

EDGE-RELATED RESPONSES OF UNDERSTORY PLANTS TO AGGREGATED RETENTION HARVEST IN THE PACIFIC NORTHWEST

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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. We 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 sixteen 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 harvested 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. Our results suggest that, over short time frames, 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.

Key words: community composition; edge effects; forest borders; forest management; forest remnants; green-tree retention; logging effects; plant communities; *Pseudotsuga menziesii*; understory; vegetation; vegetation gradients.

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, clear-cut 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 clear-cut 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 nonnative species (Forest Ecosystem Management Assessment Team 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, which 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

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PLATE 1. Examples of vegetation structure after harvest at four positions along a study transect: (top left) aggregate center, (top right) aggregate edge, (lower left) harvest-area edge, and (lower right) harvest area. Photo credit: David Phillips.

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, we examine short-term responses (one and two years 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 us to reliably quantify the spatial pattern, magnitude, and time course of vegetation responses in 1-ha forest aggregates retained during timber harvest. We 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) can we detect 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)?

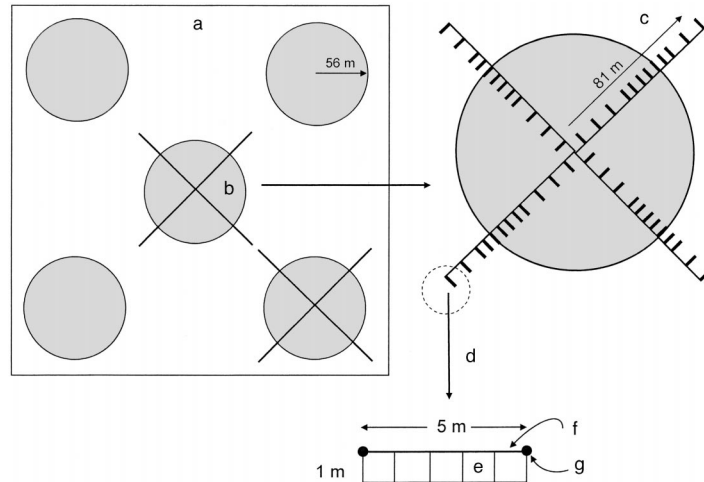


FIG. 1. Position of forest aggregates within a 13-ha harvest unit (a). Data were collected in two undisturbed forest aggregates (b) at each site, along transects (c) originating at the center of each aggregate and ending 25 m into the surrounding harvested area. Twelve bands (d) were established at 5–10 m intervals along each transect; each band consisted of five 1-m² subplots (e) within which we 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).

METHODS

Study sites

Our 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 ~70–80 years 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 m²/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 oregonum* 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 years 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 den-

sity, and basal area averaged 39 m, 740 trees/ha, and 73 m²/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. 1a). 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 harvested 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. 1b), we established four perpendicular transects (Fig. 1c), 81 m in length, which extended in cardinal directions from the

aggregate center and ended 25 m into the surrounding area to be harvested (see Plate 1). 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. 1c). Thus, bands were spaced at 5-m intervals on both sides of the forest edge, where we expected steep gradients in vegetation response, and at 10-m intervals elsewhere. Each band (Fig. 1d) consisted of five, 1-m² subplots (Fig. 1e), within which we 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, we 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. 1f), using the line-intercept method. Light availability, which correlates with many other physical factors (e.g., temperature, humidity, and soil moisture [Matlack 1993]), was estimated with a CI-110 digital canopy imager with a 150° lens (CID, Inc., Camas, Washington, USA). Digital photographs were taken from the end points of each band (Fig. 1g) 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 to minimize direct exposure to sun (Easter and Spies 1994). Digital images were analyzed using Scanopy 2.0b software (Regent Instruments Inc., Quebec City, Quebec, Canada) to calculate percent open sky (Anderson 1964, Canham 1988).

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, we 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, we computed mean values for each of the eight sample distances in each aggregate.

We 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 contribu-

tions 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):

$$PD = 100 \times \left\{ 1 - 2 \times \left[\frac{\sum \min(\text{cov}_{0i}, \text{cov}_{1i})}{\sum (\text{cov}_{0i} + \text{cov}_{1i})} \right] \right\} \quad (1)$$

where cov_{0i} and cov_{1i} 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.—We 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; we 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, cover, and PD) and distance from the aggregate edge ($n = 32$; i.e., eight distances by four 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), we used one-way ANOVAs (Sokal and Rohlf 1981) to compare the mean response of transects representing the four cardinal di-

TABLE 1. Results of two-sample *t* tests (df = 6) comparing environmental variables in forest aggregates (*n* = 4) and adjacent areas of harvest (*n* = 4).

| Parameter | Mean (SE) | | <i>t</i> | <i>P</i> |
|-----------------------------|-------------------|---------------|----------|----------|
| | Forest aggregates | Harvest areas | | |
| 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 |

rections (*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, we 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 harvested areas; however, cover of disturbed soil did not differ significantly between environments (Table 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 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. 2a).

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-m² 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. 2a). At the same time, a total of 15 early-seral taxa colonized sample bands (Table 3), with individual aggregates gaining an average of fewer than one species and adjacent areas of harvest an average of nine (Fig. 2b). In harvest areas, richness of early-seral species nearly doubled from year one to two (Fig. 2b).

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, nonsignificant change); however, the difference between environments was not significant in year two (Table 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 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 2), and for 17 of the 29 common species, mean cover differed more than twofold between environments.

After treatment, most species declined in cover in both environments (Fig. 3); however, the average magnitude of decline was greater in harvest areas than in aggregates (39 vs. 12%). 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. 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 5); however, these increases were largely restricted to a distance of ~10–15 m from the edge (Fig. 4a and b). Cover of disturbed soil did not show a significant correlation with proximity to edge (Table 5), although there were several relatively high values within 5 m of the forest margin (Fig. 4c).

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 5, Fig. 5); however, the strength of this relationship increased with time (Table 5). There were only two occurrences of early-seral species in the aggregates, both within 10 m of the edge (Fig. 5). Change in community composition

TABLE 2. Frequency (percentage of bands) and mean cover of species found before treatment in areas to be retained as forest aggregates and those to be harvested.

| Species | Forest aggregates (<i>n</i> = 128) | | Harvest areas (<i>n</i> = 62) | |
|---------------------------------|-------------------------------------|-----------|--------------------------------|-----------|
| | Frequency (%) | Cover (%) | Frequency (%) | Cover (%) |
| Grasses | | | | |
| <i>Bromus vulgaris</i> | 15 | t | 13 | t |
| Ferns and fern allies | | | | |
| <i>Pteridium aquilinum</i> | 81 | 3.4 | 74 | 3.2 |
| <i>Polystichum munitum</i> | 1 | t | 3 | 0.1 |
| <i>Blechnum spicant</i> | 1 | t | 2 | t |
| <i>Athyrium filix-femina</i> | | | 5 | 0.1 |
| <i>Adiantum pedatum</i> | | | 2 | t |
| <i>Lycopodium clavatum</i> | | | 2 | t |
| Forbs | | | | |
| <i>Viola sempervirens</i> | 74 | 0.3 | 67 | 0.3 |
| <i>Pyrola secunda</i> | 60 | 0.2 | 54 | 0.2 |
| <i>Clintonia uniflora</i> | 52 | 0.4 | 48 | 0.5 |
| <i>Achlys triphylla</i> | 48 | 3.7 | 48 | 4.0 |
| <i>Pyrola picta</i> | 46 | 0.1 | 38 | 0.1 |
| <i>Xerophyllum tenax</i> | 45 | 2.6 | 48 | 5.6 |
| <i>Trillium ovatum</i> | 36 | 0.1 | 38 | 0.1 |
| <i>Smilacina stellata</i> | 32 | 0.3 | 34 | 0.3 |
| <i>Goodyera oblongifolia</i> | 27 | 0.1 | 15 | t |
| <i>Anemone deltoidea</i> | 22 | t | 25 | 0.1 |
| <i>Hieracium albiflorum</i> | 16 | t | 20 | t |
| <i>Listera caurina</i> | 16 | t | 13 | t |
| <i>Pyrola asarifolia</i> | 15 | 0.1 | 23 | 0.1 |
| <i>Smilacina racemosa</i> | 14 | 0.1 | 16 | 0.1 |
| <i>Vancouveria hexandra</i> | 14 | 0.2 | 11 | 0.1 |
| <i>Trientalis latifolia</i> | 9 | t | 8 | t |
| <i>Tiarella trifoliata</i> | 5 | t | 15 | 0.1 |
| <i>Pedicularis racemosa</i> | 5 | t | 13 | t |
| <i>Campanula scouleri</i> | 3 | t | 3 | t |
| <i>Disporum hookeri</i> | 3 | t | 2 | t |
| <i>Galium triflorum</i> | 2 | t | 7 | t |
| <i>Adenocaulon bicolor</i> | 2 | t | 2 | t |
| <i>Streptopus amplexifolius</i> | 2 | t | | |
| <i>Viola glabella</i> | 1 | t | 5 | t |
| <i>Osmorhiza chilensis</i> | 1 | t | 2 | t |
| <i>Actaea rubra</i> | 1 | t | | |
| <i>Aquilegia formosa</i> | 1 | t | | |
| <i>Pyrola aphylla</i> | 1 | t | | |
| <i>Asarum caudatum</i> | | | 8 | 0.1 |
| <i>Nothochelone nemorosa</i> | | | 2 | t |
| Subshrubs | | | | |
| <i>Chimaphila umbellata</i> | 84 | 1.8 | 69 | 1.9 |
| <i>Linnaea borealis</i> | 81 | 0.7 | 85 | 1.0 |
| <i>Rubus ursinus</i> | 77 | 0.7 | 70 | 0.7 |
| <i>Cornus canadensis</i> | 72 | 2.6 | 72 | 2.4 |
| <i>Rubus lasiococcus</i> | 59 | 0.5 | 64 | 0.5 |
| <i>Chimaphila menziesii</i> | 27 | 0.1 | 26 | t |
| <i>Rubus nivalis</i> | 3 | 0.1 | 2 | t |
| Shrubs | | | | |
| <i>Vaccinium membranaceum</i> | 66 | 2.6 | 74 | 3.9 |
| <i>Berberis nervosa</i> | 63 | 7.5 | 54 | 5.6 |
| <i>Vaccinium parvifolium</i> | 53 | 1.2 | 64 | 1.9 |
| <i>Vaccinium ovalifolium</i> | 38 | 4.1 | 34 | 4.7 |
| <i>Pachistima myrsinites</i> | 38 | 0.3 | 31 | 0.5 |
| <i>Gaultheria ovatifolia</i> | 32 | 0.4 | 41 | 0.4 |
| <i>Rosa gymnocarpa</i> | 30 | 0.4 | 13 | 0.2 |
| <i>Sorbus</i> spp. | 16 | t | 13 | t |
| <i>Symphoricarpos mollis</i> | 13 | 0.2 | 5 | t |
| <i>Acer circinatum</i> | 9 | 2.2 | 21 | 2.7 |
| <i>Rubus parviflorus</i> | 5 | 0.1 | 2 | t |
| <i>Gaultheria shallon</i> | 3 | 0.1 | 8 | 0.5 |
| <i>Alnus sinuata</i> | 2 | t | 7 | 1.0 |
| <i>Acer glabrum</i> | 2 | t | 3 | t |
| <i>Menziesia ferruginea</i> | 2 | t | 2 | 0.2 |
| <i>Amelanchier alnifolia</i> | 2 | t | 2 | t |
| <i>Ribes lacustre</i> | | | 2 | t |

Notes: Mean cover of <0.05% is indicated by t (trace); *n* = total number of sample bands.

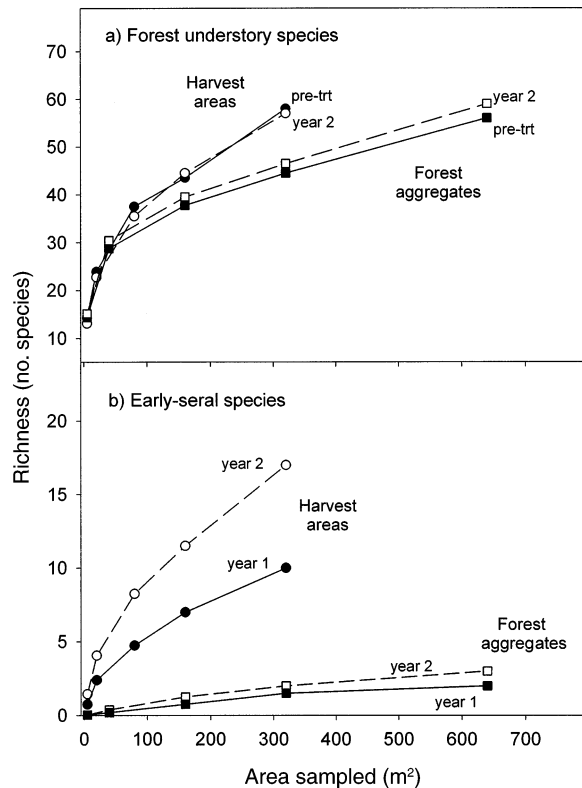


FIG. 2. Species-area curves for (a) forest understory species (before and two years after treatment) and (b) early-seral species (one and two years after treatment), in forest aggregates (squares) and harvest areas (circles). Open symbols represent year 2, solid symbols represent (a) pre-treatment and (b) year 1, respectively. Points along curves (from left to right) represent means for bands, transects, individual aggregates or surrounding harvest areas, sites, and the entire study area.

(PD) increased significantly with proximity to edge (Table 5), due in large part to changes at the forest margin (0–5 m; Fig. 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 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. 7a). Of the eight species that showed significant negative correlations between change in cover and edge proximity (Fig. 7a), five also showed significant negative correlations with light availability (Fig. 7b) and six with cover of logging slash (Fig. 7c). 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 our work. First, in a strict sense, our 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 clear-cut 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 our 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, our conclusions are limited to short-term (two-year) responses. We acknowledge this limitation as we interpret our results, and we 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, our 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 harvested 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

TABLE 3. Frequency (percentage of bands) and mean cover of early-seral taxa found two years after treatment in forest aggregates and harvest areas.

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

Notes: Mean cover of <0.05% is indicated by t (trace); n = total number of sample bands.

those in adjacent harvest areas. Despite these differences, there was substantial year-to-year variation within aggregates (PD of ~20%). Some of this variation is attributable to edge effects (see *Gradients in response within forest aggregates*). 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. 2005). 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. Our 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 shrubs, many of

TABLE 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 ($n = 4$).

| | Mean (SE) | | t | P |
|--|-------------------|---------------|-------|--------|
| | Forest aggregates | Harvest areas | | |
| 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 |

Note: A mean change of <0.5 species per band is indicated by t (trace).

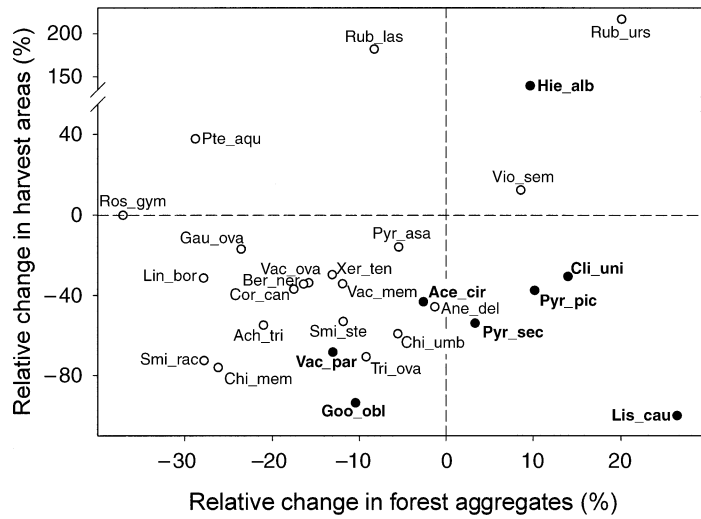


FIG. 3. Relative change in cover of individual species in harvest areas and in forest aggregates two years after treatment. Note the different scales of the *x*- and *y*-axes. Solid circles and bold labels indicate species with significant differences between environments (based on *t* tests); open circles represent nonsignificant 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 ovalifolia* (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 three or more aggregate/harvest area pairs and 10% of all sample bands are illustrated.

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 our 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

our ability to demonstrate significant differences). These observed declines are consistent with the results of long-term studies of succession in clear-cut forests of western Oregon (Halpern 1989, Halpern and Spies 1995).

Liliaceous herbs were also sensitive to timber harvest on our 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 per-

TABLE 5. Spearman rank correlation coefficients (r_s ; $n = 32$) between distance from edge or environmental variables and change in community-level attributes for each sample date.

| Parameter | Edge proximity | | Open sky | | Logging slash | | Disturbed soil | |
|-----------------------------------|----------------|----------|----------|----------|---------------|----------|----------------|----------|
| | r_s | <i>P</i> | r_s | <i>P</i> | r_s | <i>P</i> | r_s | <i>P</i> |
| 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 |

Notes: For edge proximity, negative coefficients indicate declines with proximity to forest edge.

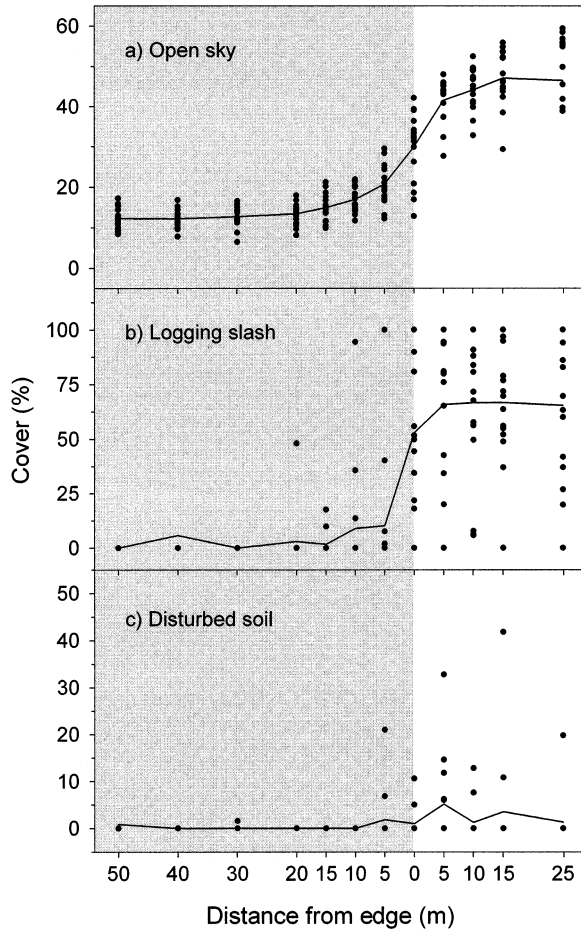


FIG. 4. (a) Open sky, (b) cover of logging slash, and (c) cover of disturbed soil with distance from the edges of forest aggregates. Lines represent mean values ($n = 16$) at each sampled distance. Points in the shaded region represent bands within the aggregates.

formance 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 we observed in harvested 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 com-

munity composition were most apparent at the forest border (0–5 m). We 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). We anticipate gradual increases in richness near aggregate edges with time, as early-seral species become more abundant in adjacent harvested 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 our Washington sites. These differences may reflect contrasting levels of microclimatic stress (the Klamath region is substantially warmer and drier than our study area) or the short time frame of our 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 our 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

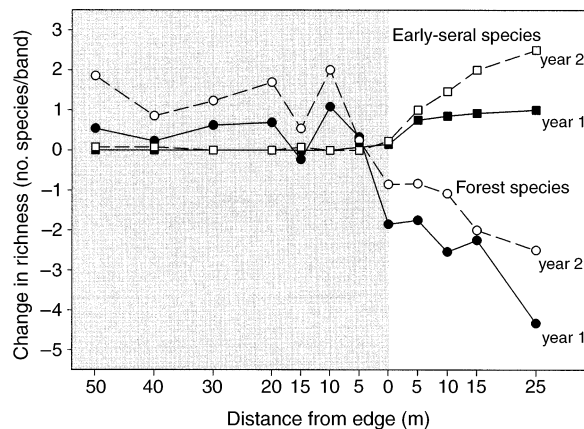


FIG. 5. Changes in richness of forest understory (circles) and early-seral (squares) species with distance from the edges of forest aggregates. Values represent mean differences ($n = 16$) in band-level richness between pre- and post-treatment measurements (solid symbols, year 1; open symbols, year 2). Points in the shaded region represent bands within the aggregates.

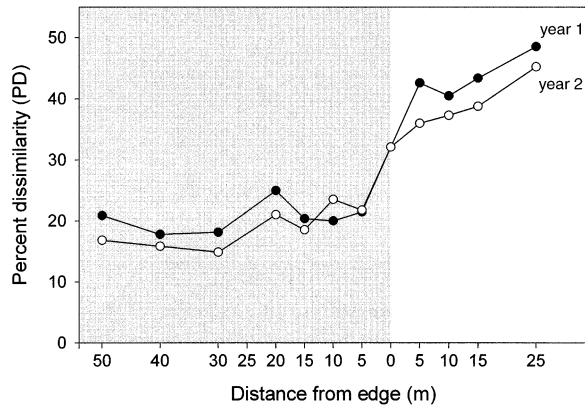


FIG. 6. Changes in community composition with distance from the edges of forest aggregates. Values represent mean percent dissimilarity ($n = 16$) between pre- and post-treatment composition at each distance (solid circles, year 1; open circles, year 2). Points in the shaded region represent bands within the aggregates.

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 our sites. First, they colonized infrequently in the harvested portions of treatment units. This contrasts with the typical pattern of abundant establishment after clear-cut 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-arming" 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 our sites, the structure of mature, Douglas-fir forests may present a barrier to dispersal even before self-arming 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., Wisser et al. 1998). In our montane forests, 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 10–15 m wide band, leaving ~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 (Reifsnnyder 1965, Geiger 1966, Reifsnnyder 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

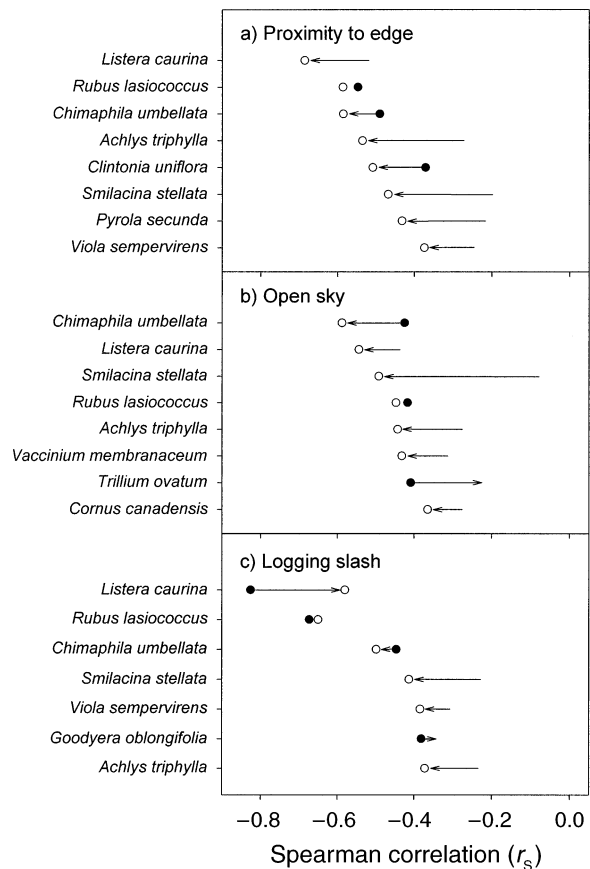


FIG. 7. Spearman rank correlation coefficients (r_s ; $n = 32$) between change in species abundance within forest aggregates and (a) edge proximity, (b) percent open sky, or (c) cover of logging slash, one and two years after treatment. For edge analyses, negative correlations indicate a decline with proximity to forest edges. Solid circles indicate significant first-year relationships, and open circles indicate 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 three or more aggregate/harvest area pairs and 10% of all bands were tested, and only those species with significant relationships ($P \leq 0.05$) are illustrated.

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 (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 we did not quantify herbivory, we 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 we 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). Our results suggest that, over short time frames, 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.

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