performed for four separate groups: residual herbs, invading herbs, residual shrubs, and invading shrubs. Although I present some initial analysis for shrubs and herbs as a whole, this classification averages out what is often the strikingly different behavior of the residual and invading species.

To determine the changes in plant cover over time, I took the differences in cover on each of the plots between successive sampling dates. Wilcoxon's signed rank test was used to test whether the difference between years was different from zero. To examine the dynamics of tree change around canopy closure, I calculated the change in tree cover from 1979 to 1994 for all plots and then split the changes up into their four quartiles. The first quarter of the changes lay between -36% and 21%, the second from 22 to 53%, the third from 54 to 85%, and the group with the greatest change increased between 86 and 195% in this period. These percents are differences between two additive cover values; they do not express percent change. Spearman's rank correlation was used to test the within-year relationship between shrubs or herbs and trees and between herbs and shrubs. The within-year correlation with tree cover serves as an estimate of the understory species tolerance of tree cover.

For each section of results in this thesis (usually a table), the significance of the p-values was adjusted for simultaneous inference using the Bonferroni sequential procedure (Rice, 1989). This procedure corrects the significance level for each test based on the total number of hypotheses tested and where each test falls on the list of ranked p-values.

Individual species

All species that played major roles in the pre-logging forest or in the clearcut environment were examined for their response to canopy closure. I examined all species that Charlie Halpern had reported showing greater than 1% cover or 20% frequency for at least one year in the clearcut (Halpern, 1989). The few species that did not make this list but that had measured more than 0.1% cover in the pre-logging forest were also included (Dyrness, 1973). A list of all these species and their common names appears in Appendix A.

Several indices of abundance and change were calculated for each species. Cover and frequency were calculated for each year. For a given species, the frequency of that species is the number of plots on which it was present divided by the total number of plots. The change in cover from 1979 to 1994 was calculated for each species for each plot. Wilcoxon's signed rank test was used to determine whether these changes were significantly different from zero. For each species, relative cover was calculated by dividing each year's average cover by the average from 1979 for that species. Groups of species that responded similarly to tree cover increase were tested for their within-year correlation with tree cover. Spearman rank correlations were used for this analysis.

Results

Trends in herb, shrub, and tree cover

Total tree cover increased significantly in each year until 1987; it plateaued and exhibited non-significant decreases from 1987 to 1994 (Figure 1, Table 1). Herb cover increased significantly from 1979 to 1981, and then declined significantly in all subsequent years except 1987 (Figure 1, Table 1). Shrub cover followed a pattern similar to that of herb cover, peaking 2 years later, in 1983. Total herb, shrub and tree cover values intersected around 1983, after which tree cover dominated (Figure 1).

Figure 1: Herb, shrub and tree cover from 1979 to 1994. Error bars are one S.E. around the mean.

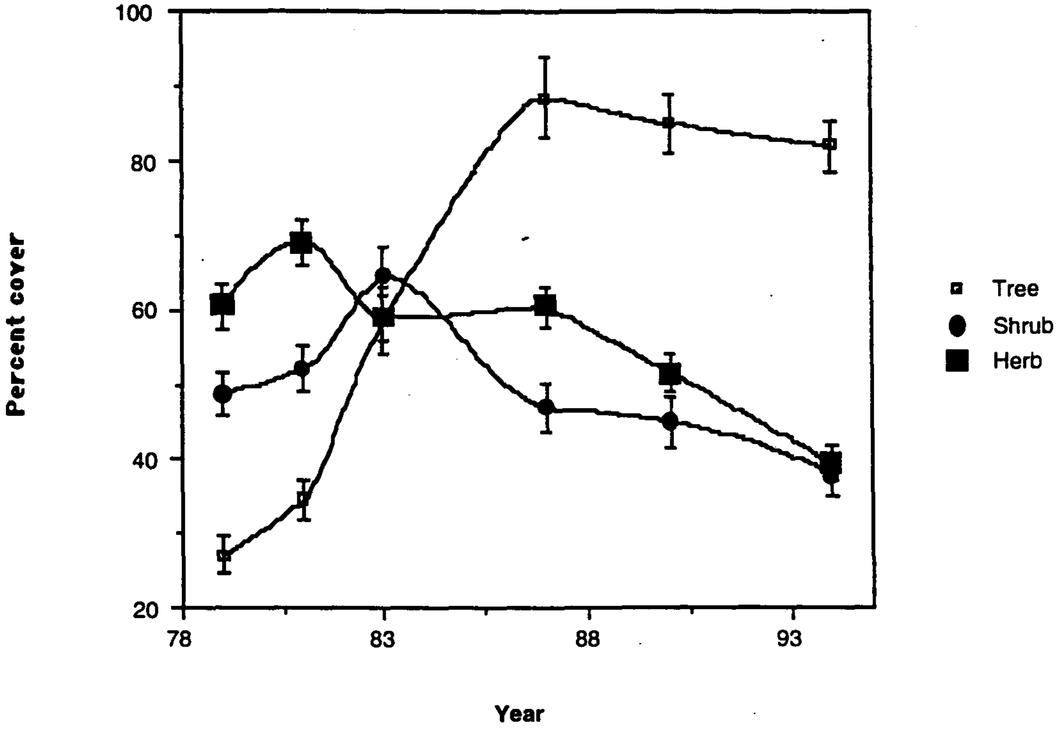
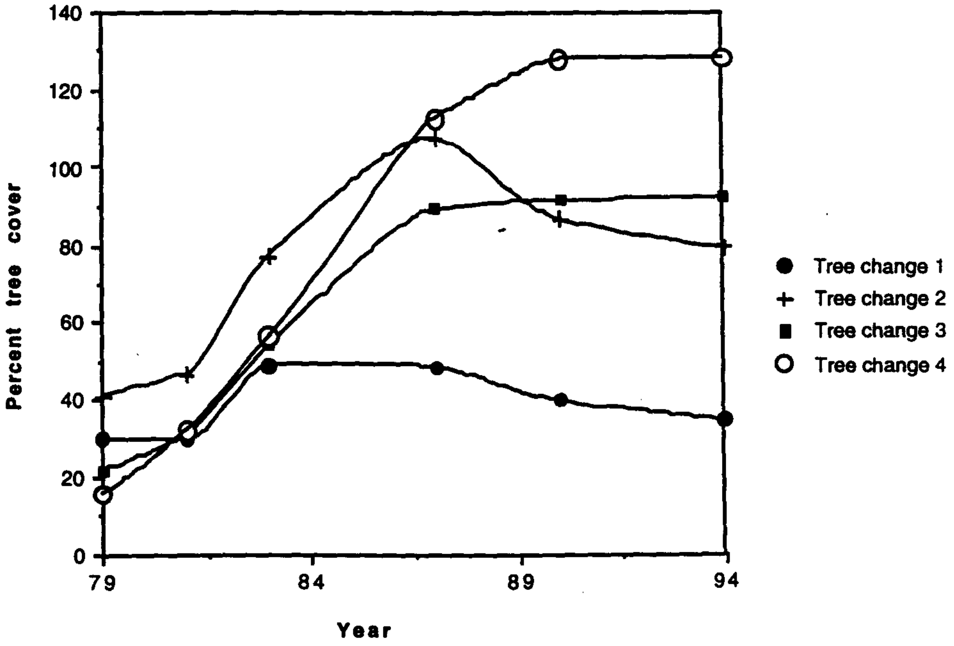


Table 1: Cover values for herbs, shrubs, and trees for the years 1979 to 1994. Understory cover = shrub cover + herb cover. Standard errors of means in parentheses. Stars indicate that the difference between a year and the previous year was significantly different from zero in Wilcoxon's signed rank test. The significance level was 0.05, adjusted by the Bonferonni sequential method.

	1979	1981	1983	1987	1990	1994
Herb						
Total	61 (3.2)	69* (3.0)	59* (2.9)	61 (2.9)	52* (2.6)	40* (2.2)
Residual	45 (2.7)	49* (2.6)	45 (2.6)	49 (2.6)	43* (2.2)	33* (2.0)
Invading	16* (1.6)	20* (1.7)	14* (1.5)	12* (1.5)	9.1* (1.4)	6.2* (1.2)
Shrub						
Total	49 (2.9)	52 (3.1)	64.* (3.9)	47* (3.3)	45 (3.4)	38* (2.8)
Residual	16 (2.0)	18 (2.1)	24* (2.7)	29* (2.8)	32 (3.0)	32 (2.7)
Invading	32 (2.5)	34 (2.7)	40.3* (3.2)	19* (2.2)	13* (1.8)	6.6* (1.1)
Under-story	109 (4.2)	121* (4.6)	123 (5.0)	108* (4.5)	97* (4.4)	78* (3.8)
Tree	27 (2.3)	35* (2.8)	59* (4.6)	88* (5.3)	85 (4.0)	82 (3.4)

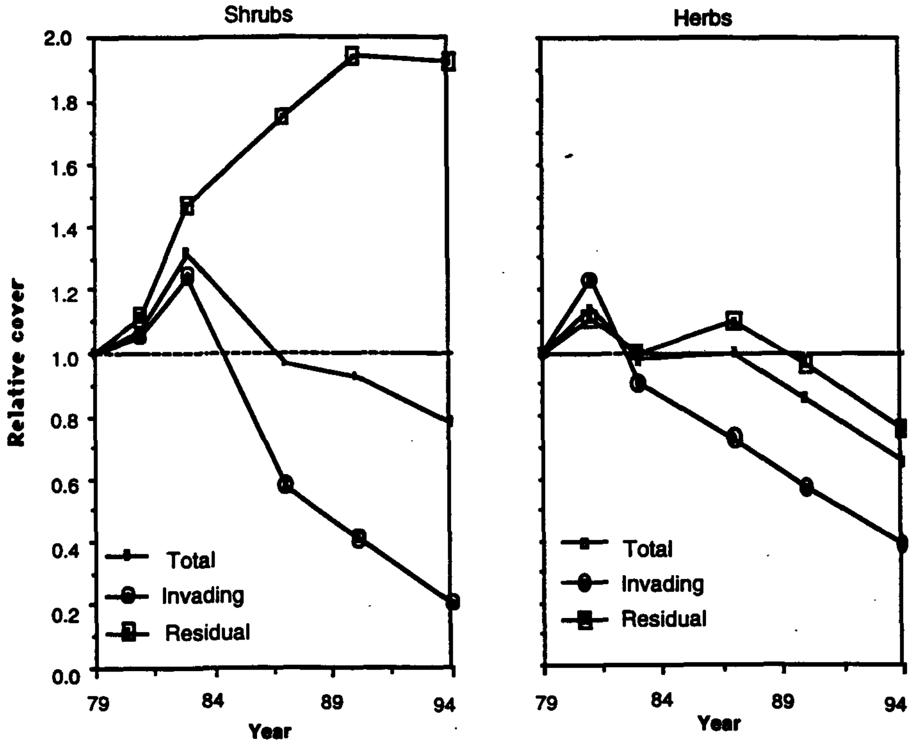
Figure 2: Four categories of tree increase. Groups were divided according to their total increase from 1979 to 1994. Group 1 = -36 to +21%; Group 2 = 22 to 53%; Group 3 = 54 to 85%; Group 4 = 85 to 195%.



When tree increases are divided into four groups, all four groups start at 20-40% cover (Figure 2). One group of plots barely increased in cover. The two groups of plots with intermediate increases in cover plateaued in 1987, while the most prolific quarter did not plateau until 1990 (Figure 2).

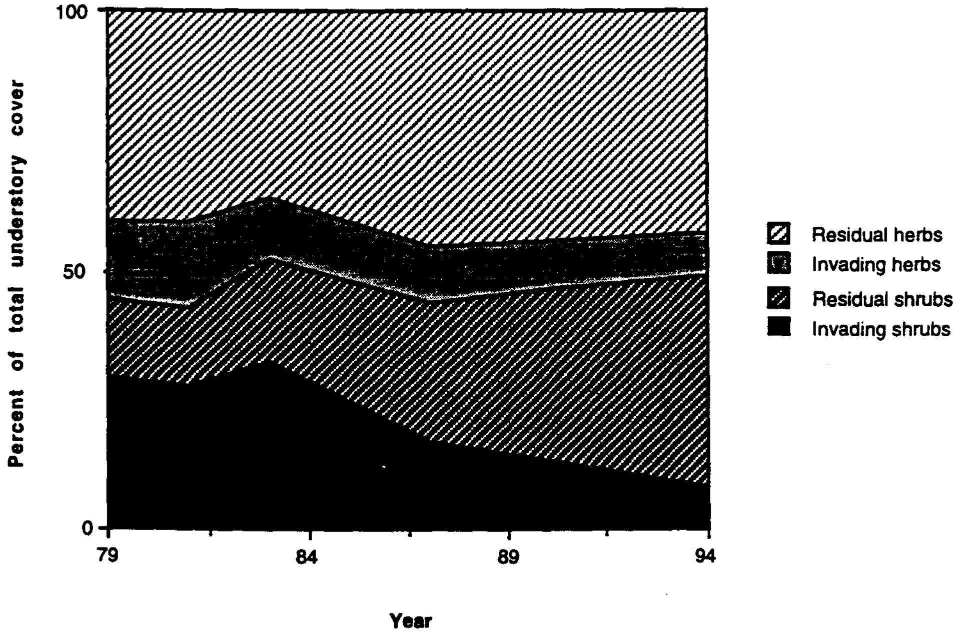
Residual and invading herb and shrub species showed different patterns of decline in response to canopy closure. Residual herb cover did not decline significantly until 1990, declining to about 75% of its 1979 value by 1994 (Table 1, Figure 3). Invading herb cover, on the other hand, peaked in 1981 and by 1994 had declined to less than 40% of its 1979 value. Over the period of this study, residual shrubs nearly doubled in cover, showing the greatest increases in 1983 and 1987 (Table 1, Figure 3). Invading shrub cover began to decline after 1983 and ended at 20% of its initial value .

Figure 3: Trends of herb and shrub cover over time. Values relative to 1979 cover.



Total understory cover declined by 37% of its 1979 value. Residual herbs comprised a constant proportion of understory cover from 1979 to 1994, about 40% (Figure 4). Invading herbs comprised a smaller percent of the total understory, 15% in 1979 and only 8% in 1994. Shrubs together comprised about 40% of the understory throughout this period; in 1979, the composition was 30% invading and 15% residual while in 1994 it was 8% invading and 41% residual (Figure 4).

Figure 4: Percent composition of total understory cover over time



Correlations between herbs or shrubs and tree cover

Invading herbs were negatively correlated with tree cover in every year after 1979 (Table 2). Residual and invading shrubs were also negatively correlated with tree cover, but these relationships were significant only in 1994 and 1987-94, respectively. Residual herbs remained non-significantly positively correlated with tree canopy cover throughout the study. The magnitude of the correlation between residual herbs and tree cover declined with time while the magnitude of the correlation between both shrub groups and tree cover increased with time.

Table 2: Within-year Spearman rank correlation of herbs and shrubs with tree cover. Stars indicate significance at 0.05 level corrected with the Bonferroni sequential procedure.

	1979	1981	1983	1987	1990	1994
Herbs						
Residual	0.18	0.12	0.17	0.12	0.08	0.01
Invading	-0.16	-0.35*	-0.33*	-0.37*	-0.29*	-0.25*
Shrubs						
Residual	-0.03	-0.06	-0.07	-0.18	-0.18	-0.25*
Invading	-0.02	-0.17	-0.13	-0.24*	-0.32*	-0.23*

Residual herbs were non-significantly positively correlated with total shrub cover throughout the study (Table 3). Invading herbs were significantly negatively correlated with shrub cover in 1979; the correlation was non-significant in all other years.

Table 3: Within-year Spearman rank correlations of herbs with total shrub cover. Stars indicate significance at the 0.05 level, corrected according to the Bonferonni sequential method.

	1979	1981	1983	1987	1990	1994
Residual	0.13	0.14	0.15	0.15	0.17	0.16
Invading	-0.31*	0.00	-0.03	-0.02	-0.04	0.02

Individual species

Almost all invading species declined sharply in response to tree cover increase (Table 4). Some, such as *Senecio sylvaticus, Conyza canadensis, Agoseris* spp., *Cirsium* spp, and *Gnaphalium microcephalum* already measured below 0.1% cover in 1979. Herb species showing significant declines over the 1979 to 1994 period included *Epilobium paniculatum* and *Epilobium angustifolium, Anaphalis margaritica,* and *Bromus* spp.. The two major invading shrubs, *Ceanothus velutinus* and *Ceanothus sanguineus* also declined significantly in response to tree canopy closure. The only invading species to show a significant increase in cover between 1979 and 1994 was the exotic herb *Lactuca muralis*. Invading species still present on more than 10% of the plots in 1994 included *Epilobium angustifolium, Lactuca muralis, Collomia heterophylla, Ceanothus sanguineus, Pteridium aquilinum* and *Rubus parviflorus*.

Table 4: Wilcoxon's signed rank tests for changes in individual invading species over time. * = significant at 0.05 level, significance corrected by rank. ** = significant at 0.005 level. See Appendix A. for common names.

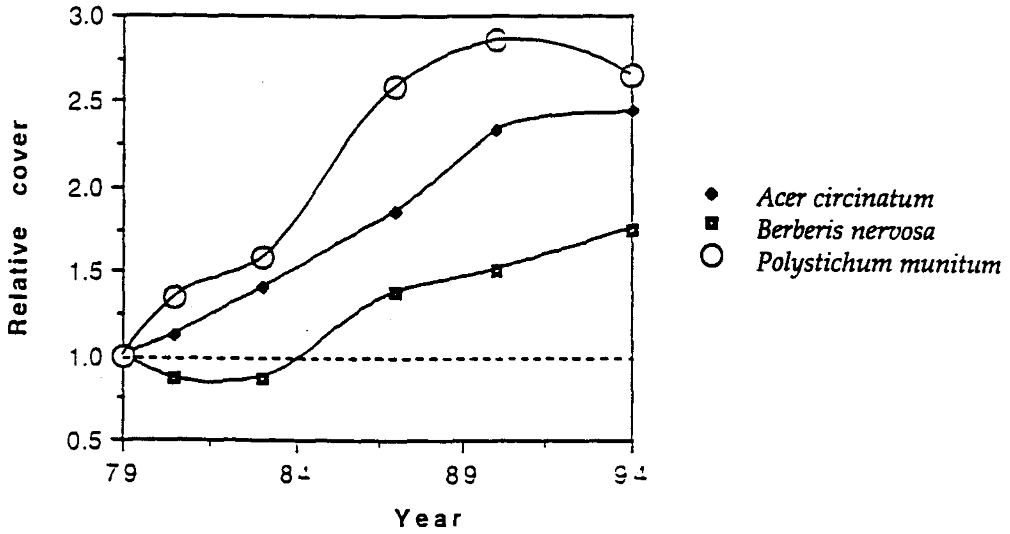
	Initial cover (S.E.)	Change in cover(S.E.)	Sig.	1994 frequency
Herbs				
Agoseris spp.	0.001 (0.001)	0.008 (0.008)	NS	1.6
Anaphalis margaritica	1.8 (0.32)	-1.7 (0.32)	**	5.2
Bromus spp.	0.14 (0.06)	-0.22 (0.17)	NS	9.8
Cirsium spp.	0.009 (0.007)	-0.009 (0.007)	NS	0
Collomia heterophylla	0.43 (0.15)	-0.38 (0.15)	NS	31
Epilobium paniculatum	1.1 (0.29)	-1.1 (0.29)	**	9.3
Epilobium angustifolium	4.6 (0.55)	-4.5 (0.55)	**	15
Gnaphalium microcephalum	0.005 (0.002)	0.008 (0.008)	NS	1.6
Pteridium aquilinum	2.7 (0.91)	0.19 (0.81)	NS	14
Rubus leucodermis	0.12 (0.07)	-0.10 (0.07)	NS	1.6
Senecio sylvaticus	0.001 (0.001)	-0.001 (0.001)	NS	0
Vicia americana	0.13 (0. 08)	-0.02 (0.05)	NS	2.1
Shrubs				
Ceanothus velutinus	13.2 (1.8)	-13.2 (1.8)	**	1.0
Ceanothus sanguinius	10.2 (1.6)	-8.5 (1.5)	**	16
Rubus parviflorus	4.2 (1.1)	-2.6 (1.2)	NS	22
Salix spp.	1.6 (0.64)	-0.61 (0.53)	NS	5.7
Exotics				
Hypericum perforatum	0.002 (0.001)	0.07 (0.02)	*	8.8
Lactuca muralis	0.27 (0.17)	0.004 (0.072)	*	16

Residual species showed a variety of responses to canopy closure (Table 5). These responses were divided between woody and herbaceous growth habit, rather than the height classification used to divide the herb and shrub categories. Woody species increased in cover between 1979 and 1994, while herbaceous species declined.

Table 5: Wilcoxon's signed rank tests for changes in individual residual species over time. * = significant at 0.05 level, significance corrected by rank. ** = significant at 0.005 level.

	Initial cover (S.E.)	Change (S.E.)	Sig.	1994 frequency
Ruderal				
Rubus ursinus	18.5 (1.6)	-1.6 (0.94)	NS	86
Sun-loving herbs				
Hieracium albiflorum	0.26 (0.05)	-0.18 (0.05)	*	28
Trientalis latifolia	2.9 (0.31)	-2.5 (0.31)	**	62
Whipplea modesta	2.8 (0.63)	-2.0 (0.54)	NS	35
Shade-loving herbs				
Coptis laciniata	0.48 (0.16)	-0.33 (0.16)	NS	21
Oxalis oregana	0.68 (0.32)	-0.26 (0.26)	NS	3.6
Rubus nivalis	0.06 (0.02)	-0.05 (0.02)	NS	3.6
Viola sempervirens	0.39 (0.09)	-0.18 (0.10)	NS	36
Forest herbs				
Festuca occidentalis	0.31 (0.11)	-0.24 (0.11)	NS	16
Galium spp.	1.1 (0.20)	-1.1 (0.20)	**	2.6
Linnea borealis	1.9 (0.47)	-0.87 (0.55)	NS	22
Vancouveria hexandra	1.2 (0.51)	-0.89 (0.49)	NS	16
Rare forest herbs				
Chimaphila umbellata	0.02 (0.01)	-0.006 (0.009)	NS	0.5
Goodyera oblongifolia	0.005 (0.005)	<0.001 (0.006)	NS	1.6
Synthyris reniformis	0	0.02 (0.01)	NS	3.1
Mesic-site woody species				
Acer circinatum	8.9 (1.5)	12.8 (1.9)	**	63
Berberis nervosa	5.5 (0.78)	4.1 (0.91)	**	68
Polystichum munitum	3.7 (0.68)	6.1 (1.0)	**	66
Xeric-site woody species				
Corylus cornuta	1.7 (0.71)	0.63 (0.48)	*	14
Gaultheria shallon	5.3 (1.0)	0.76 (0.98)	*	40
Rhododendron macrophyllum	3.5 (0.90)	1.6 (0.85)	NS	16
Vaccinium parvifolium	0.93 (0.31)	0.68 (0.32)	*	20

Figure 5: Patterns of response of residual woody species to canopy closure. Cover values are relative to 1979 cover.


A. Mesic-site Woody Species

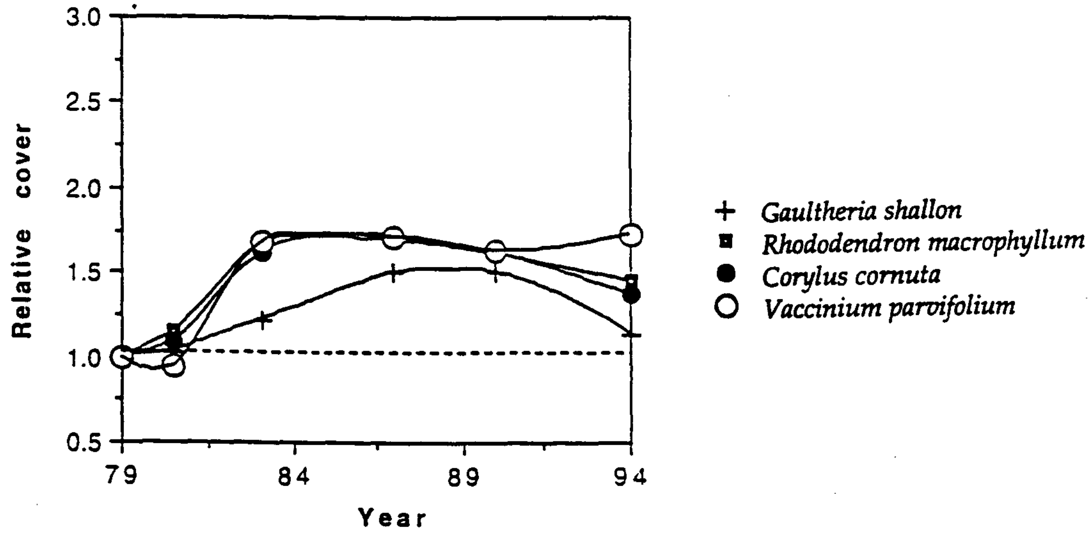
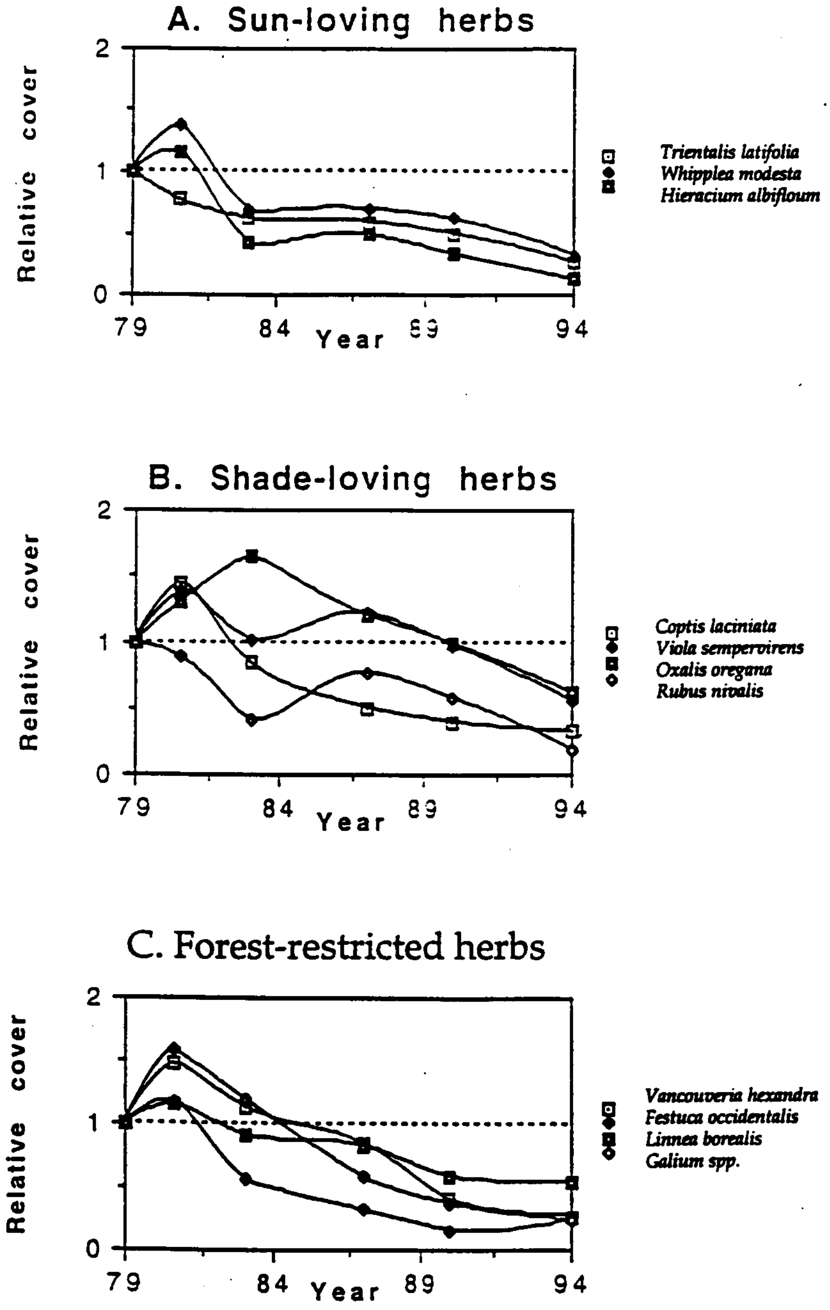

B. Xeric-site Woody Species

Figure 6: Patterns of response of residual herbaceous species to canopy closure. Cover values are relative to 1979 cover.



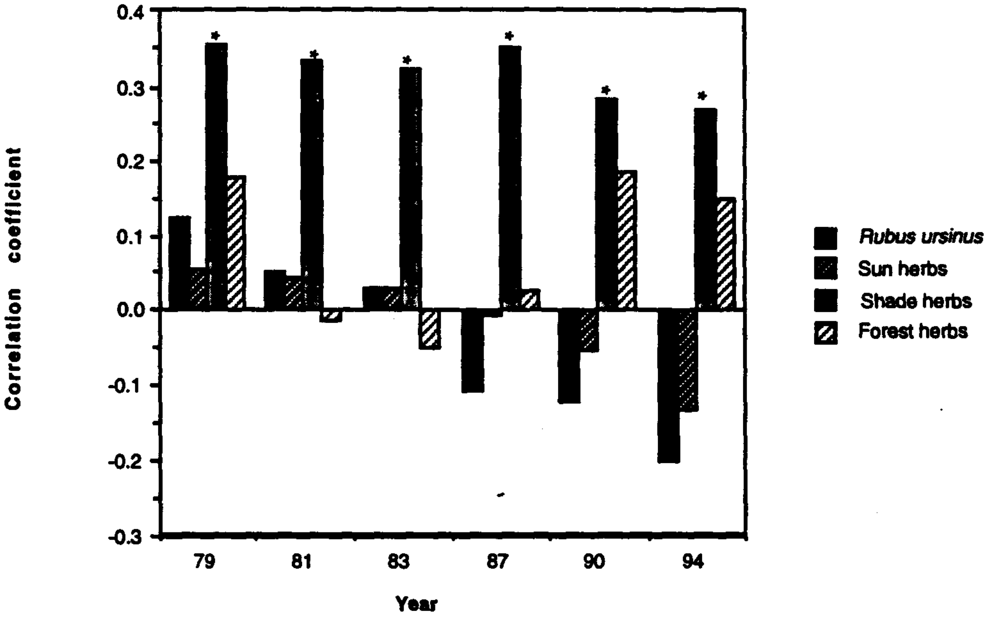
The woody species characteristic of mesic (wet) communities, *Acer circinatum, Polystichum munitum,* and *Berberis nervosa,* showed increases even after canopy closure (Figure 5.A). Species of higher-light or xeric (dry) communities, *Gaultheris shallon, Corylus cornuta, Rhododendron macrophyllum,* and *Vaccinium parvifolium,* increased until canopy closure and then plateaued or declined (Figure 5.B).

Herbaceous species declined regardless of their association with higher or lower light levels. The sun-loving herbs (species that had exceeded 5% cover or 20% frequency in the clearcut environment) declined sharply in 1983 and then showed gradual declines (Figure 6.A). The sun-loving species *Trientalis latifolia* and *Hieracium albiflorum* were the only two herbaceous species whose decline from 1979 to 1994 was significantly different from zero (Table 5). Shade-loving herbs (species that had achieved 1-5% cover in at least on year in the clearcut) tended to begin their declines a few years later; they lost as much of their cover, however, as the sun-loving species had (Figure 6.B). Forest-restricted herbs are those species that were important in the pre-disturbance forest but did not make a significant contribution to the clearcut flora. Their declines were very similar to those of the other herbs (6.C).

Rubus ursinus was extremely abundant in the clearcut and achieved this abundance in the harsh environment of the early clearcut. *Rubus ursinus,* although a residual in these watersheds, can be classified as a disturbance-loving (ruderal) species. It declined in cover to the same degree as the other herbs. Its final frequency, however, was much higher than any other residual herb (Table 5).

Correlations of residual herb groups with tree cover corresponded well to their success in the clearcut. The shade-loving herbs were significantly positively correlated with tree canopy cover throughout the period from 1979 to 1994 (Figure 7). *Rubus ursinus* and the sun-loving herbs were positively correlated with tree cover before canopy closure and negatively correlated afterwards. The forest species showed no clear pattern of association with tree canopy cover.

Figure 7: Spearman rank correlations between residual herbaceous species and tree cover. Stars indicate significance at 0.05 level, corrected using the Bonferroni sequential method.



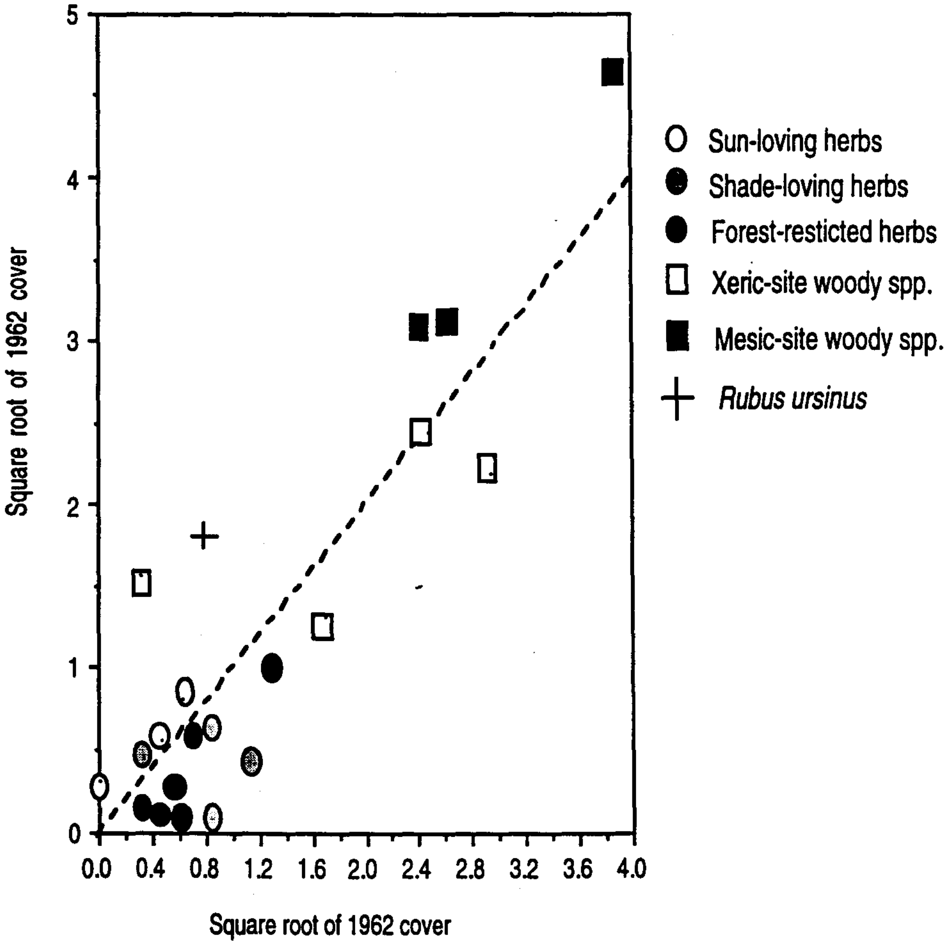
Neither mesic nor xeric-site woody species showed a significant or consistent pattern of association with tree canopy cover (Table 6). Xeric-site woody species tended to be slightly more positively associated with tree canopy cover than mesic ones did.

Table 6: Spearman rank correlations between residual woody groups and tree cover. No correlations were significant at the 0.10 level.

	1979	1981	1983	1987	1990	1994
Xeric	0.18	0.18	0.15	0.07	0.13	0.01
Mesic	0.05	0.03	0.09	0.07	0.00	-0.08

Shade-loving herbs, mesic-site woody species, and the ruderal *Rubus ursinus* were the only groups showing consistently higher percent cover in 1994 than they had in 1962 (Figure 8). Forest-restricted and shade loving herbs were well below their pre-logging cover. Xeric site woody species fell near their 1962 cover, some below and some above.

Figure 8: Relationship of 1994 cover to 1962 cover. Dashed line represents equal cover in the two years. The square root of cover values was used to allow visual separation of points.



Discussion

Canopy closure

Canopy closure on both watersheds in this study occurred in 1987, 24 years after logging was initiated. This event represents the peak in cover for trees that had been growing slowly since logging. Each of the species groups examined in this thesis started at minimal or no cover after slash burning and increased to peak in cover 2-24 years after logging. Residual shrubs and woody herbs were the only species that had not yet peaked 31 years after logging. The pattern of successive peaks of different growth-forms resembles the traditional sequence of physiognomic succession: herbs are succeeded by shrubs that are in turn overtopped by trees (Grime, 1979; Clements, 1916).

The trends in understory species cover observed from 1979 to 1994 can be interpreted only in the context of events earlier in succession. Invading herbs peaked five years after clearcutting; their decline from 1979 to 1994 represent the final stages of 20 years of decline. The decline of invading herbs began before tree cover was very high and was probably due to competition from other understory species. Residual herbs peaked about 10 years after disturbance and declined very gradually until 1987, 24 years after logging. The increases of residual and invading herbs from 1979 to 1981 or 1983 are at most tiny reversals in an overall pattern of decline and may be artifacts of the differences between crew's cover estimations. The decline of residual herbs after canopy closure is their first sharp decline. Invading shrubs increased gradually in cover for the first 20 years after disturbance, peaking in 1983 (Halpern and Franklin, 1990). Residual shrubs showed the same pattern of gradual increase, but had not yet stopped increasing.

By 1994, total understory cover had declined by about 37% from its pre-canopy-closure maximum. This decline is typical of events in young closed-canopy forests. In the Washington Cascades, Long and Turner (1975) found that understory biomass decreased by almost 50% between 20 and 40 years after logging. This initial decline is part of a long term dearth of understory cover. Paul Alaback (1982), working in Southeast Alaska, found that understory biomass peaked about 20 years after disturbance and then declined until the 50-year point. Understory biomass did not begin to increase again until 100 years after disturbance.

Understory species success in relation to their shade-tolerance

Almost all of the herbaceous species that I examined in this analysis declined in the period from 1979 to 1994. All of the woody species, which included all of the shrubs and several herbs, increased in cover between 1979 and 1994. The division between woody and herbaceous growth habit predicts behavior at canopy closure better than the division of herb and shrub layers by height did. Nevertheless, most of my analysis was done with the herb/shrub rather than the herbaceous/woody distinction. Examining these results, it is important to remember that the residual herbs include some woody species.

Invading herbs were negatively correlated with tree cover throughout this study. Their shade-intolerance probably explains the earlier initiation of their decline on the clearcut. Residual herbs were slightly positively correlated with tree cover, tolerating the increasing tree canopy until canopy closure. After canopy closure, however, the rate of residual herb decline was almost identical to that of the invading herbs. Shade-loving residual herbs fared no better at canopy closure than sun-loving species that had grown well in the clearcut.

Rubus ursinus and the sun-loving herbs, *Trientalis latifolia, Whipplea modesta,* and *Hieracium albiflorum,* thrived in the clearcut, showing at least 5% cover in the first 5-10 years after logging. They declined sharply at canopy closure. These species seemed to succeed best at an intermediate level of tree cover. Before canopy closure, they were positively correlated with tree cover, while in the lower-light environment after canopy closure, they preferred areas with less tree cover. The species of the old-growth forest understory that achieved between 1 and 5% cover in the clearcut were *Coptis laciniata, Oxalis oregana, Viola sempervirens,* and *Rubus nivalis.* These species declined just as sharply after canopy closure as the sun-loving species, despite the fact that they were strongly positively correlated with tree cover throughout this period.

Why should apparently shade-loving plants decline as canopy closure occurs? All plants that obtain their energy from photosynthesis require a certain level of light to maintain their energy balance. Shade-loving plants are those that are better able to tolerate lower light levels, either because of lower growth or metabolic rates or greater photosynthetic efficiency (Bazzaz, 1979). These plants may also be unable to grow under high light levels because they are out-competed by species better able to exploit the environment or because they are unable to tolerate the moisture-stress of a drier environment. Shade-loving plants will have an optimal shading environment in which their light and moisture requirements are met and they can out-compete other species.

In old-growth forests, most forest herbs find their optimal habitat in canopy gaps (Stewart, 1988; Spies, 1991). Canopy gaps transmit about 25% of full sunlight, while only 5% of full sunlight reaches the forest floor through tree canopies (Messier, 1992). Understory species shun the areas under the dense canopies of Western hemlock, which transmit about half as much light as Douglas-fir does (Stewart, 1988; Spies, 1991) Young forests have few canopy gaps, and may have very dense canopies. At its extreme, the deep shade under a closed young forest canopy is tolerated only by bryophytes (Franklin and Dyrness, 1973; Alaback, 1982). As canopy closure proceeds, the partial-shade habitat optimal for most forest plant species disappears just as quickly as the few remaining sunny spots.

The forest-restricted herbs that did not measure 1% cover or 20% frequency in any year of the clearcut, *Linnea borealis*, *Festuca occidentalis*, the *Galium* species, and *Vancouveria hexandra*, showed very similar patterns of decline to the other herbs. One would have predicted that the forest-restricted species would have shown the most positive correlation with tree canopy. In fact it was the shade-loving herbs, species that had made minor appearances in the clearcut, that were highly positively correlated with tree cover. This pattern suggests that the forest-restricted herbs were absent from the clearcut not because they could not tolerate the light levels but because of their inability to survive slash burning or competitive interactions with some of the invading species.

In the traditional view of physiognomic succession, the shrubs represent a shade-intolerant group that are quickly eliminated by tree cover (Grime, 1979). In this study, the shade-intolerant invading shrub species of the clearcut behaved according to the traditional model and declined just before canopy closure. They were replaced, however, by residual woody species. Residual shrubs and woody herbs were increasing in cover after canopy closure rather than declining. The physiognomic model of succession assumes that the slow growth rate of woody species determines at which point in succession they peak in abundance. The increases in residual woody species after canopy closure suggest that shade-tolerance may also influence the presence of woody species in the successional sequence.

The two *Ceanothus* species were the major invading shrubs in the clearcut. Their distribution on the watersheds seemed to be determined both by their occurrence in the seedbank and by the degree of disturbance by burning (Halpern, 1989). Both *Ceanothus* species achieved maximum covers of 10 to 15%, and frequencies of about 30%. *Ceanothus velutinus* started declining 10 years after clearcutting while *Ceanothus sanguineus* did not begin to decline until 1983, 20 years after clearcutting. Both frequency and cover of *Ceanothus velutinus* declined drastically at canopy closure in 1987, to 0.5% cover and 1% frequency. *Ceanothus sanguineus* declined more gradually; by 1994, however, it rated only 16% frequency and 2% cover.

Residual xeric-site woody species increased almost two-fold in cover between 1983 and 1987 and then began a gradual decline. *Gaultheria shallon* (salal) was the major member of this group, contributing 6% cover and 40% frequency in 1994. *Rhododendron macrophyllum* and *Corylus cornuta* reached 2-5% cover in 1994 but were present on only about 15% of the plots. *Vaccinium parvifolium* was also present on about 15% of plots but contributed less than 1% cover. This group was not significantly correlated with tree cover. Their ability to increase in cover in the relatively shady environment from 1979 to 1983, however, reflects an ability to withstand the effects of shading.

Gaultheria shallon (salal) has been extensively researched because it may compete with conifer seedlings. I will examine its response to shading in detail as a representative of the xeric-site woody species. Using data from several studies, Long and Turner (1975) found that at a stand level, salal biomass declined logarithimically with overstory tree biomass. Long and Turner (1975) found that salal decreased by 30% from 20 to 40 year old stands, while Schoonmaker and McKee (1988) found that it increased slightly during this same period.

Salal grows faster in full sunlight than in extreme shade; at light levels equivalent to that in a forest gap, however, it grows almost as well as in full sun (Messier, 1992). Under extremely reduced light levels salal switches its biomass allocation from roots to leaves and produces larger, thinner leaves than it would in the sun. By modifying its morphology to capture as much light as possible, salal is able to survive under deep shade. Messier (1992) suggests that under a forest canopy, however, salal grows so slowly that it does not compete significantly with conifers. Despite its ability to survive in shady conditions, salal thrives only when it receives at least partial sunlight. Xeric-site shrubs as a group appeared to tolerate canopy closure initially but then began to gradually decline. The delayed reaction of these shrubs may reflect their ability to survive shading for only a limited period of time.

The only group of species continuing to increase after canopy closure were the mesic-site woody species. These species are major components of old-growth forest understories (Franklin and Dyrness, 1973). In this study, *Acer circinatum* (vine maple), *Berberis nervosa* (Oregon grape), and *Polystichum munitum* (sword fern) all showed 10-20% cover and 65% frequency in 1994. Although this group as a whole was not significantly correlated with tree cover, their presence on such a high percentage of the plots reflects a relatively high degree of shade-tolerance. This shade-tolerance probably accounts for their success after canopy closure.

Vine maple grows well in the understory of old-growth forests but is only moderately shade-tolerant. It was the most frequently present woody species in Watersheds 1 and 3 before logging, and contributed the most cover (Dyrness, 1973). Russel (1974) found that vine maple abundance depends on the amount of light reaching the understory. It is excluded from young forest with extremely dense canopies (Russel, 1974). In low-light environments, vine maple stems sprawl close to the ground; it reproduces asexually by rooting where the limbs touch the ground. In more open environments, vine maple assumes an upright morphology and reproduces sexually (Anderson, 1969). Although more shade-tolerant than salal, vine maple tolerates rather than excels in the shaded environment of the young forest.

Oregon grape shows moderate shade-tolerance and is common in the understories of closed-canopy young forests (Pojar and MacKinnon, 1994). Sword fern thrives in the moist, shady understory environment. The lack of correlation between the mesic-site woody group and tree cover disguises the fact that vine maple was negatively correlated with tree cover while sword fern was positively correlated with tree cover.

The watersheds examined in this study do not support the view that young forests have completely depauperate understories. Seven years after canopy closure, light levels in the understories of these watersheds were high enough to permit an average additive understory cover of 80%. The light levels in the understory in this study are probably intermediate between a typical naturally regenerated forest and a typical intensively managed stand. The success of woody species in the early closed-canopy forest of this study support the model in which young forest understories are dominated by relatively few species of woody plants. The success of residual woody species in the shaded understory combines the ability of some species to survive in the shaded understory and of other species to excel there.

The role of plant regeneration

The dynamics of forest understory species after canopy closure may be related to factors other than shade tolerance *per se*. Grubb (1977) suggests that plants have specific habitat requirements for successful regeneration. These requirements may be different than the habitat requirements of the adult portion of the life-cycle and thus provide a novel force structuring the plant community (Grubb, 1977). Lack of regeneration can result from failure to reproduce, disperse, or establish successfully.

Understory species populations have three sources within young managed forests: plants that survive through the clearcut phase, plants that result from asexual reproduction of the survivors, and plants germinating from seed. Sexual reproduction provides the only means of dispersal into areas not occupied at the time of canopy closure. Although many forest understory species survive in low light environments, they are not likely to reproduce sexually (Niesenbaum, 1993). If plants within, or adjacent to, a forest stand do produce seed, the availability of favorable microsites for initiation may be limiting (Grubb, 1977; Eriksson and Ehrlen, 1992).

The environment of the understory is determined by the intersection of the patterns of the tree canopy and of the forest floor. Because few trees die in the young forest, the forest floor becomes a uniform mat of conifer leaf litter, unbroken by fallen logs, tip-up mounds or pits. Litterfall from coniferous trees provides a physical barrier between seeds and the soil as well as an unfavorable chemical environment (Del Moral and Cates, 1971). Tip-up mounds and pits and fallen logs provide favorable initiation sites for forest species, perhaps because they are relatively free of litter (Beatty, 1984; Thompson, 1980). The pattern of the forest canopy is projected onto the forest floor, influencing light and water availability. Germination and early survival of plants is determined in part by the light environment. Germination and survival through the fourth year of several forest herbs was found to be lower in young than in old-growth stands, probably as a result of lower light levels in the young stand (Tappeiner and Alaback, 1989). Inability to regenerate in the forest understory may explain the declines of shade-tolerant residual herb species that I observed.

Given the limitations on sexual reproduction in the forest environment, many forest understory species rely on clonal reproduction. Their presence in the understory of the young forest is determined by the presence of persistent populations from earlier in succession (Hughes et al., 1988). In the current study, the sun-loving herbaceous species had consistently higher frequencies than the shade-loving and forest herbs (30 *versus* 15-20%). Woody species also tended to enter the closed-canopy phase with greater than 30% frequency. The success of herbaceous species in the forest understory appears to be limited both by their ability to survive in the clearcut environment and by their ability to reproduce in the forest understory.

Long-term changes in the flora of a managed landscape

If species are rare or absent during the stem-exclusion phase of forest succession that dominates managed forests, their long-term persistence in the landscape may be threatened. Species eliminated under the closed canopy will be unable to take advantage of the high light levels when the site is logged again (Eriksson and Ehrlen, 1992). M. O. Hill, studying plantations of introduced conifers in Britain, suggested that many understory species may be lost entirely from managed landscapes. In Britain, as is often the case in the Pacific Northwest, stands are logged before tree growth and mortality has created canopy gaps. Hill reports decreased abundance of understory species in the second rotation of stand regeneration as compared to the first rotation. Duffy and Meir (1992), reporting the lack of recovery of Appalachian understory herbs 80 years after logging, predicted a decline in understory diversity if current logging regimes are maintained.

Changes due to disturbance

The increased frequency of disturbance resulting from logging may lead to changes in the flora of the landscape. One model predicts that disturbance-dependent (ruderal) species will increase in proportion to the frequency and geographical extent of disturbance in the landscape (Denslow, 1980). The prediction that communities subject to more frequent disturbance would be richer in early-successional species while rarely disturbed communities would contained more late-successional species was validated for a variety of community types (Denslow, 1980). Early and late-successional species in Denslow's discussion are distinguished primarily by their dispersal abilities and seedling competitive abilities. Denslow suggests that in communities where the disturbance regime has changed, species composition will be in flux (Denslow, 1980).

In my analysis, I found that many disturbance-dependent (invading) species were still present in the 30 year old forest. Because most are declining, it is impossible to predict whether they will still be present at 70 to 80 years after logging when the watershed would normally be logged again. Any invading species that do persist in the young forest, however, would have a great colonization advantage after the next removal of the canopy. The invading herbs *Epilobium angustifolium, Lactuca muralis, Collomia heterophylla, Vicia americana, Bromus vulgaris, Ceanothus sanguinius,* and *Pteridium aquilinum* all showed greater than 0.04% cover in 1994, 30 years after logging. Of these, only *Epilobium angustifolium* had been present in the pre-disturbance forest. Invading herbs and shrubs each accounted for about 10% of the understory cover in 1994, 7 years after canopy closure.

Rubus ursinus provides the best example of a species that seems likely to capitalize on an increased frequency of disturbance. It showed the highest frequency of any species in this study, always present on at least 85% of the plots. It retained this frequency after canopy closure even though its cover declined by 80%. In the old-growth forest, by contrast, it had been a minor species (Dyrness, 1973). If *Rubus ursinus* is able to persist at its elevated frequency through the rest of a logging rotation, its cover in the next clearcut would probably be even higher. The success of *Rubus ursinus* suggests that species able to capitalize on disturbance but also able to persist under lower light levels may be the most successful species of the managed landscape.

Advantage of species that increase in the young forest

Any herbaceous species that increase in cover after canopy closure are likely to be very successful in a managed landscape dominated by young forests. Two groups show a potential to exploit the young forest environment. The first group are exotic species introduced from other communities that have yet to be 'tested' in this landscape. The presence of exotic species able to succeed in young forests is limited by their ability to disperse. Disturbance by logging provides an opportunity for an invasion. Humans and their vehicles often serve as vectors for invading species. The two exotic herbs examined in this analyses did not decline in response to canopy closure. *Lactuca muralis*, an exotic introduced from Eurasia, retained constant cover and was present on one third of the plots after canopy closure. Schoonmaker and McKee (1988), in contrast, had found *Lactuca muralis* absent in forests more than 20 years old. *Hypericum perforatum*, an exotic species that is a serious weed in pastures and fields, increased from negligible cover to 1% cover in the period of this study. Its frequency increased from 2% to 10%. These exotic species show the potential to become a new part of the permanent forest flora.

The second group likely to succeed in a managed landscape are any residual species adapted to exploit the young forest environment. Tom Spies (1991) compared cover and frequency of understory species in young (30-80 year old), mature (80-180 year old), and old-growth (200-800 year old) forests in the Oregon Cascades. *Chimaphila menziesii* (Menzies' pipsissewa) was the only species to show significantly higher cover in young than in mature or old growth stands. This species was the only herbaceous residual in my analysis that increased substantially with canopy closure. While not common in either the old-growth or the clearcut, *Chimaphila menziesii* increased almost tenfold in cover and frequency between 1979 and 1994. In the deeply shaded regions of the watersheds, young *Chimaphila menziesii* individuals were common in some regions relatively devoid of other understory plants (pers. obs.).

Species abundance in the young and old-growth forest

While the old-growth forest represented the most common forest age of this region before the advent of Europeans, young forests now make up most of forest lands (Cascade Center for Ecosystem Management, 1993). By comparing plant composition between the two forest types, one can begin to predict which species will be lost in a managed landscape. In my analysis, the relationship of herbaceous species to their pre-logging cover seemed to be determined primarily by their success in the clearcut. Sun-loving species that did well in the clearcut remained above their old-growth cover, while species that were less successful in the clearcut were well below old-growth levels. The abundance of woody species, on the other hand, was determined not by their abundance in the clearcut but by their ability to tolerate canopy closure.

Relation of this study to other results

The reactions of species groups to canopy cover found in this study are similar to those found in other studies. In a comparison of different aged sites on the H. J. Andrews, Schoonmaker and McKee (1988) found identical patterns of peak abundance and of decline for residual and invading shrubs and herbs. In their study, residual shrub cover declined from the 30 to the 40-year-old stand. In the Cedar River watershed in the Washington Cascades, invading species were absent in closed canopy stands, residual woody species showed higher cover in the closed canopy stands, and residual herbaceous species showed similar cover before and after canopy closure (Long, 1977).

The previous studies that have examined the effect of canopy closure on understory species have used the chronosequence approach. The use of a series of stands of different ages to approximate what might happen through time on one stand confounds the effects of time and site history. The abundance of a forest herb depends so strongly on the historical presence of the species and on disturbance history that few clear "trends" are observed when comparing different aged sites.

Attempts to predict the fates of individual herb species meet with the further complication that successional trends in understory species abundance differ between stands in different regions of the Pacific Northwest. In Tom Spies' (1991) classification of understory species by forest age classes, species showed different age-class preferences in different regions of the Pacific Northwest. As discussed in the introduction, young stands may have relatively open or densely closed canopies. The dynamics of understory species over time will be very different in differently-structured stands.

The results from this study should be applied with caution to young forests with a different canopy density or management history from that of the watersheds of this study. Dynamics of individual species are likely to be depend strongly on specifics of individual sites. Both this analysis and the published chronosequence studies suggest, however, that species groups defined by growth-habit (woody vs. herbaceous), shade-tolerance, and success in the clearcut environment may show consistent reactions to canopy closure in young managed forests.

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Appendix A.

Common names for species attaining 1% cover or 20% frequency in at least one year in the clearcut or 0.1% cover in the old-growth forest. Names from Pojar and MacKinnon (1994).

Invading species

Latin names	**Common names**
Herbs	
Senecio sylvaticus	Wood groundsel
Epilobium paniculatum	Tall annual willowherb
Epilobium angustifolium	Fireweed
Agoseris spp.	Agoseris
Cirsium spp.	Thistle
Gnaphalium microcephalum	Slender cudweed
Anaphalis margariticea	Pearly everlasting
Rubus leucodermis	Black-cap
Collomia heterophylla	Vari-leaved collomia
Vicia americana	American vetch
Bromus spp.	Brome
Shrubs	
Ceanothus velutinus	Snowbush
Ceanothus sanguineus	Redstem
Pteridium aquilinum	Western Bracken
Rubus parviflorus	Thimbleberry
Salix spp.	Willow
Exotics	
Lactuca muralis	Wall-lettuce
Hypericum perforatum	Klamath weed

Appendix A. continued

Residual species **Latin names**	**Common names**
Ruderal	
Rubus ursinus	Trailing blackberry
Sun-loving herbs	
Trientalis latifolia	Star flower
Whipplea modesta	Whipple vine
Hieracium albiflorum	Hawkweed
Shade-loving herbs	
Viola sempervirens	Evergreen violet
Oxalis oregana	Oxalis
Rubus nivalis	Dwarf bramble
Forest herbs	
Coptis laciniata	Gold-thread
Vancouveria hexandra	Inside-out flower
Festuca occidentalis	Western fescue
Linnea borealis	Twinflower
Galium spp.	Bedstraw
Rare forest herbs	
Chimaphila umbellata	Prince's pine
Goodyera oblongifolia	Rattlesnake plantain
Synthyris reniformis	Spring queen
Mesic-site woody species	
Acer circinatum	Vine maple
Polystichum munitum	Sword fern
Berberis nervosa	Oregon grape
Xeric-site woody species	
Rhododendron macrophyllum	Pacific rhododendron
Gaultheria shallon	Salal
Corylus cornuta	California hazel
Vaccinium parvifolium	Red huckleberry

Appendix B.

List of all species appearing on watersheds 1 and 3 between 1979 and 1994. Classification by growth-form and successional status according to Dyrness (1973) and Halpern (1987). Growth forms: H=herb, S=shrub, T=tree. Successional status: R=residual, I=invading. Question marks indicate that the species had not been classified.

	Growth form	Successional status
Aceraceae		
Acer circinatum	S	R
Acer glabrum	S	I
Acer macrophyllum	T	R
Anacardiaceae		
Rhus diversiloba	S	R
Apocynaceae		
Apocynum androsaemifolium	H	I
Araliaceae		
Aralia californica	H	I
Aristolochiaceae		
Asarum caudatum	H	R
Berberidaceae		
Achlys triphyllum	H	R
Berberis nervosa	H	R
Vancouveria hexandra	H	R
Betulaceae		
Alnus rubra	T	R
Alnus sinuata	S	I
Corylus cornuta var. californica	S	R
Campanulaceae		
Campanula scabrella	H	I
Campanula scouleri	H	I

	Growth form	Successional status	
Caprifoliaceae			
Linnea borealis	H	R	
Lonicera ciliosa	H	I	
Lonicera spp.	H	I	
Sambucus caerulea	S	I	
Symphoricarpus mollis	H	I	
Caryophyllaceae			
Arenaria macrophylla	H	I	
Cerastium arvense	H	I	
Cerastium spp.	H	I	
Cerastium vulgatum	H	I	
Cerastium viscosum	H	I	
Stellaria crispa	H	?	
Stellaria spp.	H	?	
Celastraceae			
Pachistima myrsinites	H	I	
Compositae			
Adenocaulon bicolor	H	R	
Agoseris aurantiaca	H	I	
Agoseris grandiflora	H	I	
Agoseris heterophylla	H	I	
Agoseris spp.	H	I	
Anaphalis margariticea	H	I	
Arnica discoidea	H	R	
Chrysanthamum leucanthemum		H	I
Cirsium arvense	H	I	
Cirsium brevistylum	H	I	
Conyza canadensis	H	I	
Gnaphalium microcephalum	H	I	
Hieracium albiflorum	H	R	
Hypocheris radicata	H	I	
Lactuca biennis	H	I	
Lactuca muralis	H	I	
Lactuca serriola	H	I	
Madia gracilis	H	I	
Madia madioides	H	I	
Petasites frigidus	H	I	
Senecio bolanderi	H	I	
Senecio jacobaea	H	I	
Senecio sylvaticus	H	I	

	Growth form	Successional status
Compositae continued		
Taraxicum officinale	H	I
Tragapogon dubius	H	I
Tragapogon spp.	H	I
Convolvulaceae		
Convolvulus nyctagineus	H	I
Cornaceae		
Cornus nutallii	T	R
Crassulaceae		
Sedum oreganum	H	I
Cruciferae		
Cardamine integrifolia	H	?
Cardamine oligosperma	H	I
Cardamine pulcherrima	H	I
Cardamine spp	H	I
Crepis capillaris	H	I
Cupressaceae		
Libocedrus decurrens	T	?
Cyperaceae		
Carex deweyana	H	I
Carex spp.	H	I
Carex rossii	H	I
Ericaceae		
Arbutus menziesii	T	I
Arcostaphylos columbiana	S	I
Chimaphila menziesii	H	R
Chimaphila umbellata	H	R
Gaultheria shallon	H	R
Pyrola asarifolia	H	R
Pyrola picta	H	R
Pyrola secunda	H	R
Rhododendron macrophyllum	S	R
Vaccinium membranaceum	S	R
Vaccinium parvifolium	S	R
Vaccinium spp	S	R

	Growth form	Successional status
Equisetaceae		
Equisetum arvense	H	I
Equisetum tenax	H	I
Fagaceae		
Castanopsis chrysophylla	T	R
Fumariaceae		
Dicentra formosa	H	I
Graminae		
Agrostis tenuis	H	I
Agrostis alba	H	I
Agrostis diegoensis	H	I
Agrostis exarata	H	I
Agrostis spp.	H	I
Aira caryophyllea	H	I
Bromus ciliatus	H	I
Bromus spp.	H	I
Bromus sitchensis	H	I
Bromus vulgaris	H	R
Cyanosurus echinatus	H	I
Deschampsia elongata	H	I
Elymus glaucus	H	I
Festuca myuros	H	I
Festuca occidentalis	H	R
Festuca spp.	H	I
Festuca subulata	H	I
Holchus lanatus	H	I
Holcus spp.	H	I
Lolium perenne	H	I
Melica harfordii	H	I
Melica spp.	H	I
Melica subulata	H	I
Stipa occidentalis	H	I
Tristeum canadensis	H	I
Tristeum spp.	H	I
Grossulariaceae		
Ribes sanguineum	S	I
Ribes lacustre	S	I
Ribes lobbii	S	I
Ribes spp.	S	I

	Growth form	Successional status
Hydrangeaceae		
Whipplea modesta	H	R
Hydrophyllaceae		
Nemophila parviflora	H	I
Phacelia heterophylla	H	I
Hypericaceae		
Hypericum perforatum	H	I
Iridaceae		
Iris chrysophylla	H	I
Iris spp.	H	I
Iris tenax	H	I
Juncaceae		
Juncus spp.	H	I
Luzula parviflora	H	I
Luzula spp.	H	I
Luzula campestris	H	I
Leguminosae		
Lathyrus polyphyllus	H	I
Leguminosae spp.	H	I
Lotus crassifolius	H	I
Lotus micranthus	H	I
Lotus purshianus	H	I
Lupinus latifolius	H	I
Trifolium microcephalum	H	I
Vicia americana	H	I
Lilaceae		
Brodiaea congesta	H	I
Clintonia uniflora	H	R
Disporum hookeri	H	R
Disporum smithii	H	R
Disporum spp.	H	R
Lilium washingtonianum	H	R
Smilacina racemosa	H	R
Smilacina stellata	H	R
Smilacina spp.	H	R
Trillium ovatum	H	R
Xerophyllum tenax	H	R

	Growth form	Successional status
Labiatae		
Stachys cooleyae	H	I
Stachys mexicana	H	I
Onagraceae		
Circea alpina	H	R
Epilobium angustifolium	H	I
Epilobium minutum	H	I
Epilobium paniculatum	H	I
Epilobium watsonii	H	I
Orchidaceae		
Coralorhiza mertensiana	H	R
Goodyera oblongifolia	H	R
Habenaria uniflora	H	I
Listera caurina	H	?
Listera cordata	H	R
Oxalidaceae		
Oxalis oregana	H	R
Pinaceae		
Pinus lambertiana	T	R
Pinus monticola	T	I
Psuedotsuga menziesii	T	R
Taxus brevifolia	T	R
Thuja plicata	T	R
Tsuga heterophylla	T	R
Polemoniaceae		
Collomia heterohpylla	H	I
Gilia capitata	H	I
Phlox adsurgens	H	I
Polypodiaceae		
Adiantum pedatum	H	R
Athyrum filix-femina	H	R
Blechnum spicant	H	R
Cysopteris fragilis	H	I
Pteridium aquilinum	H	I
Polystichum munitum	H	R

	Growth form	Successional status
Portulaceae		
Monita sibirica	H	I
Montia parvifolia	H	I
Montia perfoliata	H	I
Poylgoniaceae		
Polygonum spp.	H	R
Rumex acetosella	H	?
Primulaceae		
Trientalis latifolia	H	R
Ranunculaceae		
Actea rubra	H	R
Anemone lyalii	H	R
Anemone deltoidea	H	R
Coptis laciniata	H	R
Ranunculus uncinatus	H	I
Rosaceae		
Amalancher alnifolia	S	I
Aruncus sylvester	H	I
Fragaria spp.	H	I
Fragaria vesca	H	I
Holodiscus discolor	S	R
Oemleria cerasiformis	S	I
Potentilla glandulosa	H	I
Prunus emarginata	T	I
Rosa gynocarpum	S	R
Rubus luecodermis	S	I
Rubus nivalis	H	R
Rubus parviflorum	S	I
Rubus ursinus	H	R
Rhamnaceae		
Ceanothus integerrimus	S	I
Ceanothus sanguineus	S	I
Ceanothus velutinius	S	I
Rhamnus purshiana	T	R
Rubiaceae		
Galium aparine	H	I
Galium oreganum	H	R
Galium triflorum	H	R

	Growth form	Successional status
Salicaceae		
Populus tremuloides	T	I
Salix scouleriana	S	I
Salix sitchensis	S	I
Saxifragaceae		
Boykinia elata	H	I
Heuchera micrantha	H	I
Mitella ovalifolium	H	I
Tellima grandiflora	H	I
Tiarella trifoliata	H	R
Tolmeia menziesii	H	?
Saxifraga occidentalis	H	I
Synthyris reniformis	H	R
Schrophulariaceae		
Castilleja hispida	H	I
Mimulus alsinoides	H	I
Mimulus guttatus	H	I
Mimulus spp.	H	I
Penstamon serrulatus	H	I
Penstamon spp.	H	I
Selaginellaceae		
Selaginella wallacei	H	I
Umbelliferae		
Osmorhiza chilensis	H	I
Valerianaceae		
Valeriana scouleri	H	I
Violaceae		
Viola glabella	H	I
Viola sempervirens	H	R