Effects of timber harvest and forest edges on abundance, viability, and physiology of understory plants in *Pseudotsuga* forests of western Washington

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Abstract

Effects of timber harvest and forest edges on abundance, viability, and physiology of understory plants in *Pseudotsuga* forests of western Washington

Cara Ritchie Nelson

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College of Forest Resources

There is widespread interest in the ecological effects of timber harvest, the resultant fragmentation of forest habitat, and the increased area of forest edges. However, there has been surprisingly little research devoted to the consequences of these management activities for understory plants. I investigated short-term responses of understory plants to timber harvest and creation of edges in aggregated retention harvest units at two sites in the western Cascade Range of Washington. Pre- and post-treatment abundance of vascular plants and ground-layer bryophytes was measured in four, 1-ha aggregates (patches of intact forest) and in surrounding harvest areas along 16 transects placed perpendicular to the edges of these aggregates. For three late-seral herbs, *Asarum caudatum, Clintonia uniflora,* and *Pyrola picta*, demographic data (ramet survival, clonal growth, flowering rate, and seedling density) were collected before and for 2 yr after treatment within nine plots in the harvest area and nine in adjacent undisturbed forest. For these same species, morphological and physiological acclimation to removal of the forest overstory was assessed by comparing leaf mass per unit area and leaf chlorophyll content from 20 leaves of plants representing each environment (harvest area and undisturbed forest). Two years after logging, 25% of common vascular plants and 60% of common bryophytes showed significant harvest-related declines in abundance. Forest aggregates retained populations of species that disappeared from or declined substantially in harvest areas, but showed edge-related changes in plant abundance. Within

aggregates, herbaceous species showed larger declines in abundance with proximity to edge than did shrubs or bryophytes, with declines becoming more prominent over time. *Asarum*, *Clintonia*, and *Pyrola* showed different demographic and physiological responses to timber harvest, suggesting that late-seral species that are assumed to respond similarly to timber harvest and associated environmental stresses employ different strategies for re-establishment and long-term recovery. Forest aggregates, which are integral components of current harvest prescriptions, may be especially important as refugia for those plant species that require long periods of time to recover from harvest-related declines.

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Introduction

Concern over widespread loss and fragmentation of late-seral forests has led to substantial changes in timber harvest practices on public lands in the Pacific Northwest. Over the last decade, clearcut logging has been replaced by structural retention harvest (USDA and USDI 1994, Franklin et al. 1997). Despite increasing application of retention harvest, the ecological benefits and silvicultural tradeoffs of this approach have not been quantified. My research represents one part of a larger experiment, the Demonstration of Ecosystem Management Options (DEMO) study, which tests the effects of varying levels and patterns of structural retention harvest on various forest ecosystem components (Aubry et al. 1999, Halpern et al. 1999a). I focus on the efficacy of aggregated retention harvest for conservation of forest understory plants by examining: the direct effects of timber harvest with aggregated retention on the abundance of forest herbs, shrubs, and ground-layer bryophytes; the demographic and physiological responses of late-seral herbs to disturbance and environmental change; the extent to which forest aggregates serve as refugia for disturbance-sensitive plants; and the degree to which species within forest aggregates are influenced by edge-effects.

I have divided this dissertation into three chapters. In the first two chapters, I address short-term responses of vascular plants (Chapter 1) and ground-layer bryophytes (Chapter 2) to aggregated retention harvest. Specifically, I compare post-harvest changes in species richness, community composition, and individual species abundance in harvest areas to those in forest aggregates; describe patterns of response with respect to proximity to forest edge; and assess the environmental correlates of these patterns. In Chapter Three, I undertake a comparative study of three late-seral herbs —*Asarum caudatum*, *Clintonia uniflora*, and *Pyrola picta* — to explore the demographic and physiological trends that underlie species' declines following harvest, as well as species' abilities to acclimate to post-harvest environmental conditions.

This dissertation makes several important contributions to knowledge about the ecology of understory plants in managed landscapes. Previous investigations of understory plant responses to timber harvest have been limited to coarse measures of species' response (e.g., frequency of occurrence or cover) and have not examined the demographic or physiological bases of these responses (e.g., Halpern 1989, Duffy and Meier 1992, Roberts and Zhu 2002). My research documents the demographic trends that underlie patterns of species decline, and the relative abilities of species to adjust to changes in environment. This study is also the first to use an experimental approach with pre- and post-treatment measurements of permanent plots, to assess edge-related responses of understory plants. Previous studies have employed a retrospective or chronosequence approach to reconstruct spatial or temporal patterns of change across forest edges (e.g., Wales 1972, Palik and Murphy 1990, Brothers and Spingarn 1992, Fraver 1994, Matlack 1994, Harper and Macdonald 2001). However, these approaches often fail to account for the patchy distributions of most forest herbs, and potentially confound edge-related responses (or their absence) with variation in the original abundance or distribution of species. Finally, mine is the first study of bryophyte responses to forest edges in the Pacific Northwest. The combination of community, demographic, and physiological studies provides critical information for the conservation of understory plants in managed forests of the Pacific Northwest and elsewhere.

Chapter One

Effects of timber harvest and forest edges on understory herbs and shrubs

Abstract

Aggregated retention of overstory trees is now a standard component of timber harvest prescriptions on federal lands in the Pacific Northwest. Patches of remnant forest retained during harvest are thought to enhance the structural and biological diversity of managed forests, but the extent to which they maintain components of the original understory or promote recovery in adjacent harvest areas has not been tested. I examined short-term (1- and 2-yr) responses of understory plants to disturbance and creation of edges in structural retention harvest units at two sites in the western Cascade Range of Washington. Pre- and post-treatment abundance of vascular plants was measured in four (two at each site), 1-ha aggregates (patches of intact forest) and in surrounding harvest areas along 16, 81-m-long transects placed perpendicular to the edges of these aggregates. Two years after treatment, aggregates had gained an average of two forest species (vs. a loss of two in adjacent areas of harvest) and less than one early-seral species (vs. a gain of nine in adjacent areas of harvest). Aggregates supported populations of late-seral species that disappeared from or declined substantially in harvest areas. However, aggregates showed edge-related changes in plant abundance: one third of common understory herbs declined significantly in cover toward the edge, and changes in community composition were distinctly higher within 5 m of the edge than in the aggregate center. Early-seral species established infrequently within the aggregates, and only within 10 m of the edge. Herbaceous species generally showed larger declines in abundance with proximity to edge than did shrubs, with declines becoming more prominent over time. My results suggest that, over short timeframes, forest aggregates of one or more hectares may play an important role in maintaining plant species richness and composition in forests managed for timber harvest. Assessing the longer term

stability of forest aggregates and the degree to which they influence recovery in adjacent areas of harvest will require continued observation.

Introduction

Concern over widespread loss and fragmentation of late-seral forests has led to substantial changes in timber harvest practices on public lands in the Pacific Northwest. Over the last decade, clearcut logging has been replaced by structural retention harvest (USDA and USDI 1994, Franklin et al. 1997). For example, on federal lands within the range of the northern spotted owl (*Strix occidentalis caurina*), forest managers are now required to retain live trees on at least 15% of the area of each harvest unit, with 70% of this retention in undisturbed patches (forest aggregates) of 0.2 - 1.0 ha and the remainder as individual, dispersed trees. In contrast to clearcut logging, aggregated retention is assumed to: (1) provide residual structures similar to those left by natural disturbances such as wildfires and windstorms, (2) retain biological elements of the original forest, (3) provide refugia and local sources of propagules for disturbance-sensitive species that are eliminated from harvest areas, and (4) create barriers to invasion of early-seral and non-native species (FEMAT 1993, Franklin et al. 1997). Despite recent widespread application of aggregated retention, the ecological benefits or silvicultural tradeoffs of this approach are not well understood. The research reported here represents part of a larger experiment, the Demonstration of Ecosystem Management Options (DEMO) Study, that tests many of these assumptions in mature forests of the Pacific Northwest (Aubry et al. 1999, Halpern et al. 1999a).

Although small forest remnants can have high conservation value (e.g., Shafer 1995, Williams-Linera et al. 1995, Turner et al. 1996), their composition, structure, and function may be diminished as a result of fragmentation and edge influences. Small forest fragments are susceptible to species' extirpations arising from demographic and environmental stochasticity (e.g., population fluctuations, chance disturbance events, or extreme weather) (Diamond 1984, Gilpin and Soulé 1986). In addition, edge effects (see reviews in Ranney 1977 and Murcia 1995), manifested primarily through changes in microclimate, can reduce the effectiveness of small forest remnants for maintaining forest species. Light, temperature, wind speed, humidity, and soil moisture can differ substantially between forest-edge and interior environments, with the depth-of-edge influence varying greatly by variable of interest, edge orientation (aspect), and ecosystem type (e.g., Raynor 1971, Kapos 1989; Williams-Linera 1990; Chen et al. 1993, 1995; Matlack 1993). In an investigation of microclimatic gradients across upland forest edges in the Pacific Northwest, Chen et al. (1995) documented that significant changes in solar radiation and soil moisture extended 30-60 m from the edge of old-growth Douglas-fir (*Pseudotsuga menziesii*) forests, but changes in wind speed and relative humidity extended considerably further (> 240 m). Forest understory responses to edge-related gradients in microclimate have not been studied in these forests.

In this paper I examine the short-term responses (1- and 2-yr after harvest) of forest understories to recently created edges in mature Douglas-fir forests in western Washington. Past studies of understory plant response to forest edges have employed a retrospective or chronosequence approach to reconstruct spatial or temporal patterns of change (e.g., Wales 1972, Palik and Murphy 1990, Brothers and Spingarn 1992, Fraver 1994, Matlack 1994, Harper and Macdonald 2001). However, these approaches often fail to account for the patchy distributions of most forest herbs, and potentially confound edge-related responses (or their absence) with variation in the original abundance or distribution of species. This study is the first to use an experimental approach with detailed pre- and post-treatment measurements on permanent plots, to assess edge-related responses of understory plants. This design enables me to reliably quantify the spatial pattern, magnitude, and time course of vegetation responses in 1-ha forest aggregates retained during timber harvest. I pose five questions about early patterns of vegetation change: (1) Do species richness and community composition remain stable in forest aggregates? (2) Do aggregates retain disturbance-sensitive herbs that decline in, or are lost from, adjacent areas of harvest? (3) Within forest aggregates, (a) are there edge-related gradients in vegetation response (changes in species richness, community composition, or abundance of individual species) and (b) if so, do these gradients correlate with changes in light availability or disturbance? (4) Do vegetation responses within forest aggregates vary with edge orientation (aspect)?

Methods

Study sites

My study sites, Butte and Paradise Hills, lie along the west slope of the Cascade Range in southern Washington on the Gifford Pinchot National Forest. Butte (46°22'07" N, 121°34'40" W) is located at an elevation of 1012-1122 m in the *Tsuga heterophylla* zone (Franklin and Dyrness 1973). Slopes average 40% and face southeast. Soils are well drained and fairly shallow, consist of loamy sands derived from residuum and colluvium, and are covered by a shallow surface layer of volcanic ash originating from the 1980 eruption of Mount St. Helens (Wade et al. 1992). Forests are ca. 70-80 yr old and dominated by *Pseudotsuga menziesii*; *Tsuga heterophylla* and *Thuja plicata* are also common (Halpern et al. 1999a). Prior to harvest, overstory canopy height, stem density, and basal area averaged 36 m, 1150 trees/ha, and 56 m^2/ha, respectively. Dominant understory species included *Tsuga heterophylla*, *Thuja plicata*, *Acer circinatum*, *Berberis nervosa*, *Pteridium aquilinum*, *Achlys triphylla*, and *Chimaphila umbellata*; ground-layer bryophytes averaged 7% cover, with *Rhytidiopsis robusta* and *Eurhynchium oreganum* as the most common species.

Paradise Hills (46°00'46" N, 121°56'34" W) is located at an elevation of 957-1000 m in the *Abies amabilis* zone (Franklin and Dyrness 1973). Slopes are gentle (averaging 18%) and face east to northeast. Soils are deep sandy loams derived from volcanic ash and pumice, till, and residuum (Wade et al. 1992). Forests are 110-140 yr old and are dominated by *Pseudotsuga menziesii*, with *Tsuga heterophylla*, *Thuja plicata*, and *Abies amabilis* as common associates (Halpern et al. 1999a). Prior to harvest, canopy height, stem density, and basal area averaged 39 m, 740 trees/ha, and 73 m^2/ha, respectively. Dominant understory species included *Tsuga heterophylla*, *Abies amabilis*, *Vaccinium membranaceum*, *V. ovalifolium*, *Xerophyllum tenax*, *Achlys triphylla*, and *Cornus canadensis*; ground-layer bryophytes averaged 23% cover, with *Rhytidiopsis robusta* and *Hypnum circinale* as the most common species.

Harvest histories

Within a 13-ha harvest unit at each site, five 1-ha (56-m radius) circular forest aggregates were retained (Fig. 1.1, a). In the surrounding area, all merchantable trees (> 18 cm diameter at breast height) were cut and removed (using a helicopter at Butte and a combination of tracked shovel loaders and rubber-tired skidders at Paradise Hills). Non-merchantable subcanopy trees were retained in the harvest areas at Butte, but were felled at Paradise Hills. Compacted soil in skid trails (present between aggregates at Paradise Hills) was loosened with a tracked excavator, and then covered with logging slash; elsewhere, slash was left in place. Yarding was completed in July 1997 at Butte and in September 1997 at Paradise Hills (for details see Halpern and McKenzie 2001).

Sampling design

Pre-treatment sampling was conducted from 1 July to 9 September 1996 and post-treatment sampling from 5 July to 15 September 1998 (year 1) and 12 July to 14 September 1999 (year 2). At each site, two of the five circular aggregates marked for retention were randomly selected. In each of these (Fig. 1.1, b), I established four perpendicular transects (Fig. 1.1, c), 81 m in length, which extended in cardinal directions from the aggregate center and ended 25 m into the surrounding area to be harvested. Twelve bands of permanent plots were established along each transect, eight in the area marked for retention (at distances of 0, 5 10, 15, 20, 30, 40, and 50 m from the edge) and four in the area marked for harvest (at distances of 5, 10, 15, and 25 m from the edge) (Fig. 1.1, c). Thus, bands were spaced at 5-m intervals on both sides of the forest edge, where I expected steep gradients in vegetation response, and at 10-m intervals elsewhere.

Each band (Fig. 1.1, d) consisted of five, 1-m^2 subplots (Fig. 1.1, e), within which I estimated the cover of all vascular plant species. When species-level identifications were not possible, taxa were recorded at the generic level. Nomenclature follows Hitchcock and Cronquist (1973).

To explore possible correlates of vegetation change, I quantified cover of logging slash and soil disturbance (year 1) and light availability (year 2). Cover of logging slash and disturbed soil was estimated along the interior edge of each band (Fig. 1.1, f), using the line-intercept method. Light availability, which correlates with many other physical factors (e.g., temperature, humidity, soil moisture; Matlack 1993), was estimated with a CI-110 digital canopy imager with a 150-degree lens (CID Inc., Vancouver, WA). Digital photographs were taken from the end points of each band (Fig. 1.1, g) at a height of 1 m from the ground surface. Photographs were taken between 20 June and 15 July, either before 08:00 or after 18:00 hr to minimize direct exposure to sun (Easter and Spies 1994). Digital images were analyzed using Scanopy 2.0b software (Regent Instruments Inc. 1999) to calculate percent open sky (Anderson 1964, Canham 1988).

Data are archived at the Oregon State University Forest Science Data Bank (FSDB; http://www.fsl.orst.edu/lter/data.cfm?topnav=8).

Data manipulation and response variables

Prior to statistical analysis, band-level means were calculated for cover of individual species and light availability, and band-level species richness was tallied. To compare responses in the two post-treatment environments, I generated mean values for individual forest aggregates and for surrounding harvest areas (n = 32 bands per aggregate, n = 16 bands per adjacent area of harvest). To analyze spatial gradients in vegetation response within aggregates, I computed mean values for each of the eight sample distances in each aggregate.

I considered three types of response variables: species richness, community composition, and species abundance (percent cover). Species richness was plotted at a range of spatial scales — number of species per band, per transect, per forest aggregate or adjacent harvest area, per study site, and for both sites combined. However, statistical comparisons of richness between post-treatment environments were limited to band-level values because sampling intensity differed in forest aggregates and harvest areas. To quantify the contributions of the original forest flora and ruderal, open-site species to changes in richness, separate calculations were made for species classified *a priori* as "forest understory" and "early-seral," respectively (based on Halpern 1989). Changes in community composition were expressed as the percent dissimilarity (PD) between pre- and post-treatment measurements, using the quantitative form of Sørensen's community coefficient (Mueller-Dombois and Ellenberg 1974):

$$\mathrm{PD} = 100*(1-2*(\Sigma \min [cov_{0i}, cov_{ti}] / \Sigma [cov_{0i} + cov_{ti}])) \qquad (1)$$

where cov_{0i} and cov_{ti} are band-level cover of species i in pre- and post-treatment samples, respectively. Separate calculations were made for each post-treatment sampling date (year 1 and 2).

To standardize for spatial variation in species richness and abundance prior to treatment, a "change value" was computed for each variable as the arithmetic difference between pre- and post-treatment values. Separate calculations were made for each post-treatment sampling date.

Statistical analyses

Relative stability of forest aggregates.—I assessed the comparative responses of vegetation in forest aggregates and adjacent areas of harvest (Questions 1 and 2) by conducting a series of two-sample *t*-tests (Sokal and Rohlf 1981) using mean "change values" (or mean PD for community composition) as the measure of response. Separate tests were conducted for first- and second-year changes. Tests of individual species' responses were limited to the 29 taxa present prior to treatment in at least three of the four aggregate/harvest area pairs and 10% of all sample bands; I refer to these as "common species."

Edge-related gradients in vegetation response and physical environment within aggregates.— Edge-related gradients in vegetation response (Question 3a) were assessed by calculating Spearman rank correlation coefficients (Sokal and Rohlf 1981) between mean values of vegetation variables (changes in richness and cover, and PD) and distance from the aggregate edge ($n = 32$; i.e. 8 distances x 4 aggregates), with separate analyses for each post-treatment year. Edge-related patterns in richness of early-seral species were not examined, because these taxa were rarely found in the aggregates (see *Results*). Species-level analyses were limited to the 29 common taxa noted above. Environmental variables (open sky, logging slash, and disturbed soil) were also correlated with distance from edge and with vegetation responses (Question 3b).

Effects of edge orientation on vegetation response.— To determine if understory responses were influenced by edge orientation (Question 4), I used one-way ANOVAs (Sokal and Rohlf 1981) to compare the mean response of transects representing the four cardinal directions ($n = 4$). For each response variable, a mean "change value" (or PD for community composition) was calculated from the eight bands representing each transect within each aggregate. Separate tests were conducted for first- and second-year changes.

All statistical analyses were conducted with Systat version 10 (SPSS 2001), with an alpha level of 0.05 as the criterion for reporting statistical significance. Given the number of tests conducted, I do not focus on the statistical significance of any particular test result, but rather emphasize the frequency or proportion of significant responses among the groups of species or variables tested.

Results

Differences between forest aggregates and adjacent areas of harvest

Post-harvest light availability, logging slash, and disturbed soil.— Percent open sky and cover of logging slash were significantly lower in forest aggregates than in adjacent harvest areas; however, cover of disturbed soil did not differ significantly between environments (Table 1.1). Although logging operations were designed to minimize disturbance to aggregates, logging slash fell into 20% of the bands (primarily along the edges), and harvest-related soil disturbance was observed in 5%.

Changes in species richness and composition.—Prior to treatment, a total of 61 vascular plant taxa were observed (Table 1.2); all were classified as forest understory species. Species richness was not evenly distributed within sites: at most spatial scales, richness was higher in areas targeted for harvest than in areas that would remain uncut (Fig. 1.2 a).

Two years after treatment, none of the 29 common species were extirpated from sample bands in harvest areas at Butte, but two (*Chimaphila menziesii* and *Listera caurina*) were lost from Paradise Hills. Individual aggregates (each sampled with 32, 5-m^2 bands) gained an average of two forest species, and adjacent areas of harvest (sampled with half as many bands) lost an average of two species (Fig. 1.2 a). At the same time, a total of 15 early-seral taxa colonized sample bands (Table 1.3), with individual aggregates gaining an average of fewer than one species and adjacent areas of harvest an average of nine (Fig. 1.2 b). In harvest areas, richness of early-seral species nearly doubled from year one to two (Fig. 1.2 b).

At the scale of individual bands, changes in richness of forest species were significantly greater (declined) in harvest areas than in aggregates (where there was minimal, non-significant change); however, the difference between environments was not significant in year two (Table 1.4). Increases in richness of early-seral species and changes in community composition (percent dissimilarity, PD) were significantly greater in harvest areas than in aggregates (Table 1.4), with levels of significance increasing from year one to two.

Abundance of individual species.— Prior to treatment, forest understory species varied considerably in their distribution and abundance within sites; 16% were restricted either to the areas that would remain uncut or to those that would be harvested (Table 1.2), and for 17 of the 29 common species, mean cover differed more than two-fold between environments.

After treatment, most species declined in cover in both environments (Fig. 1.3); however, the average magnitude of decline was greater in harvest areas than in aggregates (39 vs. 12% respectively). Eight species showed significant differences in response between environments; seven of these (*Acer circinatum*, *Clintonia uniflora*, *Goodyera oblongifolia*, *Listera caurina*, *Pyrola picta*, *P. secunda*, and *Vaccinium parvifolium*) declined more in harvest areas than in aggregates, and one (*Hieracium albiflorum*) increased more in harvest areas (Fig. 1.3).

Gradients in environment and vegetation response within forest aggregates

Spatial gradients in light availability, logging slash, and soil disturbance.— Within forest aggregates, percent open sky and cover of logging slash increased significantly with proximity to forest edge (Table 1.5); however, these increases were largely restricted to a distance of ca. 10-15 m from the edge (Fig. 1.4 a and b). Cover of disturbed soil did not show a significant correlation with proximity to edge (Table 1.5), although there were several relatively high values within 5 m of the forest margin (Fig. 1.4 c).

Spatial gradients in species richness and community composition.— Within forest aggregates, proximity to edge explained little of the variation in the change in richness of forest species (Table 1.5, Fig. 1.5); however, the strength of this relationship increased with time (Table 1.5). There were only two occurrences of early-seral species in the aggregates, both within 10 m of the edge (Fig. 1.5). Changes in community composition (PD) increased significantly with proximity to edge (Table 1.5), due in large part to changes at the forest margin (0-5 m) (Fig. 1.6). Change in forest species richness showed a significant negative correlation with light availability, slash accumulation, and cover of disturbed soil; change in community composition (PD) showed a significant positive correlation with light availability and slash accumulation (Table 1.5).

Spatial gradients in species abundance.— Herbaceous species were more affected by proximity to edge than were shrubs, and the number and strength of significant relationships increased with time: declines were significant for three herbaceous species in year one and eight in year two, but not for any shrubs in either year (Fig. 1.7 a). Of the eight species that showed significant negative correlations between change in cover and edge proximity (Fig. 1.7 a), five also showed significant negative correlations with light availability (Fig. 1.7 b) and six with cover of logging slash (Fig. 1.7 c). No species showed a significant positive correlation between abundance and proximity to edge.

Effects of edge orientation.— Edge orientation did not affect species richness, composition or cover of individual species within forest aggregates: of 64 tests, only one resulted in a significant effect.

Discussion

It is important to acknowledge several limitations of my work. First, in a strict sense, my inferences about disturbance and edge effects apply to structural retention harvests of mature forests implemented as part of the Northwest Forest Plan (USDA and USDI 1994). Harvest-related disturbance, microclimate, and associated edge-effects may differ in traditional clearcut units in which the contrast between harvest area and intact forest is more pronounced (*cf.* Chen et al. 1993, 1995). Species may show different responses to disturbance and edge in these contexts, and direct comparisons with my work should be made with caution. Second, the forest aggregates used in this study were of fixed size and shape (1-ha circles); edge-related gradients might have differed in smaller or larger patches or in patches with a greater edge-to-area ratio. Thus, additional research on the influence of patch size and shape would make an important contribution to future harvest design (but see *Management considerations* below). Finally, my conclusions are limited to short-term (two-year) responses. I acknowledge this limitation as I interpret my results, and I speculate about future trends. Although longer term observations (in progress) might lead to different conclusions, it is critical to document these initial responses both to understand the time course and mechanisms of response, and to establish a reference point for assessing future change.

Pre-treatment data, which are rare in ecological studies of forest edges, were critical for discriminating between patterns that may have arisen from spatial distributions in the original forests and those due to harvest or edge effects. For example, prior to treatment, species richness was higher in areas that were subsequently logged than in those that remained as aggregates, and many species were either restricted to, or had greater abundance in, one of the two environments. Without knowledge of these initial conditions, some differences in the richness or abundance of forest species might have been erroneously attributed to treatment effects, and some treatment effects might not have been detected. Thus, my results clearly demonstrate the importance of pre-treatment data in documenting and interpreting responses to harvest and creation of forest edges.

Forest aggregates vs. adjacent harvest areas

Compared to harvest areas, forest aggregates showed minimal change in species richness and composition two years after treatment. Aggregates were largely resistant to colonization by early-seral species, and changes in composition were small compared to those in adjacent harvest areas. Despite these differences, there was substantial year-to-year variation within aggregates (PD of ca. 20%). Some of this variation is attributable to edge effects (see below). However, similar levels of compositional change were observed in adjacent control treatments (undisturbed forest) sampled as part of a broader study of vegetation responses to varying levels and patterns of green-tree retention (Halpern et al. *in press*). It is likely that patterns of precipitation and temperature — which varied considerably among sampling years — and their effects on plant phenology were the primary drivers of compositional change within forest aggregates.

In the short term, forest aggregates can serve as refugia for shade-tolerant herbs that are extirpated from, or decline in, adjacent areas of harvest. One quarter of the species tested showed significantly greater declines in harvest areas than in aggregates, and two formerly common species, *Chimaphila menziesii* and *Listera caurina*, disappeared from harvest areas at Paradise Hills. My estimates of the frequency and magnitude of species declines may be low, given that all sample bands in harvest areas were located within 25 m of an aggregate. Declines should be less pronounced in these areas (due to shading from aggregates) than in more exposed portions of harvest units. Thus, because most forest species do not maintain a viable seed bank (e.g., Halpern et al. 1999b), local persistence in and subsequent dispersal of seeds from aggregates may greatly facilitate reestablishment of populations in harvested areas.

Forest aggregates may be particularly important for orchids and ericaceous herbs and sub-shrubs, many of which are obligate mycotrophs (Castellano and Trappe 1985). These species may decline in logged areas due to associated loss of mycorrhizal fungi (Schoenberger and Perry 1982, Amaranthus 1992). Both of the common orchids *(Goodyera oblongifolia* and *Listera caurina*) and two of five common ericaceous herbs (*Pyrola picta* and *P. secunda)* showed significant declines in harvest areas on my sites. Declines for two additional ericaceous species (*Chimaphila menziesii* and *C. umbellata*) were more than 50% greater in harvest areas than in aggregates (although small sample size limited my ability to demonstrate significant differences). These observed declines are consistent with the results of long-term studies of succession in clearcut forests of western Oregon (Halpern 1989, Halpern and Spies 1995).

Liliaceous herbs were also sensitive to timber harvest on my sites. Of five common species, the cover of four (*Clintonia uniflora, Smilacina racemosa*, *S. stellata,* and *Trillium ovatum)* declined over 40% more in harvest areas than in forest aggregates. *Clintonia uniflora*, which showed a significant difference in performance between environments, may be sensitive to logging disturbance, because its long, slender rhizomes (Antos 1988) are easily severed. Loss of physiological integration among ramets (Salzman and Parker 1985, Alpert and Mooney 1986, Hutchings and Bradbury 1986, Marshall 1990) may lead to reduced plant density or vigor, as I observed in harvest areas. Declines in abundance may also result from photoinhibition (Powles 1984) related to prolonged exposure to high levels of solar radiation, or from herbivory. Members of the Liliaceae are highly palatable to deer (*Odocoileus* spp.) and other herbivores (Anderson 1994) that often respond positively to canopy removal and creation of edges (Alverson et al. 1988).

Gradients in response within forest aggregates

Within forest aggregates, spatial gradients in community composition, species richness, and the abundance of individual forest species correlated to varying degrees with proximity to forest edge. Changes in community composition were most apparent at the forest border (0-5 m). I also found slightly reduced richness at the edge, reflecting declines of some forest species and minimal establishment of early-seral species. This overall decline in richness in newly created edges contrasts with studies of older edges that support greater diversity of species (Gysel 1951, Brothers and Spingarn 1992, Burke and Nol 1998). I anticipate gradual increases in richness near aggregate edges with time, as early-seral species become more abundant in adjacent harvest areas.

Although none of the common shrub species showed significant response, eight of 23 common herbs declined near edges. All but one of these herbs showed similar preference for forest-interior environments in a study of older forest edges in the Klamath Mountains of California (Frost 1992, Jules et al. 1999). However, eight other "interior" species from the Klamath study showed no response to edge at my Washington sites. These differences may reflect contrasting levels of microclimatic stress (the Klamath region is substantially warmer and drier than my study area) or the short timeframe of my study. Most forest herbs are clonal and, during short periods of unfavorable resource conditions, many are capable of drawing upon nutrient reserves (Eriksson and Jerling 1990) or of physiological integration among ramets (Salzman and Parker 1985, Alpert and Mooney 1986, Hutchings and Bradbury 1986, Marshall 1990). With time, however, reserves may be depleted and rhizome connections may decay. On my sites, a marked increase from year one to two in both the number of species showing significant declines and the magnitude of decline suggests that edge effects will become more apparent with time.

Recruitment of early-seral species within forest aggregates was rare and limited to within 10 m of the edge. Although edge susceptibility to invasion varies within and among regions (Murcia 1995), others have observed similar depth of penetration (< 15 m) of early-seral species (Matlack 1994, Burke and Nol 1998, Cadenasso and Pickett 2001, Honnay et al. 2002). Several factors may have limited invasion of forest aggregates by these species on my sites. First, they colonized infrequently in the harvested portions of treatment units. This contrasts with the typical pattern of abundant establishment after clearcut logging and broadcast burning in this region (Dyrness 1973, Schoonmaker and McKee 1988, Halpern 1989) and may be attributable to high levels of logging slash (nearly 70% cover), limited ground disturbance (< 3% cover of disturbed soil), and absence of fire on these sites. Second, woody vegetation at the margins of forest aggregates may have limited dispersal of early-seral species by physical obstruction (Wales 1967, Ranney et al. 1981, Brothers and Spingarn 1992, Cadenasso and Pickett 2001). Typically, this "self-armoring" of forest edges occurs over time, through increased growth of shrubs and trees in response to elevated light at the forest margin (Brothers and Spingarn 1992, Cadenasso and Pickett 2001). However on my sites, the structure of mature, Douglas-fir forests may present a barrier to dispersal even before self-armoring begins. Third, recruitment is likely to have been limited by inadequate conditions for germination. Even if seeds had been present in the soil (e.g., Halpern et al. 1999b) or had dispersed into the aggregates, the virtual absence of disturbed soil (< 5% of bands, < 1% cover) may have prevented germination and establishment. Despite limited occurrence of early-seral species during the period of observation, it is possible for some exotic taxa to invade forests more slowly, and their abundance may increase over time (e.g., Wiser et al. 1998). In my montane forest sites, the only species with this potential is *Lactuca muralis,* and to date, its distribution is limited to harvest areas.

Increased light availability and harvest-related disturbance were limited to a 10- to 15-m-wide band, leaving approximately 50% of the forest aggregate unchanged for these attributes. However, this large outer band was notably altered, with logging slash covering 38% of the ground surface and open sky roughly double that at the center of the aggregate. Elevated light to a depth of 15 m is consistent with values reported by other investigators for temperate and tropical forest edges (Reifsnyder 1965, Geiger 1966, Reifsnyder et al. 1971, Bruner 1977, Burke and Nol 1998, Williams-Linera et al. 1998), but slightly lower than the 30- to 60-m penetration of short-wave solar radiation reported by Chen et al. (1995) for edges adjacent to old-growth forest in the Cascade Range of Washington and Oregon.

Almost 30% of species tested showed significant negative correlations with light availability. Many of these species reach maximum abundance in late-seral forests (Spies 1991) and are adapted to moist, shaded microsites. Some understory species may be able to avoid or tolerate elevated light and associated declines in surface soil moisture at forest margins by adjusting leaf position, morphology, or resource allocation (Powles 1984) or by relying on clonal integration and exploitation of new habitats (Alpert and Mooney

1986, Sutherland and Stillman 1988, Stuefer et al. 1996). Others, however, may not possess these avoidance mechanisms and may experience photoinhibition (Jurik et al. 1979, Powles 1984) within edge zones.

Some species showing edge-related declines in abundance may be responding to factors other than light availability. For instance, *Listera caurina* and *Rubus lasiococcus* showed stronger relationships with cover of slash than with open sky, suggesting that burial disproportionately affects their survival or growth. Herbivory, which can decrease the size and reproductive output of *Clintonia* in eastern deciduous forests (Anderson 1994, Balgooyen and Waller 1995), may be a factor in the edge-related decline of *C. uniflora*, which was not correlated with any of the environmental variables measured. Although I did not quantify herbivory, I did find evidence (scat and travel paths) of elk (*Cervus elaphus*) and deer more frequently within forest aggregates after treatment.

Edge orientation can influence vegetation response in other forest types (Wales 1972, Ranney et al. 1981, Palik and Murphy 1990, Brothers and Spingarn 1992), presumably through moderation of microclimate (Chen et al. 1995). Although I detected no effect of orientation in the current study, it may become increasingly important if edge effects become more prominent with time.

Management considerations

Identifying minimum sizes for protected areas is an important issue in conservation biology (Meffe and Carroll 1994). Although large reserves are clearly necessary for many ecosystem processes and components (e.g., interior-forest microclimate [Chen et al. 1995] and wide-ranging carnivores [Picton 1979, Newmark 1987]), smaller forest remnants also may have high conservation value, especially in landscapes that are intensively managed for timber production. Investigators working in different forest ecosystems have found that small patches (2 - 9 ha) of intact forest may retain interior-forest vegetation (Ranney 1977, Levenson 1981, Kapos 1989, Matlack 1994) and that depth-of-edge influence does not vary with patch size (Brothers and Spingarn 1992, Young and Merriam 1994, Burke and Nol 1998). My results suggest that, over *short timeframes*, aggregates of at least 1 ha in size may play an important role in protecting late-seral plant species through retention harvest of mature, Douglas-fir forest. However, temporal trends suggest that edge effects judged to be small in the short term may become more prominent with time. Additional research at these and other sites in the Pacific Northwest is necessary to identify the temporal and spatial scales over which forest aggregates serve their intended ecological functions.

Table 1.1. Results of two sample *t*-tests ($df = 6$) comparing environmental variables in forest aggregates ($n = 4$) and adjacent areas of harvest ($n = 4$).

	Mean (SE)			
	Forest aggregates	Harvest areas	*t*	*P*
Open sky (%)	17 (1.3)	45 (2.6)	-9.79	<0.001
Cover of logging slash (%)	10 (0.7)	66 (6.0)	-9.24	0.002
Cover of disturbed soil (%)	1 (0.2)	3 (1.1)	-2.07	0.084

Table 1.2. Frequency (% of bands) and mean cover of species found before treatment in areas scheduled to be retained as forest aggregates ($n = 128$ sample bands) and those to be harvested ($n = 62$ sample bands). Mean cover of < 0.05% is indicated by t (trace).

	Forest aggregates		Harvest areas (prior to logging)	
Species	Frequency (%)	Cover (%)	Frequency (%)	Cover (%)
Grasses				
Bromus vulgaris	15	t	13	t
Ferns and fern allies				
Pteridium aquilinum	81	3.4	74	3.2
Polystichum munitum	1	t	3	0.1
Blechnum spicant	1	t	2	t
Athyrium filix-femina			5	0.1
Adiantum pedatum			2	t
Lycopodium clavatum			2	t
Forbs				
Viola sempervirens	74	0.3	67	0.3
Pyrola secunda	60	0.2	54	0.2
Clintonia uniflora	52	0.4	48	0.5
Achlys triphylla	48	3.7	48	4.0
Pyrola picta	46	0.1	38	0.1
Xerophyllum tenax	45	2.6	48	5.6
Trillium ovatum	36	0.1	38	0.1
Smilacina stellata	32	0.3	34	0.3
Goodyera oblongifolia	27	0.1	15	t
Anemone deltoidea	22	t	25	0.1

Table 1.2. continued

	Forest aggregates		Harvest areas (prior to logging)	
Species	Frequency (%)	Cover (%)	Frequency (%)	Cover (%)
Hieracium albiflorum	16	t	20	t
Listera caurina	16	t	13	t
Pyrola asarifolia	15	0.1	23	0.1
Smilacina racemosa	14	0.1	16	0.1
Vancouveria hexandra	14	0.2	11	0.1
Trientalis latifolia	9	t	8	t
Tiarella trifoliata	5	t	15	0.1
Pedicularis racemosa	5	t	13	t
Campanula scouleri	3	t	3	t
Disporum hookeri	3	t	2	t
Galium triflorum	2	t	7	t
Adenocaulon bicolor	2	t	2	t
Streptopus amplexifolius	2	t		
Viola glabella	1	t	5	t
Osmorhiza chilensis	1	t	2	t
Actaea rubra	1	t		
Aquilegia formosa	1	t		
Pyrola aphylla	1	t		
Asarum caudatum			8	0.1
Nothochelone nemorosa			2	t
Sub-shrubs				
Chimaphila umbellata	84	1.8	69	1.9
Linnaea borealis	81	0.7	85	1.0

Table 1.2. continued

	Forest aggregates		Harvest areas (prior to logging)	
Species	Frequency (%)	Cover (%)	Frequency (%)	Cover (%)
Rubus ursinus	77	0.7	70	0.7
Cornus canadensis	72	2.6	72	2.4
Rubus lasiococcus	59	0.5	64	0.5
Chimaphila menziesii	27	0.1	26	t
Rubus nivalis	3	0.1	2	t
Shrubs				
Vaccinium membranaceum	66	2.6	74	3.9
Berberis nervosa	63	7.5	54	5.6
Vaccinium parvifolium	53	1.2	64	1.9
Vaccinium ovalifolium	38	4.1	34	4.7
Pachistima myrsinites	38	0.3	31	0.5
Gaultheria ovatifolia	32	0.4	41	0.4
Rosa gymnocarpa	30	0.4	13	0.2
Sorbus spp.	16	t	13	t
Symphoricarpos mollis	13	0.2	5	t
Acer circinatum	9	2.2	21	2.7
Rubus parviflorus	5	0.1	2	t
Gaultheria shallon	3	0.1	8	0.5
Alnus sinuata	2	t	7	1.0
Acer glabrum	2	t	3	t
Menziesia ferruginea	2	t	2	0.2
Amelanchier alnifolia	2	t	2	t
Ribes lacustre			2	t

Table 1.3. Frequency (% of bands) and mean cover of early-seral taxa found two years after treatment in forest aggregates and harvest areas. *n* = total number of sample bands. Mean cover of < 0.05% is indicated by t (trace).

	Forest aggregates (*n* = 128)		Harvest areas (*n* = 62)	
Species	Frequency (%)	Cover (%)	Frequency (%)	Cover (%)
Grasses, sedges, and rushes				
Poaceae spp.			6	t
Carex deweyana			5	t
Agrostis sp.			2	t
Carex spp.			2	t
Festuca sp.			2	t
Luzula campestris			2	t
Forbs				
Senecio sylvaticus	1	t	31	t
Epilobium watsonii	1	t	11	0.2
Cirsium vulgare			29	0.1
Lactuca muralis			13	t
Epilobium angustifolium			11	t
Hypochaeris radicata			6	t
Epilobium spp.			5	t
Epilobium paniculatum			3	t
Fragaria vesca			3	t
Anaphalis margaritacea			2	t
Lactuca serriola			2	t
Trifolium sp.			2	t

Table 1.4. Results of two sample *t*-tests (*df* = 6) comparing changes in species richness (number of species per band) and community composition (percent dissimilarity, PD) in forest aggregates (*n* = 4) and adjacent areas of harvest (*n* = 4). A mean change of < 0.5 species per band is indicated by t (trace).

	Mean (SE)			
	Forest aggregates	Harvest areas	*t*	*P*
Change in forest species richness				
Year 1	t (0.2)	-2 (0.6)	3.37	0.032
Year 2	1 (0.3)	-1 (0.8)	2.17	0.073
Change in early-seral species richness				
Year 1	t (<0.1)	1 (0.3)	-2.48	0.048
Year 2	t (<0.1)	1 (0.4)	-3.28	0.017
Percent dissimilarity (PD)				
Year 1	22 (0.4)	43 (4.5)	-4.83	0.003
Year 2	21 (0.6)	39 (2.2)	-8.10	<0.001

Table 1.5. Spearman rank correlation coefficients (r, $n = 32$) between distance from edge or environmental variables and change in community-level attributes for each sample date. Probabilities of significance (P) are shown in parentheses. For edge proximity, negative coefficients indicate declines with proximity to forest edge.

	Edge proximity	Open sky	Logging slash	Disturbed soil
	r (*P*)	*r* (*P*)	*r* (*P*)	*r* (*P*)
Environmental variables				
Open sky (%)	0.80 (<0.001)			
Cover of logging slash (%)	0.72 (<0.001)	0.56 (0.001)		
Cover of disturbed soil (%)	0.24 (0.180)	0.20 (0.268)	0.22 (0.218)	
Change in forest species richness				
Year 1	-0.32 (0.073)	-0.49 (0.004)	-0.42 (0.017)	-0.26 (0.151)
Year 2	-0.44 (0.011)	-0.60 (<0.001)	-0.44 (0.012)	-0.40 (0.023)
Percent dissimilarity (PD)				
Year 1	0.41 (0.022)	0.41 (0.019)	0.35 (0.053)	0.06 (0.738)
Year 2	0.73 (<0.001)	0.62 (<0.001)	0.48 (0.006)	0.15 (0.407)

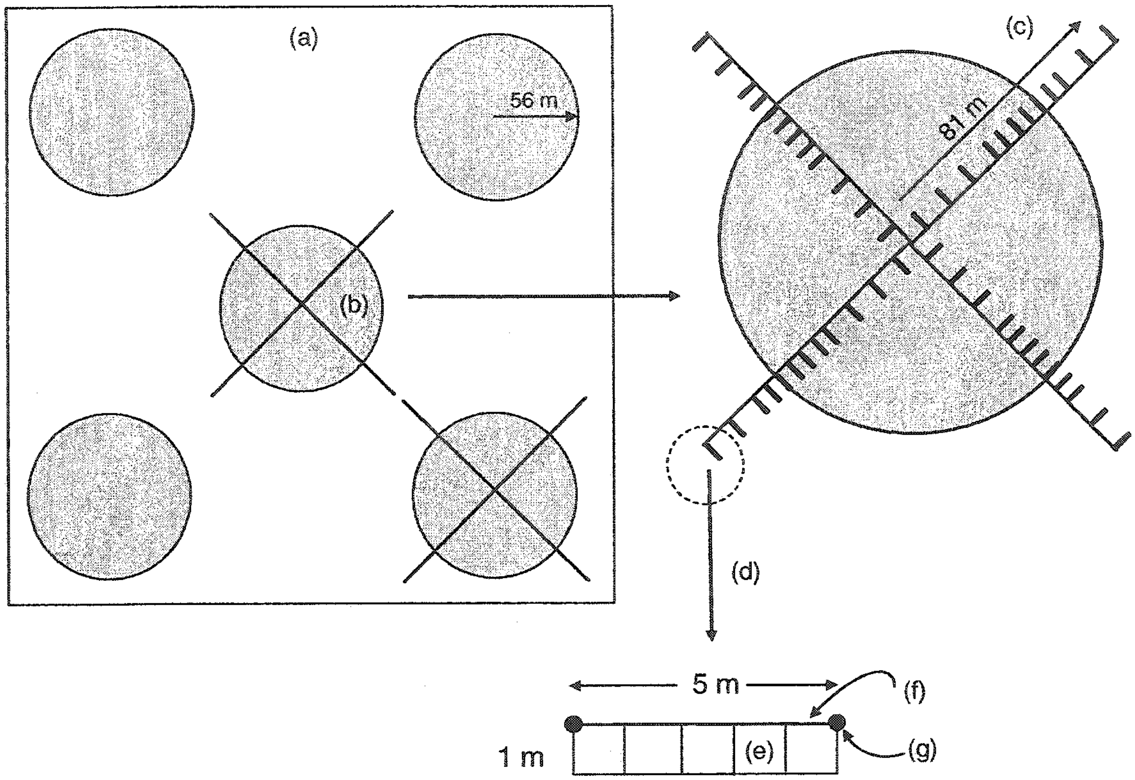

Figure 1.1. Position of forest aggregates within a 13-ha harvest unit (a). Data were collected in two, undisturbed forest aggregates (b) at each site, along transects (c) originating at the center of each aggregate and ending 25 m into the surrounding harvest area. Twelve bands (d) were established at 5-10 m intervals along each transect; each band consisted of five, 1-m^2 subplots (e) within which I estimated cover of all vascular plant species. Cover of logging slash and disturbed soil were sampled along the interior edge of each band (f) and light availability at the two interior endpoints (g).

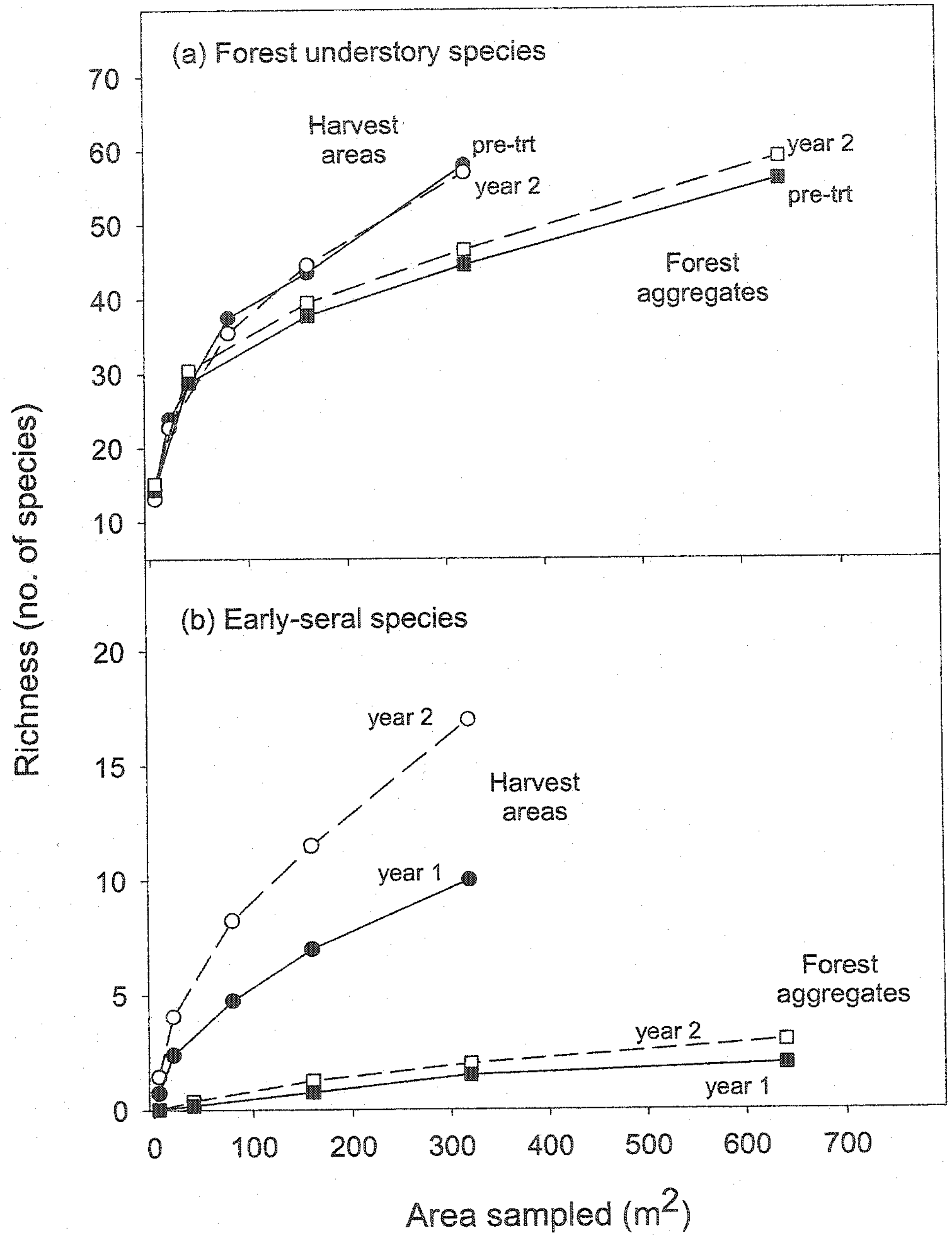

Figure 1.2. Species area curves for (a) forest understory species (before and 2 yr after treatment) and (b) early-seral species (1 and 2 yr after treatment), in forest aggregates (squares) and harvest areas (circles). Points along curves (from left to right) represent means for bands, transects, individual aggregates or surrounding harvest areas, sites, and entire study.

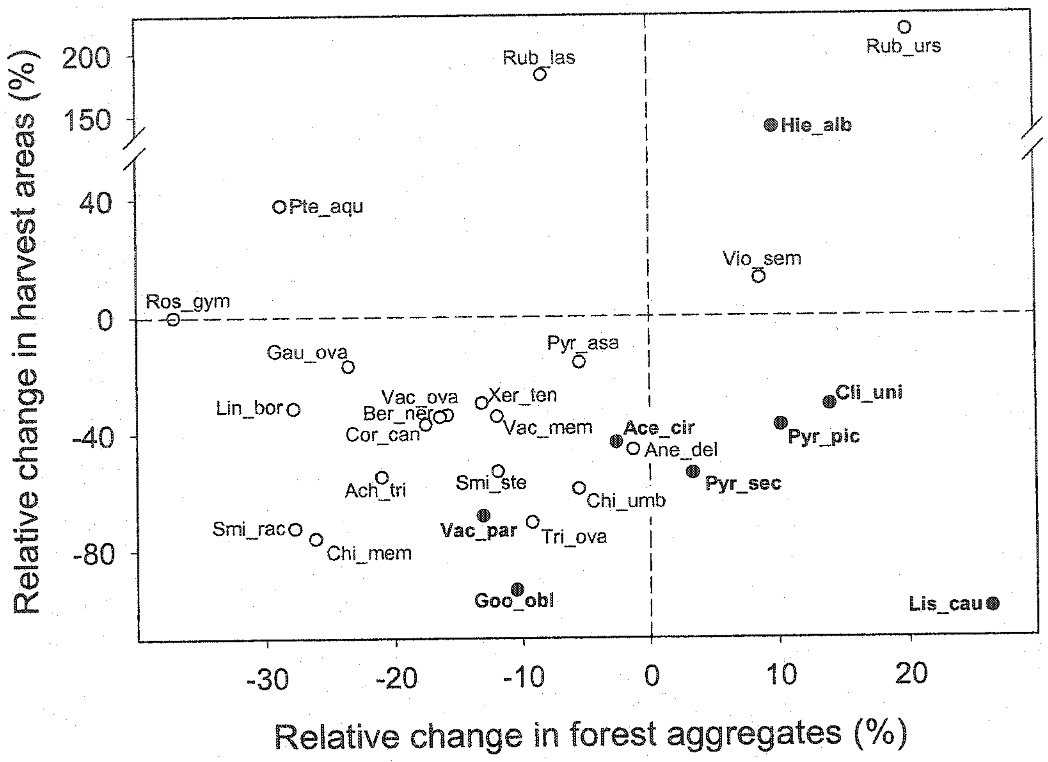

Figure 1.3. Relative change in cover of individual species in forest aggregates and harvest areas, 2 yr after treatment. Note different scales of x and y axes. Closed circles and bold labels indicate species with significant differences between environments (based on *t*-tests), and open circles non-significant relationships. Species codes (and probabilities of significance, *P*) are: Ace_cir = *Acer circinatum* (0.038), Ach_tri = *Achlys triphylla* (0.055), Ane_del = *Anemone deltoidea* (0.105), Ber_ner = *Berberis nervosa* (0.482), Bro_vul = *Bromus vulgaris* (0.342), Chi_men = *Chimaphila menziesii* (0.134), Chi_umb = *C. umbellata* (0.093), Cli_uni = *Clintonia uniflora* (0.047), Cor_can = *Cornus canadensis* (0.485), Gau_ova = *Gaultheria ovatifolia* (0.491), Goo_obl = *Goodyera oblongifolia* (0.002), Hie_alb = *Hieracium albiflorum* (0.017), Lin_bor = *Linnaea borealis* (0.390), Lis_cau = *Listera caurina* (0.030), Pte_aqu = *Pteridium aquilinum* (0.089), Pyr_asa = *Pyrola asarifolia* (0.343), Pyr_pic = *P. picta* (0.050), Pyr_sec = *P. secunda* (0.011), Ros_gym = *Rosa gymnocarpa* (0.248), Rub_las = *Rubus lasiococcus* (0.114), Rub_urs = *R. ursinus* (0.094), Smi_rac = *Smilacina racemosa* (0.307), Smi_ste = *S. stellata* (0.103), Tri_ova = *Trillium ovatum* (0.120), Vac_mem = *Vaccinium membranaceum* (0.253), Vac_ova = *V. ovalifolium* (0.321), Vac_par = *V. parvifolium* (0.038), Vio_sem = *Viola sempervirens* (0.869), and Xer_ten = *Xerophyllum tenax* (0.078). Only those species present prior to treatment in ≥ 3 aggregate/harvest area pairs and 10% of all sample bands are illustrated.

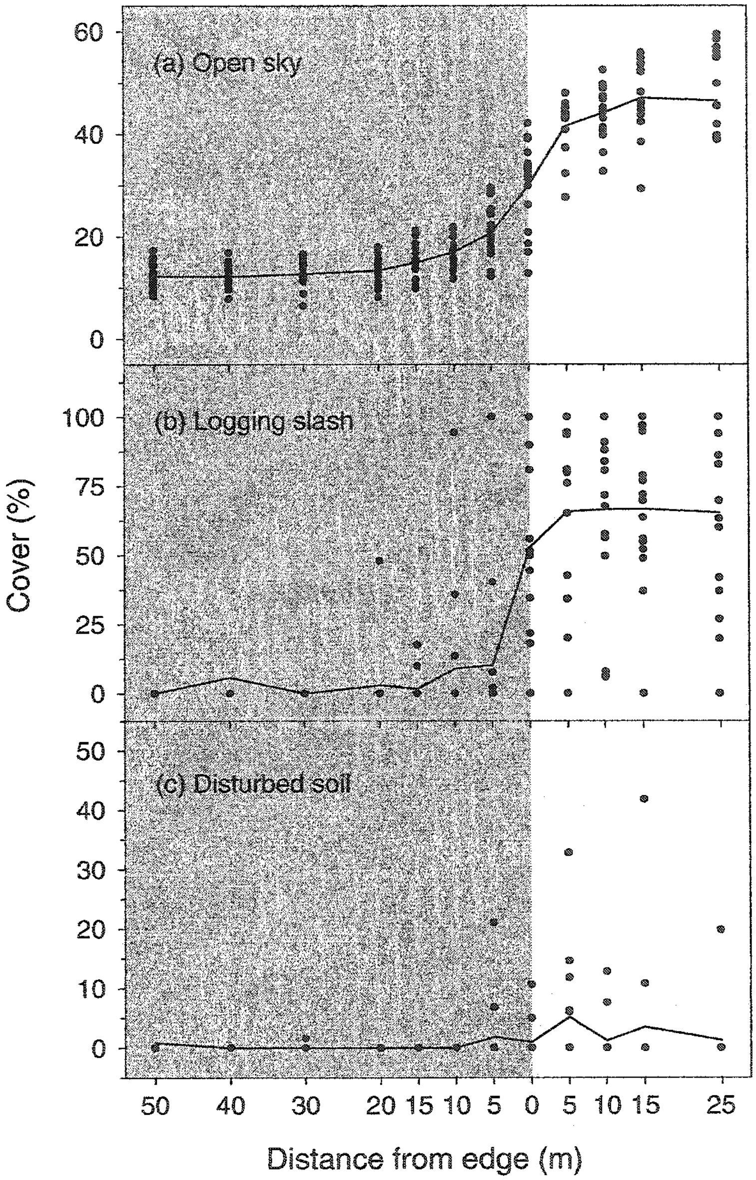

Figure 1.4. (a) Open sky, (b) cover of logging slash and (c) cover of disturbed soil with distance from the edges of forest aggregates. Lines represent mean values (*n* = 16) at each sampled distance. Points in the shaded region represent bands within the aggregates.

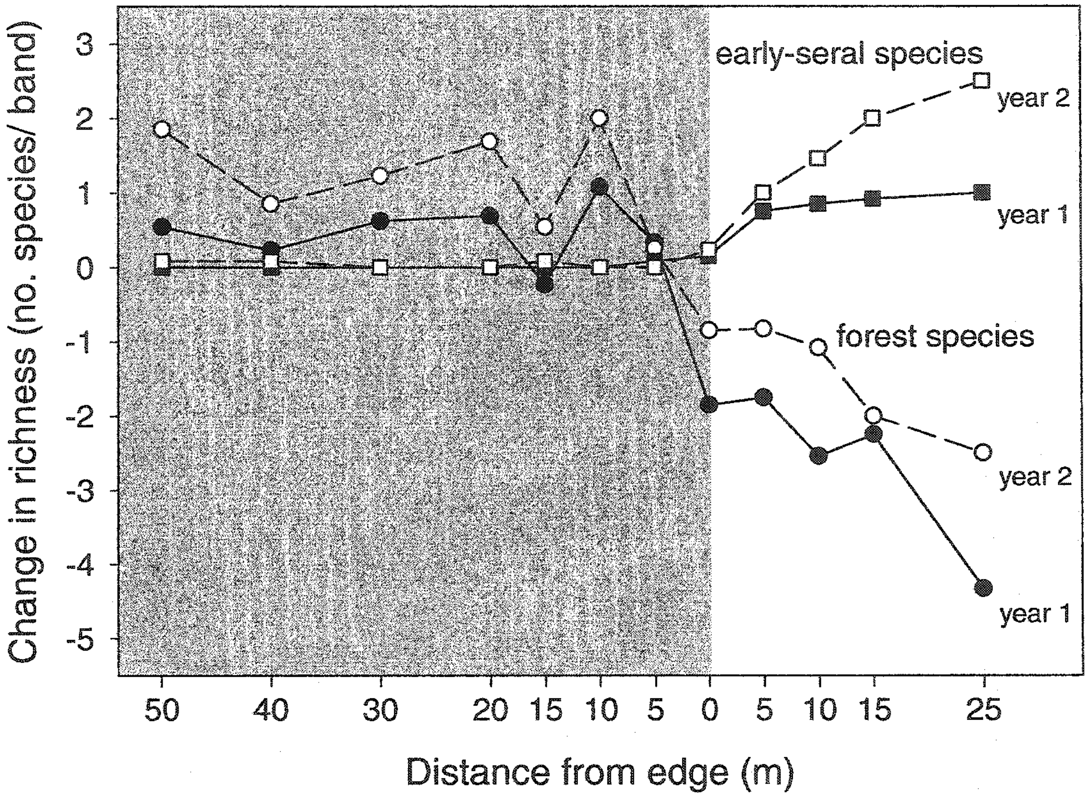

Figure 1.5. Changes in richness of forest understory (circles) and early-seral (squares) species with distance from the edges of forest aggregates. Values represent mean differences ($n = 16$) in band-level richness between pre- and post-treatment measurements (closed symbols = year 1, open symbols = year 2). Points in the shaded region represent bands within the aggregates.

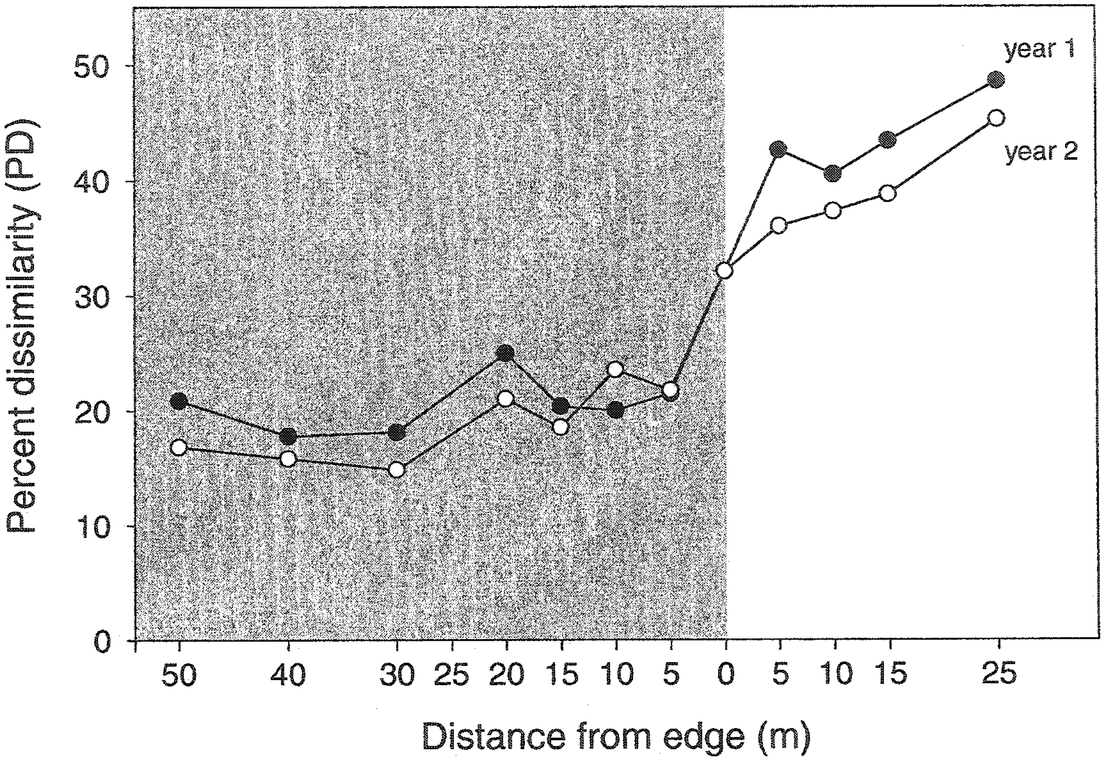

Figure 1.6. Changes in community composition with distance from the edges of forest aggregates. Values represent mean percent dissimilarity (*n* = 16) between pre- and post-treatment composition at each distance (closed circles = year 1, open circles = year 2). Points in the shaded region represent bands within the aggregates.

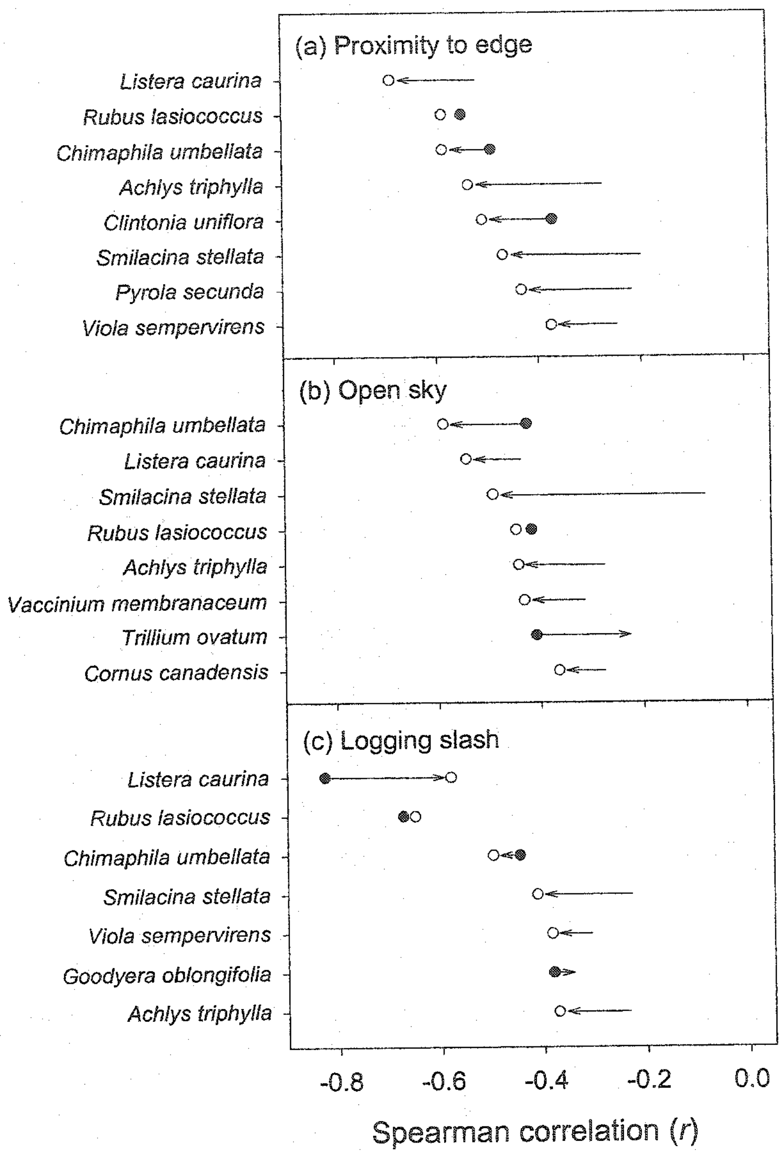

Figure 1.7. Spearman rank correlation coefficients (r, $n = 32$) between change in species abundance within forest aggregates and (a) edge proximity, (b) percent open sky, or (c) cover of logging slash, one and two years after treatment. For edge analyses, negative correlations indicate a decline with proximity to forest edges. Closed circles indicate significant first-year relationships, and open circles significant second-year relationships. Absence of circles indicates non-significant relationships. Arrows illustrate the direction and magnitude of change in response from year 1 to 2. Only those species present prior to treatment in ≥ 3 aggregate/harvest area pairs and 10% of all bands were tested, and only those species with significant relationships ($P \leq 0.05$) are illustrated.

Chapter Two

Effects of timber harvest and forest edges on ground-layer bryophytes

Abstract

Over the past several decades, there has been increasing interest in the effects of timber harvest, habitat fragmentation, and the resultant increase in edge habitat. Most research to date has focused on animal or vascular plant responses; few studies have addressed effects on bryophytes, despite their importance in forest ecosystems. I examined short-term responses of ground-layer bryophytes to disturbance and creation of edges in structural retention harvest units at two sites in the western Cascade Range of Washington, USA. Pre- and one year post-treatment abundance of bryophytes were measured in four, 1-ha aggregates (patches of intact forest) and in surrounding logged areas, using 16, 81-m long transects placed perpendicular to the edges of these aggregates. One year after harvest, species richness, total cover, and frequency of most taxa declined significantly within harvest areas. In contrast, minimal change was observed within forest aggregates. Species richness declined with proximity to the aggregate border; however, only one common species, *Scapania bolanderi*, exhibited a significant decline in frequency near the edge, suggesting that local extirpations of less common species account for observed richness trends within aggregates. My first-year results suggest that forest patches of at least 1 ha may play an important role in maintaining common bryophyte species in forests subjected to harvest with aggregated retention. However, future monitoring of these sites will be necessary to determine whether the diversity and strength of edge-effects will increase over time.

Introduction

There is global interest in the effects of timber harvest, habitat fragmentation, and the resultant increase in edge habitat on forest ecosystems. Although many investigations of vascular plant responses to harvest (e.g., Halpern 1989, Duffy and Meier 1992) and edges (Murcia 1995) have been conducted, bryophytes (mosses and liverworts) have received limited attention. This gap in information is conspicuous given that bryophytes contribute greatly to biodiversity in forest ecosystems (FEMAT 1993). For instance, over 450 species of mosses and 170 species of liverworts inhabit old-growth forests of the Pacific Northwest (Lawton 1971), with roughly 20% endemic to the region or to western North America (Christy and Wagner 1996). In addition to comprising a large proportion of the forest flora, bryophytes contribute substantially to net primary productivity (Binkley and Graham 1981, Longton 1984, den Ouden and Alaback 1996), enhance retention of nutrients and moisture (Rieley 1979), provide food and habitat for invertebrates (Gerson 1982), are used as nesting materials for small mammals and birds (Schofield 1985, FEMAT 1993), and are economically important as special forest products (Peck and McCune 1997). Thus, understanding the consequences of timber harvest and forest fragmentation for bryophytes is of critical conservation and management concern.

Several aspects of the biology and ecology of forest bryophytes suggest that they should be more sensitive to disturbance than are associated vascular plants. First, because of their small stature, bryophytes on the forest floor are highly susceptible to mechanical damage or burial during harvest operations. Second, because they lack true roots and protective leaf cuticles, bryophytes have limited control over water uptake and loss. Although species of some habitats are very tolerant of desiccation (Proctor 1981, Bewley and Krochko 1982), shade-adapted bryophytes have limited capacity to recover from prolonged periods of drying (Proctor 2000). Thus, individuals that survive the direct effects of timber harvest may not tolerate the warmer, drier conditions found in post-harvest environments. Third, if bryophyte species are locally extirpated, reestablishment may be slow (Alaback 1982) because of dispersal limitations and other constraints (Söderström 1990). Although little is known about bryophyte responses to harvest in temperate forests, harvest-related declines have been reported for boreal forests (Hannerz and Hånell 1997, Jalonen and Vanha-Majamaa 2001, Newmaster and Bell 2002).

Opportunities for recovery of bryophyte communities following timber harvest may be enhanced by retention of undisturbed forest patches (Söderström et al. 1992), such as those left as part of structural retention harvests (for information on retention harvests, see Franklin et al. 1997). However, the extent to which forest remnants provide refugia for bryophyte species will depend on the degree to which they are compromised by edge effects. Light, temperature, wind speed, humidity, and soil moisture can differ substantially between forest-margin and interior environments, with depth-of-edge influence varying greatly among variables and among edges of different orientations (i.e. aspects) (Chen et al. 1993, 1995). Although relationships between vascular plant composition or abundance and proximity to edge have been examined in some temperate forest ecosystems (Wales 1972, Palik and Murphy 1990, Brothers and Spingarn 1992, Fraver 1994, Matlack 1994, Nelson and Halpern *in press*), similar studies of bryophytes have not been conducted (but see Luczaj and Sadowska 1997).

This study addresses first-year responses of ground-layer bryophytes to timber harvest with aggregated retention (in the form of undisturbed 1-ha forest patches) in the western Cascade Range of Washington. It is part of a larger experiment, Demonstration of Ecosystem Management Options (DEMO), which tests the effects of varying levels and patterns of green-tree retention on diverse groups of forest organisms in the Pacific Northwest (Aubry et al. 1999, Halpern et al. 1999a). I address the following questions: (1) Do bryophyte species richness and abundance decline after timber harvest? (2) If so, are declines correlated with harvest-related ground disturbance or elevated light levels, or moderated by the presence of residual herb or shrub cover? (3) Do 1-ha forest aggregates adjacent to harvested areas provide short-term refugia for bryophyte species? (4) Within these aggregates, does proximity to edge explain variation in bryophyte richness or abundance, and if so, are edge-related patterns correlated with ground disturbance, light availability, or cover of herbs or shrubs? (5) Do bryophyte responses within forest aggregates vary as a function of edge orientation? (6) Are bryophytes more responsive to timber harvest or creation of forest edges than co-occurring vascular plants?

Methods

Study sites

My study sites, Butte and Paradise Hills, are on the west slope of the Cascade Range in southern Washington on the Gifford Pinchot National Forest. Butte (46°22'07" N, 121°34'40" W) is located at an elevation of 1012-1122 m in the *Tsuga heterophylla* zone (Franklin and Dyrness 1973). Slopes average 40% and face southeast. Soils are well drained and fairly shallow, consist of loamy sands derived from residuum and colluvium, and are covered by a shallow surface layer of volcanic ash originating from the 1980 eruption of Mount St. Helens (Wade et al. 1992). Forests are ca. 70-80 yr old and dominated by *Pseudotsuga menziesii*; *Tsuga heterophylla* and *Thuja plicata* are also common (Halpern et al. 1999a). Prior to treatment, canopy height, stem density, and basal area averaged 36 m, 1150 trees/ha, and 56 m^2/ha, respectively; common understory species included *Tsuga heterophylla*, *Thuja plicata*, *Acer circinatum*, *Berberis nervosa*, *Pteridium aquilinum*, *Achlys triphylla*, and *Chimaphila umbellata*; and ground-layer bryophytes averaged 7% cover, with *Rhytidiopsis robusta* and *Eurhynchium oreganum* most common.

Paradise Hills (46°00'46" N, 121°56'34" W) is located at an elevation of 957-1000 m in the *Abies amabilis* zone (Franklin and Dyrness 1973). Slopes are gentle (averaging 18%) and primarily face east to northeast. Soils are deep sandy loams derived from volcanic ash and pumice, till, and residuum (Wade et al. 1992). Forests are 110-140 yr old and are dominated by *Pseudotsuga menziesii*, with *Tsuga heterophylla*, *Thuja plicata*, and *Abies amabilis* as common associates (Halpern et al. 1999a). Prior to treatment, canopy height, stem density, and basal area averaged 39 m, 740 trees/ha, and 73 m^2/ha, respectively; species common in the understory included *Tsuga heterophylla*, *Abies amabilis*, *Vaccinium membranaceum*, *V. ovalifolium*, *Xerophyllum tenax*, *Achlys triphylla*, and *Cornus canadensis*; and ground-layer bryophytes averaged 23% cover, with *Rhytidiopsis robusta* and *Hypnum circinale* as most common.

Harvest treatments

Within a 13-ha harvest unit at each site, five 1-ha (56 m radius) circular forest aggregates were retained (Fig. 2.1, a). In the surrounding area, all merchantable trees (> 18 cm diameter at breast height) were cut and removed (using a helicopter at Butte and a combination of tracked shovel loaders and rubber-tired skidders at Paradise Hills). Non-merchantable subcanopy trees were retained in harvest areas at Butte but were felled at Paradise Hills. Compacted soil in skid trails (present between aggregates at Paradise Hills) was loosened with a tracked excavator, and then covered with logging slash; elsewhere, slash was left in place. Yarding was completed in July 1997 at Butte and in September 1997 at Paradise Hills (for details see Halpern and McKenzie 2001).

Sampling design

Pre-treatment sampling was conducted from 1 July to 9 September 1996 and post-treatment sampling from 5 July to 15 September 1998. At each site, two of the five circular aggregates marked for retention were randomly selected. In each of these (Fig. 2.1, b), I established four perpendicular transects (Fig. 2.1, c), 81 m in length, which extended in cardinal directions from the center and ended 25 m into the surrounding area to be harvested. Twelve bands of permanent plots were established along each transect, eight in the area marked for retention (at distances of 0, 5, 10, 15, 20, 30, 40, and 50 m from the edge) and four in the area marked for harvest (at distances of 5, 10, 15, and 25 m from the edge) (Fig. 2.1, c). Thus, bands were spaced at 5-m intervals on both sides of the forest edge, where I expected steep gradients in vegetation response, and at 10-m intervals elsewhere.

Each band (Fig. 2.1, d) consisted of five, 0.1-m^2 microplots (Fig. 2.1, e), within which I estimated total cover (vertical projection) of ground-layer bryophytes and cover of individual species, including epilithic, epixylic, and epigeic taxa (but not epiphytic taxa present as litter fall). Where microplots fell on coarse woody debris or the bases of shrubs or trees, sampling was limited to within 1 m of the forest floor. When species could not be reliably identified in the field, specimens were collected from outside the sample bands, identified in the lab, and archived for future reference. Specimens could not be collected directly from sample bands without compromising future sampling. This was particularly problematic for *Brachythecium,* as several species that can not be distinguished without the aid of a microscope co-occurred on sample bands. As a consequence, data for all species of *Brachythecium* were combined for statistical analyses. Nomenclature follows Anderson et al. (1990) for mosses and Stotler and Crandall-Stotler (1977) for liverworts. In addition to data on bryophytes, I also measured: (1) total cover of herbaceous species (including ferns, graminoids, and low-growing woody species) and of tall shrubs within five, 1-m^2 subplots (Fig. 2.1, f); (2) cover of logging slash and disturbed soil along the interior edge of each band using the line-intercept method (Fig. 2.1, g); and (3) cover of open sky at the two endpoints of each band using a CI-110 digital canopy imager with 150-degree lens (CID Inc., Vancouver, Washington; Fig. 2.1, h).

Data are archived at the Oregon State University Forest Science Data Bank (FSDB; http://www.fsl.orst.edu/lter/data.cfm?topnav=8).

Statistical analyses

I used changes (post- minus pre-treatment values) in species richness or abundance as measures of response to harvest or creation of forest edge, because bryophytes exhibited considerable spatial variation in richness and abundance prior to timber harvest. Changes in mean species richness (number of taxa per sample band), mean total bryophyte cover, and frequency of occurrence (percentage of bands) of individual species were computed for each aggregate, for each adjacent area of harvest, and for each sample distance within each aggregate. Statistical tests of species' responses were limited to taxa that prior to treatment (1) occurred in at least three of the four replicates (i.e. forest aggregate/surrounding harvest area pairs) and (2) had greater than 10% frequency (percentage of all possible bands).

Responses in harvest areas and forest aggregates. —Paired *t*-tests (Sokal and Rohlf 1981) were used to compare pre- and post-treatment values of species richness, total cover, and individual species' frequencies within each environment (harvest areas and forest aggregates; $n = 4$) (Questions 1 and 3). To explore the possible correlates of change in harvest areas (Question 2), I computed Spearman rank correlation coefficients (Sokal and Rohlf 1981) between changes in richness or abundance and habitat variables (cover of logging slash, disturbed soil, open sky, herbs, and tall shrubs).

Edge-related gradients within forest aggregates. — To assess relationships between bryophyte responses and proximity to aggregate edge (Question 4), I computed Spearman rank correlation coefficients between changes in richness or abundance and distance from edge. I then explored possible correlates of edge-related gradients by computing Spearman rank correlation coefficients between these same bryophyte response variables and habitat variables. To test whether responses within forest aggregates varied with edge orientation (Question 5), I used one-way analysis of variance (ANOVA; (Sokal and Rohlf 1981) to compare mean changes in richness and abundance for transects representing the four cardinal directions (four transects per direction); transect means were computed from the eight bands representing the forested portion of each transect.

Comparative responses of life forms. —To place bryophyte responses within the context of other groups of understory plants (herbs and tall shrubs), I compared the sensitivities of these three life forms to timber harvest and creation of forest edges (Question 6). For each life form at each replicate (forest aggregate/harvest area pair, $n = 4$), I computed an index of sensitivity to harvest, S_h, as the difference between the proportional change in total cover in the harvest area ($n = 16$ bands) and that in the "interior" of the aggregate ($n = 16$ innermost bands), thus adjusting for "background" variation in undisturbed forest. One-way ANOVA was then used to compare S_h values among life forms.

Sensitivity to edge, S_e, was computed as the Spearman rank correlation coefficient between changes in total life form cover and proximity to edge ($n = 32$, i.e. 4 aggregates x 8 distances). The strength and significance of correlations were compared among life forms.

All statistical analyses were conducted using Systat 10.0 (SPSS 2001), with an alpha level of 0.05 as the criterion for reporting statistical significance.

Results

Prior to treatment, a total of 36 bryophyte taxa (28 mosses and eight liverworts) were identified in sample bands (Table 2.1). Of these, 22 were found both in areas scheduled for retention and for harvest (Table 2.1) and 12 were found at both study sites. Eight taxa (six mosses and two liverwort) met my criteria for statistical analysis — presence prior to treatment at three or more replicates (forest aggregate/harvest area pairs) and greater than 10% frequency (percentage of all possible bands); I refer to these as "common taxa." Species richness (number of taxa per band) and total cover did not differ significantly between areas scheduled for retention and for harvest (3.7 vs. 3.9 species, $t = 0.324$, $P = 0.757$; 9.4 vs. 8.9% cover, $t = 0.113$, $P = 0.914$).

Responses within harvest areas

After one year, bands in harvest areas showed significant declines in species richness and total cover (closed circles, Fig. 2.2). Nearly 90% of taxa found before treatment declined in frequency; of the eight taxa tested, declines were significant for five (Fig. 2.3 a). Seven uncommon taxa (*Blepharostoma trichophyllum*, *Eurhynchium pulchellum*, *Trachybryum megaptilum*, *Orthotrichum* sp., *Plagiomnium insigne*, *Plagiothecium laetum*, and *Rhytidiadelphus loreus*) disappeared completely from sample bands, but four appeared (*Ditrichum montanum*, *Hygrohypnum bestii*, *Pleurozium schreberi*, and *Polytrichum juniperinum*).

Declines in species richness correlated significantly with open sky and logging slash, and declines in total cover correlated significantly with open sky, logging slash, and disturbed soil (Table 2.2). However, these declines were reduced significantly at higher levels of tall shrub cover (Table 2.2). Similarly, for four of eight taxa considered, declines in frequency correlated significantly with cover of logging slash and/or disturbed soil, and for five taxa declines were significantly reduced at higher levels of herb or shrub cover (Table 2.2).

Responses within forest aggregates

In contrast to patterns in harvest areas, species richness and total cover changed minimally within forest aggregates (open circles, Fig. 2.2). Changes in frequency of common taxa were also non-significant (Fig. 2.3 b). One uncommon species (*Ditrichum montanum*) disappeared from sample bands within forest aggregates, but four others appeared (*Lepidozia reptans*, *Plagiothecium undulatum*, *Pleurozium schreberi*, and *Racomitrium heterostichum*).

Edge-related gradients within forest aggregates

Within forest aggregates, declines in species richness were significantly correlated to proximity to edge (Fig. 2.4 a; Table 2.3), but changes in total cover were not (Fig. 2.4 b; Table 2.3). Of eight taxa considered, only *Scapania bolanderi* showed a significant decline in frequency with proximity to edge, and there were virtually no significant correlations between bryophyte responses and habitat variables (Table 2.3). No significant differences in richness, total cover, or species' frequencies were found among transects representing contrasting edge orientations (one-way ANOVAs: $0.116 < P < 0.963$).

Comparative responses of life forms

Relative to vascular plant groups, bryophytes appeared more sensitive to timber harvest, but less responsive to creation of forest edges. Although differences among life forms were not significant, bryophytes showed the greatest sensitivity to harvest (S_h): relative declines in total cover averaged 61 vs. 31 and 44% for herbs and tall shrubs, respectively (Fig. 2.5). In contrast, the correlation between total cover and proximity to forest edge (S_e) was non-significant for bryophytes, but highly significant for herbs ($r = -0.48$, $P = 0.006$).

Discussion

My results clearly show the sensitivity of ground-layer bryophytes to logging disturbance. One year after treatment, species richness, total cover, and frequency of common taxa declined significantly within harvest areas. Similar responses have been observed in *Picea* forests of Finland and Sweden. One year after clearcut logging, Jalonen and Vanha-Majamaa (2001) observed 60 and 94% declines in richness and total cover, respectively. Similarly, Hannerz and Hånell (1997) observed 64-89% reduction in cover of common species, seven to eight years after harvest. On my sites, harvest-related declines were greatest in areas with heavy slash deposition, soil disturbance, and low tree cover. In the short term, burial by slash and soil disturbance, processes by which bryophytes may be immediately destroyed, appear to play larger roles in observed declines than does overstory removal. However, the influence of canopy openings may increase with time, as changes in microclimate associated with overstory removal may induce longer-term declines in bryophyte abundance. Reduction in the amount or quality of substrates, particularly moist, well-decayed coarse woody debris, may also contribute to declines in abundance (Söderström 1988, Rambo 1998); however, I did not examine this relationship.

In disturbed areas, bryophyte populations may require long periods of time to recover initial abundance (e.g., Alaback 1982, Zobel and Antos 1997). Many bryophyte species are prolific spore producers in suitable habitats (Miles and Longton 1992). However, spore production depends on adequate moisture, which may not be available in the warmer, drier post-harvest environment. Moreover, recruitment of spores from adjacent stands may be limited by dispersal ability (Wyatt 1982); short spore lifespan (Tan and Pocs 2000); or inability of spores to survive desiccation, extreme temperature, or exposure to ultraviolet radiation during dispersal (van Zanten and Pocs 1981, Miles and Longton 1992, Tan and Pocs 2000). Recovery also may be delayed until adequate microclimatic conditions and substrates develop within the regenerating forest (Edwards 1986, Söderström 1988, Lesica et al. 1991, Frisvoll and Prestø 1997).

In contrast to responses in harvest areas, bryophyte communities within forest aggregates remained relatively stable. Although edge environments were characterized by increased light availability and ground disturbance to a distance of 15 m (Nelson and Halpern *in press*), total bryophyte cover and frequency of most common taxa did not show strong edge-related responses one year after timber harvest. The sole taxon to show a significant decline was *Scapania bolanderi*, the most common liverwort on my sites. This result supports previous suggestions that liverworts are more sensitive to changes in humidity and temperature than are mosses (Söderström 1988, Frisvoll and Prestø 1997).

The general absence of immediate declines in abundance of common species does not preclude the possibility that edge-related gradients will develop with time. Although the contrast in microclimatic conditions is most extreme immediately after edges are formed (Williams-Linera 1990, Matlack 1993), plant responses are likely to lag behind environmental changes. I observed this phenomenon with forest herbs on my sites: the proportion of species that showed significant edge-related declines increased from 10 to 28% over two years (Nelson and Halpern *in press*). Similar patterns may develop over time in the bryophyte community.

Despite the relative insensitivity of common species, I did detected significant edge-related declines in species richness, consistent with patterns reported in boreal forests (Luczaj and Sadowska 1997). These declines thus reflect local loss of relatively uncommon taxa. Small sample sizes and patchy distributions limited my ability to test the individual responses of these less common species. However, many are epixylic (Rambo 1998) and are particularly sensitive to changes in substrate quality (Söderström 1988, Rambo 1998) resulting from exposure to increased light. Future sampling of specialized habitats will be necessary to determine the relative sensitivity to edges of less common taxa and the extent to which substrate requirements control species responses.

Implications for conservation and management

Ground-layer bryophytes appear more sensitive to the direct effects of timber harvest than do vascular plants and likely require longer periods for recovery from disturbance. Thus, management strategies specific to bryophyte conservation are necessary to ensure adequate protection for these organisms in managed landscapes. Retention of live trees may moderate the effects of clearcut logging (Hannerz and Hånell 1997, Jalonen and Vanha-Majamaa 2001); however, some forest-floor bryophytes may require conditions that are only met in undisturbed forest and may disappear from areas where even moderate timber extraction has occurred (Söderström 1988).

Aggregated retention of live trees may provide a refugium for disturbance-sensitive species and a local dispersal source for re-colonization of harvested areas once microclimatic conditions become suitable for establishment. However, the efficacy of remnant forest patches will depend on their size and the degree to which habitat conditions are not compromised by edge phenomena. In the mature coniferous forests that I studied, 1-ha remnant patches appear sufficiently large to buffer common ground-layer bryophytes from the direct effects of harvest, but may not be large enough to prevent declines of less common species. I expect that remnants smaller than 0.5 ha will be strongly influenced by microclimatic and disturbance effects (elevated levels of light, disturbed soil, and deposition of logging slash), which penetrated up to 15 m (ca. 50% of the area) into my aggregates. There is evidence from *Picea* forests in Finland that very small patches (0.01-0.02 ha) do not prevent short-term declines in bryophyte richness or abundance (Jalonen and Vanha-Majamaa 2001). In combination, these results suggest that current standards for structural retention on federal "matrix" lands in the Pacific Northwest (USDA and USDI 1994), which allow for aggregates as small as 0.1 ha, may not be adequate to retain the diversity and abundance of bryophyte species found in older, undisturbed forests. Longer term studies in these and other fragmented forests will be critical for improving standards for bryophyte protection in managed landscapes.

Table 2.1. Bryophyte species constancy (number of replicates, maximum of 4) and frequency of occurrence (percentage of all bands) prior to treatment. Asterisks denote liverworts.

	Forest aggregates		Harvest areas (prior to logging)	
Species	Constancy	Frequency	Constancy	Frequency
Rhytidiopsis robusta	4	85	4	80
Dicranum fuscescens	4	51	4	38
Hypnum circinale	4	36	3	30
Eurhynchium oreganum	4	28	4	28
Brachythecium leibergii	4	21	4	16
Dicranum tauricum	4	20	4	31
Scapania bolanderi *	4	15	4	20
Ptilidium californicum *	4	14	3	18
Pseudoleskea stenophylla	3	6	3	11
Pseudotaxiphyllum elegans	3	20	2	11
Aulacomnium androgynum	2	17	2	16
Brachythecium starkei	2	9	3	21
Brachythecium velutinum	2	9	3	10
Rhizomnium glabrescens	2	6	2	8
Pohlia nutans	2	5	2	13
Cephalozia lunulifolia *	2	2	2	5
Brachythecium asperrimum	2	6	1	3
Trachybryum megaptilum	2	2	1	5
Lophozia spp. *	2	2	1	2
Cephalozia bicuspidata *	2	2		
Hylocomium splendens	2	2		

Table 2.1. continued

	Forest aggregates		Harvest areas (prior to logging)	
Species	Constancy	Frequency	Constancy	Frequency
Mnium spinulosum	2	2		
Brachythecium hylotapetum	1	1	3	10
Plagiothecium laetum	1	2	2	5
Blepharostoma trichophyllum *	1	2	1	2
Brachythecium albicans	1	2		
Scapania umbrosa *	1	2		
Claopodium bolanderi	1	1		
Ditrichum montanum	1	1		
Isothecium stoloniferum	1	1		
Lophocolea heterophylla *	1	1		
Drepanocladus aduncus			1	2
Eurhynchium pulchellum			1	2
Orthotrichum spp.			1	2
Plagiomnium insigne			1	2
Rhytidiadelphus loreus			1	2

Table 2.2. Spearman rank correlation coefficients (*r*) between bryophyte responses (changes in species richness, total cover, and species frequency) in harvest areas and habitat variables (post-treatment cover of logging slash [Slash], disturbed soil [Dsoil], open sky [Osky], herbs [Herb], and tall shrubs [Shrub]). Only those taxa present prior to treatment in $\geq$ 3 replicates (forest aggregate/harvest area pairs) and with > 10% frequency (percentage of all possible bands) were considered for species-level tests. Probabilities of statistical significance are coded as: ** = $P \leq 0.01$ or * = $0.01 < P \leq 0.05$.

	Slash	Dsoil	Osky	Herb	Shrub
Species richness	-0.62 **	-0.27	-0.58 **	0.27	0.43 **
Total cover	-0.62 **	-0.47 **	-0.42 **	0.24	0.34 *
Species frequency					
Brachythecium spp.	-0.14	0.05	-0.09	-0.11	0.17
Dicranum fuscescens	-0.34 *	-0.31 *	-0.34	-0.04	-0.07
Dicranum tauricum	-0.20	0.10	-0.10	-0.08	0.38 **
Eurhynchium oreganum	-0.28	-0.13	-0.36	0.42 **	0.02
Hypnum circinale	-0.22	-0.36 *	-0.18	0.03	-0.10
Ptilidium californicum	-0.32 *	-0.18	-0.33	0.20	0.36 *
Rhytidiopsis robusta	-0.57 **	-0.46 **	-0.40	0.18	0.36 *
Scapania bolanderi	-0.21	-0.17	-0.19	0.10	0.35 *

Table 2.3. Spearman rank correlation coefficients (*r*) between bryophyte responses (changes in species richness, total cover, and species frequency) within forest aggregates and proximity to forest edge (Edge), or habitat variables (post-treatment cover of logging slash [Slash], disturbed soil [Dsoil], open sky [Osky], herbs [Herb], and tall shrubs [Shrub]). See Table 2.2 for other details.

	Edge	Slash	Dsoil	Osky	Herb	Shrub
Species richness	-0.43 *	-0.34	-0.04	-0.21	0.06	0.44
Total cover	0.24	-0.23	-0.23	0.29	0.04	0.09
Species frequency						
Brachythecium spp.	0.00	-0.05	0.19	0.21	-0.20	0.27
Dicranum fuscescens	-0.14	-0.26	-0.15	-0.17	-0.20	-0.23
Dicranum tauricum	0.00	-0.12	0.22	0.20	-0.21	0.43
Eurhynchium oreganum	-0.29	-0.12	-0.09	-0.41 *	0.50	-0.08
Hypnum circinale	0.08	-0.03	-0.31	0.16	-0.08	-0.25
Ptilidium californicum	-0.23	-0.11	-0.01	-0.09	0.04	0.35
Rhytidiopsis robusta	0.25	-0.12	-0.22	0.30	-0.15	0.16
Scapania bolanderi	-0.38 *	-0.26	-0.03	-0.11	0.23	0.43

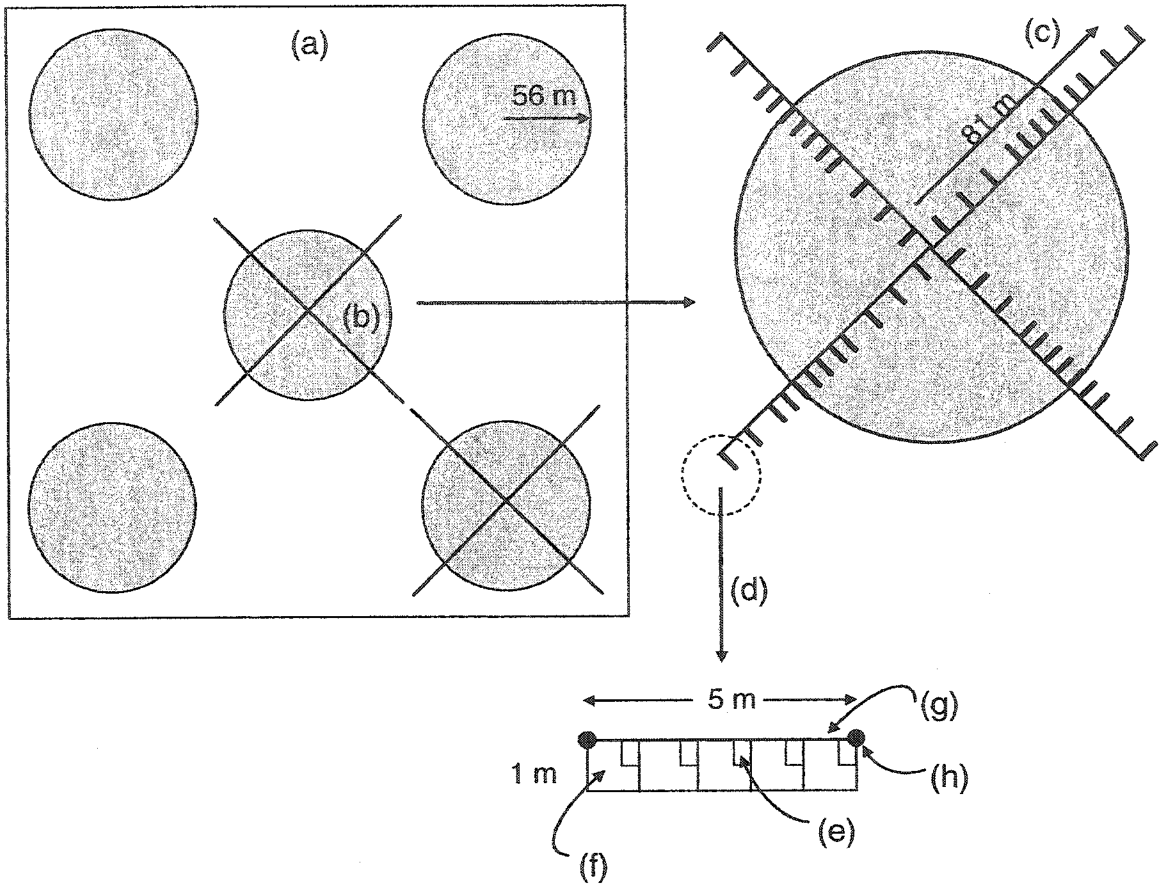

Figure 2.1. Arrangement of forest aggregates within the 13-ha harvest units (a). Sampling was conducted in and adjacent to two aggregates (b) at each site. Transects (c), oriented in cardinal directions, originated at the center of each aggregate, and extended 25 m into the adjacent harvest area. Twelve, 1 x 5 m bands (d) were established at 5- to 10-m intervals along each transect. Each band consisted of five, 0.1-m^2 microplots (e) for sampling bryophytes and five, 1-m^2 subplots (f) for sampling herbs and tall shrubs. Harvest-related disturbance (cover of logging slash and disturbed soil) was sampled along the interior edge of each band (g), and cover of open sky at the two endpoints (h).

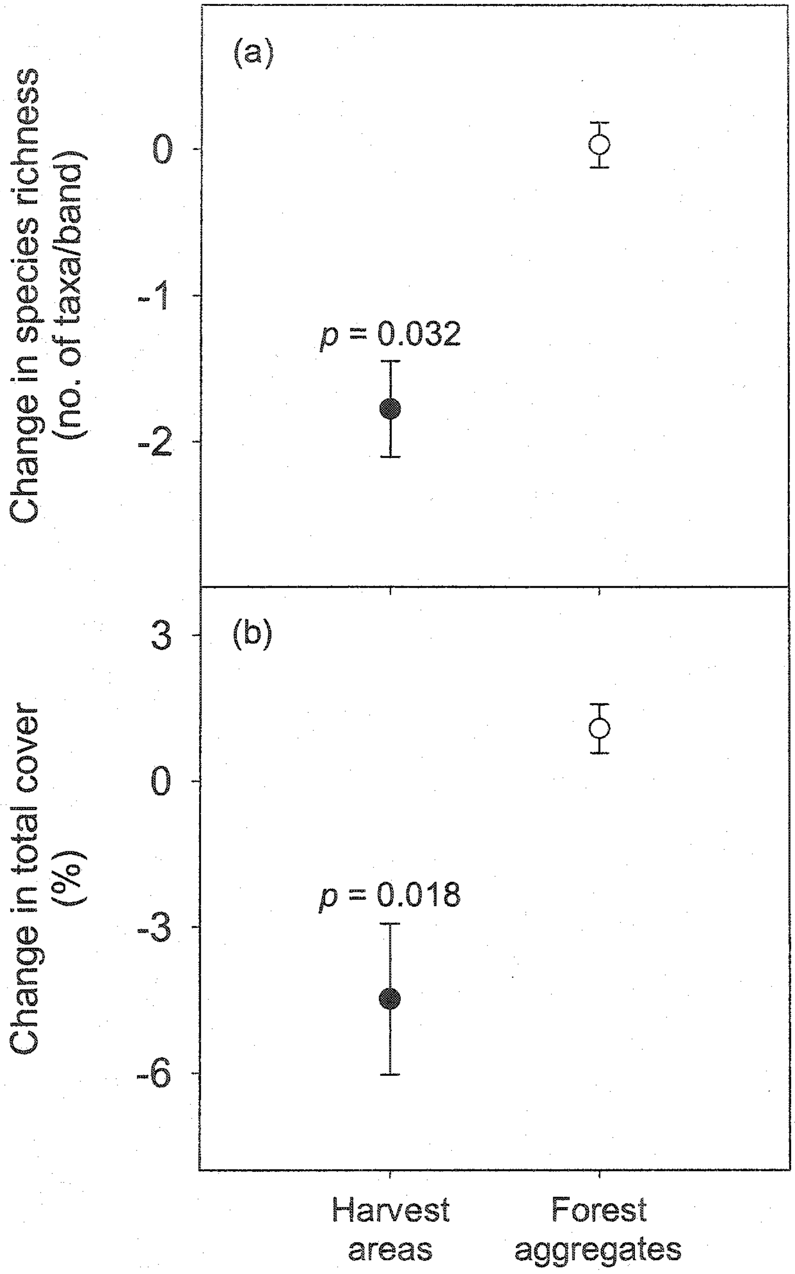

Figure 2.2. Mean changes (±1 SE) in (a) species richness and (b) total cover in harvest areas (closed circles) and forest aggregates (open circles) one year after treatment. *P* values are shown where pre- and post-treatment means differed significantly based on a paired *t*-test ($n = 4$).

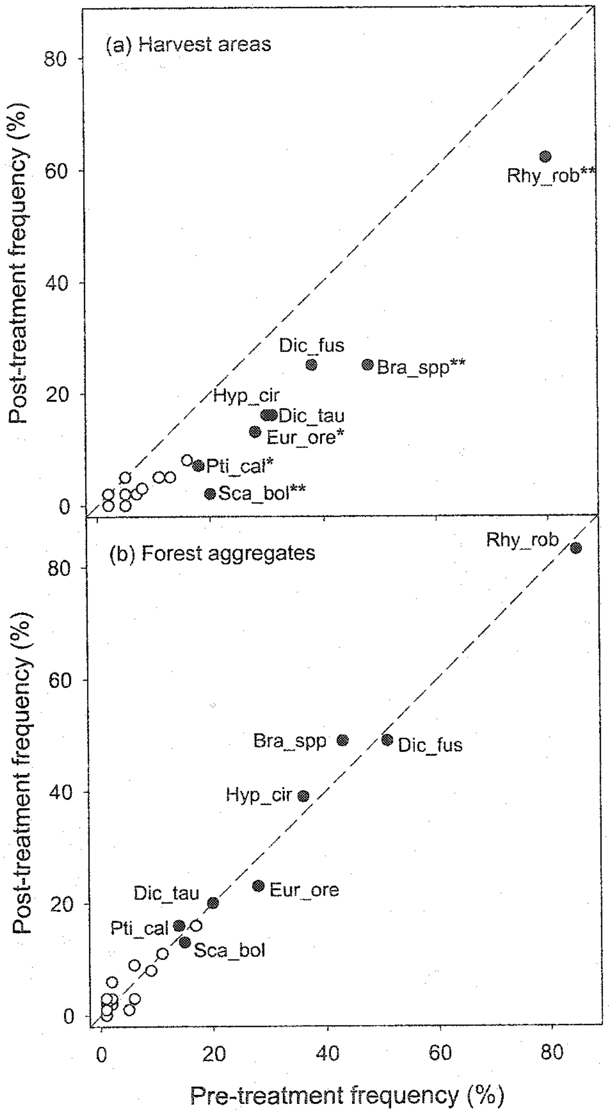

Figure 2.3. Mean frequency ($n = 4$) of individual bryophyte taxa before and after treatment in (a) harvest areas (25 taxa) and (b) forest aggregates (28 taxa). Only taxa present before treatment are plotted. Taxa present prior to treatment in ≥ 3 replicates (forest aggregate/harvest area pairs) and with > 10% frequency (percentage of all possible bands) are plotted with closed circles and coded as: Bra_spp = *Brachythecium* spp., Dic_fus = *Dicranum fuscescens*, Dic_tau = *Dicranum tauricum*, Eur_ore = *Eurhynchium oreganum*, Hyp_cir = *Hypnum circinale*, Pti_cal = *Ptilidium californicum*, Rhy_rob = *Rhytidiopsis robusta*, and Sca_bol = *Scapania bolanderi*. Probabilities of significance (based on paired t-tests, $n = 4$) are coded as: ** = $P \leq 0.01$ or * = $0.01 < P \leq 0.05$. Less common taxa are plotted with open circles.

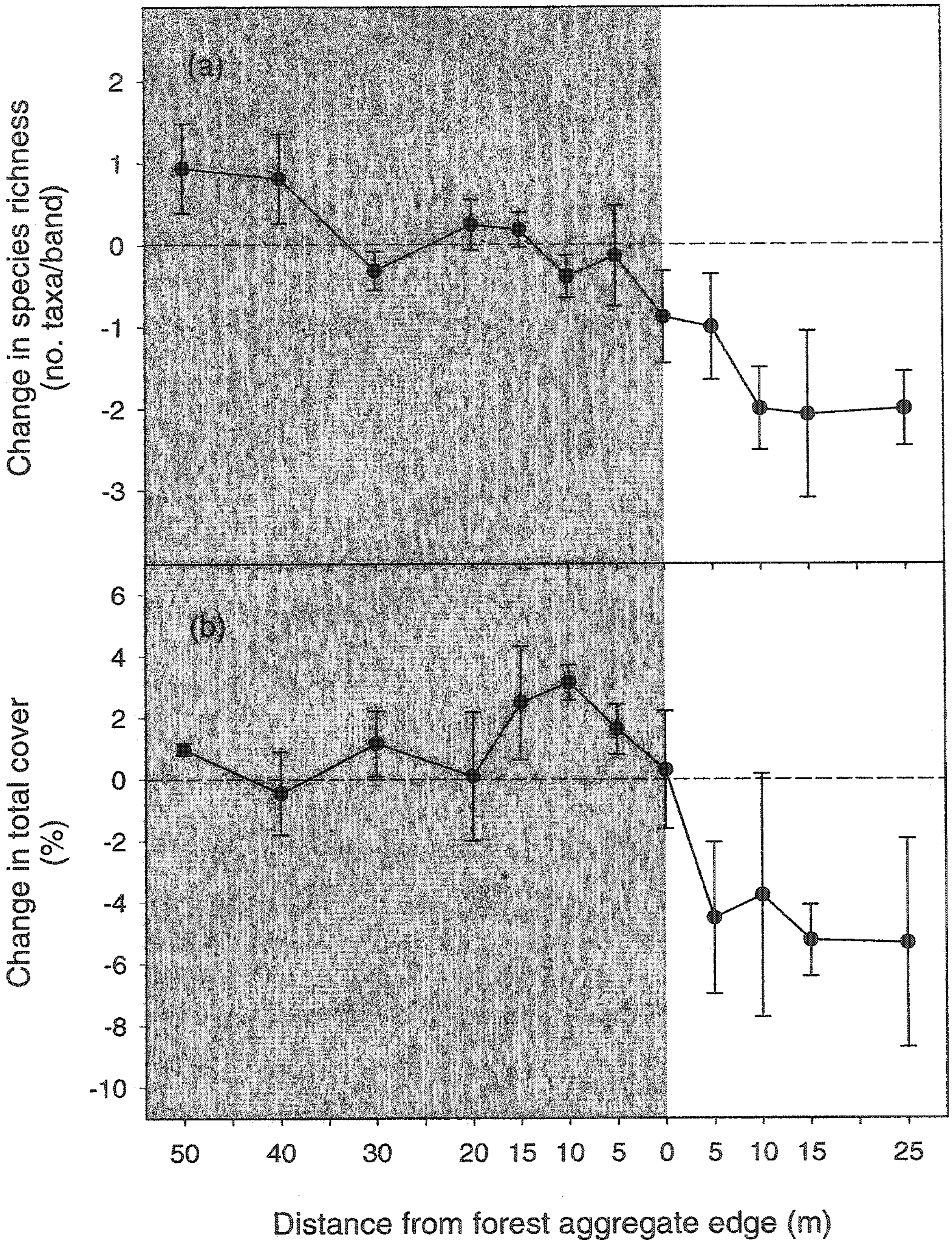

Figure 2.4. Changes in (a) species richness and (b) total cover with proximity to forest aggregate edge. Values represent mean differences (±1SE) (*n* = 16) between pre- and post-treatment measurements at each distance. Points in the shaded region represent bands within forest aggregates.

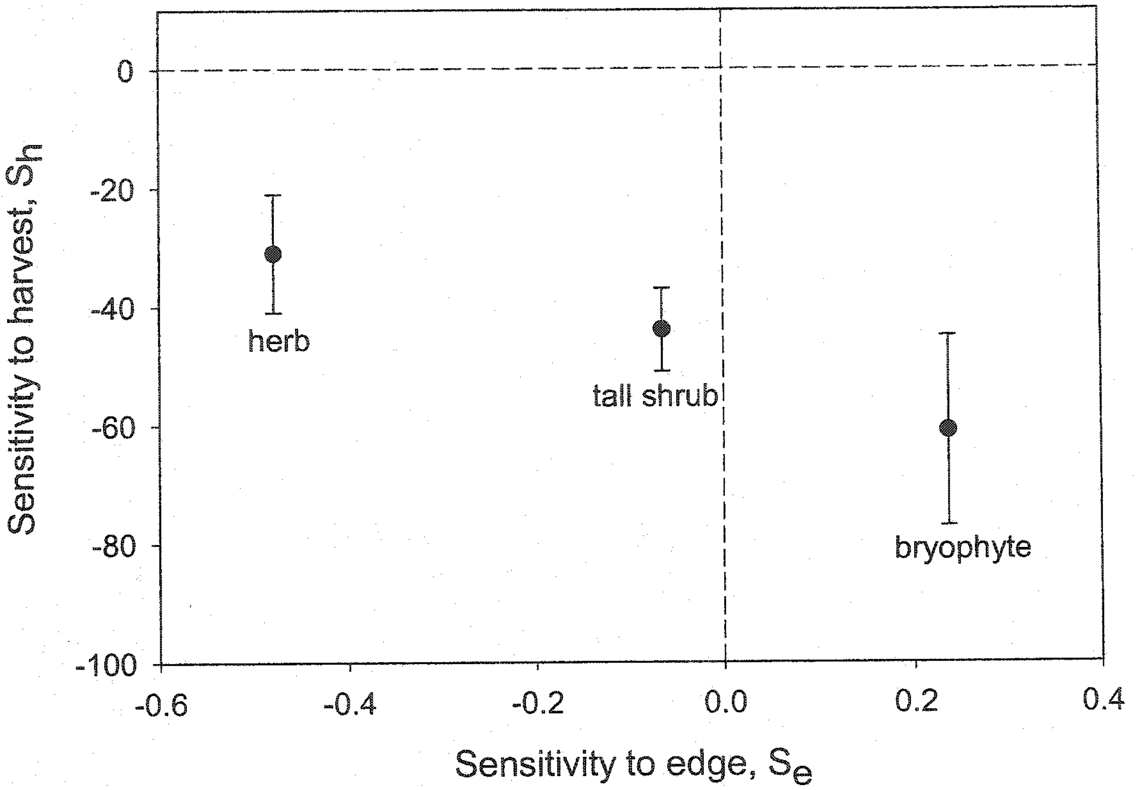

Figure 2.5. Sensitivity of understory life forms (bryophyte, herb, and tall shrub) to timber harvest and forest edge. At each replicate (forest aggregate/harvest area pair), sensitivity to harvest, S_h, was computed as the difference between the proportional change in total life form cover in the harvest area (*n* = 16 bands) and in the "interior" of the aggregate (*n* = 16 innermost bands); points represent means (±1 SE) (*n* = 4 replicates). Sensitivity to edge, S_e, was calculated as the Spearman rank correlation coefficient between the change in total cover of each life form and proximity to edge (*n* = 32, 4 aggregates x 8 distances).

Chapter Three

Demographic responses to timber harvest and acclimation to environmental change for three late-seral forest herbs: *Asarum caudatum, Clintonia uniflora,* and *Pyrola picta*

Abstract

Although many herbs associated with late-seral forests show dramatic declines in abundance after timber harvest, some are able to persist through the early stages of forest development. Persistence depends on the demographic and morphological traits of species and on their potential to acclimate physiologically to abrupt changes in environment. However, these traits and abilities are not well understood for most forest herbs. I studied demographic responses to timber harvest and physiological acclimation to post-harvest conditions of three clonal herbs (*Asarum caudatum, Clintonia uniflora,* and *Pyrola picta*) that are characteristic of late-seral forests of the Pacific Northwest, but vary in belowground morphology and leaf duration. Ramet density, leaf area, survival, clonal growth, and flowering rates were measured before and for 2 yr after logging in 9, 1 x 4 m plots in a 13-ha harvest unit and in 9 control plots in adjacent undisturbed forest. Acclimation to increased solar radiation was assessed by comparing leaf mass per unit area (LMA) and chlorophyll *a*: *b* ratios in first-year leaves of each species in recently harvested and undisturbed environments ($n = 20$ leaves per species per environment). The abundance of all three species declined substantially in the harvest area after treatment, with *Pyrola* exhibiting the greatest decline. Two years after logging, survival of *Asarum* ramets was significantly lower and survival of *Clintonia* ramets was significantly higher in the harvest area than in the undisturbed forest. For both species, clonal growth in the harvest area was more than double that in the forest. In contrast, survival and growth of *Pyrola* were similar between environments. Although all three species had higher LMA in the harvest area, only *Clintonia* had a higher chlorophyll *a*: *b* ratio, suggesting that *Clintonia* may be better able to utilize increased light than *Asarum* or *Pyrola*. My results indicate that late-seral species that are assumed to respond

similarly to timber harvest and associated environmental stresses vary in their demographic and physiological responses to disturbance, in part due to variation in belowground morphology and leaf duration.

Introduction

Many herbs associated with mature and late-seral forests initially decline in abundance after timber harvest (MacLean and Wein 1977, Halpern 1989, Duffy and Meier 1992, Halpern and Spies 1995, Meier et al. 1995, Nelson and Halpern *in press*), but some are able to recover from the direct effects of logging and to persist through early stages of forest succession (e.g., Halpern 1989). Persistence depends on species' demographic and morphologic traits and on their potential to acclimate physiologically to abrupt environmental change. Despite increasing concern over plant conservation in managed landscapes (Halpern and Spies 1995), little is known about the effects of disturbance on the population dynamics of forest herbs or their physiological acclimation to environmental stress. This comparative study of three late-seral herbs —*Asarum caudatum*, *Clintonia uniflora*, and *Pyrola picta* — explores the demographic trends that underlie species' declines following timber harvest, the ability of species to acclimate to post-harvest environmental conditions, and the life history traits that are associated with these trends and abilities.

In most temperate and boreal forests, a majority of understory herbs are clonal (e.g., Sobey and Barkhouse 1977, Antos and Zobel 1985a). For clonal plants, meristem demography (birth and death of plant modules or ramets) has been used to study growth patterns and to estimate fitness (Bazzaz and Harper 1977, Fagerström 1992, Wikberg 1995, Bonser and Aarssen 1996, Lezberg et al. 2001). Fitness of most forest understory plants is largely determined by survival and growth, rather than fecundity (Fagerström 1992, Silvertown et al. 1993, Salomonson et al. 1994). Sexual reproduction generally has limited influence on population persistence in undisturbed forest and, for most forest herbs, seedling establishment is rare (Bierzychudek 1982). Despite the limited contribution of sexual reproduction, forest herbs in favorable microsites do produce flowers and, although flowering may not be indicative of reproductive success, it is an important indicator of habitat suitability (Pitelka et al. 1980, Geber et al. 1997, Lindh 2003).

Clonal forest herbs employ a wide range of architectures and growth strategies (Sobey and Barkhouse 1977, Antos and Zobel 1984, Antos 1988). Variation in belowground morphology, including rhizome thickness and depth, distance between ramets (internode length) (Sobey and Barkhouse 1977), and degree of physiological integration of ramets (Pitelka and Ashmun 1985, Marshall 1990), may affect species' responses to timber harvest and associated changes in environment. Mechanical disturbance associated with timber harvest can reduce ramet survival by removing or burying plants or by severing rhizomes. Species with thin rhizomes that lie along the forest floor may experience greater declines from soil disturbance than species with more robust rhizomes or rhizomes that are positioned further below the soil surface. Some plants exhibit plasticity in rhizome internode length, producing both long and short shoots, while others have more rigid architecture (e.g., de Kroon et al. 1994). The ability to vary internode length may facilitate escape from adverse conditions, movement into new environments, and acquisition of resources at multiple locations (Slade and Hutchings 1987, Hutchings 1988, van Groenendael et al. 1996). Physiological integration allows ramets in more favorable environments to supply photosynthate to those in less favorable locations (Hartnett and Bazzaz 1985) and can increase ramet survival and clonal performance in heterogeneous (Salzman and Parker 1985) or marginal environments (Alpert and Mooney 1986). Loss of physiological integration may be especially detrimental to species for which survival or growth is correlated with clonal fragment size (e.g., Cain and Damman 1997).

Species adapted to shade differ in their abilities to acclimate to high-light environments, due to varying ability to adjust leaf morphology or biochemistry (Powles 1984).

Although increased light can increase rates of photosynthesis (Augspurger 1984, Burton and Mueller-Dombois 1984), exposure to higher-than-normal irradiance can cause high-light, high-temperature, and water-deficit stress in shade-adapted species (Osmond 1983), leading to high rates of photoinhibition, photorespiration, and photodestruction of chlorophyll (photooxidation) (Powles 1984, Pearcy et al. 1989). In high-light environments, ramets with even mild water stress may exhibit signs of photoinhibition, while photosynthetic rates of well-watered plants may not be reduced (Gauhl 1976).

Plants have evolved numerous forms of photosynthetic acclimation to high-light conditions. Two common responses are to adjust the ratio of leaf mass to surface area (LMA) and the chlorophyll content of leaves (Gamon and Pearcy 1989). The rate of photosynthesis in a shade leaf is limited by its rate of light capture. Shade plants maximize the area of light interception by having larger and thinner leaves, less conducting tissue, and a lower ratio of internal to external surface (lower LMA) than do sun plants. In addition, shade plants allocate more resources to light capture and production of chlorophyll *b* (Chl *b*) than to maintenance of photosynthetic reaction centers and associated production of chlorophyll *a* (Chl *a*) (Pearcy and Sims 1994). However, for photosynthetic efficiency in high-light conditions, plants need thicker leaves with taller or more layers of palisade cells and higher Chl *a*: Chl *b* ratios (Lambers et al. 1998); without these or other modifications, plants growing in high-light environments will not be able to utilize additional energy available for photosynthesis and may ultimately suffer from damage to the photosynthetic apparatus (Powles 1984).

Leaf lifespan, which is inversely correlated with net photosynthetic capacity (Reich et al. 1991), varies considerably among forest herbs and may influence the potential for acclimation to high-light environments. Several authors suggest there is a simple tradeoff between leaf persistence and leaf productivity (Kikuzawa 1991, Reich et al. 1992, Gower et al. 1993): plants with persistent leaves allocate more resources to leaf mechanical strength or chemical defenses from herbivores or pathogens than do plants with leaves of short duration, but at the expense of assimilatory potential. Thus, short-lived leaves are at an advantage in high-light environments. In addition, short leaf duration allows more rapid acclimation to changes in light availability, because the sun or shade character of a leaf is largely determined during leaf development, which may occur during the growing season before emergence (Lambers et al. 1998). Thus, whole plant acclimation may be delayed until all shade leaves are replaced with ones that are acclimated to high light. However, some plants can change LMA in mature leaves by producing an additional layer of palisade parenchyma upon exposure to increased irradiance (Bauer and Thöni 1988).

This study explores demographic responses to timber harvest and acclimation to environmental change for three rhizomatous herbs, *Asarum caudatum, Clintonia uniflora,* and *Pyrola picta,* characteristic of late-seral forests in the Pacific Northwest. These species were chosen because they differ in belowground morphology and leaf lifespan, and have the potential to show different responses to disturbance. Demographic data were collected before and for two years after logging in a timber harvest unit and an adjacent undisturbed forest. Morphology and chlorophyll content of first year leaves were assessed two years after harvest for each species in each environment. I address the following questions: (1) Does timber harvest affect the abundance or demographic patterns (ramet survival, clonal growth, rate of flowering, or seedling establishment) of *Asarum caudatum, Clintonia uniflora*, or *Pyrola picta*? (2) If so, does initial ramet density affect the magnitude of response? (3) Do changes in abundance or demographic trends vary with post-harvest ground conditions or cover of associated herbs or shrubs? (4) Do species acclimate to post-harvest conditions by changing leaf mass per unit area or Chl *a*: Chl *b* ratios?

Methods

Study species

Asarum caudatum (Aristolochiaceae) — *Asarum caudatum* (hereafter, *Asarum*) is a mat-forming, evergreen perennial herb found in moist, shaded forests at low to mid elevations from British Columbia to Oregon and as far east as Montana (Hitchcock and Cronquist 1973). Although little is known about the disturbance ecology of *Asarum* in the Cascade Mountains, Frost (1992) found that, in the Klamath Mountains of California, it was significantly less abundant in clearcuts than in forest interiors.

Asarum has stout rhizomes with relatively short internode segments, up to two cordate to reniform leaves per ramet, and solitary purple to dark brown flowers (Fig. 3.1 a). Individual leaves may persist for up to three years (personal observation). There is little information on the morphology and life history of *Asarum caudatum;* more is known about *A. canadense* of eastern North America. Flowers of *A. canadense* produce up to ca. 30 seeds (Muir 1995, Cain and Damman 1997). Seedlings germinate during the growing season in which they are produced; roots are initiated first, but shoots are not formed until the following spring (Baskin and Baskin 1986). Rates of seedling establishment are generally high relative to other rhizomatous forest herbs (Damman and Cain 1998). Plants must be several years old before they can produce two leaves or more than one ramet, and flowering only occurs in ramets that have two leaves (Damman and Cain 1998). Clonal-fragments with a larger number of ramets have higher rates of ramet survival, flowering, and seedling establishment than do those with fewer ramets (Cain and Damman 1997).

Clintonia uniflora (Liliaceae) — *Clintonia uniflora* (hereafter, *Clintonia*) is widely distributed in moist forests at low to subalpine elevations from Alaska to California. Its range extends inland to southwestern Alberta, Montana, Idaho, and eastern Oregon

(Hitchcock and Cronquist 1973). In some forests of the Pacific Northwest, *Clintonia uniflora* attains highest abundance in old-growth stands (Halpern and Spies 1995) and declines in those that have been logged and burned (Halpern 1989, Nelson and Halpern *in press*).

Ramets of *Clintonia* have one to three oblong or elliptic leaves that are arranged in basal rosettes (Fig. 3.1 b) and generally persist for only one growing season. Ramets produce solitary white flowers with single metallic-blue fruits. In undisturbed forest, *Clintonia* blooms infrequently: only 14% of study plants at sites in old-growth western hemlock-silver fir forests in the Oregon Cascade Range had flowers (Antos 1988). Seedling establishment also appears to be low (personal observation). In contrast, *Clintonia* has relatively high rates of vegetative spread (Antos 1988). Rhizomes are thin and fragile, but are relatively plastic with respect to variation in shoot and internode length (Antos 1988).

In eastern North America *C. borealis* has been relatively well studied (Tam 1956, Carter and Vogelman 1968, Siccama et al. 1970, Sobey and Barkhouse 1977, Bierzychudek 1982). *Clintonia borealis* does not flower until it is ca. 10 yr old, flower primordia are formed during the year prior to flowering, and fruits produce 10-15 seeds (Pitelka et al. 1985). Ramets typically senesce in late summer, after one or two rhizomes are produced (Pitelka et al. 1985). These rhizomes produce the following year's ramets. If a ramet only produces one rhizome, there will be no net clonal growth, as the rhizome will produce only a replacement ramet (Pitelka et al. 1985). Plants that produce a second rhizome, however, also produce a second ramet, and thus undergo clonal growth (Pitelka et al. 1985). Pitelka et al. (1985) found that survivorship and reproduction of *C. borealis* is correlated with ramet size.

Pyrola picta (Ericaceae) — *Pyrola picta* (hereafter, *Pyrola*) is a relatively common plant at low to mid elevations in dry to moist coniferous forests from British Columbia to southern California, and as far east as the Rocky Mountains (Hitchcock and Cronquist 1973). In the Washington Cascade Range, *Pyrola* reaches maximum abundance in mature and old-growth forest (Spies 1991) and declines in abundance in harvested areas (Halpern and Spies 1995, Nelson and Halpern *in press*).

Pyrola picta is an evergreen perennial with a basal rosette of leaves, branching rhizomes (Haber 1987) (Fig. 3.1 c), and strong associations with both ericoid and arbutoid mycorrhizae (Largent et al. 1980, Haber 1987). Leaves have relatively long lifespan (> 3 yr), and their morphology varies with environment: plants growing in drier environments have more epicuticular waxes, smooth leaf margins, and more abundant stomata on lower leaf surfaces than do plants in moist environments (Haber 1987). In addition, plants in drier and sunnier habitats tend to have two layers of palisade cells (Copeland 1947). Although *Pyrola* can reproduce sexually, seedling establishment is rare (personal observation). Flowering scapes are produced from lateral buds or on side branches on the rhizome and typically contain up to 25, 6- to 8-mm-long, yellowish- or greenish-white flowers (Haber 1987).

Study site

This study was conducted in the Gifford Pinchot National Forest in southwestern Washington (46°22'07" N, 121°34'40" W), in conjunction with the Demonstration of Ecosystem Management Options (DEMO) experiment (Aubry et al. 1999, Halpern et al. 1999a). Sampling occurred in and adjacent to a 13-ha aggregated retention harvest unit, in which all merchantable trees (> 18 cm diameter at breast height) were cut and yarded by helicopter except for two 1-ha patches of forest that were retained in opposite corners of the unit (for details see Halpern and McKenzie 2001). The site is located at 1012-1122 m elevation in the *Tsuga heterophylla* zone (Franklin and Dyrness 1973). Slopes average 40% and face southeast. Soils are well drained and fairly shallow, consist of loamy sands derived from residuum and colluvium, and are covered by a shallow surface layer of volcanic ash originating from the 1980 eruption of Mount St. Helens (Wade et al. 1992).

Forests are ca. 70-80 yr old and dominated by *Pseudotsuga menziesii*; *Tsuga heterophylla* and *Thuja plicata* are also common (Halpern et al. 1999a). Prior to treatment, canopy height, stem density, and basal area averaged 36 m, 1150 trees/ha, and 56 m^2/ha, respectively. Dominant understory species included *Tsuga heterophylla, Thuja plicata, Acer circinatum, Berberis nervosa, Pteridium aquilinum, Achlys triphylla*, and *Chimaphila umbellata.*

Sampling design

Plant demographic traits — Pre-harvest sampling was conducted from 21 July to 5 September 1997. In the planned harvest unit and adjacent forest, I identified groups of ramets of each study species (hereafter, "patches") based on four criteria: (1) included $\geq$ 15 ramets within a patch, (2) located > 15 m from neighboring plants of the same species, (3) located > 60 m from the harvest-unit edge, and (4) fit within a 1 x 4 m plot (to facilitate access to all ramets with minimal ground disturbance). From patches that met these criteria, 18 plots per species were randomly selected, with half in each environment. Within each plot, all ramets were numbered with an aluminum tag to monitor survival over time. The length and width of each leaf were measured for each ramet; these dimensions were then multiplied to estimate leaf area, and leaf areas were summed for all ramets in a plot. The number of ramets with flowers was counted, but seed production was not censused because destructive sampling and seed removal would have compromised future sampling. Finally, total cover of herbaceous species (including sub-shrubs) and shrubs was estimated in each plot. Because I did not excavate rhizomes, I could not determine ramet connections or the number of clonal fragments in each patch.

Post-harvest sampling, conducted from 6 August to 17 September in 1998 (year 1) and from 2 August to 12 September in 1999 (year 2), included all measurements taken during the initial sampling. In each post-harvest year, tagged ramets that survived were re-measured, and new ramets (produced through clonal growth) and seedlings (germinants with cotyledon leaves) were tagged and measured. In addition, harvest-related soil disturbance and cover of logging slash were quantified for plots in the harvest area (year 1 only). Cover of slash was recorded by density class: "light slash" included non- or minimally overlapping wood or foliage; "moderate slash," multiple overlapping pieces; and "heavy slash," entirely overlapping pieces. A single plot could contain more than one slash-density class. The presence of logging slash did not prevent relocation of ramets. When necessary, slash was carefully lifted and replaced and, with very few exceptions, all tags were relocated and ramet status assessed.

Leaf mass per unit area and chlorophyll content — On 24 and 25 July 1999 (year 2), one first-year leaf from each of 20 randomly selected ramets of each study species was collected from each environment (harvest area and adjacent undisturbed forest). Leaves were placed on ice and stored in the dark until processed. Within 12 hr of collection, two disks (each 1.13 cm^2) were cut from each leaf and placed in light-proof glass vials with 6 ml of N, N-dimethylformamide. Vials were stored in the dark at 2°C for 7 days, after which absorbance of Chl *a* ($A_{664.5}$) and Chl *b* (A_{647}) was read in 1.00 cm cuvettes using a Beckman DU-64 spectrophotometer (following methods of Brown 2000). Chlorophyll content (Chl *a* and Chl *b*) was calculated using the extinction coefficients provided in Inskeep and Bloom (1985). Leaves were dried for 48 hours at 70°C. Dry weights were determined using a Mettler balance, and leaf area was obtained by calculating the mean of three readings from a Li-Corr 3100 leaf area meter. Leaf mass per unit area (LMA) was calculated as dry weight divided by area.

Statistical analyses

To test for effects of timber harvest on abundance and demographic responses (Question 1), and to assess the significance of initial ramet density on the magnitude of response (Question 2), I conducted a series of ANCOVAs (Sokal and Rohlf 1981), with environment (undisturbed forest vs. harvest area) as the main effect and pre-treatment ramet density as the covariate. Prior to conducting ANCOVA, a general linear model (Sokal and Rohlf 1981) was used to test the assumption of no interaction between environment and pre-treatment ramet density. If a significant interaction was found, ANOVA (Sokal and Rohlf 1981) was used to compare species response between environments, and Pearson correlations (Sokal and Rohlf 1981) were used to test for significant relationships between species response and initial ramet density in each environment. Separate tests were performed for each post-harvest year (1 and 2).

For ANCOVA and ANOVA models, two measures of change in abundance were considered: the difference in ramet density and in leaf area between post- and pre-treatment values. Demographic variables included ramet survival, clonal growth, flowering rate, and seedling density. Ramet survival was calculated as the percentage of ramets present in the previous year that were also present in the current year. Clonal growth was expressed as the quotient of the number of new, vegetatively produced ramets in the current year and the total number of ramets in the previous year. Flowering rate was calculated as the percentage of ramets with flowers in the current year. Seedling density was expressed as the number per m^2. All response variables were square-root transformed to correct for unequal variance between environments.

Relationships between species' responses in harvest areas and post-treatment ground conditions or cover of associated vegetation (Question 3) were assessed with Pearson correlations between abundance or demographic response variables (see above) and cover of disturbed soil, logging slash (light, moderate, or heavy), herbs, and shrubs.

To test whether plants in the harvest area acclimated to post-harvest light conditions (Question 4), I conducted a series of *t*-tests (Sokal and Rohlf 1981) for between-environment differences in leaf morphology (LMA) and Chl *a*: Chl *b* ratio.

All statistical analyses were conducted using Systat 10.0 (SPSS 2001), with an alpha level of 0.05 as the basis for reporting statistical significance.

Results

Prior to timber harvest, ramet density, total leaf area, and flowering rate were similar between environments for all three species (Table 3.1). Seedlings were present only for *Asarum*, which showed no difference in density between environments (Table 3.1).

Changes in ramet density and leaf area

In year 1, density of ramets of all species (Fig. 3.2 a-c) and leaf area of *Clintonia* and *Pyrola* (Fig. 3.2 e, f) declined in the harvest area, and these changes were significantly greater than in undisturbed forest. In three of six tests, the magnitude of first-year declines was related to initial ramet density, with patches of greater density experiencing smaller declines (significant covariate; Fig. 3.2 c-e).

In year 2, there was no significant difference in either measure of abundance for *Asarum* or *Clintonia*. However, ramet density and leaf area of *Pyrola* remained significantly more depressed in the harvest area than in undisturbed forest (Fig. 3.2 c, f). In harvest areas, initial patch density moderated the decline in ramet density of *Asarum* and *Clintonia,* and in leaf area of *Asarum* (significant positive correlations, Table 3.2). In contrast, in undisturbed forest, initial patch size was negatively correlated with change in ramet density of *Clintonia* (Table 3.2).

Post-treatment demographic trends

In year 1, *Asarum* had significantly lower ramet survival, clonal growth, and flowering in the harvest area than in undisturbed forest (Fig. 3.3 a-c). In year 2, percent survival and flowering remained depressed in the harvest area (Fig. 3.3 a, c), but clonal growth increased (Fig. 3.3 b). Although mean *Asarum* seedling density was greater in the harvest area (1.2/m^2 in yr 1; 4.9/m^2 in yr 2) than in undisturbed forest (0.4/m^2 in yr 1; 0.7/m^2 in yr 2), the differences were not statistically significant.

In year 1, *Clintonia* had significantly lower ramet survival in the harvest area than in undisturbed forest (Fig. 3.3 d), but clonal growth was similar between environments (Fig. 3.3 e). In contrast, in year 2, survival and growth were significantly higher in the harvest area than in undisturbed forest (Fig. 3.3 d, e). Flowering was rare in both environments (Fig. 3.3 f), and no seedlings were found.

In year 1, *Pyrola* experienced significantly lower ramet survival and flowering in the harvest area than in undisturbed forest, but no difference in clonal growth (Fig. 3.3 g-i). In year 2, survival and growth were similar between environments (Fig. 3.3 g-h). Ramets in the harvest area did not produce flowers, but an average of 3% of ramets in the forest did (Fig. 3.3 i). No seedlings were found in either environment.

Demographic patterns for *Clintonia* and *Pyrola* were not correlated with initial patch density. However, for *Asarum*, ramet survival (yr 1) and seedling densities (yr 1 and 2) were positively correlated with initial ramet density in the harvest area, but not in undisturbed forest (Table 3.2).

Relationships with ground conditions and understory vegetation

Survival of ramets of all three species and changes in leaf area of *Pyrola* (Table 3.3) were negatively correlated with cover of heavy slash. In contrast, survival and clonal growth of *Asarum* were positively correlated with cover of light and moderate slash. Herb and shrub cover moderated declines in ramet density for *Asarum* and *Clintonia*, clonal growth of *Clintonia,* and survival of *Pyrola* ramets (Table 3.3).

Post-harvest leaf mass per unit area and chlorophyll content

Two years after harvest, LMA was significantly greater in the harvest area than in undisturbed forest for all species (Fig. 3.4 a). Leaf chlorophyll ratios differed significantly between environments for *Asarum* and *Clintonia*, but not for *Pyrola*: for *Asarum*, Chl *a*: Chl *b* ratio was significantly lower in the harvest area than in the forest

(Fig. 3.4 b); *Clintonia* showed the opposite trend, with significantly higher Chl *a*: Chl *b* ratio in the harvest area than in the forest (Fig. 3.4 b).

Discussion

Direct effects of timber harvest

For all three species, abundance (ramet density and leaf area) declined substantially in the harvest area directly after treatment, with greater losses of leaf area than of ramet density. In the undisturbed forest, year-to-year variation in ramet density was relatively small (< 20%), but declines in leaf area were surprisingly large, illustrating the potential for plant cover to vary annually in what are thought to be fairly stable forests. Most previous studies of plant responses to timber harvest have relied on plant cover rather than ramet density as a basis for assessing performance (e.g., Halpern 1989, Duffy and Meier 1992, Roberts and Zhu 2002, Ramovs and Roberts 2003, Nelson and Halpern *in press*). My results suggest that, relative to ramet density, cover-based assessments may overestimate the magnitude of species' declines.

All three species experienced similar rates of first-year ramet survival. Ramet mortality correlated with cover of heavy logging slash (entirely overlapping pieces of foliage and wood). Piles of slash, often > 1 m tall, consisted of dense accumulations of foliage and woody material that restricted ramet emergence. Forest herbs with long rhizomes can reemerge following shallow burial, but do not survive deep burial (> 15 cm) (Antos and Zobel 1985b). In contrast to heavy slash, light and moderate slash (non- or minimally-overlapping material) and cover of associated vegetation moderated declines in abundance, survival, and growth. Moderate amounts of shade provided by logging slash or taller vegetation may ameliorate potentially stressful levels of light or elevated temperatures on the forest floor.

Species responses to post-harvest environmental conditions

Asarum caudatum — Two years after harvest, there was no difference in the abundance (leaf area, ramet density) of *Asarum* in the undisturbed forest and harvest area. However, demographic trends and leaf chlorophyll patterns suggest that *Asarum* may not be acclimating to post-harvest environments. First, ramet survival and flowering remained depressed in the harvest area, patterns consistent with previous observations (Cain and Damman 1997, Damman and Cain 1998). Second, although *Asarum* responded to increased light in the harvest area by increasing LMA, leaves had lower Chl *a*: Chl *b* ratios than did leaves in the undisturbed forest — trends that would not be beneficial under greater levels of irradiance (Anderson and Osmond 1987, Anderson et al. 1988). As a consequence, photosynthetic rates in harvest areas may be compromised. This conclusion is supported by preliminary comparative analyses of leaf gas exchange: *Asarum* showed reduced rates of photosynthesis in the harvest area relative to undisturbed forest (unpublished data).

Despite short-term recovery of abundance in the harvest area due to increased clonal growth, I predict longer-term population declines for *Asarum*. High rates of clonal growth are unlikely to be sustained given low survival, lack of biochemical leaf acclimation, and reduced rates of photosynthesis. Furthermore, *Asarum*'s "rigid" architecture and short rhizome segments restrict movement into more favorable microsites. In addition, flowering has high resource costs (Muir 1995) and may be further reduced or eliminated in the harvest area as clonal stores become depleted. Although post-treatment density of seedlings did not differ between environments, future reductions in flowering may limit seedling establishment, further reducing potential for recovery. Damman and Cain (1998) found that ramet density of *A. canadense* decreased over time in early successional habitats, but remained stable in late-successional forest. To ensure long-term persistence, they estimated a minimum viable population size three orders of magnitude greater in early successional than in late-seral forest.

Clintonia uniflora — Two years after harvest, ramet density and leaf area of *Clintonia* were similar between environments, and survival and clonal growth in the harvest area surpassed that in the undisturbed forest, suggesting successful acclimation. Three biological traits may account for *Clintonia*'s ability to adjust to high light environments. First, dimorphic rhizomes allow *Clintonia* to respond to temporal and spatial variation in environment by changing ramet positions; ramets in unfavorable locations can be replaced by others in more favorable habitats (e.g., areas with local shade) via growth of long shoots (Antos 1988). Second, high levels of physiological integration (as reported for *C. borealis* [Ashmun et al. 1982]), may increase survival through resource sharing and nutrient recycling from dead ramets (Pitelka et al. 1985). There is only weak support for this possible mechanism in my study: although pre-treatment density of ramets positively affected post-treatment density, I did not find similar relationships with ramet survival or clonal growth. Finally, because *Clintonia* exhibits annual turnover of leaves, it can quickly adjust leaf morphology and physiology to respond to environmental change. Both LMA and Chl *a*: Chl *b* ratios were higher in the harvest area than in undisturbed forest, thus, *Clintonia* showed high phenotypic plasticity in response to changing light availability. Similar observations have been made for *Clintonia borealis* (Ashmun and Pitelka 1985, Pitelka et al. 1985).

Clintonia's fairly rapid recovery of abundance in the current study contrasts with reports of local extirpation after timber harvest elsewhere in the Pacific Northwest (Halpern and Spies 1995). However, this difference in response may be attributable to differences in disturbance history. Until recently, forest managers have used broadcast burning to remove logging slash, to facilitate planting of tree seedlings, and to reduce competition from residual vegetation. Declines of some forest species may result primarily from this type of burning, rather than from physical disturbances associated with logging (Bradley 1984, Halpern 1989); greater survival of *Clintonia* on my sites may be explained by the absence of broadcast burning. In addition, trees were yarded by helicopter, with only minimal disturbance to forest soils (Halpern and McKenzie 2001). With long, slender, rhizomes located in the upper layers of the soil, *Clintonia* may be especially susceptible to ground-based harvest operations that disturb soils and disrupt the physiological integration of ramets.

Pyrola picta — *Pyrola* showed distinctly slower recovery of abundance in harvest areas than did *Asarum* or *Clintonia*. Although second-year survival and clonal growth were similar between environments, ramet density and leaf area remained significantly depressed due to the magnitude of first year declines.

Pyrola also showed the greatest change in LMA in response to timber harvest. Others have found substantial differences in leaf morphology in different environments: Copeland (1947) found that plants in relatively dry habitats had more layers of palisade cells than did plants in moister environments, and Haber (1987) found that open-grown plants had more obvious epicuticular wax, smoother leaf margins, and more abundant stomata on lower leaf surfaces. In fact, *Pyrola* exhibits such a wide range of leaf morphologies that there has been confusion about its taxonomic classification; some have classified plants in open habitats as *P. dentata* or *P. pallida* (Hitchcock and Cronquist 1973, Haber 1987), although generally they are recognized as the same species (Haber, 1987).

Despite large changes in leaf morphology, *Pyrola* did not alter leaf chlorophyll ratio in response to timber harvest. Wesser (1991) found that *P. secunda* (which also occurs in the study area) was inflexible to changes in light, maintaining constant Chl *a*: Chl *b* ratios under widely varying irradiances. *Pyrola*'s inability to adjust leaf photopigments does not appear to affect survival or growth. One possible explanation is that *Pyrola* employs other strategies to acclimate to increased irradiance. In a comparison of photosynthesis rates of leaves in undisturbed forest and harvest areas (unpublished data), those in the harvest area had higher rates of photosynthesis at high irradiance than did those growing in undisturbed forest exposed to the same levels of light. This suggests that *Pyrola* acclimates to increased irradiance by adjusting electron transport, or photophosphorylation and carbon assimilation, but not its light harvesting system. This strategy has been observed in other shade-adapted species, including *Tradescantia albiflora* (Chow et al. 1991). However, it is also possible that relatively high rates of survival and clonal growth reflect short-term reliance on belowground stores rather than acclimation of its photosynthetic apparatus.

Conclusions

It is generally assumed that species associated with late-seral forests respond similarly to disturbance and environmental stress. My comparative studies suggest, however, that there can be considerable variation in demographic and physiological response, related to variation in belowground morphology and leaf duration. *Clintonia* shows the greatest potential for recovery after logging, arising from its dimorphic rhizomes, annual turnover of leaves, and capacity to adjust Chl *a*: Chl *b*. However, *Clintonia* has shallow, fragile rhizomes that are sensitive to burning and mechanical disturbance, and recovery may be limited in areas of intensive ground disturbance. By contrast, *Asarum*'s relatively inflexible architecture and perennial leaves limit its potential for acclimation. Although it may utilize stored resources to persist in marginal habitat for short periods of time, long-term persistence in stressful environments appears unlikely given poor ramet survival and limited "mobility." The dynamics and potential for recovery of *Pyrola* are less clear. Patterns of survival and growth in the harvest area may reflect either physiological acclimation unrelated to changes in leaf chlorophyll (e.g., reallocation of resources within mature leaves) or reliance on resources stored in belowground structures. If *Pyrola* can adapt physiologically, it may be able to persist in harvested environments, although recovery will be slow. However, if plants must rely on underground stores, ramet densities are likely to decline dramatically in future years. Knowledge of species demographic and physiological responses to disturbance and environmental stress are thus useful in understanding their spatial and temporal dynamics. Even among species that are viewed as functional equivalents (clonal, shade-tolerant, forest herbs), caution must be exercised in generalizing about the population change that will result from a major disturbance and the plant characteristics that will contribute to adjustment or recovery in the post-harvest environment.

Table 3.1. Ramet density (no./m^2), total leaf area (cm^2/m^2), flowering rate (% of ramets with flowers), and seedling density (no./m^2) for *Asarum caudatum*, *Clintonia uniflora*, and *Pyrola picta* prior to treatment in areas to be harvested and adjacent forest. No *Clintonia* or *Pyrola* seedlings were observed. Test statistics (t) and probability values (P) are from t-tests ($n = 9$ in each environment).

	Forest				Harvest area (prior to logging)					
	Mean	SE	Min	Max	Mean	SE	Min	Max	t	P
Asarum caudatum										
Ramet density (no./m^2)	9	2	4	23	10	3	4	34	-0.3	0.768
Leaf area (cm^2/m^2)	588	248	86	2489	478	172	102	1775	0.4	0.720
Flowering (% of ramets)	2.1	1.1	0.0	8.9	6.7	3.0	0.0	23.1	-1.4	0.180
Seedling density (no./m^2)	0.3	0.2	0.0	2.0	0.5	0.2	0.0	1.8	-0.5	0.642
Clintonia uniflora										
Ramet density (no./m^2)	5	1	4	10	6	1	4	12	-0.4	0.703
Leaf area (cm^2/m^2)	310	66	81	639	342	60	159	693	-0.4	0.722
Flowering (% of ramets)	<0.1	<0.1	<0.1	0.4	0.1	0.1	<0.1	0.5	-0.1	0.933
Pyrola picta										
Ramet density (no./m^2)	10	1	5	15	10	2	5	22	-0.1	0.957
Leaf area (cm^2/m^2)	257	28	168	452	253	34	160	473	0.1	0.941
Flowering (% of ramets)	7.0	1.2	0.0	13.3	17.0	5.4	0.0	44.0	-1.8	0.107

Table 3.2. Correlations (Pearson *r*) between abundance or demographic variables and pre-treatment ramet density in undisturbed forest and harvest areas. Probabilities of significance (P) ≤ 0.05 are in bold font. Tests were conducted only for those variables showing a significant interaction between environment and pre-treatment ramet density (see *Methods: Statistical analyses*).

	Pre-treatment ramet density			
	Forest		Harvest	
	r	*P*	*r*	*P*
Asarum caudatum, yr 1				
Survival	-0.41	0.275	0.71	**0.033**
Seedling density	-0.08	0.835	0.93	**0.001**
Asarum caudatum, yr 2				
Change in ramet density*	0.38	0.309	0.81	**0.008**
Change in total leaf area*	-0.03	0.942	0.70	**0.038**
Seedling density	-0.05	0.890	0.91	**<0.001**
Clintonia uniflora, yr 2				
Change in ramet density*	-0.78	**0.013**	0.89	**0.002**
Change in total leaf area*	-0.65	0.061	0.56	0.352

* For change variables, positive correlation coefficients (*r*) indicate that patches of greater pre-treatment ramet density experienced smaller declines (or larger increases) in post-treatment ramet density or leaf area than those with lower initial ramet density; negative coefficients indicate that patches of greater initial density experienced larger declines (or smaller increases) in ramet density or leaf area.

Table 3.3. Significant correlations (Pearson *r*) between species responses in the harvest area (changes in ramet density and leaf area, survival, and clonal growth) and cover of logging slash (light, moderate, or heavy) or plant cover (herbs and shrubs). See *Methods* for a description of slash-density classes. Separate tests were conducted for first- and second-year responses; underscored values represent second-year responses. Probabilities of statistical significance are coded as: * = $P \leq 0.05$, ** = $P \leq 0.01$, and *** = $P \leq 0.001$. Correlations with disturbed soil were not significant.

	Cover of logging slash			Plant cover	
	Light	Moderate	Heavy	Herbs	Shrubs
	r	*r*	*r*	*r*	*r*
Asarum caudatum					
Change in density				0.70*	$\underline{0.91}$***
Change in leaf area					$\underline{0.72}$*
Survival	0.71*		-0.77*		
Clonal growth		0.71*			
Clintonia uniflora					
Change in density					0.81**
Survival			-0.88**		
Clonal growth				$\underline{0.86}$**	0.92***
Pyrola picta					
Change in leaf area			-0.78*, -$\underline{0.72}$*		
Survival			-0.67*	0.68*	0.81**

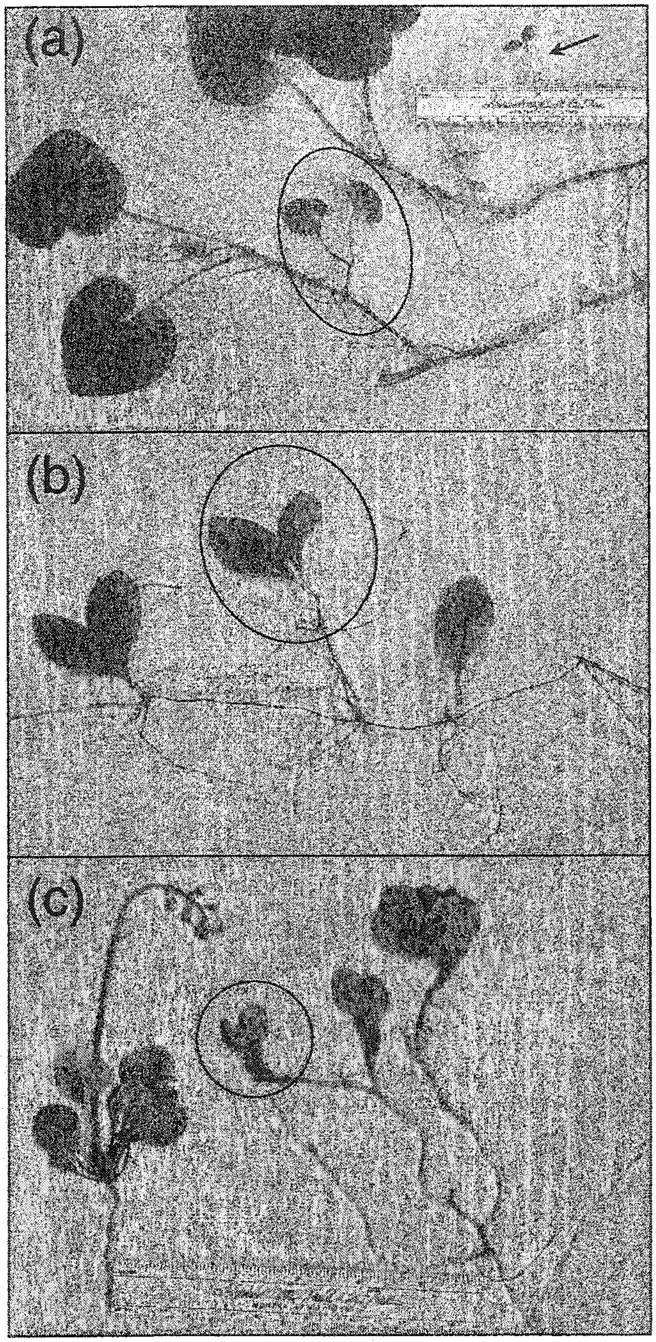

Figure 3.1. Clonal fragments of *Asarum caudatum* (a), *Clintonia uniflora* (b), and *Pyrola picta* (c) illustrating individual ramets (circled) and root system distribution and morphology. The arrow in (a) points to a seedling (germinant with cotyledon leaves).

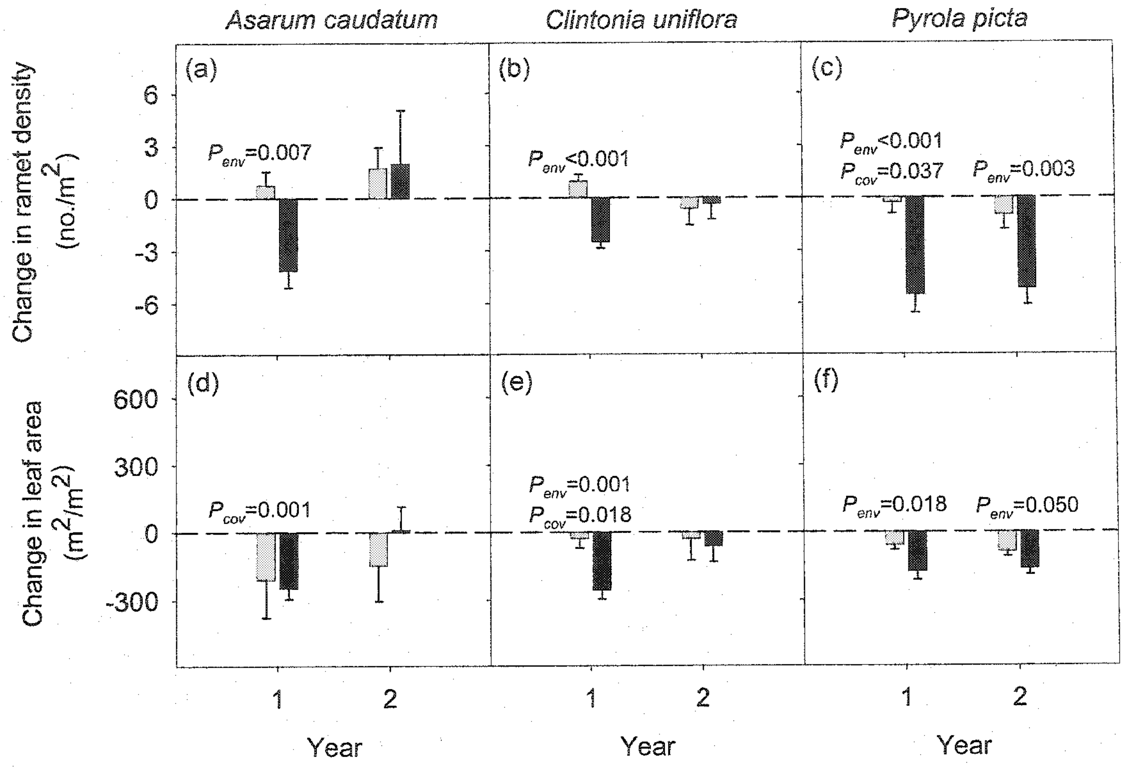

Figure 3.2. Changes in ramet density (a-c) and total leaf area (d-f) for *Asarum caudatum*, *Clintonia uniflora*, and *Pyrola picta* in undisturbed forest (light shading) and adjacent harvest area (dark shading), one and two years after treatment. Bars indicate mean changes (post minus pre-treatment values) ±1 SE. P_{env} values indicate significant differences in response between environments based on ANCOVA; P_{cov} values indicate a significant effect of the covariate, pre-treatment ramet density, on species response. For year 2 comparisons of *Asarum* and *Clintonia,* there was a significant interaction between environment and pre-treatment ramet density, thus ANOVA was used to compare responses between environments and Pearson correlations (see Table 3.2) were used to assess relationships between species' responses and initial ramet density in each environment.

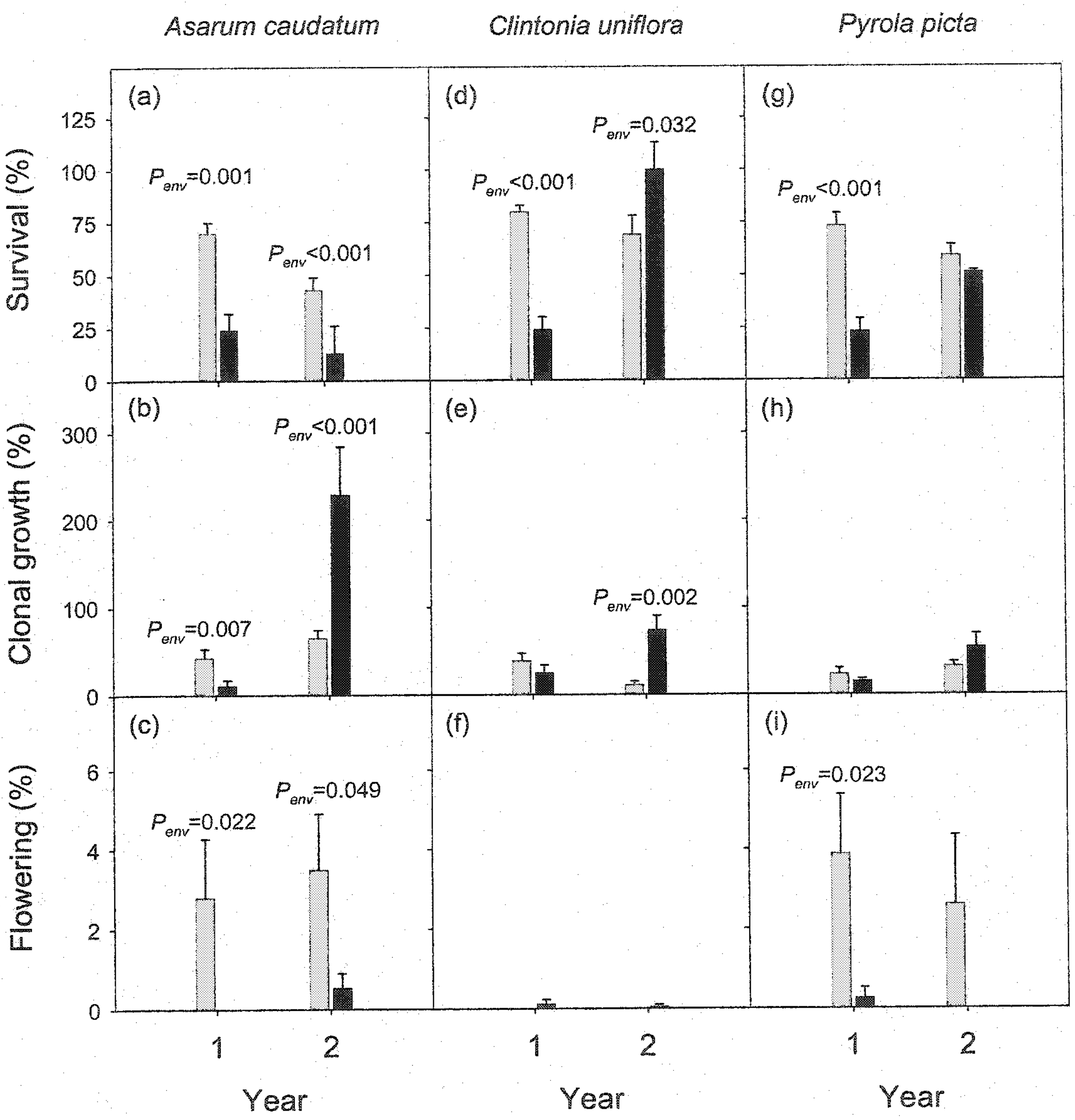

Figure 3.3. Post-treatment percent survival (a-c), clonal growth (d-f), and flowering (g-i) for *Asarum caudatum*, *Clintonia uniflora*, and *Pyrola picta* in undisturbed forest (light shading) and adjacent harvest area (dark shading). Values are means ±1 SE. P_{env} values indicate significant differences in response between environments based on ANCOVA; no test resulted in a significant covariate. For year 1 comparisons of *Asarum* ramet survival, there was a significant interaction between environment and pre-treatment ramet density, thus ANOVA was used to compare responses between environments, and Pearson correlations (see Table 3.2) were used to assess relationships between ramet survival and initial ramet density in each environment.

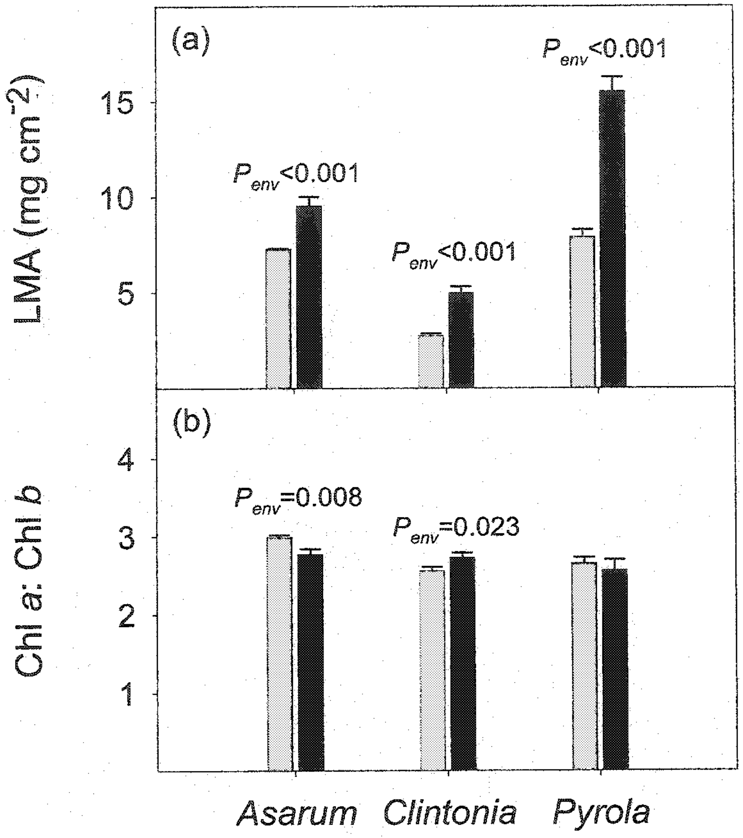

Figure 3.4. Leaf mass per unit area (LMA; a) and Chl *a*: Chl *b* ratio (b) for *Asarum caudatum*, *Clintonia uniflora*, and *Pyrola picta* in undisturbed forest (light shading) and adjacent harvest area (dark shading) 2 yr after treatment. Values are means ±1 SE. *P* values indicate significant differences in response between environments based on a paired *t*-test ($n = 20$ in each environment).

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VITA

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