

Bibit Halliday Traut,¹ Department of Botany & Plant Pathology, Oregon State University, Corvallis, Oregon 97331-2902

and

Patricia S. Muir², Department of Botany & Plant Pathology, Oregon State University, Corvallis, Oregon 97331-2902

Relationships of Remnant Trees to Vascular Undergrowth Communities in the Western Cascades: a Retrospective Approach

Abstract

Managers of federal forests in the U.S. Pacific Northwest are charged with managing timber harvest while maintaining ecosystem functions and biological diversity associated with old, unmanaged forests. Thus, timber-oriented management is being replaced by ecosystem management, which includes leaving live trees (green trees), snags, and coarse woody debris after harvest. We used a retrospective approach to assess potential effects of green-tree retention on vascular undergrowth in the western Cascades of Oregon. Fourteen natural two-storied stands of remnant trees (> 300 yr) over 65-125 yr old regeneration were paired with neighboring stands of the same age but lacking remnants. Species richness and cover of shrubs, all herbs, and late-successional shrubs and herbs did not differ systematically between stands with and without remnant trees. However, communities of herbs and shrubs varied with the percentages (% BA/ha) of Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) in the regeneration, which varied with remnant densities. Regeneration densities and percentages of western hemlock in the regeneration were positively correlated with remnant tree densities. In contrast, percentages of Douglas-fir in the regeneration and overall conifer volume were negatively correlated with remnant densities. Undergrowth cover and species richness was generally greater in relatively open, Douglas-fir dominated forests, which were associated with physiographically drier sites and fewer remnant trees. Results for these natural, two-storied stands suggest that variable levels of green-tree retention in managed forests may provide for a diversity of undergrowth communities

Introduction

The preservation of biological diversity is one of the most important environmental priorities today (Lubchenco et al. 1991). In the U.S. Pacific Northwest (PNW), concern focuses on loss of biotically rich and structurally complex old-growth forest (FEMAT 1993). These forests provide habitats for many organisms (Norse 1990), whereas stands managed for maximum timber productivity typically have fewer of the structural and compositional features that provide the diversity of habitats on which many species depend (e.g., Alaback 1982, Franklin and Spies 1991, Hansen et al. 1991). Old-growth forests of the PNW are characterized by several structural features, including a multi-layered canopy consisting of living and dead trees and abundant coarse woody debris (Franklin et al. 1981). The mosaic of gaps and shaded areas allows a spatially heterogeneous understory and a rich assemblage of plant spe-

cies (Franklin and Spies 1991). Some surveys show that management practices that interfere with the development of old-growth structural features may result in a long-term loss of species diversity (e.g., Halpern 1993). Thus, forest managers, who are required to manage for timber production, as well as maintenance or enhancement of ecosystem functions and biological diversity (Kessler et al. 1992; Swanson and Franklin 1992; R.O.D. 1994), are now charged with fostering structural and compositional heterogeneity in forests.

Much of the original old-growth forest area of the Pacific Northwest has been harvested, with a two-thirds decrease in old-growth area over the last five decades (Bolsinger and Waddell 1993). Efforts to protect remaining old-growth stands are important for protection of old-growth associated species, but re-creation of such systems may also be invaluable (R.O.D. 1994). Management techniques may be able to accelerate the development of structural features characteristic of old-growth forests, including large trees over intermediate canopy layers with abundant standing and down coarse woody debris (CWD). Consequently, forest managers are beginning to apply "ecosystem management" techniques in forests within the range

¹Current address: Bibit Halliday Traut, Graduate Group in Ecology, Wildlife, Fish and Conservation Biology, One Shields Ave, University of California, Davis, CA 95616; e-mail: bhtraut@ucdavis.edu.

²Author to whom correspondence should be addressed.

of the Northern Spotted Owl (*Strix occidentalis*), seeking to re-create structurally diverse stands by carrying through harvest some of the structural legacy of the former stands (e.g. large green trees, CWD, and snags; FEMAT 1993, R.O.D. 1994). These techniques, in part, mimic natural disturbances (e.g., fire), which often leave standing green trees and snags, as well as CWD (Swanson and Franklin 1992). However, these changes are being implemented with little data on long term effects, particularly whether they will enhance biotic diversity or communities characteristic of older forests (but see, Aubry et al. 1999; Halpern et al. 1999).

Unmanaged forests in the western Cascades of Oregon consist of a mosaic of stands that were created and influenced by fires (Morrison and Swanson 1990, Agee 1991) and other disturbances. Past disturbances of diverse intensity and frequency left varying numbers of remnant trees, creating a variety of stand structures. This variation presents the opportunity to examine the relationships of remnant tree carry-over to the structure and composition of resulting stands. Natural, two-storied stands (remnant trees over regeneration) created by fire may be analogous to stands that are being created by ecosystem management techniques, projected into the future. A retrospective approach allows insights into the possible consequences of these techniques without waiting decades for results from newly manipulated stands to become apparent (Swanson and Franklin 1992).

We used a retrospective approach to examine the apparent effects of variations in ecosystem carryover, specifically remnant tree densities, on abundance and species composition of herbs and shrubs in rotation-aged stands (65-125 yr). We assessed whether simple univariate measures, such as species richness or cover, differed systematically between stands with remnant trees and those without remnants. In addition, we analyzed composition of herb and shrub communities, and relationships between those communities and overstory characteristics. The results are important to our basic understanding of influences on undergrowth, which have been little studied in natural two-storied stands of this region (Hansen et al. 1991). (We use the term "undergrowth," rather than "understory" to emphasize that our focus was on herbs and shrubs, with understory trees excluded.) This study also provides important information for forest managers, who need to as-

sess probable consequences of remnant, overstory trees on undergrowth diversity, abundance, and communities. Parallel studies on the same sites examined relationships of remnant trees to growth of conifer regeneration (Zenner 1994; Acker et al. 1998; Zenner et al. 1998) and canopy epiphytic lichens (Peck and McCune 1997).

While our retrospective approach allows us to anticipate some potential effects of logging with green-tree retention on undergrowth, such an approach has limitations. For example, the natural, two-tiered stands that we studied originated after fire, not after timber harvest, which may influence responses. Thus, apparent responses to remnant density may, in fact, be responses to variation in disturbance intensity that led to differential survival of remnant trees. Our approach allows us to assess correlations between undergrowth and overstory characteristics, but our ability to infer causation is limited.

Study Area

This study was conducted on the Willamette National Forest, Oregon, within the *Tsuga heterophylla* (western hemlock) zone (Franklin and Dyrness 1973) of the central western Oregon Cascades at elevations between 520 and 850 m. All sites were within the *Tsuga heterophylla*/*Berberis nervosa* (TSHE/BENE) and *Tsuga heterophylla*/*Berberis nervosa*-*Gaultheria shallon* (TSHE/BENE-GASH) associations (Hemstrom et al. 1987). These plant associations are among the most common in the Willamette National Forest and are similar to one another in that they are typically found at mid-elevations on moderately productive, well-drained sites. We restricted sites to these two associations to minimize among-site environmental variation, although TSHE/BENE sites tend to be more mesic than TSHE/BENE-GASH sites. Stands were sampled on a range of aspects and topographic positions.

Methods

Plot Selection

Natural two-storied stands of mature remnant trees (≥ 300 yr) over well-stocked rotation-aged regeneration (65-125 yr old) were selected based on suggestions by U.S. Forest Service personnel and on field inspection. Remnant trees are those that were dominant or co-dominant at the time of the

regeneration-initiating disturbance. We reduced inter-stand heterogeneity by choosing only stands that appeared to originate after wildfire (e.g., fire scars on remnants), rejecting stands originating after other disturbances, such as wind storms or selective harvesting. To maximize our ability to infer effects potentially attributable to remnant trees (as opposed to those attributable to abiotic variables), we paired study plots: one plot with remnant trees (3 - 57 trees per ha) paired with a plot without remnants. Thus, each site had to be large enough (1-2 ha) to include two areas; one with remnants (remnant megaplot) and one without remnants (non-remnant megaplot). Edges of megaplot pair members were 5 - 50 m apart. Edge effects resulting from proximity to clearcuts were minimized by locating sites at least 20 m, and generally much farther, from the edge of a clearcut. Final sample size was 14 pairs of plots. All sites were sampled between late June and early September, 1993.

Plot Design

On each site, trees, herbs and shrubs were measured within a pair of nested, concentric, fixed-radius plots (Figure 1). Remnant trees and aspects

of the physical environment were measured in the largest circular plots ("megaplots," 30.9 m radius, area = 3000 m²). Tree regeneration, herbs, and shrubs were measured in smaller "detection plots" (radius = 12.62 m, area = 500 m², Figure 1), which were centered within megaplots (one per megaplot). (Detection plots were so-named, as they were the areas in which undergrowth was measured to detect potential remnant effects.) Sampled areas within remnant and non-remnant plots were separated by at least 30 m, a distance over which remnant effects on regeneration are likely to be minimal (Hoyer 1993). Sparse remnant trees may influence regeneration or undergrowth, yet may be missed in smaller plots (such as the detection plot); measurement of remnants in the larger megaplot minimized this potential problem. Within detection plots, 10 subplots (radius = 2 m) were randomly placed, each with three microplots (0.2 x 0.5 m) for a total of 30 microplots per detection plot (Figure 1).

Plot Measurements

Megaplots

Slope, aspect, physiographic class, coarse woody debris and remnants were measured or recorded

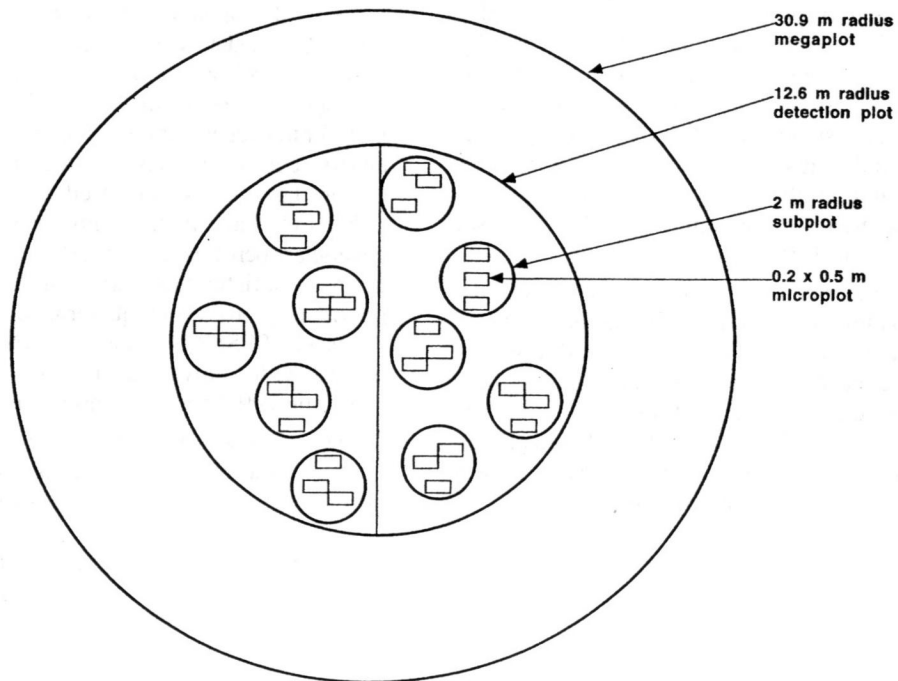


Figure 1. Sampling schematic, showing shrub subplots and herb microplots within the detection plot portion of the megaplot. A pair of such megaplots was established at each of the 14 sites.

in the megaplots as follows. Physiographic classes were based on aspect and topographic position, ranked to reflect increasing potential moisture status as influenced by these factors (1 = W, SW, S facing middle/upper slopes; 2 = SE, NW facing middle/upper slopes; 3 = N, NE, E facing middle/upper slopes; modified from Kessell 1979; Rose 1994). For each remnant tree, we recorded species, diameter at breast height (dbh), height, and two perpendicular crown radii. Ages of most remnants were determined from increment cores taken at breast height. The post-disturbance stand had been affected not only by current remnants, but also by remnants that died over its history. Thus, dead remnant trees were assigned to a decay class (Bartels et al. 1985; Neitro et al. 1985) and measured variously depending on decay class. Trees of decay classes 1, 2 and 3 (class 1 being least decayed) were measured in the same way as live remnants when possible, including the extraction of increment cores (for methods, see Zenner 1994). Remnants in more advanced decay classes were excluded from remnant tree analyses, on the assumption that they were dead throughout the post-disturbance stand's history (Acker et al. 1998). The following remnant tree variables were then calculated: density (trees/ha), total basal area at time of stand initiation (henceforth, total BA; m²/ha), live BA (m²/ha), live volume (m³/ha), and live crown area (m²/ha) (see Acker et al. 1998 and Zenner et al. 1998 for calculations and rationale).

Detection Plots

We measured species and dbh of all trees (dbh \geq 20 cm) in detection plots and calculated density, BA, species composition (percent of BA) and volume of conifers and hardwoods in the post-disturbance stand (Zenner 1994). Coarse woody debris and snags (diameter \geq 10 cm) were measured, and number (no./ha), volume, and cover or basal area were determined (for methods see Zenner et al. 1998).

Species richness of shrubs and herbs in detection plots was based on measurements in subplots and microplots (see below) and a 30 min ocular inspection of each detection plot. The time-constrained ocular inspection was intended to increase the species lists over those based on sub- and microplot sampling, yet maintain consistency in sampling intensity across sites.

Sub- and Microplots

Shrub cover was estimated in subplots (2 m radius) using a modified Daubenmire cover-class scale which approximates an arcsine squareroot transformation (1 = <1%, 2 = 1-5%, 3 = 5-25%, 4 = 25-50%, 5 = 50-75%, 6 = 75-95%, 7 = 95-99%, 8 = >99%; Muir and McCune, 1988). Shrubs were defined structurally as all vascular species > 0.5 m and < 3 m in height. Herbaceous plants taller than 0.5 m (e.g., *Polystichum munitum* and *Pteridium aquilinum*) were included with shrubs because their influences on the herb stratum (e.g., light interception) may be similar to those of shrubs. Because some species were in both herb and shrub strata, as defined by height, a given species may be represented in both layers for a plot.

We measured tree canopy cover (subcanopy and canopy trees combined, but excluding tall shrubs such as *Acer circinatum*) using a convex spherical densiometer. We took readings in the four ordinal directions from the center of each subplot ("wedge method"; Strickler 1959). The densiometer was fastened and leveled at 1.1 m above the ground on a pole at plotcenter. Canopy cover values for each subplot were averaged to give detection plot-level estimates of cover.

Herb cover was estimated in microplots (0.2 x 0.5 m) using the cover-class scale used for shrubs. All vascular plants \leq 0.5 m tall were considered "herbs." Nomenclature follows Hitchcock and Cronquist (1973).

Data Analysis

Data on shrubs and herbs were analyzed separately. Cover data were aggregated to the detection plot level by summing across subplots and microplots. Henceforth, "plot" refers to detection plots for tree regeneration, CWD, herbs, and shrubs and to megaplots for remnant trees (live and dead). Cover-class values were used in most analyses, rather than back-transforming to mid-points of cover-class percentages, because cover-class scores improve statistical properties of the data by approximating an arcsine squareroot transformation. We used SPSS/PC+ Version 4.0 (Norusis/SPSS Inc. 1988) for univariate analyses and PC-ORD (McCune 1993) for multivariate analyses.

We tested whether remnant and nonremnant plots differed in shrub and herb cover and species richness, using comparisons of means and

standard errors. We also tested whether richness of species considered to be late-successional (FEMAT 1993) differed between remnant and nonremnant plots. Late-successional species included *Achlys triphylla*, *Adenocaulon bicolor*, *Anemone deltoidea*, *Chimaphila menziesii*, *C. umbellata*, *Coptis laciniata*, *Corallorhiza maculata*, *C. mertensiana*, *Disporum hookeri*, *Goodyera oblongifolia*, *Hypopitys monotropa*, *Monotropa uniflora*, *Pyrola picta*, *Trillium ovatum*, *Vaccinium parvifolium*, *Vancouveria hexandra*, and *Whipplea modesta*. We tested whether species richness or cover of all herbs and of late-successional herbs was correlated with overstory attributes, using Spearman's rank correlation.

To describe and interpret species compositional patterns and their relationships to site variables, we analyzed the species cover data using nonmetric multidimensional scaling ordination (NMS; Kruskal 1964; Mather 1976) with a Sorenson distance measure for each layer (shrub and herb) and for late-successional species. Outliers were plots whose average distances were greater than 2.5 standard deviations from the mean distance; two such plots were omitted. We examined correlations of environmental variables with ordination axes, using Pearson's r and overlays of environmental variables on ordination diagrams. We rotated axes by 15° for shrub ordinations to maximize the variance of important environmental variables (variables with the highest r^2) along them (McCune 1993). Apparently strong relationships between individual species and environmental variables (suggested by overlays of environmental variables on ordination diagrams and correlation coefficients ≥ 0.3) were then analyzed directly using Pearson correlations, as were correlations among environmental variables. Because we made multiple comparisons, probabilities associated with correlation coefficients should be interpreted with caution.

Results

Relationships Among the Remnant Trees, the Regeneration Cohort and Environmental Variables

Remnant tree density in megaplots ranged from 3 to 57 trees/ha, (live remnants only) with an average of 21 remnants per hectare. Density of all live trees (remnants + regeneration) ranged from 440 to 1920 trees/ha and averaged 894 trees/ha

(see Zenner et al. 1998 for a complete listing of overstory characteristics in remnant and nonremnant plots). Canopy cover percentages were always $> 92\%$ and averaged 96% . All remnant tree attributes (total BA [at time of stand initiation], live BA, total volume, crown area) were highly inter-correlated ($P \leq 0.01$, minimum $r = 0.38$; see Zenner et al. 1998, for details). As remnant density increased, percentages of western hemlock (% BA/ha) generally increased, and percentages of Douglas-fir and overall conifer volume (m^3/ha) decreased (Pearson's $r = 0.61$, -0.62 , and -0.67 respectively; all $P \leq 0.01$).

The characteristics of the regeneration cohort of trees were also interrelated. Canopy cover (including remnants and regeneration trees) was positively correlated with the percentage of western hemlock and negatively correlated with the percentage of Douglas-fir in stands (% BA/ha basis; $r = 0.39$ and -0.39 , respectively, $P \leq 0.05$). Regeneration conifer volume was positively correlated with the percentage of Douglas-fir and negatively correlated with the percentage of western hemlock in stands ($r = 0.52$ and -0.50 , respectively; $P \leq 0.05$), consistent with Rose (1994) and Rose and Muir (1997). In contrast to results for regeneration volume, regeneration density was positively correlated with the percentage of western hemlock in the regeneration ($r = 0.32$), implying an abundance of relatively small stems in stands with regeneration dominated by western hemlock, a result consistent with others (e.g., Edmonds et al. 1993). Regeneration density was negatively correlated with the cover of CWD ($r = -0.39$; $P \leq 0.05$).

Abiotic site characteristics were correlated with regeneration characteristics as well. Conifer volume generally decreased as elevation increased ($r = -0.39$; $P \leq 0.05$), probably reflecting a decrease in the relative abundance of Douglas-fir at higher elevations. Conifer volume was also lower on steeper slopes ($r = -0.50$; $P \leq 0.05$), but regeneration density increased with slope steepness ($r = 0.49$; $P \leq 0.05$). Canopy cover and relative abundance of western hemlock (% BA/ha) were positively correlated with physiographic conditions (1 [relatively xeric] – 3 [relatively mesic]; $r = 0.52$ and 0.73 , respectively, $P \leq 0.05$), whereas the relative abundance of Douglas-fir was negatively correlated with physiographic moisture status ($r = -0.74$, $P < 0.05$).

Relationships of Communities to Overstory and Environment

No systematic differences in herb or shrub cover, or in species richness of herbs, shrubs or late-successional species were detected between remnant and nonremnant plots (Traut 1994). Further, the paired plots did not separate into groups (remnant vs. non-remnant plots) on community ordinations. However, communities did vary along gradients that were related to remnant trees, hence we focus on patterns across all plots, rather than on differences between plot pairs.

Shrubs

We found a total of 24 shrub species across all plots, with a mean alpha diversity of 8.4 species per plot. Multivariate analyses revealed relationships of remnant trees to shrub communities (Table 1). Cover of 8 of the 24 shrub species increased

TABLE 1. Pearson correlations (r) of shrubs, remnant and regenerating trees, and environmental variables with ordination axes (NMS). Only correlations $\geq \pm 0.37$ ($P \leq 0.05$) with one or more axes are shown.

Species/Variable	Axis 1	Axis 2
Shrubs		
<i>Acer circinatum</i>	-0.34	0.70
<i>Acer macrophyllum</i>	0.57	-0.35
<i>Castanopsis chrysophylla</i>	0.43	-0.36
<i>Gaultheria shallon</i>	0.78	-0.54
<i>Polystichum munitum</i>	0.07	0.51
<i>Pteridium aquilinum</i>	0.66	-0.22
<i>Rhododendron macrophyllum</i>	-0.02	-0.47
<i>Rosa gymnocarpa</i>	0.55	-0.19
<i>Rubus ursinus</i>	0.80	-0.28
<i>Symphoricarpos mollis</i>	0.56	-0.23
<i>Tsuga heterophylla</i>	0.43	-0.09
Summed cover of shrub species	0.07	-0.97
Remnant and Regenerating Trees, Environmental Variables		
Remnant density (trees/ha)	-0.53	-0.18
Remnant BA (total; m ² /ha)	-0.48	-0.05
Remnant BA (live, m ² /ha)	-0.44	-0.03
Remnant volume (m ³ /ha)	-0.39	-0.03
Remnant crown area (m ² /ha)	-0.38	0.00
<i>Tsuga heterophylla</i> regeneration (% BA)	-0.43	-0.23
<i>Pseudotsuga menziesii</i> regeneration (% BA)	0.46	0.23
Regeneration conifer volume (m ³ /ha)	0.56	0.05
Regeneration density (trees/ha)	-0.38	-0.15
Slope (%)	-0.40	0.07

along the first NMS ordination axis, while remnant trees (remnant density, total and live BA, volume, and crown area) decreased (R^2 for Axis 1 = 0.36). Percentages of western hemlock in the regeneration and regeneration density also decreased along Axis 1. In contrast, the percentage of Douglas-fir in the regeneration and overall conifer volume increased along this axis (Table 1). The only abiotic environmental variable correlated ($P \leq 0.05$) with Axis 1 was slope steepness, which increased as remnants increased and as cover by most shrub species decreased. Stands with greater numbers of remnants tended to be at higher elevations, although the correlation of elevation with Axis 1 ($r = -0.31$) was not statistically significant at $P \leq 0.05$. While several shrub species were strongly correlated with the second ordination axis, it was not related to overstory or measured abiotic site variables (Table 1; R^2 for Axis 2 = 0.32).

Herbs

We found a total of 52 herb species across all plots, with a mean alpha diversity of 10.1 species per plot. Variation in herb communities was predominantly accounted for by the second axis of the herb ordination (R^2 for Axis 2 = 0.52), which was most strongly related to relative abundances of Douglas-fir and western hemlock in the regeneration (Table 2). Correlations of remnant tree attributes with this second axis of herb ordinations were suggestive, but not statistically significant (maximum $r = 0.34$ [remnant density]; $0.05 < P < 0.1$). While weaker, these correlations were similar to those for shrub communities, in that cover of several herb species was negatively correlated with remnant attributes and positively correlated with the relative abundance of Douglas-fir. Summed cover across herb species and cover by 10 of the 52 individual species was negatively correlated with this axis ($P \leq 0.05$), as was the percentage of Douglas-fir in the regeneration. *Polystichum munitum* was the only herb species that was positively correlated with this axis. Herb community composition also varied along another axis (Axis 1, $R^2 = 0.29$), and several species were strongly correlated with this gradient. However, Axis 1 was only weakly related to overstory variables (maximum $r = 0.30$ for regeneration volume), and slope was the only abiotic site variable with which it was correlated.

TABLE 2. Pearson correlations (r) of herbs, regenerating trees, and environmental variables with ordination axes (NMS). Only correlations $\geq \pm 0.37$ ($P \leq 0.05$) with one or more axes are shown.

Species/Variable	Axis 1	Axis 2
Herbs		
<i>Acer macrophyllum</i>	0.57	-0.35
<i>Achlys triphylla</i>	0.26	-0.45
<i>Amelanchier alnifolia</i>	-0.57	0.15
<i>Berberis nervosa</i>	0.21	-0.80
<i>Calypso bulbosa</i>	-0.38	0.00
<i>Collomia heterophylla</i>	-0.47	0.07
<i>Galium triflorum</i>	-0.42	0.05
<i>Gaultheria shallon</i>	0.70	-0.59
<i>Linnaea borealis</i>	0.22	-0.45
<i>Polystichum munitum</i>	-0.06	0.62
<i>Pteridium aquilinum</i>	0.49	-0.35
<i>Pyrola asarifolia</i>	0.33	-0.37
<i>Rosa gymnocarpa</i>	0.32	-0.53
<i>Rubus ursinus</i>	0.52	-0.55
<i>Symphoricarpos mollis</i>	0.34	-0.47
<i>Synthris reniformis</i>	-0.57	0.15
<i>Viola sempervirens</i>	0.16	-0.38
<i>Whipplea modesta</i>	0.13	-0.46
Summed cover across herb species	-0.01	-0.89
Regenerating Trees and Environmental Variables		
<i>Pseudotsuga menziesii</i> regeneration (% BA)	0.12	-0.71
<i>Tsuga heterophylla</i> regeneration (% BA)	-0.09	0.69
Slope (%)	-0.39	0.15

Late-successional species

Multivariate analysis revealed relationships of late-successional species' (FEMAT 1993; see Methods) communities to canopy cover, abundance of CWD, regeneration tree density, and elevation (Table 3). As for ordinations involving all herb species, remnant tree variables were not directly related to either ordination axis. However, by contrast with results for shrubs and all herb species, percentages of western hemlock and Douglas-fir in the regeneration were not directly correlated with the axes of variation in late-successional herb communities (maximum $r = 0.29$).

The first axis of this ordination was most strongly related to canopy cover and CWD cover and volume, which were negatively correlated with this axis (R^2 for Axis 1 = 0.27). Relatively open plots (lower canopy cover) generally contained *Achlys triphylla*, *Adenocaulon bicolor*, *Anemone*

TABLE 3. Pearson correlations (r) of late-successional species, remnant and regenerating trees, and environmental variables with ordination axes (NMS). Only correlations $\geq \pm 0.37$ ($P \leq 0.05$) with one or more axes are shown.

Species/Variable	Axis 1	Axis 2
Species		
<i>Achlys triphylla</i>	0.38	0.09
<i>Adenocaulon bicolor</i>	0.42	0.16
<i>Allotropa virgata</i>	-0.07	0.51
<i>Anemone deltoidea</i>	0.77	0.08
<i>Chimaphila menziesii</i>	0.62	0.54
<i>Chimaphila umbellata</i>	0.30	0.55
<i>Coptis laciniata</i>	0.13	0.69
<i>Corallorhiza maculata</i>	-0.49	-0.16
<i>Corallorhiza mertensiana</i>	-0.42	-0.13
<i>Disporum hookeri</i>	0.16	-0.37
<i>Goodyera oblongifolia</i>	0.32	-0.39
<i>Hypopitys monotropa</i>	-0.42	-0.03
<i>Monotropa uniflora</i>	-0.18	-0.41
<i>Pyrola picta</i>	-0.02	0.61
<i>Trillium ovatum</i>	-0.19	-0.63
<i>Vaccinium parvifolium</i>	-0.42	0.07
<i>Vancouveria hexandra</i>	0.47	0.00
<i>Whipplea modesta</i>	0.75	0.06
Remnant and Regenerating Trees		
Canopy cover (%)	-0.64	-0.03
CWD cover (%)	-0.42	-0.29
CWD volume (m ³ /ha)	-0.37	-0.30
Regeneration density (trees/ha)	0.02	0.38
Environmental Variables		
Elevation (m)	0.17	0.46

deltoidea, *Chimaphila menziesii*, *Vancouveria hexandra*, and *Whipplea modesta*. Plots with greater canopy cover and abundance of CWD were typified by the presence of *Vaccinium parvifolium*, *Corallorhiza maculata*, *C. mertensiana*, and *Hypopitys monotropa*.

The second axis of the ordination of late-successional species' communities was most strongly related to elevation, with *Allotropa virgata*, *Chimaphila menziesii*, *Chimaphila umbellata*, *Coptis laciniata*, and *Pyrola picta* typical of plots at higher elevations (R^2 for Axis 2 = 0.24). Regeneration density also increased with elevation along this axis.

Species richness

The most species-rich plots tended to have higher percentages of Douglas-fir relative to western hemlock in the regeneration and more open canopies (Table 4). These plots also tended to be

TABLE 4. Correlations between herbaceous species richness and environmental variables (Spearman's correlation coefficients; probabilities are ≤ 0.05 except where indicated). % PSME and % TSHE are percentages of *Pseudotsuga menziesii* and *Tsuga heterophylla*, respectively, on a basal area basis; physiographic classes were ranked, with 1 = driest and 3 = moistest, as indicated by slope, aspect, and topographic position; "late-successional" species are based on FEMAT (1993).

Richness Component	Canopy Cover (%)	% PSME	% TSHE	Physiographic Class
All Herbaceous Species	-0.56	0.72	-0.74	-0.55
Late-successional Species	-0.38	0.48	-0.48	-0.27 ^{ns}

^{ns} = $P > 0.05$

physiographically drier. Patterns in species richness for late-successional species paralleled those for all herb species, in that richness increased with the relative abundance of Douglas-fir and decreased with the relative abundance of western hemlock. Correlations of late-successional herb species richness with overstory attributes were weaker than were correlations of those attributes with richness across all herb species (Table 4).

Summary and Discussion

Species Richness and Cover

We had anticipated that species richness or cover, particularly for late-successional species, might be higher in remnant than in non-remnant plots. For example, remnant trees might ameliorate site conditions after disturbance, potentially enhancing survival or establishment of herb and shrub species in the years immediately following the disturbance. In addition, remnant survival suggests that the regeneration-initiating disturbances (in the case of our plots, fires) were less intense in remnant than in nonremnant plots. Lower intensity disturbances might be expected to enhance post-disturbance survival of undergrowth species. The lack of systematic pairwise differences between remnant and nonremnant plots in species richness or cover that we found could result from several factors, including: (1) pre-disturbance differences in species composition or abundance that persisted through the disturbance via survival of roots, rhizomes or seeds; (2) effects of remnants on density and species composition of re-

generating trees, whose effects on undergrowth may have obscured direct remnant or disturbance-intensity effects (see below); or (3) other site-to-site differences that overwhelmed remnant or disturbance-intensity effects on undergrowth. Our retrospective approach does not allow us to distinguish between these, or other, influences.

Shrub and Herb Communities

Analyses of herb and shrub communities suggested, however, that remnant trees may have influenced their development, at least indirectly. While remnant density or basal area itself was not always correlated with axes of variation in shrub and herb communities, remnant characteristics were generally correlated with composition and density of the regeneration trees, which were, in turn, strongly related to the undergrowth communities.

For example, major axes of variation in shrub and herb communities were always correlated with the relative abundance of Douglas-fir and western hemlock in the regeneration, or with density of regeneration trees. Further, cover by several individual herb and shrub species decreased as the relative abundance of western hemlock increased. Relative abundance of western hemlock and density of regeneration trees was higher when remnant density (or BA) was higher, while relative abundance of Douglas-fir in the regeneration was generally higher when remnants were sparser. Shadier conditions associated with remnant trees may have enhanced the relative success of western hemlock compared to Douglas-fir on remnant plots, as western hemlock is more shade-tolerant than Douglas fir (Burns and Honkala 1990). The relative abundance of Douglas-fir also tended to be higher on physiographically drier sites, which supported lower remnant densities. Physiographically drier conditions on sites with lower remnant densities may have been more suitable for Douglas-fir than for the relatively moisture-demanding western hemlock.

The inverse relationship of cover by several shrub species to remnant density, BA, volume and crown area may have been mediated by the relative abundance of western hemlock regeneration. Overstory influences could act via the canopy (e.g., light or moisture interception), the soil (e.g., litter chemistry and accumulation), or both. Western hemlock and Douglas-fir have different influences on the understory environment (e.g., Alaback 1982, Stewart 1986). For example, less

direct light comes through relatively dense hemlock canopies than through those of Douglas-fir (Stewart 1986, 1988) and therefore, greater development of many shrub species often occurs under Douglas-fir than under western hemlock. In addition, sunflecks, which can be important to many understory species (Pearcy 1983), may be more frequent under Douglas-fir than under western hemlock (Antos and Zobel 1984). We found that cover of *Gaultheria shallon* and *Acer circinatum* was negatively correlated with the relative abundance of western hemlock ($r = -0.46$ for both; $P \leq 0.05$). Both *G. shallon* and *A. circinatum* are sensitive to overstory density, and often show increased growth in thinned stands (Tappeiner and Zasada 1993). *Gaultheria shallon*, although not highly shade-tolerant, may do well under a uniform, somewhat open canopy (Messier 1992), as is often found in stands dominated by Douglas-fir. With regard to *A. circinatum*, Anderson (1967) found a positive correlation between its density and basal area of Douglas-fir within the stand, and Stewart (1986) found that it was more commonly present in stands dominated by Douglas-fir than in those dominated by western hemlock, consistent with our findings. Of course, Douglas-fir and western hemlock have differential effects on site factors in addition to light, such as moisture interception (e.g., Voigt 1960, Rothacher 1963) and litter chemistry, and these differences may also have influenced shrub communities.

Several herb species that were negatively correlated with the relative abundance of western hemlock (based on the ordination of herb communities), and thus positively correlated with the relative abundance of Douglas-fir, are typical of drier sites (e.g. *G. shallon*, *Whipplea modesta*, *Linnaea borealis*; Zobel et al. 1976; Gagnon and Bradfield 1986). Hence, differences among sites in moisture status as well as differences in light regime may have been influential. Relationships of undergrowth communities to physiographic moisture status were also suggested by overlays of physiographic classes on an ordination of herb and shrub communities together, which revealed that plots with lower shrub and herb cover tended to be physiographically moister (Traut 1994). The negative correlation between herb species richness and physiognomic moisture status that we observed is consistent with results from other studies of forests in the region, which have found that

species richness often is higher in relatively dry forest communities (e.g., Zobel et al. 1976). There were some exceptions to the generally lower cover on physiographically-moister sites, however, such as *Coptis laciniata*, which commonly indicates moist sites (Hemstrom et al. 1987), and which was more abundant in western hemlock-dominated sites. Because physiographically moister sites supported more remnants and more western hemlock in the regeneration, we are unable to separate potential physiographic influences on undergrowth communities from influences mediated by overstory composition (including remnants), however it is likely that both types of influences are important. (Note that we did not measure soil moisture status directly.)

Three of the late-successional species characterizing plots with relatively high canopy and CWD cover were mycotrophs (*Corallorhiza maculata*, *C. mertensiana* and *Hypopitys monotropa*; Hitchcock and Cronquist 1973, Furman and Trappe 1971). Logs may help to maintain mycorrhizal associates of these species through stand-initiating disturbances and in post-disturbance stands (Spies et al. 1988). The mycorrhizae associated with *H. monotropa* are compatible with western hemlock (Furman and Trappe 1971), the most abundant conifer in stands with higher canopy and CWD cover. Coarse woody debris also provides a favorable substrate for many non-mycotrophic species (Stewart 1986), such as *Vaccinium parvifolium*, which occurred commonly on logs, and whose cover was associated with relatively abundant CWD. Finally, CWD may also influence soil moisture and stand humidity (Franklin et al. 1981). Coarse woody debris can retain water throughout the summer and also provide shade and diminished wind at the forest floor, thereby reducing evaporation. We found that two species often associated with mesic sites, *Trillium ovatum* and *Polystichum munitum* (Hitchcock and Cronquist 1973), tended to be more abundant in plots with more CWD.

Herbaceous species richness and abundance often decrease with canopy closure (e.g., Alaback 1984; Stewart 1988; Oliver and Larsen 1990; Duffy and Meier 1992), and the communities that we studied were probably affected variously by this stage in stand development. All of our sites had apparently advanced to or through the self-thinning (Drew and Flewelling 1979) or stem-exclusion (Oliver and Larson 1990) phase (Zenner et

al. 1998). However, the effects of this stage on the undergrowth were probably more intense in the relatively dense, hemlock-dominated stands than in the stands dominated by Douglas-fir, with their relatively open canopies. In extreme cases, all herbaceous plants may die under dense stands of western hemlock (Alaback 1982). Another sampling of these stands in the future, when the undergrowth has recovered further from canopy closure, might result in different interpretations of relationships between remnant trees and undergrowth than those offered here; the longevity of shade-tolerant herbs during the stem-exclusion stage is not well-understood (North et al. 1996).

Answers to questions about the influence of remnant, overstory trees on undergrowth communities are important but difficult to find, because these new forest management techniques are only now being implemented (Aubry et al. 1999; Halpern et al. 1999). Retrospective studies such as this can, however, help us to understand and predict potential long-term consequences of these techniques (Swanson and Franklin 1992). Long-term consequences may differ substantially from those that would be predicted based on study over shorter time periods. For example, a study that assessed initial (16 month) responses of understory plant diversity to a green-tree retention harvest found that herb and shrub species richness and evenness were significantly higher in the green-tree retention cut than in an adjacent clearcut and an intact 65-yr old forest (North et al. 1996). Further, cover by shade-tolerant plants was greater in the retention cut than in the clearcut. Our results suggest that such early differences in undergrowth between green-tree retention cuts, clearcuts, and intact forests might not persist. Studies of species' attributes likely to affect survival, re-establishment, and reproduction under alternative forest management scenarios are needed, as are long-term monitoring studies to follow consequences of such management practices (see Halpern et al. 1999).

Limitations in the analogy between our natural, two-tiered stands and those that will result from timber harvesting with green-tree retention must be borne in mind. For example, harvesting will not always be followed by burning, while the regeneration in our sites was initiated after fires. It is unclear to what extent the absence of

fire in managed stands will affect their successional trajectories compared to those followed in natural, fire-origin stands. How will planting of trees in particular densities and species mixtures in managed stands affect undergrowth compared to effects apparently associated with natural regeneration, as occurred on our sites? Will the spatial pattern of green-tree retention (aggregated versus clumped, for example) affect responses in the undergrowth? Despite these limitations, our study does provide some insights for forest managers and ecologists on potential effects of green-tree retention on undergrowth communities.

Our results underscore the importance of defining management goals. We suggest that if the goal is simply to foster high vascular species richness and cover, then stands with relatively open canopies, higher percentages of Douglas-fir, and fewer remnant trees might be favored. However, if goals include provision of habitats suitable for a wide range of plant communities, then retention of variable numbers of remnant trees may be desirable. The potential importance of retaining remnant trees is substantiated by a parallel study (conducted in the same plots as those used here), which reported that biomass of alectorioid and cyanolichens, both often associated with older forests, was greater in plots with remnant trees than in those lacking remnants at low elevations (Peck and McCune 1998). Our results also reinforce the importance of CWD as an important habitat component.

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