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Source: *Ecological Applications*, Vol. 15, No. 1 (Feb., 2005), pp. 175-195
Published by: Ecological Society of America
Stable URL: http://www.jstor.org/stable/4543344
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Ecological Applications, 15(1), 2005, pp. 175–195
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INITIAL RESPONSES OF FOREST UNDERSTORIES TO VARYING LEVELS AND PATTERNS OF GREEN-TREE RETENTION

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Abstract. Timber harvest with "green-tree" retention has been adopted in many temperate and boreal forest ecosystems, reflecting growing appreciation for the ecological values of managed forests. On federal forest lands in the Pacific Northwest, standards and guidelines for green-tree retention have been adopted, but systematic assessments of ecosystem response have not been undertaken. We studied initial (1–2 yr) responses of vascular understory communities to green-tree retention at six locations (blocks) in western Oregon and Washington, using a factorial design with retention at contrasting levels (15% vs. 40% of initial basal area) and spatial patterns (trees dispersed vs. aggregated in 1-ha patches). Direction of compositional change (expressed in ordination space) was similar among treatments within each block, but the magnitude of change was consistently larger at 15% than at 40% retention; pattern of retention had little effect on compositional change. Despite major changes in vegetation structure, early-seral (ruderal) herbs contributed little to plant abundance and richness in most treatments. For many forest understory groups, declines in abundance or richness were significantly greater at 15% than at 40% retention. However, pattern of retention had surprisingly little effect on treatment-level response; although changes within forest aggregates were small, declines in adjacent areas of harvest were generally greater than those in corresponding dispersed treatments. Late-seral herbs were particularly sensitive to these effects, with more frequent extirpations from plots within the harvested portions of aggregated treatments than from dispersed treatments. Plot-to-plot variation in understory abundance and richness within treatments increased after harvest, but level and pattern of retention had little effect on the magnitude of this change. We suspect that the initial responses of forest understories to green-tree retention are mediated, in large part, by associated patterns of disturbance and slash accumulation that differ significantly with level and pattern of retention. Because these represent short-term responses, future sampling will be necessary to understand the broader implications of structural retention harvests. We predict that, as effects of disturbance diminish with time, effects of canopy structure will increasingly shape patterns of compositional and structural development in the understory.

Key words: forest understory; green-tree retention; late-seral species; logging slash; Pacific Northwest; plant succession; species diversity; structural retention; timber harvest; understory variability.

INTRODUCTION

Forest management policies on federal lands in the Pacific Northwest have changed dramatically in the last decade, spurred by increasing concern over the loss and fragmentation of old-growth forests and the consequences of habitat loss and degradation for biological diversity (Forest Ecosystem Management Assessment Team 1993, Thomas et al. 1993, Tuchmann et al. 1996). It is now widely accepted that silvicultural practices that include large clearcuts, intensive site preparation, and even-aged management—designed to maximize timber production—share little in common with the natural disturbance and successional processes that shaped forest development historically in this region (Franklin et al. 1995, 2002). In various ecosystems, forest managers are attempting to balance the ecological and commodity values of forests by implementing new models of silviculture that acknowledge these differences. These models include explicit consideration of the frequency, size, and spatial distribution of disturbance, and of the types and amounts of live and dead structures that are retained through disturbance (Arnott and Beese 1997, Bergeron and Harvey 1997, Coates et al. 1997, Fries et al. 1997, Franklin et al. 2002, Palik et al. 2002).

In the Pacific Northwest (northern California, Oregon, and Washington), structural or "green-tree" retention has replaced clearcut logging on federal forest lands subject to timber harvest (those designated as

Manuscript received 24 March 2003; revised 1 March 2004; accepted 19 April 2004; final version received 17 May 2004. Corresponding Editor: D. S. Schimel.

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"matrix" lands and Adaptive Management Areas within the range of the Northern Spotted Owl; USDA and USDI 1994*a*). Federal forest management policies require that live trees are retained over at least 15% of each harvest unit, and that 70% of this retention occurs in aggregates of 0.2–1.0 ha with the remainder dispersed in small groups (<0.2 ha) or as individual trees (USDA and USDI 1994*b*, Tuchmann et al. 1996). Although these standards and guidelines were designed with the explicit goal of maintaining the diversity of species, structures, and ecological processes found in late-successional forests, they derive largely from expert opinion and practical experience, and thus reflect many assumptions and uncertainties. Moreover, these standards provide only broad guidance for a region comprised of diverse physical environments and forest types, which are likely to vary in their responses to structural retention. Given the short history of implementation and limited assessment of responses, many questions remain: Is the current minimum standard of 15% retention sufficient to maintain the organisms and processes that characterize late-seral forests in this region? What are the ecological and silvicultural tradeoffs of varying the level of retention or the spatial distribution of retained trees? Which species or groups of organisms are most sensitive to variation in the amount or spatial pattern of retention? How do responses to retention vary geographically or among forests with different initial structures or compositions? Can short-term responses be used to predict longer-term trends?

In this paper, we begin to explore some of these questions from the perspective of the forest understory with an emphasis on the structure, composition, and diversity of the vascular plant community. Our study is part of a larger experiment in structural retention harvests in the Pacific Northwest—the Demonstration of Ecosystem Management Options (DEMO) Study (Aubry et al. 1999, Halpern et al. 1999*a*). Replicated at six locations in western Oregon and Washington, DEMO represents the first large-scale experimental assessment of green-tree retention in the Pacific Northwest, encompassing studies of vegetation, wildlife, canopy arthropods, ectomycorrhizal fungi, snow hydrology, and public perceptions of alternative silvicultural approaches (Halpern and Raphael 1999).

Considerable attention has been devoted to understanding the responses of forest understory communities to clear-cutting in many temperate and boreal ecosystems (e.g., Halpern 1989, Duffy and Meier 1992, Halpern and Spies 1995, Roberts and Gilliam 1995, Hannerz and Hånell 1997, Rees and Juday 2002, Roberts and Zhu 2002). In the Pacific Northwest, many understory species are resistant to the physical disturbances or microclimatic changes associated with clearcut logging and site preparation. However, some herbaceous species associated with late-seral forests are sensitive to both ground disturbance and canopy removal, and timber harvest may result in local extirpation (Schoonmaker and McKee 1988, Halpern 1989, Halpern et al. 1992, Halpern and Spies 1995, Jules 1998). Partial retention of the overstory may ameliorate some of these impacts (North et al. 1996, Beese and Bryant 1999, Jalonen and Vanha-Majamaa 2001), although responses will vary with the level of tree retention and its spatial distribution.

Although it is reasonable to hypothesize that increases in level of retention will maintain a correspondingly higher diversity of forest organisms, few empirical data exist to evaluate this assumption, or to identify critical thresholds for local persistence of species. The spatial distribution of retention may also affect understory responses. As illustrated by shelterwood regeneration systems, moderation of stressful microclimatic conditions can be achieved for conifer seedlings by dispersed retention of relatively few overstory trees (Seidel 1979, Childs and Flint 1987). However, dispersed retention may be insufficient for forest herbs that require moist soil and shade. Under aggregated retention, amelioration of microclimatic stress is likely to be more complete, albeit spatially localized (Chen et al. 1993, 1995). Harvest units that contain undisturbed patches of forest are also more likely to retain the full array of species found in older forests (Franklin et al. 1997). Populations within aggregates may function as sources for clonal expansion or dispersal of seed into adjacent harvest areas when environmental conditions become more favorable for establishment.

Although these hypothesized relationships presume strong direct controls of residual overstory trees on understory, early responses of vegetation to harvest will also be affected by patterns of soil disturbance, physical damage, and burial by logging slash (Halpern 1988, McInnis and Roberts 1994, 1995, Roberts and Gilliam 1995, Scherer et al. 2000, Roberts and Zhu 2002). In the short term, however, it may be difficult to separate these disturbance effects from microclimatic and other effects of canopy structure, because the magnitude and spatial distribution of logging disturbance are likely to be correlated with the proportion and pattern of live trees that are retained (Halpern and McKenzie 2001).

In this study, we examine understory responses to variation in both the level (proportion of basal area) and pattern of green-tree retention. We employ an orthogonal design with two levels of retention, 15% (the current minimum specified in the Northwest Forest Plan) and 40%, and two distinct patterns, dispersed and aggregated (the latter as 1-ha circular patches). These treatments were intended to produce stark contrasts in the density and spatial distribution of residual trees, with the goal of eliciting strong responses among organisms that are sensitive to the amount or pattern of overstory structure. Because a goal of structural retention is to maintain the spatial heterogeneity of structure and composition present in older forests, we analyze

PLATE. 1. Post-harvest comparison of a 15% aggregated and 15% dispersed retention treatment. In the former, a 1-ha forest aggregate is visible in the background. Photo credit: David Phillips.

not only the differences in mean response among treatments, but also the patterns and sources of variation within treatments, and how these are influenced by level and pattern of retention. To guide these analyses we pose the following hypotheses:

Hypothesis 1: Mean treatment-level responses.—Mean changes in understory abundance, richness, and composition will be greater (a) at 15% than at 40% retention, and (b) in dispersed than in aggregated treatments (as changes within retained patches of forest will be small). (c) Late-seral herbs will show particular sensitivity to level and pattern of retention.

Hypothesis 2: Variation in response within treatments.—Harvest-related disturbance will reduce within-treatment (plot-to-plot) variation in understory abundance, richness, and composition. Loss of variability (measured by change in the coefficient of variation) will be greater (a) at 15% than at 40% retention (reflecting greater "homogenization" of plots where harvest is more intense), and (b) in dispersed than in aggregated treatments (as retained patches of forest will show minimal change).

Hypothesis 3: Forest aggregates vs. adjacent harvested areas.—Changes in understory abundance, richness, and composition will be smaller in forest aggregates than in adjacent areas of harvest.

Hypothesis 4: Mean responses in harvested areas.—Within the harvested portions of treatment units, mean changes in understory abundance, richness, and composition will be greater (a) at 15% than at 40% retention, and (b) in aggregated than in dispersed treatments (reflecting more complete removal of trees from the former).

Hypothesis 5: Variation in response within harvested areas.—Within-treatment variation in understory abundance, richness, and composition will decline in the harvested portions of treatment units. The magnitude of decline (a) will be greater at 15% than at 40% retention (see hypothesis 2a), but (b) will be greater in aggregated than in dispersed treatments (reflecting the moderating influence of residual trees in the latter).

We apply these hypotheses to a diverse array of understory responses. These include changes in species composition and in the abundance and richness of broad groups of plants that represent different understory strata or that vary in their sensitivities to disturbance or to the microclimatic changes associated with timber harvest. We also consider individual responses of late-seral herbs that show strong associations with old-growth forest, and identify the conditions (i.e., treatments and locations within treatments) under which overstory removal results in local extirpation. By exploring a diversity of responses at a range of spatial scales we are able to identify the components of the understory that are sensitive to structural retention and the elements of structural retention to which understory communities are responsive.

STUDY AREAS

Six study locations (henceforth "blocks") were selected to represent a diversity of physical environments and mature forest types at low to moderate elevations in western Oregon and Washington (see Table 1 for details). Five blocks lie in the western Cascade Range: three on the Gifford Pinchot National Forest (Washington) and two on the Umpqua National Forest (Oregon) (Fig. 1). The sixth, Capitol Forest, lies on state lands (Washington Department of Natural Resources [DNR]) in the Black Hills of southwestern Washington. A primary objective in site selection was to minimize variation in environment and vegetation among experimental units within each block. This was not always possible, however, given the total area required for each block (a minimum of 78 ha comprised of six, 13-ha experimental units). Placement of experimental units was often constrained by local topography and past management activity (harvest units and roads); although harvest units lie adjacent at some blocks, they are separated by as many as 15 km at others.

The climate of the region is maritime; summers are relatively warm and dry and winters are cool and wet

TABLE 1. Environmental and pre-harvest structural characteristics of the six experimental blocks.

	Umpqua National Forest, Oregon		Gifford Pinchot National Forest, Washington
Characteristic	Watson Falls	Dog Prairie	Butte
Environmental characteristics			
Latitude, longitude (degrees)†	43.27 N, 122.34 W	43.20 N, 122.20 W	46.37 N, 121.59 W
Elevation (m)	945–1310	1460–1710	975–1280
Slope (%)	4–7	34–62	40–53
Aspect	Flat	SW	E–SE
Precipitation (mm)‡	1443	1683	1860
Temperature, min/max§ (°C)	−3.7/26.2	−6.4/22.3	−5.5/21.5
Forest structural characteristics prior to harvest			
Stand age (yr)	110–130	165	70–80
Tree density (no./ha)‖	310–500	258–475	759–1781
Tree basal area (m^2/ha)‖	36–52	72–106	48–65
Site index (m)¶	40–43	30	27–32
Forest zone#	*Tsuga heterophylla*	*Abies concolor*	*Tsuga heterophylla*
Overstory cover (%)††	51–70	68–78	72–82
Volume CWD (m^3/ha)‡‡	67–191	50–233	91–943
Management history	salvaged dead trees (1970–1978)	thinned (1986)	none

Note: Ranges of dates represent variation among treatment units within blocks.

† Latitude and longitude at the center of each block.

‡ Estimated mean annual precipitation, derived from DAYMET (Thornton et al. 1997), a set of 1-km GIS raster coverages that were generated from meteorological records (1980–1997) and digital elevation data.

§ Estimated monthly means, derived from DAYMET; min is the January minimum temperature, and max is the August maximum.

‖ Trees ≥5.0 cm dbh.

¶ Height of Douglas-fir at 50 yr.

Defined by potential climax tree species.

†† Estimated using a moosehorn densiometer at the end points of each transect (eight points per plot).

‡‡ Volume of coarse woody debris estimated with the planar intercept method (Brown 1974) along four 6 m long transects per plot.

with most precipitation falling between October and April (Franklin and Dyrness 1973; Table 1). Soils vary in depth and texture, but most are moderately deep and well-drained loams to loamy sands derived from andesite, breccia, or basalt parent materials, or from pumice deposits (Radtke and Edwards 1976, Pringle 1990, Wade et al. 1992).

Pseudotsuga menziesii dominated the overstory in each block, although stand age, structure, composition, and disturbance and management histories differed among blocks (Table 1; Aubry et al. 1999, Halpern et al. 1999*a*).

METHODS

Experimental design

The full experimental design consists of six, 13-ha green-tree retention treatments, including a control (Fig. 1), replicated at each of the six blocks. In this paper we utilize five of these treatments (described in Table 2): the control (100% retention) as a reference, and four that can be analyzed as a fully balanced, two-factor design that contrasts the level (15% vs. 40% of original basal area) and spatial pattern (aggregated vs. dispersed) of overstory retention (see Plate 1). We do not consider the 75% retention treatment in this paper.

Harvest methods and post-harvest management activities

Within each block, harvest was completed within in a period of 3–7 mo in 1997 or 1998 (Table 3). Methods of yarding, treatment of logging slash, and specifications for planting of seedlings varied among blocks (depending on topography, forest type, post-harvest ground conditions, and local management practices; Table 3), but these were applied consistently to all treatment units within a block (Aubry et al. 1999). Where terrain was steep, logs were removed by helicopter or suspension cables; where slopes were more gentle, logs were removed with ground-based equipment (tracked shovel loaders and/or rubber-tired skidders; Table 3). Treatment of non-merchantable trees (subcanopy stems <18 cm dbh) varied among blocks. They were felled at Paradise Hills, felled if damaged at Watson Falls, and left standing at Butte; non-merchantable trees were largely absent in the remaining blocks (Table 3). At four of six blocks, tree canopies were yarded attached to the upper bole to reduce accumulations of logging slash, but residual material was left in place. At Watson Falls, however, depth of slash was considered excessive by local managers and tree limbs and small boles were systematically removed and piled onto temporary skid roads leaving a 5–15 cm layer of slash on site. Slash piles were covered with plastic and burned when conditions were cool and wet. To ensure minimum levels of tree regeneration (as specified by federal resource management plans), conifer seedlings were planted in the harvested portions of all experimental units, but at densities lower than those used in conventional oper-

TABLE 1. Extended.

Gifford Pinchot National Forest, Washington		Department of Natural Resources, Washington
Little White Salmon	Paradise Hills	Capitol Forest
45.86 N, 121.69 W	46.01 N, 121.99 W	46.90 N, 123.14 W
825–975	850–1035	210–275
40–66	9–33	28–52
NW–NE	various	various
1968	2968	1973
−4.3/24.0	−4.0/22.1	−0.1/24.1
140–170	110–140	65
182–335	512–1005	221–562
61–77	59–87	54–73
30	26–33	37–41
Abies grandis	*Abies amabilis*	*Tsuga heterophylla*
55–71	73–91	69–85
73–289	126–230	131–216
none	none	second growth (natural regeneration)

ations (Table 3). Responses of planted seedlings are not considered in this paper.

Field sampling

Plot layout and timing of sampling.—Within each 13-ha treatment unit, a systematic grid (i.e., 7 × 9 or 8 × 8 points at 40-m spacing; Fig. 2) was installed prior to harvest. At a subset of grid points, permanent vegetation plots were established, varying in number and spatial distribution by treatment (Table 2, Fig. 2). In the control and dispersed-retention treatments (characterized by relatively homogenous post-harvest environments), 32 plots were established at alternate grid points (Fig. 2a). In the aggregated treatments (characterized by two distinct post-harvest environments), plots were established at all grid points within the forest aggregates and at a subset of points in each of the surrounding harvest areas (Fig. 2b), yielding a total of 32 (15%A) or 36–37 (40%A) plots per treatment (Table 2). Grid points on the edges of forest aggregates were not sampled, although sample transects within the aggregates extended to within 6 m of the edge (Fig. 2).

Pre- and post-harvest sampling was staggered in time among blocks (Table 3). Post-harvest data were taken during the first growing season after harvest at five blocks, but during the second growing season at Dog Prairie, where initial sampling was terminated by a hailstorm that stripped foliage before measurements could be completed.

Measurements of vegetation, soil disturbance, and ground-surface conditions.—At each sampled grid point, understory strata (herbs, tall shrubs, tree seedlings, and saplings) were sampled with a series of transects and nested subplots (Fig. 2c). We used the line intercept method to estimate the cover of each tall shrub species (typically >1 m tall at maturity) along four, 6 m long transects (Fig. 2d). Maximum height of the tall shrub layer was estimated at 1-m intervals along the same transects. Coniferous saplings (0.1–1.0 m tall) were tallied in four, 1 × 6 m subplots bordered on one side by each transect (Fig. 2e). Species in the herb layer (graminoids, herbs, ferns, and subshrubs/low shrubs [typically <1 m tall at maturity]) were sampled in six, 0.2 × 0.5 m microplots spaced at 1-m intervals along each transect (yielding 24 microplots per plot; Fig. 2f). Within each microplot, we recorded species presence (from which we generated plot-level frequency, range of 1–24) and total cover of the herb layer (maximum of 100%). The same microplots were used to tally tree seedlings (natural regeneration <10 cm tall) by species. Plant nomenclature follows Hitchcock and Cronquist (1973) and Hickman (1993).

Soil disturbance and ground-surface conditions were sampled after harvest as possible covariates in analyses of treatment effects. Using the intercept lines employed for tall shrubs (Fig. 2d), we estimated cover and depth of slash (needles, leaves, and branches <10 cm in diameter), as well as cover of logs (≥10 cm in diameter), intact forest floor, disturbed soil, and other ground-surface characteristics (for details see Halpern and McKenzie 2001).

Response variables and data aggregation

Given the diversity of species (>300 taxa) and large floristic differences among blocks, species-specific analyses generally were not practical. Instead we consider 12 understory response variables that fall into four general classes—plant abundance, plant height, species richness, and species composition (see Table 4 for a list of response variables and their pre-harvest means and ranges). Five of these represent the abundance or height of major growth forms: cover of the herb layer (maximum of 100%), summed cover of tall shrub species (potentially >100%), mean maximum height of the tall shrub layer, density of seedlings, and density of saplings. From microplot- or transect-level

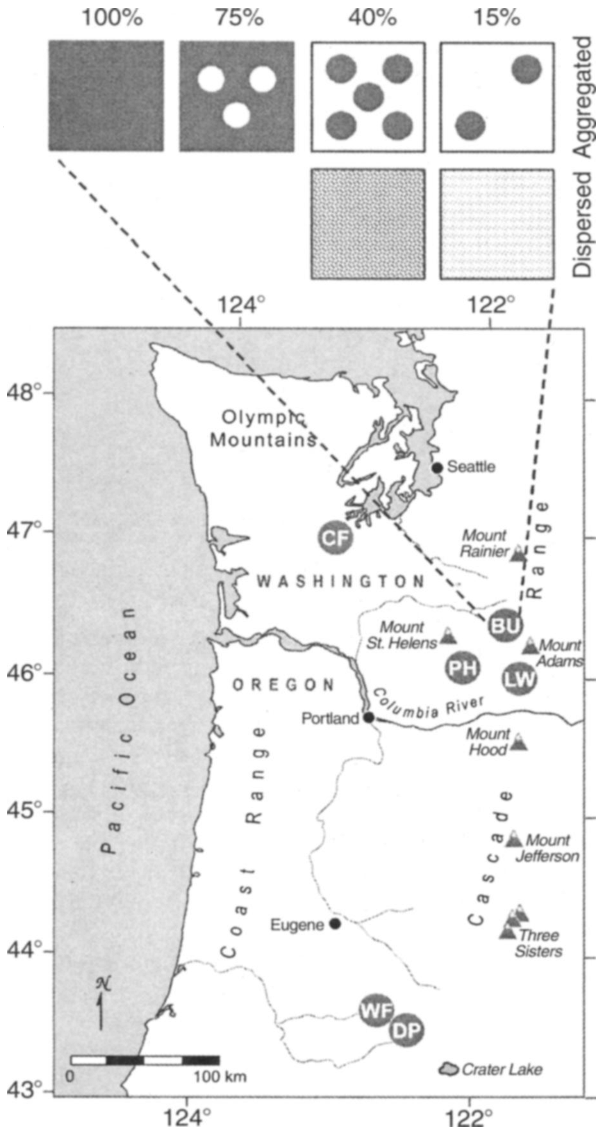

FIG. 1. Locations of the six experimental blocks and schematic representation of the harvest treatments. We do not consider 75% retention in this paper. Dark gray areas represent uncut forest (100% and 75% retention treatments) or 1-ha forest aggregates (15%A and 40%A treatments). Block codes are, from north to south: CF, Capitol Forest; BU, Butte; PH, Paradise Hills; LW, Little White Salmon; WF, Watson Falls; DP, Dog Prairie. The schematic diagram is reprinted from Halpern and McKenzie (2001: Fig. 1), with permission from Elsevier Science.

data we generated plot-level means for each variable. Species in the herb layer were further analyzed by "seral status" to distinguish among taxa with differing successional roles and sensitivities to disturbance (Dyrness 1973, Halpern 1989, Halpern and Spies 1995). Species were assigned to one of three groups: (1) Early-seral herbs are annual, biennial, and perennial herbs (native and exotic) that typically dominate early successional communities; these taxa are characterized by long-distance seed dispersal (or buried viable seed), rapid growth rates, and high fecundities (76 taxa). (2) Forest herbs are characteristic understory species found beneath a broad range of canopy conditions and through most stages of stand development (66 taxa). (3) Late-seral herbs are species that reach maximum abundance in old-growth forests and are sensitive to canopy removal or disturbance (42 taxa). For each of these three groups we calculated a plot-level "summed frequency" (the sum of the frequencies of all species in a plot, henceforth "frequency") and richness (number of species per plot), which yielded six additional response variables (Table 4). The final response variable, compositional change, was computed as the percent dissimilarity (PD) between the pre- and post-harvest composition of the herb layer within each plot. PD derives from the quantitative form of Sørensen's community coefficient (Mueller-Dombois and Ellenberg 1974) and is calculated as follows:

$$\mathrm{PD} = 100 \times \left\{1 - 2 \times \left[\frac{\sum \min(frq_{0i}, frq_{1i})}{\sum (frq_{0i} + frq_{1i})}\right]\right\} \qquad (1)$$

where frq_{0i} and frq_{1i} are the frequencies of species i before and after harvest, respectively. PD can range from 0 (no change in frequency of any species) to 100 (no species in common).

Treatment unit means and coefficients of variation (CVs) were computed from pre- and post-harvest plot-level means for each of the 12 response variables. For the aggregated retention treatments, post-harvest means and CVs were computed as weighted averages to adjust for unequal areas and sampling intensities in the two post-harvest environments (forest aggregates and adjacent areas of harvest; Fig. 2). We observed considerable variation among treatments for many response variables prior to harvest. To standardize for this initial variation, we computed the difference between pre- and post-harvest means as the measure of treatment-level response and used these difference values in subsequent univariate analyses (see *Methods: Data analyses*).

Data analyses

Detrended correspondence analysis (DCA, Hill and Gauch 1980) was used to graphically portray the overall compositional response of the herb layer. In preliminary analyses, large floristic differences among blocks masked the variation associated with treatments. Thus, separate ordinations were run for each block using a sample-by-species matrix with 10 samples representing the average composition of each of five treatments (15%A, 15%D, 40%A, 40%D and 100%), before and after harvest. Average frequency was used as the measure of species abundance, with frequencies in the aggregated treatments computed as weighted means (see *Methods: Response variables and data aggregation*).

TABLE 2. Description of treatments and sampling intensity within treatments.

Treatment	Code	Treatment description	No. sample plots (per block) Not harvested	Harvested	Total
Control	100%	no harvest	32	0	32
75% retention	75%	not considered in this paper			
Aggregated treatments†					
Level: 40%	40%A	five 1-ha aggregates	24–25	12	36–37
Level: 15%	15%A	two 1-ha aggregates	10	22	32
Dispersed treatments‡					
Level: 40%	40%D	basal area equivalent to 40%A	0	32	32
Level: 15%	15%D	basal area equivalent to 15%A	0	32	32

Note: See Figs. 1 and 2 for spatial distributions of forest aggregates and sample plots.

† All retention in 1-ha circular aggregates; all merchantable trees (>18 cm dbh) in surrounding areas were cut and removed.

‡ Retention of dominant and codominant trees evenly dispersed throughout the treatment unit.

Effects of treatments on species composition and relative abundance were inferred from the magnitude and direction of movement between pre- and post-harvest samples in ordination space (axes 1 and 2). Movement of the control treatment provided a measure of sampling error and temporal variation. Ordinations were performed with rare species downweighted, using PC-Ord version 4.0 (McCune and Mefford 1999).

We used analysis of variance (ANOVA) models to test our hypotheses about treatment-level responses and within-treatment variability. Three randomized block designs (Neter et al. 1990) were used, each with a different subset of plots or treatments to address a specific hypothesis. First, to test for effects of level or pattern of retention on treatment-level responses (hypothesis 1) or within-treatment variability (CV, hypothesis 2), we used a 2 × 2 factorial design (level = 15 or 40%, pattern = aggregated or dispersed) with treatment means and CVs based on all sample plots (32–37 plots per treatment; Table 2). Second, to compare responses between forest aggregates and adjacent areas of harvest (hypothesis 3), we used a single-factor ANOVA, with means for each post-harvest environment derived from the combined set of plots in treatments 15%A and 40%A (forest aggregates: 34–35 plots per block; adjacent areas of harvest: 34 plots per block; Table 2). Finally, to compare responses within the harvested portions of treatment units (hypotheses 4 and 5), we used the same 2 × 2 design as above, but with means and CVs derived from plots in harvested areas only (12–32 plots per treatment; Table 2).

For several response variables (tall shrub cover and height, densities of seedlings and saplings, frequency and richness of late-seral herbs), we eliminated either one or two blocks (replicates) prior to analysis because these response variables were poorly represented at these sites (see *Results*, Table 4). Levels of replication and degrees of freedom (df) in the ANOVA models vary accordingly. Thus, for the 2 × 2 designs, degrees of freedom are 5, 4, or 3 for block; 1 for level; 1 for pattern; 1 for level × pattern; and 15, 12, or 9 for error. For the single-factor ANOVAs, degrees of freedom are 5, 4, or 3 for block; 1 for environment; and 5, 4, or 3 for error.

Residual and diagnostic plots revealed minimal departures from normality and, for a very small set of models, only minimal deviation in variance among treatments. Thus, data were not transformed. Main effects (pattern or level of retention) and interactions were judged to be significant at $\alpha \leq 0.05$, although we also report marginally significant test results in the figures ($0.05 < P < 0.10$). Alpha levels were not adjusted for multiple comparisons.

For ANOVA models in which there was a significant main effect, we examined each of the ground-surface/disturbance variables (e.g., cover of slash, logs, intact forest floor, disturbed soil) as possible covariates, using likelihood-ratio tests (Pinheiro and Bates 2000), under the assumption that slash accumulation and soil disturbance can vary considerably due to local site conditions or harvest methods (Halpern and McKenzie 2001). With the exception of one test, none of the covariates proved significant, thus we do not report these results. However, several of these variables differed significantly with level and/or pattern of retention (Halpern and McKenzie 2001), thus were useful for interpreting responses to treatments (see *Discussion*). All analyses were conducted with Splus 2000 (Insightful 2000).

Finally, for each of the 42 species classified as late seral, we compared patterns of local extirpation by tabulating all cases in which a species was completely lost from all sample plots within a treatment unit. Losses were recorded separately for the two post-harvest environments in aggregated retention treatments.

RESULTS

Overall compositional changes

Ordinations of herb-layer data illustrate common patterns of compositional response to treatments within each block. Controls (100% retention) showed little

TABLE 3. Details of harvest, post-harvest, and sampling activities at the six experimental blocks.

	Umpqua National Forest, Oregon		Gifford Pinchot National Forest, Washington
Details of treatment	Watson Falls	Dog Prairie	Butte
Dates of harvest	Jun–Oct 1998	Jul–Sep 1998	May–Sep 1997
Dates of planting	Apr–Jun 1999	May–Jun 1999	Apr–May 1998
Dates of sampling			
Pre-harvest	Jun–Jul 1994, Jul–Aug 1995	Jun–Sep 1996	Aug–Sep 1994, Jul–Aug 1995
Post-harvest	Jul–Aug 1999	Jul–Aug 2000	Jul–Sep 1998
Yarding method	shovel loader	helicopter‡	helicopter‡
Non-merchantable trees‖	damaged	absent	retained
Planting density (no./ha)	476	610	551
Species¶	Psme, Pipo, Pimo	Psme, Pipo, Abmas	Psme, Pimo

Note: Ranges reflect varying dates among treatment units within blocks.

† Treatment 40%D was planted in March 2000.

‡ Tree canopies were yarded with the upper bole to reduce slash loadings.

§ Small portions (0.8–2.4 ha) of treatments 15%D, 40%A, and 40%D were yarded with a shovel loader where cables could not be used to access logs.

‖ Treatment of non-merchantable overstory trees (<18 cm dbh): absent, largely absent; damaged, felled in harvest areas, only if damaged; felled, felled in harvest areas; retained, not felled in harvest areas.

¶ Species codes: Abmas, *Abies magnifica* var. *shastensis*; Abpr, *A. procera*; Pimo, *Pinus monticola*; Pipo, *Pinus ponderosa*; Psme, *Pseudotsuga menziesii*; Thpl, *Thuja plicata*; Tshe, *Tsuga heterophylla*.

change in composition, indicating that natural, temporal variation or effects of sampling bias were small relative to treatment effects (Fig. 3). The direction of compositional change was similar among treatments within a block, with the magnitude of change consistently larger for 15% than for 40% retention. Effects of pattern of retention (aggregated vs. dispersed) were less consistent: at 40% retention, aggregated treatments showed equal or greater change than dispersed treatments, but similar trends were not apparent at 15% retention. Treatments within Capitol Forest (the lowest elevation block) showed the largest changes in composition, reflecting abundant establishment of many early-seral, and often exotic, herbs that were far less common at the remaining blocks.

Responses to treatments

Most plant groups showed large reductions in abundance (cover, density, or frequency), stature (height of tall shrubs), or richness in response to treatments (Fig. 4; see Table 4 for pre-treatment values). Early-seral herbs were the only group to increase in frequency and richness, but these changes were small (Fig. 4). Changes in the control treatments (100% retention) were consistently small and not statistically significant (P = 0.18–0.95 for 10 of 11 paired t tests of pre- and post-harvest means); late-seral herbs showed a small, but significant ($P = 0.04$) increase in frequency. Thus, differential responses to treatments were assumed to reflect the effects of level and/or pattern of retention, not temporal or sampling effects.

Mean treatment-level responses.—The magnitude of response to level of retention was consistent with our prediction (hypothesis 1a): changes in mean values were typically smaller at 40% than at 15% retention, with significant differences observed for five of 12 understory variables (Fig. 4). However, responses to pattern of retention were not consistent with hypothesis 1b: changes were not more pronounced in dispersed than in aggregated treatments. Moreover, where effects of pattern were significant (forest herb and late-seral herb richness), declines were greater in aggregated than in dispersed treatments (Fig. 4). As predicted (hypothesis 1c), late-seral herbs were sensitive to level and pattern of retention (as measured by change in richness), but not in the direction predicted for pattern (Fig. 4). We observed no significant interactions between level and pattern of retention.

Variation in response within treatments.—We hypothesized that timber harvest would reduce plot-to-plot variation within treatments, but coefficients of variation (CVs) actually increased for all response variables (except early-seral herbs; Fig. 5). We predicted greater declines in variability at 15% than at 40% retention (hypothesis 2a), and greater declines in dispersed than in aggregated treatments (hypothesis 2b), yet neither prediction was supported by our results. With the exception of early-seral herbs, mean trends suggested increased variation within treatments at lower retention (although a significant main effect was observed only for richness of late-seral herbs; Fig. 5). Pattern of retention had no detectable effect on within-treatment variation for any response variable (Fig. 5).

Responses within aggregated retention treatments

We observed large and statistically significant differences in understory response between forest aggregates and adjacent areas of harvest, consistent with hypothesis 3 (Fig. 6). Although some response variables (particularly herb cover and percent dissimilarity) showed some change within forest aggregates, the magnitude of change was significantly greater in adjacent

TABLE 3. Extended.

Gifford Pinchot National Forest, Washington		Department of Natural Resources, Washington
Little White Salmon	Paradise Hills	Capitol Forest
Mar–Oct 1998	Jun–Oct 1997	Dec 1997–May 1998
Jun 1999	Jun 1999	Jan–Feb 1999†
Jul–Sep 1995	Aug–Sep 1995	Jun–Jul 1995
Jul–Sep 1999	Aug–Sep 1998	Jun–Jul 1998
helicopter‡	shovel loader, rubber-tired skidder‡	suspension cables§
absent	felled	absent
485	485	741
Psme, Pipo, Abpr, Pimo	Psme, Abpr, Pimo, Thpl, Tshe	Psme

harvested areas. Moreover, comparable small changes were often observed in the controls.

Responses in harvested areas

Mean responses.—We hypothesized that within the harvested portions of treatment units, the magnitude of understory response would vary inversely with level of retention (hypothesis 4a), and that changes would be greater in aggregated than in dispersed treatments (hypothesis 4b). The first of these hypotheses was supported for only two of 12 understory variables (significant effects of level of retention for herb-layer PD and richness of early-seral herbs; Fig. 7). Although not statistically significant, trends for all variables in the dispersed treatments (open symbols, Fig. 7) also suggested greater change at lower retention. Effects of pattern of retention were significant for four of 12 variables (significantly greater change in aggregated treatments; Fig. 7), and for the remaining variables, trends were consistent with our prediction. Both the frequency and richness of late-seral herbs showed significantly greater declines in the harvested portions of aggregated treatments than in dispersed treatments (Fig. 7).

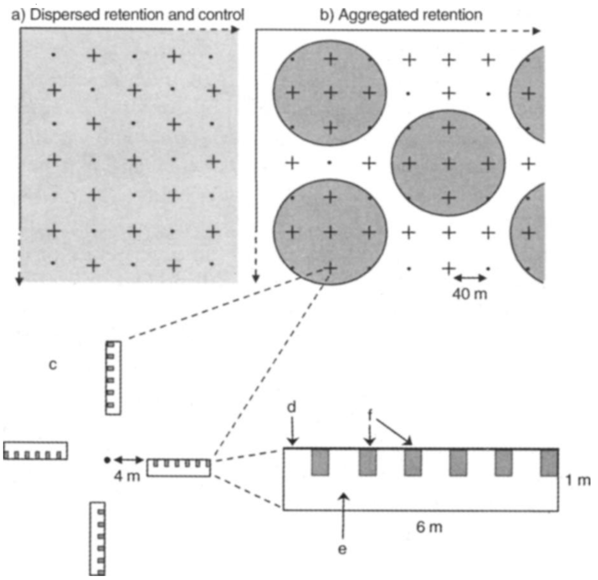

FIG. 2. Sample grid (40-m spacing) and understory sampling design. Portions of two treatment units are shown for illustration (see Fig. 1 for full representation of retention patterns and Table 2 for numbers of plots sampled per treatment). Sampling design is shown for (a) dispersed (15%D and 40%D) and control (100%) treatments, and (b) aggregated treatments (15%A and 40%A). Plus signs (+) denote sampled grid points. (c) Transect and subplot layout at sampled grid points. (d) Transect lines for tall shrubs and coarse woody debris. (e) Sapling subplot. (f) Microplots for herbs and tree seedlings. See *Methods: Field sampling* for descriptions of sampling methods.

Variation in response within harvested areas.—Within the harvested portions of treatment areas, we expected plot-to-plot variation to decline. We predicted greater declines at 15% than at 40% retention (hypothesis 5a), and greater declines in aggregated than in dispersed treatments (hypothesis 5b). Contrary to these predictions, CVs increased in the harvested portions of all treatments for all response variables (except early-seral herbs; Fig. 8). Increases were significantly greater at 15% than at 40% retention for two variables (sapling density and late-seral herb richness). Increases were significantly greater in aggregated than in dispersed treatments for two variables (forest herb and late-seral herb frequency), and marginally so for two others (herb cover and forest herb richness; Fig. 8). A significant interaction between level and pattern of retention was observed for the change in CV of seedling density (Fig. 8).

Local extirpation of late-seral species

We observed numerous instances in which late-seral species were lost from all plots within treatments or from the harvested portions of treatment areas (Table 5). Among the most sensitive of these 42 species—those lost most often and/or from the greatest number of plots—were *Chimaphila menziesii*, *Corallorhiza maculata*, *Goodyera oblongifolia*, *Pyrola secunda*, and *Listera caurina*. Local extirpation was comparable among treatments (total number of treatment-level extirpations: 40%A, 15; 40%D, 15; 15%A, 12; 15%D, 14). In aggregated treatments, however, species were commonly lost from areas of harvest (26 cases in

TABLE 4. Pre-harvest block means (and treatment-level ranges) for the understory response variables (excluding percent dissimilarity).

Response variable	Umpqua National Forest, Oregon	
	Watson Falls	Dog Prairie
Herb cover (%)†	46.3 (35.9–55.2)	18.1 (9.5–27.6)
Tall shrub cover (%)‡	8.5 (0.9–19.6)	**1.7** (0.5–2.8)
Tall shrub height (m)	0.8 (0.1–1.8)	**0.2** (0.2–0.3)
Sapling density (no./m^2)	1.29 (0.76–1.88)	0.12 (0.06–0.24)
Seedling density (no./m^2)	4.27 (1.53–7.25)	1.77 (1.11–2.15)
Early-seral herb frequency (no. microplots/plot)§	9.6 (3.7–12.1)	9.0 (1.3–15.3)
Forest herb frequency (no. microplots/plot)§	175.9 (138.2–201.6)	69.4 (34.8–122.1)
Late-seral herb frequency (no. microplots/plot)§	67.6 (59.3–81.7)	19.8 (12.5–41.7)
Early-seral herb richness (no. species/plot)	2.1 (1.0–3.0)	2.2 (0.5–3.4)
Forest herb richness (no. species/plot)	23.2 (19.4–26.4)	15.4 (10.0–21.3)
Late-seral herb richness (no. species/plot)	9.2 (8.3–10.0)	5.5 (3.2–7.7)

Notes: See *Methods: Response variables and data aggregation* for definitions of variables. Means in bold identify blocks that were not included in the ANOVA model for a particular variable (see *Methods: Data analyses*).

† Total cover of the herb layer (maximum 100%).

‡ Summed cover of tall shrub species (potentially >100%).

§ Summed frequency of all species (see *Methods*).

40%A, 25 in 15%A; Table 5). Although losses were also recorded within undisturbed forest aggregates (10 cases in 40%A, six in 15%A) and controls (five cases), the species lost typically had low initial constancy (present in only one or two plots).

DISCUSSION

In this study, we tested a simple conceptual model in which forest understory responses to structural retention are influenced both by the proportion of live trees retained through harvest and the spatial pattern in which they are retained (Franklin et al. 1997, Aubry et al. 1999). Considerable evidence exists that level of retention or conversely, intensity of overstory removal or thinning, are important in shaping understory responses to harvest in both mature and young forests (e.g., Klinka et al. 1996, Thomas et al. 1999, Bergstedt and Milberg 2001, Thysell and Carey 2001, Vanha-Majamaa and Jalonen 2001). In contrast, limited consideration has been given to the spatial pattern in which trees are retained, although pattern is often implicit in the level of retention in most traditional silvicultural systems (e.g., clear-cut, seed tree, shelterwood, and individual-tree selection) and in current applications of variable retention harvests (Beese and Bryant 1999, Jalonen and Vanha-Majamaa 2001, Sullivan et al. 2001). To our knowledge, ours is the first experimental study to explicitly consider the relative contributions of level and pattern of retention to understory response.

General responses to harvest with green-tree retention

We observed large post-harvest declines in plant cover, height of the tall shrub layer, and density of natural regeneration. Despite these major changes in vegetation structure, early-seral herbs contributed minimally to plant abundance and richness, and post-harvest communities were dominated by pre-treatment floras. As a consequence, initial compositional differences among treatment units within a block were maintained through harvest (Fig. 3). Limited development of a ruderal flora contrasts with the pattern typically observed after clear-cut logging and broadcast burning in the region (Morris 1970, Schoonmaker and McKee 1988, Halpern 1989), and with that observed by North et al. (1996) following dispersed retention in a Douglas-fir-dominated forest similar to ours. Our result may be explained, in part, by patterns of disturbance and post-harvest ground conditions. In the absence of broadcast burning (which is difficult to implement in the context of green-tree retention), cover and depth of residual slash remained high (~70–80% and 6–16 cm, respectively) and cover of exposed mineral soil, low (~6%) (Halpern and McKenzie 2001). Heavy slash loadings probably created barriers to emergence of ruderal species from the litter and soil seed banks, which can be well developed in these forests (Kellman 1974, Ingersoll and Wilson 1989, Halpern et al. 1999*b*), or obstructed seed dispersal onto potential germination sites. However, the development of this group is also likely to reflect broader (landscape-scale) patterns of seed availability. Early-seral (including exotic) taxa established in greatest abundance at our lowest elevation block, Capitol Forest, which lies within a more intensively managed forest landscape, situated closer to agricultural and other human development than the remaining blocks in the Cascade Range.

Temporal trends documented in previous studies of post-harvest succession (Halpern 1989, Halpern and Spies 1995) suggest that the abundance and richness of early-seral herbs will increase on these sites, perhaps for 3–5 yr, but given limited initial recruitment, it is unlikely that peak development will approach that observed following methods of harvest and site preparation that involve fire or mechanical removal of slash and associated exposure of mineral soil.

TABLE 4. Extended.

Gifford Pinchot National Forest, Washington			Department of Natural Resources, Washington
Butte	Little White Salmon	Paradise Hills	Capitol Forest
26.9 (20.5–29.8)	43.0 (33.1–48.9)	19.0 (7.3–29.2)	51.5 (39.4–66.2)
20.1 (11.3–33.1)	68.8 (54.5–87.7)	12.5 (4.0–28.6)	40.6 (27.2–61.5)
1.4 (0.5–2.6)	3.2 (2.7–3.6)	0.5 (0.2–0.8)	3.6 (2.3–5.0)
0.11 (0.04–0.17)	**0.02** (0.01–0.03)	0.54 (0.13–1.73)	**0.01** (0.00–0.01)
2.85 (0.61–8.09)	**0.29** (0.12–0.52)	4.71 (1.41–13.33)	**0.05** (0.00–0.20)
5.1 (2.1–7.2)	0.8 (0.5–1.4)	1.4 (0.1–4.5)	2.1 (0.8–2.8)
64.2 (60.8–80.4)	108.8 (93.7–132.1)	46.9 (20.4–81.6)	43.1 (30.7–50.1)
23.9 (17.8–32.6)	67.0 (59.4–79.5)	21.7 (9.8–50.7)	**2.8** (1.6–4.0)
1.0 (0.8–1.2)	0.4 (0.3–0.6)	0.5 (0.1–1.1)	0.8 (0.5–1.3)
12.8 (11.7–14.6)	16.6 (15.0–18.9)	10.0 (6.3–15.0)	7.4 (6.1–8.4)
5.6 (4.4–6.9)	8.4 (7.3–10.3)	5.4 (4.1–8.8)	**1.4** (1.0–1.8)

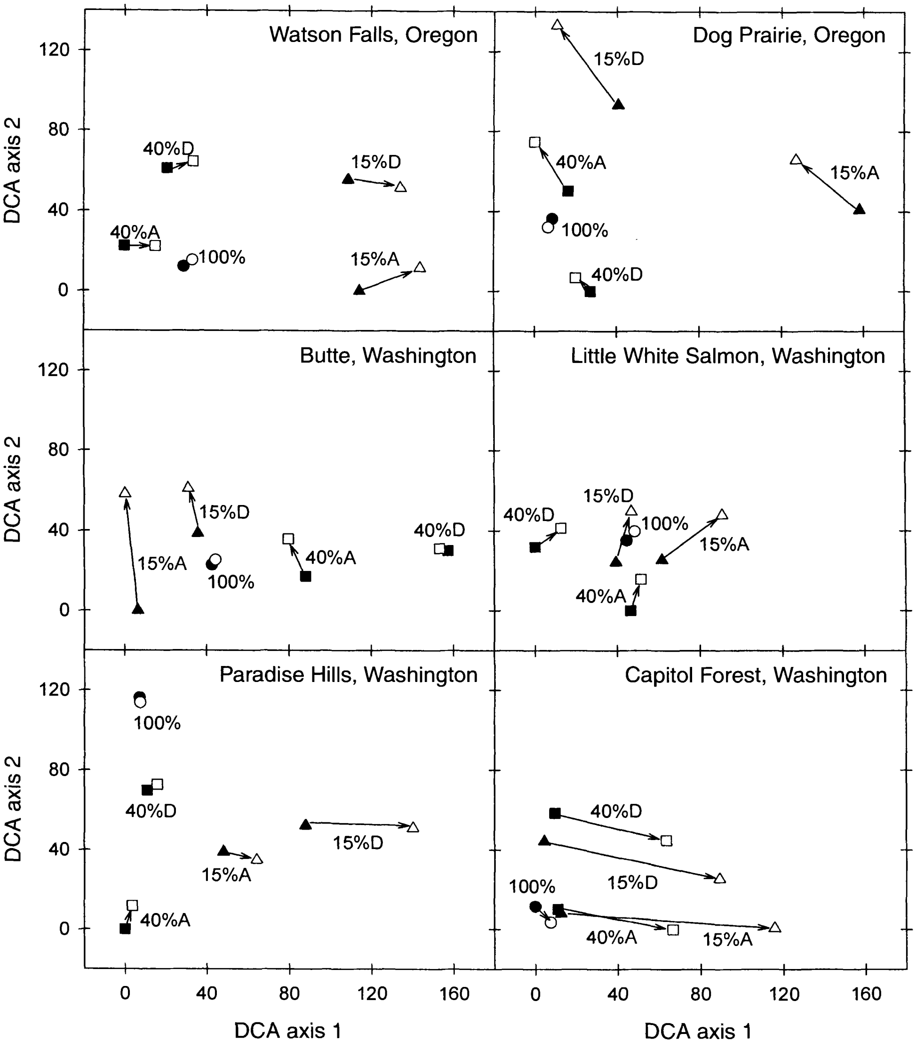

FIG. 3. DCA ordinations portraying changes in the average species composition of five retention treatments within each of the six study blocks. Solid symbols represent pre-harvest compositions, and open symbols represent post-harvest compositions. Mean treatment-level frequency was used as the measure of species abundance (see *Methods*).

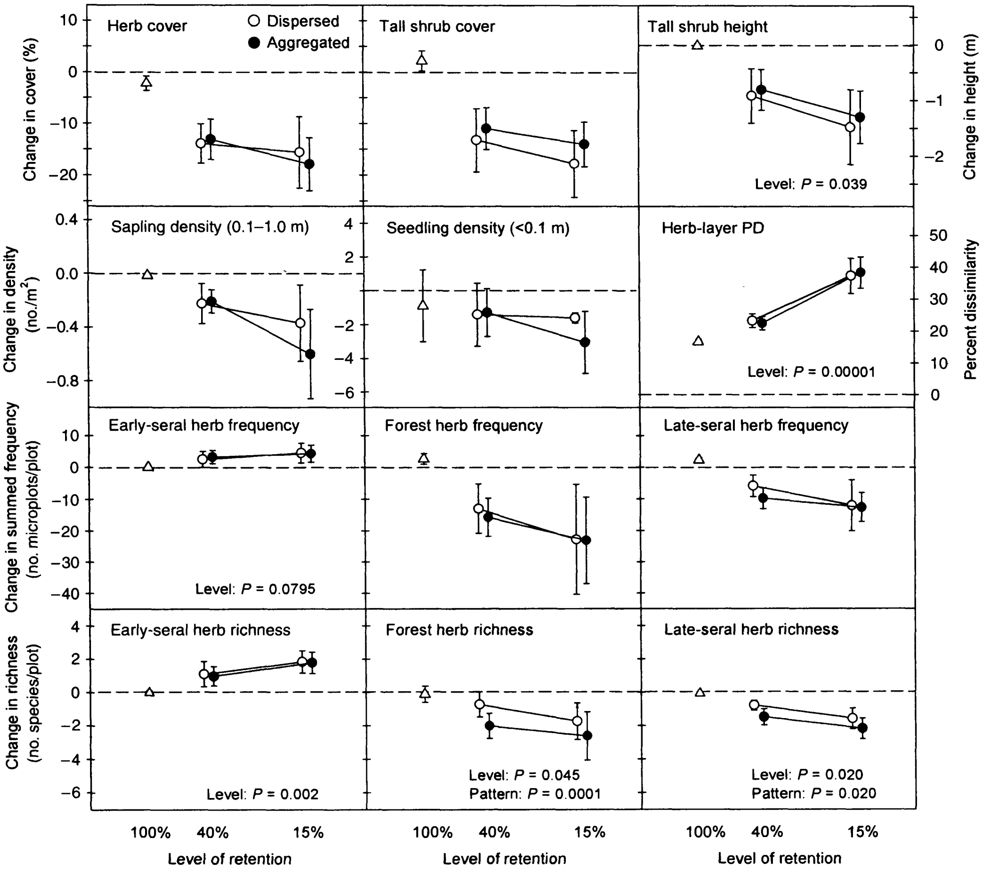

FIG. 4. Mean treatment-level responses (pre- minus post-harvest difference, or "change," ±1 SE) for each of the 12 understory variables. Solid circles represent aggregated treatments, and open circles represent dispersed treatments. Weighted means were computed for aggregated treatments (see *Methods*). Change (mean ± 1 SE) for the control treatment (open triangle) is presented for reference. P values are from two-way ANOVA models and are reported if $P < 0.10$.

Mean responses to level and pattern of retention

We hypothesized that the magnitude of change in understory abundance, richness, and composition would vary inversely with the level of overstory retention and that changes would be greater in dispersed than in aggregated treatments. For a diversity of growth forms and seral groups, level of retention had a significant and predictable effect, with greater compositional change, reduced stature of the tall shrub layer, and greater loss of forest and late-seral species at lower levels of retention. Mean trends for most remaining variables, although not statistically significant, were consistent with this pattern.

Strong understory responses to gradients of retention, similar to those reported here, have been observed for vascular understory communities in other regions, including boreal spruce forests of Finland (Jalonen and Vanha-Majamaa 2001), boreal spruce–pine forests of Sweden (Bergstedt and Milberg 2001) and coastal, montane-fir–western-hemlock forests of British Columbia (Beese and Bryant 1999). Elsewhere, relatively weak relationships between understory response and canopy retention have been observed. For example, in a comparison of clear-cut, seed-tree, and patch-cut harvests in coniferous forests of southern British Columbia, level of retention had little effect on plant abundance or richness (Sullivan et al. 2001). Likewise, in a retrospective analysis of understory response to partial cutting in hemlock–spruce forests of southeast Alaska, significant changes in community structure were not observed until >50% of overstory basal area was removed (Deal 2001). Similar stability in the ground-layer herb community was observed in selectively logged neotropical forests, but logging intensity was light, amounting to removal of ≤20 stems/ha (Costa and Magnusson 2002). Many factors may contribute to differences in response among forest ecosystems, but given the diversity of sampling approaches, scales of measurement, and measures of vegetation response, it is difficult to distinguish between system-specific patterns and sampling effects.

Three factors associated with level of retention may account for the observed patterns of response in our study: direct physical disturbance, burial by logging slash, and effects of microclimatic changes. For some response variables, such as height of the tall shrub lay-

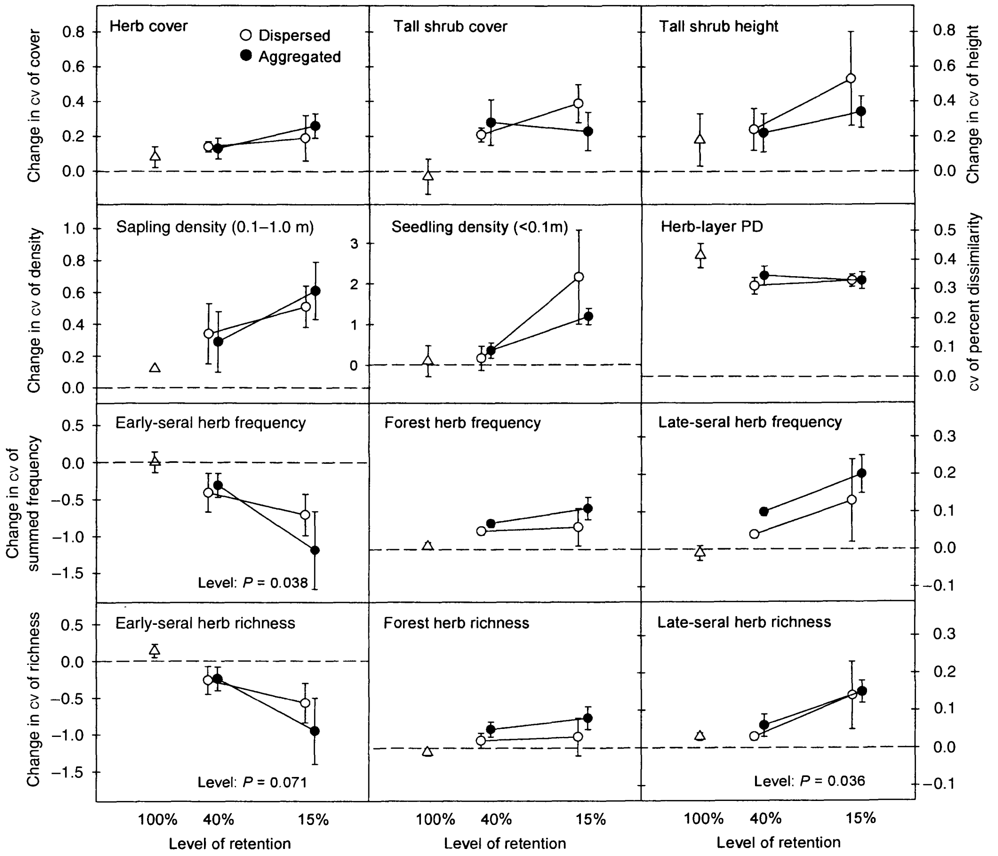

FIG. 5. Changes in within-treatment variability (CV, coefficient of variation ± 1 SE) for each of the 12 understory variables. Weighted coefficients of variation were computed for aggregated treatments. See Fig. 4 for other details.

er, initial effects of retention level were probably a direct consequence of logging disturbance, with more damage to erect woody stems in treatments where a greater proportion of trees were felled and removed (e.g., Reader et al. 1991). Similar effects were observed for sapling density (trees 0.1–1.0 m tall) in those blocks in which initial densities were high (Fig. 4; Table 4). However, the overall significance of treatment effects was probably masked by the limited potential for change in blocks with lower initial sapling densities. It was for this reason that we dropped blocks from particular analyses, but our criteria for doing so may have been too conservative.

For forest and late-seral herbs, significant declines at lower levels of retention may reflect not only increased physical disturbance, but also more complete burial beneath logging slash. In an earlier analysis of post-harvest ground conditions at these sites, we observed significantly greater cover and depth of slash and significantly greater input of large woody debris (boles ≥10 cm dbh) at 15% than at 40% retention (Halpern and McKenzie 2001). For ground-layer species, survival and subsequent expansion may be limited by the cover and depth of burial, although clonal herbs that are able to move perennating structures into more favorable environments may not be as susceptible to burial as non-clonal, "fixed-point" species (cf. Antos and Zobel 1984, 1985, Lezberg et al. 1999).

Finally, for the group of late-seral herbs, in addition to disturbance and burial effects, physiological stress may contribute to greater declines in plant frequency and richness at lower levels of retention. Although their physiological responses to canopy removal have not been studied, the species classified as late seral show a strong affinity for old-growth and forest-interior environments (Halpern and Spies 1995, Jules et al. 1999) characterized by patches of deep shade and by cool, moist, and relatively stable ground-layer microclimates (Chen et al. 1993, 1995). Thus, even if they escape direct damage from felling or yarding operations, abrupt exposure to full sun may lead to photoinhibition and loss of photosynthetic function (Powles 1984). Overstory retention, either in a dispersed or aggregated pattern could afford partial, but patchy, amelioration of extremes in light, temperature, or soil moisture (Childs and Flint 1987, Holbo and Childs 1987, Barg and Edmonds 1999). Although direct measures of insolation were not taken, estimates of overstory canopy cover suggest significant differences in shading with level of retention, particularly in dispersed treatments:

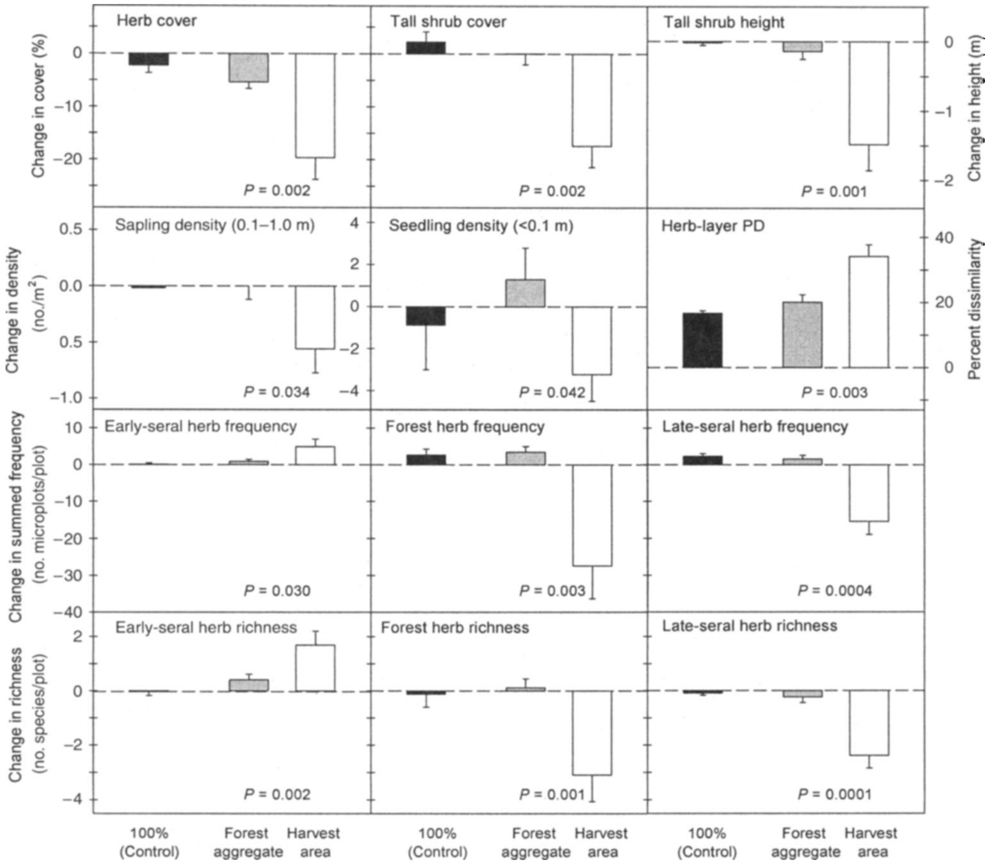

FIG. 6. Mean responses (change ± 1 SE) in forest aggregates and adjacent harvested areas for each of the 12 understory variables. Means for each post-harvest environment were derived from the combined set of plots in treatments 15%A and 40%A (forest aggregates, n = 34–35 plots per block; adjacent areas of harvest, n = 34 plots per block; Table 2). Change ± 1 SE for the control treatment (solid bar) is presented for reference. P values are from one-way ANOVA models comparing responses in aggregates and harvest areas. See Fig. 4 for other details.

post-harvest canopy cover was up to 2.5 times greater at 40% than at 15% retention (range among blocks of 47–83% and 22–48%, respectively; D. Maguire, *unpublished data*).

We anticipated strong, ameliorating effects of aggregated retention on the treatment-level responses of the forest understory. Yet, for none of our uni- or multivariate comparisons of treatment response was there an indication that forest aggregates provided this benefit. In fact, in the few instances in which pattern of retention proved significant (richness of forest and late-seral herbs), greater loss of diversity was observed in the aggregated treatments. Explanations for this counterintuitive result lie in the contrasting patterns of response in the disturbed portions of aggregated and dispersed treatments (Fig. 7). Here, we observed a strong effect of "pattern" on many herb-layer attributes, with the harvested portions of aggregated treatments showing significantly greater changes in composition and significantly greater loss of plant abundance (late-seral herbs) and richness (forest and late-seral herbs). These outcomes are consistent with our prediction about understory response within the harvested portions of treatments (hypothesis 4b) and with our earlier assessment of disturbance patterns (Halpern and McKenzie 2001). In that analysis, the harvested portions of aggregated treatments exhibited significantly greater cover of logging slash and significantly lower cover of undisturbed forest floor than did the corresponding dispersed treatments.

The benefits of aggregated retention are predictably localized, as illustrated by the marked contrasts in response in forest aggregates and adjacent areas of harvest (Fig. 6; see also Nelson and Halpern 2005). Thus, in the short term, and in the context of average treatment responses, these benefits appear to be offset by the more intensive damage that occurs where overstory removal is more complete. Perhaps the clearest illustration of these tradeoffs emerged from our analysis of species' extirpations: in aggregated treatments, species were lost more than twice as often from harvested areas as from forest aggregates. As a result, extirpations were no more common in dispersed than in aggregated treatments, contrary to our initial expectation. Because

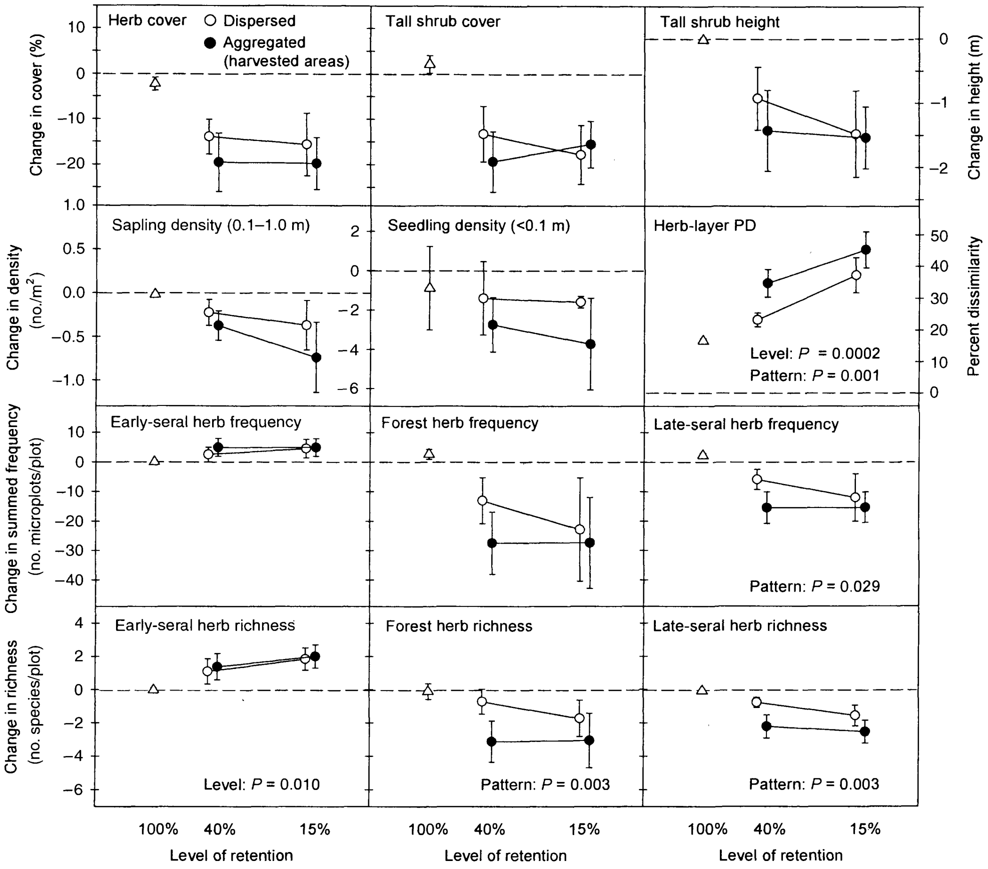

FIG. 7. Mean responses (change ± 1 SE) within the harvested portion of treatment units for each of the 12 understory variables. Note that data for dispersed treatments are the same as in Fig. 4. See Fig. 4 for other details.

many of these late-seral species exhibit patchy distributions, aggregated retention will enhance survival only when the locations of forest aggregates and plant populations coincide. If they do not, our results suggest that the probability of loss in adjacent areas of harvest will be higher than if a fully dispersed canopy were retained.

We acknowledge several possible limitations of these analyses and interpretations. First, initial survival beneath dispersed retention may not ensure long-term persistence, as stress-induced mortality may lead to gradual extirpation. Thus, the apparent benefit of a dispersed canopy may be short-lived. Second, for some taxa (particularly geophytic orchids), post-harvest losses may reflect temporary dormancy induced by environmental stress rather than mortality (Lesica and Steele 1994). Future census of these plots will clarify the nature and duration of these losses. Finally, our data represent extirpations from sample plots, not necessarily from entire experimental units; a complete inventory would be necessary to document larger-scale extinctions. Nonetheless, our plot-based sampling provides a basis for comparing the frequency and magnitude of species turnover within treatments (cf. Reader and Bricker 1992). The potential implications of these initial losses are made apparent by the results of longer-term studies in clear-cut forests. The species shown to be most sensitive in the current study—*Chimaphila menziesii*, *Corallorhiza maculata*, *Goodyera oblongifolia*, *Pyrola secunda*, and *Listera caurina*—are among those that were extirpated from sample plots monitored for >25 yr after harvest, including plots not subjected to broadcast burning of logging slash (Halpern 1989, Halpern et al. 1992, Halpern and Spies 1995). It is unclear whether environmental stress, dispersal limitation, or in some cases mycorrhizal links to trees (Simard et al. 2002) constrain species' reestablishment after harvest. Future surveys of dispersed-retention treatments and harvest areas adjacent to forest aggregates with known "source populations" may provide insights into these possibilities.

Patterns of variability within treatments

In addition to maintaining important elements of the original forest, harvest with structural retention is thought to enhance the spatial variability of residual structure and composition in the regenerating forest (Franklin et al. 1997, 2002). In mature and old forest, this variability may arise from a heterogeneous overstory, other forms of habitat variation (e.g., dense

TABLE 5. Rates of local extirpation of late-seral species among experimental treatments.

	Treatments and within-treatment environments						
		40%A			15%A		
Species	100% (*n* = 32)	Aggr. (*n* = 25)†	Harvest (*n* = 12)	40%D (*n* = 32)	Aggr. (*n* = 10)	Harvest (*n* = 22)	15%D (*n* = 32)
Watson Falls							
Chimaphila menziesii	···		···	···		1	
Corallorhiza maculata		···	1	···	···	···	···
Disporum hookerii	···	···	1	3			
Goodyera oblongifolia			9			16	17
Listera caurina			2			3	8
Listera cordata	···	···	···	4	···	···	8
Pyrola picta		3	4	2		1	···
Pyrola secunda			10		2	3	
Rubus nivalis		1	1	1		3	
Tiarella trifoliata			2				
Total no. species lost	0	2	8	4	1	6	3
Dog Prairie							
Asarum caudatum	···				1		
Chimaphila menziesii			8	3			13
Clintonia uniflora		···	1				···
Corallorhiza maculata		1	···	···	···	1	2
Goodyera oblongifolia			3			16	
Pyrola aphylla	···	···	···	1	1	2	···
Pyrola picta			1				
Pyrola secunda			4			11	3
Smilacina racemosa			4	···			
Total no. species lost	0	1	6	2	2	4	3
Butte							
Adenocaulon bicolor	1		···				
Asarum caudatum					···	1	···
Blechnum spicant		···	1	···	···	···	···
Clintonia uniflora					1		
Disporum hookerii	1	···	···	···		2	···
Goodyera oblongifolia			1	···	···	···	···
Listera caurina	···	···	···		···	···	2
Pyrola asarifolia					···	1	
Pyrola chlorantha	···		1	···		4	2
Pyrola picta				···			
Rubus nivalis			1	2			
Smilacina racemosa	···	4	···			···	···
Tiarella trifoliata					···	1	
Trillium ovatum			2		2	5	···
Total no. species lost	2	1	5	1	2	6	2
Little White Salmon							
Asarum caudatum			1	···	···	···	···
Corallorhiza maculata	···	···	···	2		2	···
Listera cordata	···	···	···	1	···	···	1
Rubus lasiococcus		2			···	···	
Total no. species lost	0	1	1	2	0	1	1
Paradise Hills							
Adenocaulon bicolor	···	···	1	···			
Asarum caudatum	···	1	···	···	···	···	1
Chimaphila menziesii		4	1				
Goodyera oblongifolia					1	1	
Listera caurina	···		4	2		1	3
Pyrola asarifolia	2	5	4	1	···	2	
Pyrola picta						···	1
Pyrola secunda				9		3	
Smilacina stellata				2	···	4	
Tiarella trifoliata			2	···			
Total no. species lost	1	3	5	4	1	5	3
Capitol Forest							
Achlys triphylla		1	···	···		1	
Chimaphila menziesii	1	···	···		···	···	1
Chimaphila umbellata	1	···	···	···	···	···	1
Corallorhiza maculata	···	···	1	···	···	2	···

TABLE 5. Continued.

	Treatments and within-treatment environments						
		40%A			15%A		
	100% (*n* = 32)	Aggr. (*n* = 25)†	Harvest (*n* = 12)	40%D (*n* = 32)	Aggr. (*n* = 10)	Harvest (*n* = 22)	15%D (*n* = 32)
Capital Forest							
Goodyera oblongifolia	...	...	...	3		...	...
Pyrola uniflora	...	...	...	1	...	1	...
Smilacina racemosa		1	...	...	...	...	...
Total no. species lost	2	2	1	2	0	3	2
Total no. species lost from all blocks	5	10	26	15	6	25	14

Notes: In aggregated treatments, data are presented separately for the two post-harvest environments: forest aggregates (Aggr.) and adjacent harvest areas (Harvest). Sample sizes (no. plots per environment) are given in the column heads. Ellipses (. . .) indicate absence prior to harvest; blanks indicate persistence in at least one plot within the post-treatment environment, and numbers represent loss from all plots in which a species was present prior to harvest. Species are listed only if they were present in at least two treatments in a block prior to harvest.

† There were 24 plots at Paradise Hills.

patches of western hemlock, canopy gaps, or patchy accumulations of coarse woody debris; Spies 1991, Spies and Franklin 1991, McKenzie et al. 2000), or natural disturbance processes (Stewart 1986, Winter et al. 2002). We expected that timber harvest would have an "homogenizing" influence on this variability and that level and pattern of retention would affect the magnitude of change. In particular, we hypothesized greater reductions in variability where harvest was either more intensive (i.e., at 15% retention) or extensive (i.e., in dispersed treatments in which all plots were disturbed).

Contrary to our expectation, plot-to-plot variation generally increased after treatment (declining only for early-seral herbs which recruited more uniformly among plots after harvest). Because the abundance and richness of most plant groups declined after harvest, increases in spatial heterogeneity can be attributed to the patchy nature of logging disturbance, which left some plots relatively unchanged and others greatly diminished for one or more understory attributes. Although level of retention had limited effect on the magnitude of change for most variables, trends were consistent and strongly suggestive of greater change at lower retention (Fig. 5). We suspect that at 15% retention, accumulations of slash and larger woody debris were sufficiently high to exceed thresholds of plant damage or burial more often—yielding greater variability among plots—than at 40% retention, where levels of slash and fresh woody debris were significantly lower (Halpern and McKenzie 2001).

Surprisingly, changes in plot-to-plot variation were unaffected by the spatial pattern of retention—aggregated and dispersed treatments showed comparable increases in CVs for all response variables (Fig. 5). Patterns of variability within the harvested portions of treatment areas provide insight into this counterintuitive result. For those variables for which significant, or marginally significant effects of pattern were detected in these areas, changes were consistently greater in aggregated than dispersed treatments (Fig. 8), thus negating the stabilizing influence of adjacent forest aggregates. As a consequence, average increases in variability were comparable among treatments.

Clearly our analyses provide a limited view of the spatial and temporal variation induced by structural retention. We quantify variation at a fairly large spatial scale (40–80 m), but relationships may differ if much of the variability associated with timber harvest or residual canopy cover occurs at a finer spatial scale (e.g., meters). Similarly, initial changes in variability reflect the patchy nature of disturbance as it influences loss of plant cover. With time, additional sources of variation (e.g., the effects of residual overstory cover on species recruitment or growth) may lead to distinctly different patterns of understory heterogeneity.

Management implications and future responses

Do our results suggest a clear difference in the response of the forest understory to different levels or spatial patterns of retention? Clearly, the magnitude of change in understory composition and structure was notably reduced from 15% to 40% retention, but for most elements of the understory, aggregated retention appeared to offer few short-term benefits over dispersed retention. The latter result was particularly surprising with respect to loss of late-seral species, the group for which aggregated retention of the overstory was presumed to be most relevant. Yet, we must temper these conclusions by acknowledging the short-term nature of our results. In large part, we have attributed observed responses to retention to associated patterns of logging disturbance and slash accumulation. However, most components of the understory are fairly resistant to large-scale disturbance (with the exception of the late-seral flora), and early successional change is characterized by fairly rapid recovery through vegetative reproduction (Halpern 1988, Halpern and Franklin 1990). As the immediate effects of disturbance

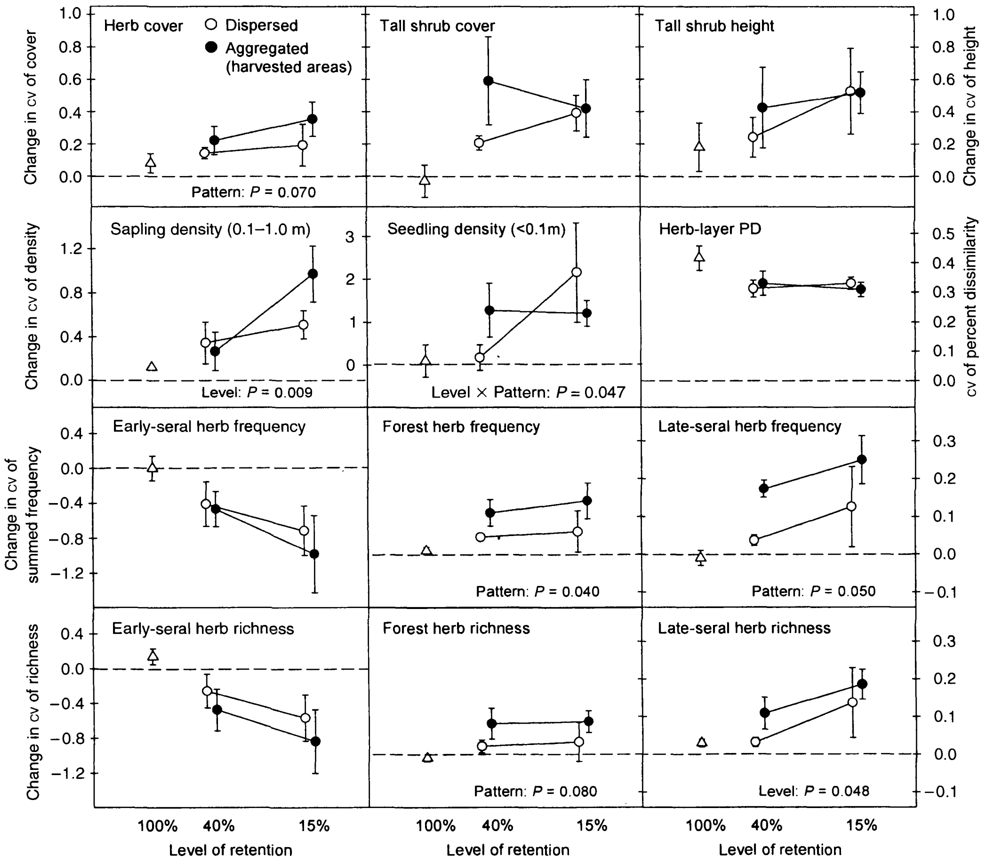

FIG. 8. Changes in within-treatment variability (CV, coefficient of variation ± 1 SE) within the harvested portion of treatment units for each of the 12 understory variables. Note that data for dispersed treatments are the same as in Fig. 5. See Fig. 4 for other details.

diminish with time, the direct and indirect effects of residual overstory structures are likely to become increasingly important. Possible insights into the longer term effects of green-tree retention may be gleaned from retrospective analyses of natural "two-storied" stands, in which young to mature forests (65–125 yr old) established after wildfire beneath a sparse overstory of remnant Douglas-fir (Rose and Muir 1997, Acker et al. 1998, Zenner et al. 1998). Comparison of plots with and without overstory remnants suggest that relatively few residual trees (i.e., 5–15 per ha) can influence the composition and growth of regenerating conifers (Acker et al. 1998, Zenner et al. 1998) which in turn, can shape patterns of herb- and shrub-layer development, presumably through effects on light availability (Traut and Muir 2000). Clearly, there are limitations to applying the results of retrospective analyses to predict the development of forests managed with green-tree retention, both with respect to their distinctly different histories of disturbance and to the comparability of the retention "treatments." Future measurements of our experimental plots will be useful in distinguishing between those outcomes that are specific to managed forests, and those that can be viewed more generally.

In developing strategies for structural retention harvest that sustain biological diversity and timber production, forest managers must weigh the ecological and silvicultural tradeoffs associated with varying levels and patterns of retention. Our vegetation studies identify some of these tradeoffs with respect to the forest understory community. Companion studies of natural regeneration, overstory mortality, bryophyte and fungal diversity, and wildlife responses will provide a broader ecological foundation from which future management decisions can be made (Aubry et al. 1999). However, longer-term observations will be necessary to distinguish between the short-term effects of disturbance and the more persistent influence of residual overstory trees.

ACKNOWLEDGMENTS

We thank Denise Liguori, David Phillips, Tammy Stout, and our numerous field assistants for help with data collection. Melora Halaj and David Phillips assisted with compiling and verifying the databases. We appreciate the tireless efforts of Gody Spycher in data management and quality assurance for the DEMO Study. For logistical support we thank Rick

Abbott, Dave Allaway, Richard Bigley, Sue Macmeeken, Jon Nakae, Ed Tompkins, and Jim White. Critiques from Joseph Antos, Keith Aubry, Tim Max, Pat Muir, Annette Olson, James Saracco, Ed Schreiner, and two anonymous reviewers greatly improved the manuscript. This is a product of the Demonstration of Ecosystem Management Options (DEMO) Study, a joint effort of the USDA Forest Service Region 6 and Pacific Northwest Research Station. Research partners include the University of Washington, Oregon State University, University of Oregon, Gifford Pinchot and Umpqua National Forests, and the Washington State Department of Natural Resources. Funds were provided by the USDA Forest Service, PNW Research Station (PNW-93-0455, PNW-97-9021-1-CA, and PNW-01-CA-11261993-091).

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