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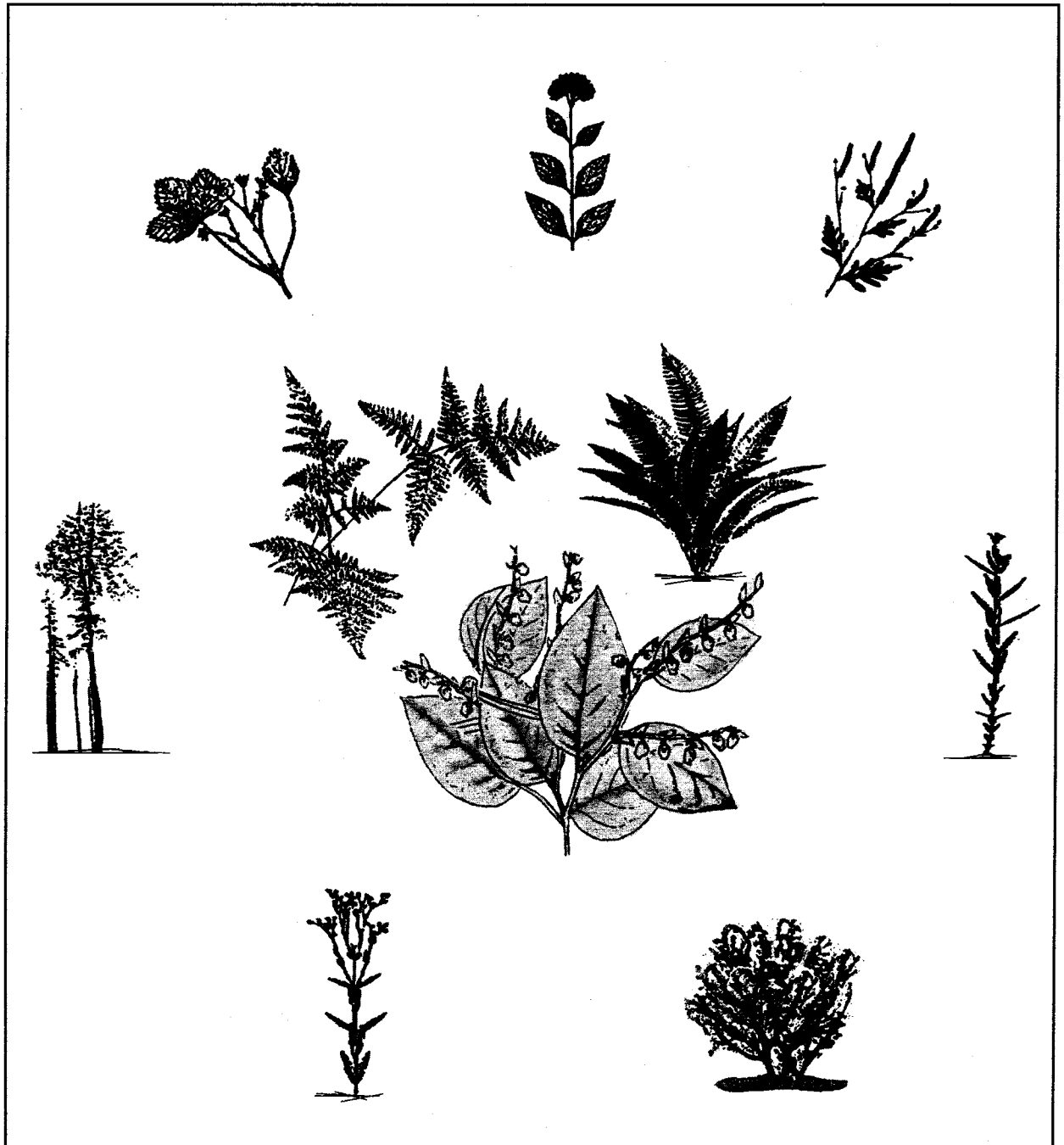
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Effects of Forest Management on Understory and Overstory Vegetation: A Retrospective Study

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Abstract

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Management for wood production through long rotations and thinning (MT) and management for biodiversity through legacy retention, protection, and no subsequent manipulation (ML) are two approaches to managing second-growth forests in the Pacific Northwest. We describe how these two strategies have affected tree size, tree density, and native and exotic vascular plant diversity and abundance.

Keywords: Diversity, second-growth, Douglas-fir, *Pseudotsuga menziesii*, understory vegetation, species richness, forest development, thinning, legacies.

Summary

We examined understory and overstory vegetation in two proximate tracts of Douglas-fir (*Pseudotsuga menziesii*) forests with divergent management histories. The two tracts regenerated from harvest of old growth in the 1920s (MT) and 1930s (ML): MT subsequently was thinned twice and contained little coarse woody debris (CWD) and few snags; ML received no management after harvest with retention of some live and dead trees and contained moderate CWD, snags, and residual trees. We compared tree density, tree size, tree size-class diversity, understory species richness and abundance, and Shannon index of vascular plant diversity (H') in the two tracts. We performed a Bray-Curtis ordination to more fully illustrate variation in the understory communities.

The MT tract had fewer and larger trees and had higher tree size-class diversity than ML. Species richness and diversity were significantly higher in MT than in ML. Total vascular plant species richness in MT (94 species) was twice that in the more densely stocked ML (47 species). Average total understory cover was much higher in MT (88 percent) than in ML (34 percent). Both tracts lacked shade-tolerant understory trees and had minimal foliage height diversity. Numerous exotic species were found in MT, but these were virtually absent in ML.

Plant communities in the two tracts differed qualitatively and quantitatively, and current conditions will differentially influence plant composition and structure after future silvicultural entries. Forest processes such as crown differentiation, decadence, and understory development are amenable to management and suggest hypotheses about development of late-seral attributes in such stands. Due to lack of legacy trees and CWD in MT, crown differentiation will occur solely within the current cohort; CWD enhancement by tree felling would reduce stand density to unacceptably low levels. Future thinnings in MT may result in further increase of already-dominant clonal understory species that, along with lack of CWD as nurse logs, could delay establishment of a shade-tolerant understory and retard development of a diverse foliage height profile. In ML, crown differentiation is less than in MT but is augmented by residual trees. The amount of CWD in ML is greater than in MT; unlike MT, live-tree densities in ML permit CWD augmentation while retaining high stocking levels. After future thinnings, shade-tolerant trees, shrubs, and herbs should be more likely to establish in ML because of less competition and more CWD as nurse logs, thereby resulting in a more rapid increase in foliage height diversity and relatively more seedling than clonal expansion in the understory in ML than in MT. Late-seral

development in both tracts will be hindered by absence of shade-tolerant understory trees. Future thinnings will increase vascular plant species richness in both tracts, but many new species will be exotics. Major challenges in forest management include minimizing spread and impact of exotics, fostering late-sera) conditions in managed stands, and, above all, ensuring continuity of natural legacy-perpetuating processes and systems.

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Introduction

A great deal of attention has been paid to management of biological diversity in forested ecosystems of the Pacific Northwest and elsewhere (see papers in Gilliam and Roberts 1995). Emerging and related concerns are the homogenization of the world's floras and the threat to native species posed by exotic species that spread in response to human activities (Soule 1990; United States Congress, Office of Technology Assessment 1993; Wilcove and others 1998; Wisser and others 1998). Recent shifts in thinking about forest management coincide with increases in human population, decreases in timber harvests, and concerns about sustainability of managed forests (Carey 1998; Kohm and Franklin 1997; McGinnis and others 1996, 1997; Perry 1998) and are manifested by a divergent paradigm of active, adaptive, and site-specific management versus passive, protective management in efforts to hasten development of late-seral forest attributes and to increase native biodiversity (Carey 1998, Carey and Curtis 1996). Though certainty of outcome is impossible, combining knowledge of past management practices, contemporary manipulations, and previously accumulated research with retrospective and experimental investigations can increase the likelihood of meeting specific objectives while retaining a wide range of future options (Carey and others 1996a, 1996b, 1999b; Spies 1997; Walters and Holling 1990).

Numerous silvicultural tools are available to forest managers and include a wide variety of harvest systems, retention levels and patterns, regeneration methods, and rotation lengths that can be applied to meet site-specific objectives (Carey and others 1996b, Curtis 1997, DeBell and others 1997, Franklin and others 1997, McComb and others 1993). However, information relating past harvest practices to current understory and overstory conditions in older, managed forests is lacking (Halpern and Spies 1995; North and others 1996; Spies 1991, 1997). Such information is needed to better predict the effects of future manipulations on biodiversity, stand development, and long-term ecosystem structure and function.

Many low- to mid-elevation forested landscapes of western Washington and Oregon currently are dominated by young (< 80 years old), even-aged stands of a single tree species (usually Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco]). Such landscapes resulted primarily from clearcuts and have created negative public perceptions as well as scientific concerns about forest management (Curtis 1997, Curtis and Carey 1996). Past management often simplified forest composition and structure. Clearcutting, burning, planting of genetically uniform trees, application of herbicides, and precommercial thinning have diverted many ecosystem resources to rapid growth of timber and fiber; fewer resources were intentionally directed to maintenance of biodiversity (Carey and others 1996a, 1996b, 1999a; Perry 1998). Nonetheless, because such young, managed stands are so widespread, they may provide the greatest short-term opportunity for management and study as they develop. With appropriate and well-designed management intervention, differentiation in such stands can probably be expedited and directed to meet a variety of specific late-successional goals (Carey and others 1996a, 1996b; Curtis and others 1998; DeBell and others 1997). With or without management, these stands are the raw material from which many old forests of the future likely will develop.

Simulation modeling (Carey and others 1996a, Carey and Curtis 1996, Lippke and others 1996), early results from young-stand manipulation experiments (Carey and others 1996b, 1999b), and retrospective studies (Carey 1995, Carey and Johnson 1995, Carey and others 1996b, 1999b) indicate that compared to no management,

management could enhance biodiversity while hastening development of late-seral forest conditions. These studies suggest that integrated strategies which include legacy retention, alternative harvest and thinning regimes, and direct habitat improvement may be necessary to enhance native biodiversity, minimize the spread of exotic species, accelerate development of late-seral conditions, and restore balance to landscape-level stand-age distributions, while providing high-quality wood, increased levels of carbon sequestration, and increased employment (Carey and Curtis 1996; Carey and others 1996a, 1999b; Curtis and Carey 1996; Lippke and others 1996).

Several replicated silvicultural experiments in developing late-seral conditions in managed stands are underway in the Pacific Northwest but are in the early phases of their response monitoring¹ (Aubry and others 1999; Carey and others 1999b). Though there is little published information on the efficacy of silvicultural interventions in accelerating forest development in young stands (Hayes and others 1997, McComb and others 1993), preliminary data suggest that thinning can stimulate understory development and the establishment and growth of shrubs and conifer seedlings, increase diversity of understory vascular plants (Bailey and Tappeiner 1998; Carey and others 1996a, 1999b; North and others 1996) and hypogeous ectomycorrhizal fungi (Colgan 1997, Colgan and others 1999), and increase abundance of some forest floor small mammals (Carey and others 1996b).

Our purpose in this paper is to consider the effects at ≥ 55 years in stand age of two commonly proposed management strategies on tree size, density, and size-class diversity and on current plant species diversity and abundance in forests of financial rotation-age, and to reflect on how past management and current conditions may affect the development of native biodiversity and late-seral attributes and the establishment of exotic species after future silvicultural entries. Our data are baseline information for a 20-year silvicultural experiment subsequently imposed on the stands.

We identified two proximate forested tracts of similar age, substrate, topography, and composition, but markedly different management histories, that illustrate commonly occurring end-of-rotation conditions in the Pacific Northwest; both were past the common age at harvest for industrial forests and approaching a historically common age of harvest on public lands. The tracts differed in amount of legacy tree, snag, and coarse woody debris (CWD) retention from the previous harvest and in subsequent tree density control through thinning. We contrast the results of the two strategies by tree size, density, and size-class diversity and plant species abundance and diversity at four spatial scales: plot, stand, block, and track levels. Plots represent within-stand variation owing to stochasticity in stand initiation and development. Among-stand variation incorporates minor effects of slope, aspect, and stochasticity in application of management. Blocks represent large-scale site differences and differences that arise as a result of timing of treatments. Between-tract variation should represent effects of management strategy.

¹Harrington, C.; Carey, A. Manuscript in preparation. Authors may be contacted at the Forestry Sciences Laboratory, Olympia, WA.

Study Area Site Selection

After a regional search for retrospective study sites in western Washington and Oregon (Thomas and others 1993), we further inspected potential sites to determine suitability as to forest homogeneity, sufficient size to allow replication of treatments, and histories representative of currently recommended strategies of legacy retention and management with thinnings. We located such an area and interested managers at the Fort Lewis Military Reservation in Thurston County, Washington. The area is part of about 6000 ha of 40- to 70-year-old second-growth Douglas-fir stands, thus allaying concerns about the potentially confounding effects that could arise due to close proximity to older forests. Within the 6000 ha were two large tracts that had markedly different management histories. Both tracts contained two management units, each large enough to accommodate four 13-ha stands. The two management units per tract, although sharing general management history, were potentially different in site, aspect, slope, time of implementation, initial forest conditions, and implementation by different operators. Differences among the four management units, except those distinguishing the two tracts, appeared small.

Physical Environment

Fort Lewis Military Reservation is in the southern Puget Trough Physiographic Province (Franklin and Dyrness 1973). Present-day land forms and soils were deposited during the recession of the Puget Lobe of the Vashon Stade of the continental glacier 13,000 to 15,000 years ago (Kruckeberg 1991). Topographic relief is moderate to rolling with occasional steeper areas surrounding small kettle depressions; topography is typical of the south-central portion of the Puget glacial lobe. The study sites are at latitude 46° 55' 42" to 46° 59' 00" N. and longitude 122° 40' to 42' E. The elevation ranged from 120 to 165 m, slopes were moderate, and aspect was variable, though tending southeast (table 1). No perennial creeks, ponds, or wetlands were in the study area. The sites were on glacial uplands, terminal moraines, and glacial till and outwash plains where root penetration into the soil is moderately shallow and drainage is classified as somewhat excessive. Soils are coarse-textured gravelly and gravelly-sandy loams of the Everett and Tenino soil series (Pringle 1990). Annual precipitation for the Fort Lewis area is 800 to 900 mm with only 10 to 15 percent of the annual precipitation falling during the peak growing months of June through September (Pringle 1990).

Vegetation and Management History

The two tracts, about 3 km apart, have experienced substantially different management, both at the time of original harvest and subsequently (table 1). Both tracts resemble the *Pseudotsuga menziesii*/*Holodiscus discolor* association of the *Tsuga heterophylla* zone of Franklin and Dyrness (1973) or the *Pseudotsuga menziesii*/*Gaultheria shallon* association of Henderson and others (1989), though Douglas-fir forests of the Puget lowlands have not been studied in great detail and may eventually be assigned to their own separate vegetative associations (Franklin and Dyrness 1973). Both tracts were even-aged Douglas-fir forests that had established by natural seedfall. Neither tract had experienced natural or prescribed fire since harvest, and we did not attribute current differences to fire. The tracts thus illustrate two possible developmental pathways and two potential endpoints in a management cycle of about 60 years, while also representing two conditions where future management to enhance biodiversity and develop late-seral conditions could occur. We refer to the two strategies as management with thinnings (MT) and management with legacies (ML).

Table 1-Characteristics of forests managed with legacies versus managed with thinning in the Puget Trough of Washington, 1991-92

Characteristic	Managed with legacies	Managed with thinning
Elevation (m)	135-165	120-150
Average slope in % (median)	17 (15)	7 (5)
Range (%)	0-55	0-28
Aspect (average in degrees)	Variable: tending SE (149°)	Variable: tending SE (131°)
Number of plots (area)	120 (25 m ²)	120 (25 m ²)
Harvest date, method, and coarse woody debris (CWD) treatment	1935-39 cut with some tree, snag, and CWD retention.	1923-27 clear cut with minimal CWD retention.
Regeneration method	Natural seeding	Natural seeding
Subsequent management	None	Commercially thinned in 1970s and late 1980s
Douglas-fir in overstory (%)	99+	95-98
Soils	Tenino series: moderately deep, well-drained soils on terminal moraines; formed in glacial till over glacial outwash	Everett series: very deep, excessively drained soils on glacial terraces and moraines; formed in glacial outwash
50-yr site index (m)/site class (King 1966) ^a	36.0-36.3/low II	39.6-40.5/high II
CWD % cover (mean ± 1 SE) ^a	7.4 ± 0.5	2.5 ± 0.2
Residual live trees (mean/ha ± 1 SE) ^a	2.7 ± 0.8	0.4 ± 0.4
Residual snags (mean/ha ± 1 SE) ^a	3.5 ± 0.7	0.0 ± 0.1

^aData from Carey and others (1999b).

Old growth in the two management units in the MT tract was clearcut in 1923-27; the subsequent regeneration was commercially thinned in the early 1970s and again in the late 1980s. During harvests in the two MT units, live and recently dead trees were removed and slash was piled and burned; few snags or residual trees, and little cover of CWD, remained in 1992 (table 1). At the time of our sampling, MT (fig. 1) was dominated by well-spaced Douglas-fir 55 to 65 cm in diameter at breast height (d.b.h.) with small numbers of black cottonwood (*Populus balsamifera* ssp. *trichocarpa* [Torr. & Gray] Brayshaw) and red alder (*Alnus rubra* Bong.). Based on 50-year site curves for Douglas-fir from King (1966), the MT tract, with stand site indices of 39.6 to 40.5 m, was site class II. The vascular plant understory was well developed and moss cover was low to moderate (Carey and others 1999b).

In contrast, old growth in the two management units in ML was cut in 1935-39 and was not further manipulated; moderate CWD and numerous legacy trees and snags remained in 1992 (table 1). In 1992, ML (fig. 2) was a closed-canopy forest dominated by closely spaced Douglas-fir 30 to 45 cm d.b.h., with a few western redcedars (*Thuja plicata* Donn ex D. Don) and Pacific yews (*Taxus brevifolia* Nutt.). Trees killed by suppression and trees with small crowns were abundant. Based on 50-year site curves for Douglas-fir from King (1966), the MT tract, with stand site indices of 36.0 to 36.3 m, also was site class II. Understory vascular vegetation in ML was sparse and forest floor mosses were abundant (Carey and others 1999b).



Figure 1-Typical understory vegetation and tree size and density conditions in the managed-with-thinning tract, summer 1992.



Figure 2-Typical understory vegetation and tree size and density conditions in the managed-with-legacies tract, summer 1992.

Methods

Sampling Design

Four 13-ha stands were located in each of the four management units (hereafter referred to as blocks) in each of the two tracts (Carey and others 1999b). The two ML blocks were Star (stands 101-104) and Stellar (stands 201-204); the two MT blocks were Farley (stands 301-304) and Hill (stands 401-404). Stand size was chosen to be as large as possible but was constrained by topography, changes in vegetation, and past management activities, including roads; 13 ha was the maximum contiguous area of homogeneous vegetation we could regularly circumscribe. An 8 by 8 sampling grid with 40-m spacing between grid points (e.g., 280 by 280 m), encompassing 7.8 ha, was surveyed in the center of each stand. Though management had been applied to blocks that were relatively homogeneous, there was within- and among- block variation in time, space, and implementation of management. We expected to capture much of the variation due to site and management differences with the four stands in each block and the two blocks in each tract. The four stands per block were selected as distinct segments of each block, and we expected greater similarity within than among blocks. We also used replication of plots within stands to assess within- and among-stand variation and block-level variability. The two blocks per tract allowed us to evaluate interblock variation that may have been caused by spatio-temporal and treatment implementation differences within the same general management strategy.

Our retrospective investigation required the use of circumscribed blocks in which the same management had been applied throughout. Within each block, the four stands were, by necessity, placed to optimize use of available space, thus assuring even, complete, and representative coverage across the blocks. Such coverage was further ensured at the stand level by sample plots being systematically located in each stand. We recognize that our sampling design lacked random assignment of treatments and disallows formal hypothesis testing, thus we used statistical analyses and tests primarily for exploratory purposes and to describe the variation encountered in our data set.

Field Sampling

Overstory and understory vegetation was sampled at or near 15 systematically located interior grid points within each of the 16 stands (240 points total), with the six interior north-south grid lines alternately containing two or three sample points. Sample points were ≥ 56 m apart. Overstory trees were measured during fall and winter 1991-92; understory vegetation was measured from June through August 1992. At each sample point, a variable-radius prism plot tally (basal area factor 30 [English]) was made. We recorded tree species and d.b.h. in centimeters for each tallied tree, measuring trees ≥ 5 cm d.b.h. For the two largest, current-stand, Douglas-fir trees per prism plot (dominants), d.b.h., height, height to live crown, and crown width were recorded. Using the volume of a cone as an idealized approximation, we derived crown volume estimates of the dominant trees based on crown width as the diameter of the cone base, and tree height minus height to live crown as the cone height.

Understory vegetation was recorded from a 2.82-m radius circular plot (25-m²) offset 5 m at a random bearing from each overstory sampling point. On understory plots we recorded percentage of cover by species, defining cover as the portion of ground covered by the vertical projection of the vegetation onto a horizontal plane. For our analysis, we grouped plants into the following life forms or functional groups: (1) tall shrubs and understory tree species typically ≥ 2 m in height but below the forest canopy, (2) low shrub species 0.5-2 m in height, (3) trailing shrubs and vine species < 0.5 m in height or scandent on other plants, (4) herbs and subshrubs, (5) ferns, (6) graminoids (members of the families Poaceae, Cyperaceae, and Juncaceae), and (7) forest-floor mosses.

Vascular plant nomenclature follows Kartesz (1994), and vascular plant species concepts and identifications are based on Hitchcock and Cronquist (1973); moss nomenclature follows Schofield (1992). Vascular plant acronyms are from the PLANTS database (USDA 1997). Vascular plant species origins (e.g., native or nonnative), autecology, and disturbance responses were based on regional guides (Hickman 1993, Hitchcock and Cronquist 1973, Klinka and others 1989, Pojar and MacKinnon 1994) and previously published studies (Dyrness 1973; Halpern 1988, 1989; Halpern and Spies 1995; Long 1977; Schoonmaker and McKee 1988; Spies 1991; Spies and Franklin 1991).

Analysis

Overstory tree-size diversity (Shannon index) was examined based on the abundance of trees in each of nine d.b.h. classes: >5-19.9 cm; ≥20-29.9 cm; ≥30-39.9 cm; ≥40-49.9 cm; ≥50-59.9 cm; ≥60-69.9 cm; ≥70-79.9 cm; >80-89.9 cm; and ≥90 cm. Measured trees were used to compute average density (for trees >15 cm d.b.h.), d.b.h., and height by stand, block, and tract. Understory vascular plant species diversity was calculated based on percentage of cover (as the measure of abundance) for each species. For understory vascular plant species, we examined species richness (the average number of species per plot), and the Shannon index of diversity which incorporates both species richness and abundance. The Shannon diversity index (H') is calculated as:

$$H' = -\sum_{i=1}^m p_i \ln p_i$$

where p_i is the proportional abundance of the i th of m groups and \ln is the natural logarithm (Magurran 1988). For the overstory, p_i is the number of trees in the i th size class divided by the sum of all trees in the m size classes in the group under consideration (e.g., stand, block, tract). For understory species, p_i is the ratio of the cover of species i to the summed cover of all m species in the group under consideration. We examined understory species richness and diversity and tree size-class diversity at the plot, stand, block, and tract levels.

To estimate species richness and to illustrate the range of variability among stands, blocks, and tracts, we generated species-area curves. To improve the precision of our estimates of stand-, block-, and tract-level species richness, we used the first-order jack-knife estimator (JN) for species richness:

$$JN = S + r1(n - 1)/n$$

where S = the number of species found in n plots, and $r1$ = the number of species found in only one plot (Heltshel and Forrester 1983, Palmer 1990).

To illustrate major gradients of plot-level variation within and among blocks and tracts, we performed a Bray-Curtis (BC) ordination. We chose BC due to its ease of ecological interpretation and its specific relevance to phytosociological data (Beals 1984). We used the Sorenson distance measure (in the form of percentage of dissimilarity or PD) to generate the ordination distance matrix and we used the variance-regression method to select reference points for the ordination axes (Beals 1984, McCune and Mefford 1997). The Sorenson distance (PD) between two plots is:

$$PD_{ij} = \frac{\sum_{k=1}^m |X_{ik} + X_{jk}|}{\sum_{k=1}^m (X_{ik} + X_{jk})}$$

where PD_{ij} = the Sorenson distance between plots i and j , m = the number of species, x_{jk} = the abundance (percentage of cover) of the k th species in plot i , and x_{ik} = the abundance (percentage of cover) of the k th species in plot j (Greig-Smith 1983, McCune and Mefford 1997). We used raw quantitative data (percentage of cover) on all vascular plant species (e.g., without transformation or relativization) from all 240 plots for the final ordination data set, calculating the first three ordination axes. The amount of variance explained by each axis was computed by subtracting the ratio of the sum of squares of the residual distance matrix to the sum of squares of the original distance matrix from one and expressed as a percentage (McCune and Mefford 1997). For frequently encountered species and for variables such as total understory cover, total moss cover, and tree density, we examined the correlation (Pearson's product-moment correlation coefficient, r) between the variable or species and each of the first three ordination axes (McCune and Mefford 1997). Using $n = 240$ ($df = 238$) to describe variation across the full plot-by-species data set, the critical value (two-tailed) of r at $\alpha = 0.01$ was 0.167 (Zar 1984). This value was used to test whether correlations differed significantly from zero.

To illustrate within- and among-stand patterns of abundance for dominant species, species groups, and for tree attributes, we generated 95-percent confidence interval graphs of the attributes for the 16 stands based on the 15 plots per stand. In an exploratory analysis, we examined differences between 2 or >2 groups with parametric t-tests or one-way analysis of variance (ANOVA), respectively, where assumptions of homoscedasticity and normality were met or were able to be met through data transformations. We used the Levene statistic (Norusis 1993) at $\alpha = 0.05$ to test for homogeneity of variance. Because of the small sample size ($n = 4$ stand means per block) used in the ANOVA groups, normality of distribution for some blocks was difficult to ascertain though such distributions approach normality under the central limit theorem. We also confirmed that assumptions were met for the eight stand means per tract. We performed block-wise one-way ANOVA to detect differences among blocks and used the Tukey's *B post hoc* test (at $\alpha = 0.05$) to identify which blocks differed. Nested ANOVAs based on plot-level data from stands within blocks within tracts were characterized by inequality of variance and lacked normal distributions that we could not correct with transformations. Nonetheless, nested ANOVAs supported our one-way ANOVAs based on stand means and demonstrated the plot- and stand-level variation that we present graphically. Though we assumed, *a priori*, that the overstory and understory would differ between ML and MT, we used ANOVAs and *post hoc* tests to assess among-block variation within and between tracts and to relate present conditions to previous management. Between-tract t-tests were performed by using the eight stand means per tract. Where data were intractable to transformation, as in testing for between-tract differences in individual species abundances and for testing for tract-level effects on frequency of individual species occurrence, we used the nonparametric Mann-Whitney U-test, and X^2 test, respectively (Norusis 1993, Zar 1984).

We calculated the indicator value (IV) for species with high frequency or abundance, or both, to identify species characterizing one or the other management strategy (Dufrene and Legendre 1997). The species IV, in percent, is its relative abundance times its relative frequency. Relative abundance is the average abundance of a species in a group of plots divided by its average abundance in all plots. Relative frequency is the percentage of the plots within a group in which a species is present (Dufrene and Legendre 1997, McCune and Mefford 1997). We then evaluated the statistical significance of the maximum IV (IV-max) for the two tracts by using a Monte Carlo method employing 1,000 permutations of the data where the resultant P-value was the proportion of permutations in which the IV-max from the randomized data set equaled or exceeded the observed IV-max. Thus, a significant IV-max indicates a species that is characteristic of a tract and that the indicator value is larger than would be expected by chance in the permutation set (Dufrene and Legendre 1997, McCune and Mefford 1997). All calculations were made with the SPSS statistical program release 6.1.2 (Norusis 1993) or with PC-ORD, a program for multivariate analysis of ecological data (McCune and Mefford 1997).

Results
Overstory Composition, Density, Size, and Size-Class Diversity

Of 1,441 live trees sampled in the two tracts, 98 percent were Douglas-fir. In ML (n = 777) 99 percent were Douglas-fir; the remaining 1 percent were western red-cedar and western hemlock. In MT (n = 664) 96 percent were Douglas fir; the remaining 4 percent were red alder, bigleaf maple, black cottonwood, and western hemlock.

Within- and among-stand variability in mean densities was higher in ML than in MT (fig. 3A). Tree density was greater in ML blocks than in MT ($df= 3, 12; F= 13.9; P < 0.01$); blocks differed significantly between, but not within, tracts. Tree density in ML was significantly greater than in MT (fig. 3B).

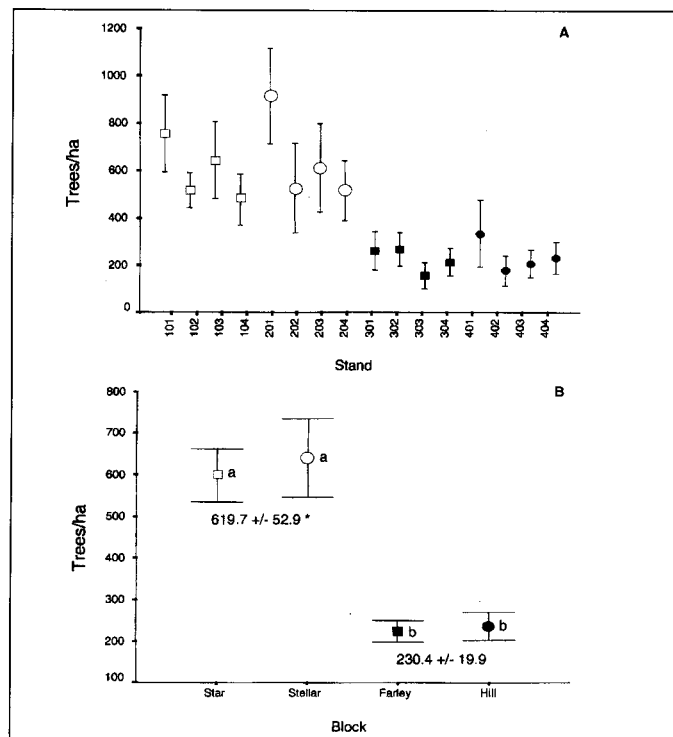


Figure 3—Mean tree density ($\pm 95\%$ CI) in trees/ha by stand (A); and mean of stand means (± 1 SE) by block (B) in forests managed with legacies (stands 101-204; Star and Stellar blocks) and managed with thinning (stands 301-404; Farley and Hill blocks), winter 1991-92. Symbols in (B) with different letters differed significantly (one-way ANOVA; Tukey's B *post hoc* test, $p = 0.05$, Norušis 1993). Numerals below symbols in (B) are tract-level tree density means ± 1 SE. The asterisk indicates a significant difference between tracts based on 8 stand means per tract (t-test, $df = 14$, $p < 0.01$). N = 15 plots per stand (A); n = 4 stand means per block (B). Star block and stands (\square); Stellar block and stands (o); Farley block and stands (\blacksquare); Hill block and stands (\bullet).

Within- and among-stand variability in d.b.h. was less in ML than in MT (fig. 4A). Blocks differed in mean d.b.h. ($df = 3, 12; F = 25.0; P < 0.01$) with blocks differing significantly between but not within tracts. Mean d.b.h. in ML (33.9 ± 1.2 cm) was significantly less than in MT (52.7 ± 1.8 cm) ($df = 14, t = 8.7, P < 0.01$). Were a constant growth rate for ML trees used, an additional 12 years (the age difference between tracts) would result in 7.4-cm increase in d.b.h., or 39 percent of the observed between-tract difference in d.b.h. Tree size-class diversity (H') was significantly greater in MT than in ML (fig. 4B).

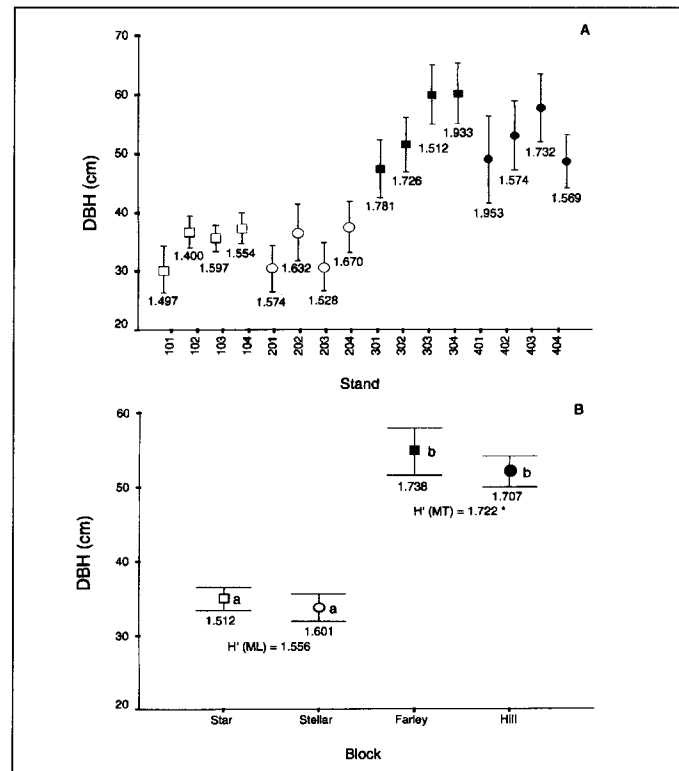


Figure 4—Mean tree dbh ($\pm 95\%$ CI) (symbols) and Shannon-Weiner diversity index (H') of tree size (numerals) by stand (A); and means of stand means (± 1 SE) by block (B) in forests managed with legacies (stands 101-204; Star and Stellar blocks) and managed with thinning (stands 301-404; Farley and Hill blocks), winter 1991-92. Symbols in (B) with different letters differed significantly in d.b.h. (one-way ANOVA based on 4 stand means per block; Tukey's B *post hoc* test, $p = 0.05$, Norušis 1993). Forest-level H' values are also shown in (B). The asterisk indicates a significant difference in H' between the two tracts based on 8 stand means per tract ($df = 14, t = 6.9, P < 0.01$). $N = 74$ to 116 trees per stand (A); $n = 4$ stand means per block (B). Star block and stands (\square); Stellar block and stands (\circ); Farley block and stands (\blacksquare); Hill block and stands (\bullet).

There were significant differences among the four blocks in dominant tree d.b.h., height, crown diameter, and crown volume but not in height-to-live-crown (table 2). Again, blocks differed significantly between but not within tracts. Dominant trees in MT were larger in diameter, taller, had wider crowns, greater heights-to-live-crown, and greater crown volume (table 2). The live-crown ratio of the dominant trees averaged 50 percent in MT and 44 percent in ML. The ratio of the d.b.h. of dominants to the d.b.h. of all prism plot trees was 1.30 ± 0.02 in ML vs. 1.18 ± 0.02 in MT.

There were significant differences among blocks in average number of species per plot, average total species per stand, and first-order jack-knife species per stand; in all cases *post hoc* tests showed that blocks differed significantly between but not within tracts (table 3). Ranking of mean number of species per plot in all 16 stands showed the MT stands to rank 1-8 and the ML stands to rank 9-16. Across all 240 plots, species richness per plot ranged from 3-15 in ML and from 5-29 in MT Understory species accumulated at distinctly lower rates in ML than in MT (fig. 5). Species

Understory Species Richness and Diversity

Table 2-Block- and tract-level dominant tree attributes for forests managed with legacies (ML) and managed with thinning (MT) with block-wise ANOVAs and between-tract t-tests^a

Tree attribute	Block ^b				Block-wise ANOVA			Tract ^c	
	Star	Stellar	Farley	Hill	F	df	P	ML	MT
Dbh (cm)	43.4±1.7 ¹ (38.6-46.5)	43.1±2.3 ¹ (37.0-46.8)	63.2±2.9 ² (57.7-70.6)	57.8±3.0 ² (52.4-65.7)	16.3	3,12	<0.001	43.3±1.3 (37.0-46.8)	60.5±2.2 (52.4-70.6)
Height (m)	33.2±0.8 ¹ (31.5-35.0)	34.1±1.2 ¹ (31.8-37.3)	42.3±0.7 ² (41.3-44.5)	41.1±0.9 ² (38.6-43.2)	24.8	3,12	<0.001	33.7±0.7 (20-30)	41.7±0.6 (40-65)
Crown diameter (m)	6.5±0.2 ^{1,2} (6.1-7.0)	6.2±0.4 ¹ (5.2-7.0)	8.8±0.5 ³ (7.5-9.8)	7.9±0.5 ^{2,3} (6.9-9.1)	9.4	3,12	0.002	6.4±0.2 (5.2-7.0)	8.4±0.4 (6.9-9.8)
Height-to-live-crown (m)	18.5±0.9 ¹ (16.5-20.7)	18.7±1.0 ¹ (16.4-20.8)	20.6±1.3 ¹ (17.9-23.6)	21.4±0.6 ¹ (19.9-22.7)	2.2	3,12	0.145	18.6±0.6 (16.4-20.8)	21.0±0.7 (17.9-23.6)
Crown volume (m ³)	185.9±17.0 ¹ (145-225)	183.2±26.7 ¹ (110-237)	515.3±91.3 ² (321-761)	371.2±49.5 ² (269-483)	8.7 ^d	3,12	0.002	184.5±14.7 (110-237)	443.2±55.3^d (269-761)

^a Star and Stellar blocks are in the ML tract; Farley and Hill blocks are in the MT tract. Block and tract data are means ± 1 SE with ranges in parentheses.

^b For a variable, blocks with different numeral superscripts differed significantly; those with the same numerals did not differ significantly (Tukey's B *post hoc* test, $p = 0.05$, Norušis 1993). N = 4 stand means per block.

^c Bold numerals indicate a significant difference between tracts for that attribute ($df = 14$, t-test, $P < 0.05$). N = 8 stand means per tract.

^d ANOVA and t-test results for crown volume were based on natural log transformed values.

Table 3-Average species richness per plot, total species per stand, 1st-order jack-knife estimate of total species per stand, and Shannon-Weiner Diversity Index for forests managed with legacies (ML) and managed with thinning (MT), with block-wise ANOVA and between-tract t-tests^a

Attribute	Block ^b				Block-wise ANOVA			Tract ^c	
	Star	Stellar	Farley	Hill	F	df	P	ML	MT
Mean species/plot	8.1±0.9 ¹ (6.8-10.5)	9.1±0.6 ¹ (7.5-10.1)	15.1±0.7 ² (14.1-17.0)	15.1±1.3 ² (12.8-17.5)	17.7	3,12	<0.001	8.6±0.5 (6.8-10.5)	15.1±0.7 (12.8-17.5)
Mean total species/stand	24.5±2.2 ¹ (20-30)	25.5±1.0 ¹ (23-28)	50.0±2.9 ² (47-54)	50.5±5.7 ² (40-65)	28.3 ^d	3,12	<0.001	25.0±1.1 (20-30)	50.2±2.7 (40-65)
1st-order jack-knife estimate of total species/stand	32.0±3.0 ¹ (26.5-40.3)	32.1±0.3 ¹ (31.4-32.7)	61.7±1.8 ² (58.3-66.1)	66.9±7.8 ² (49.3-86.5)	28.1 ^d	3,12	<0.001	32.0±1.4 (26.5-40.3)	64.3±3.8 (49.3-86.5)
Shannon-Weiner Diversity Index (H') ^e	1.40±0.16 (1.08-1.83)	1.49±0.09 (1.33-1.71)	1.67±0.04 (1.61-1.79)	1.67±0.09 (1.46-1.87)				1.45±0.09 (1.08-1.83)	<u>1.67±0.05</u> (1.46-1.87)

^a Star and Stellar blocks are in the ML tract; Farley and Hill blocks are in the MT tract. Data are means ± 1 SE with ranges in parentheses.

^b For attributes with ANOVA results shown, blocks with different numeral superscripts differed significantly; those with the same numerals did not differ significantly (Tukey's B *post hoc* test, $p = 0.05$, Norušis 1993). N = 4 stand means per block.

^c Between-tract differences were significant at $p < 0.01$ (bold), or $p < 0.05$ (underlined); t-test, $df = 14$.

^d ANOVAs for these attributes were based on natural log transformed values.

^e Only means and ranges are presented for block-level H'. ANOVA was not performed for H'.

richness per stand, block, and tract were substantially less in ML, as was the among-stand, within-tract variation (fig. 5A). Jack-knife estimates of species richness were 26 to 40 species per stand in ML and 49 to 86 species per stand in MT Species-area curves for the two blocks in each tract were nearly coincident (fig. 5B).

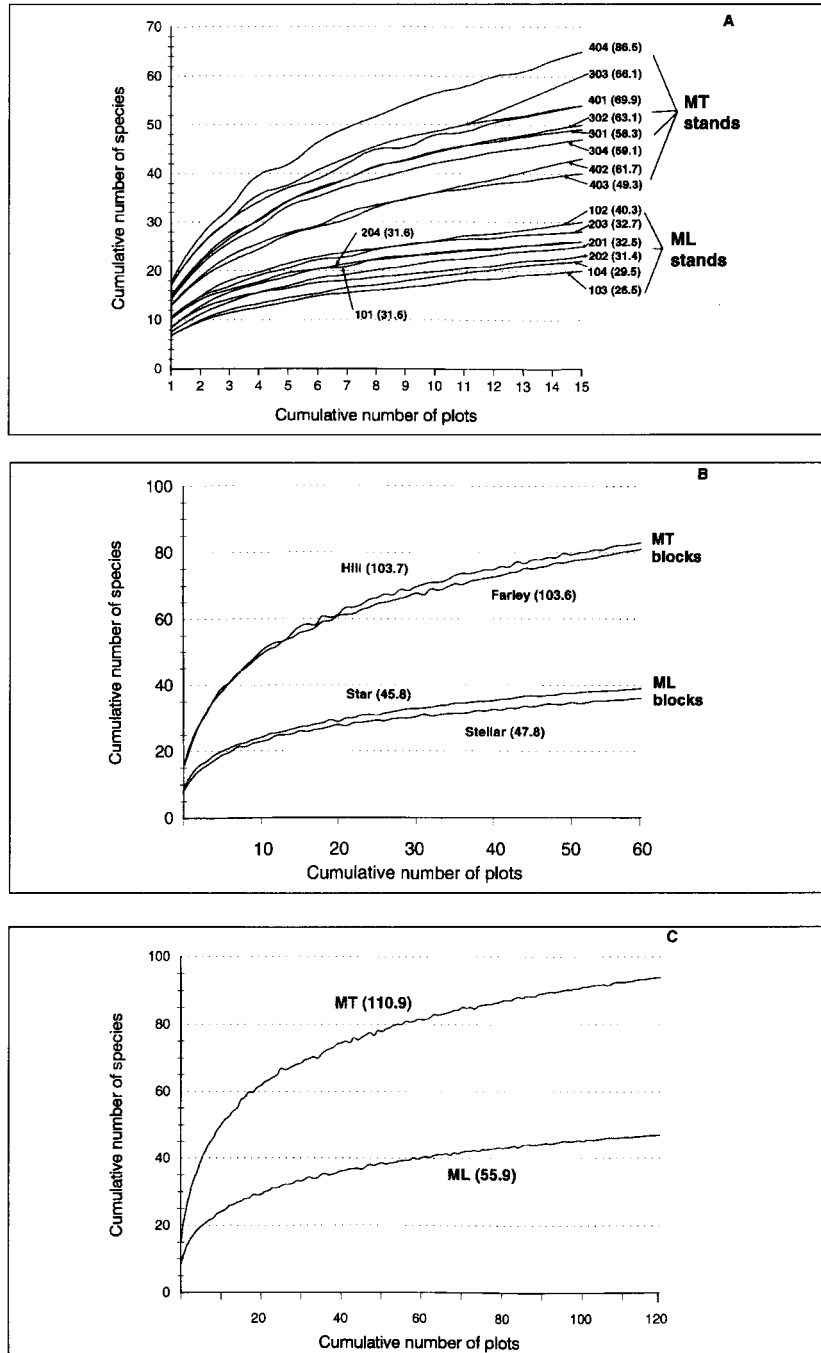


Figure 5-Species area curves for stands (A), blocks (B), and tracts (C) in forests managed with legacies (ML) and managed with thinning (MT), summer 1992. Numbers in parentheses are the first-order jack-knife estimates of stand-, block-, or tract-level species richness.

**Understory Species
Abundance and
Frequency**

At the tract level, similar patterns also were evident (fig. 5C): 94 of 98 (jack-knife estimates 111 of 114) total species were found in MT and 47 species were in ML (jack-knife estimate = 56). MT averaged more species per plot and more species per stand and was significantly more diverse than ML (table 3).

MT had greater average percentages of cover than ML for total understory, total tall shrubs, dominant low shrubs (*Gaultheria shallon*), and common ferns (*Polystichum munitum* and *Pteridium aquilinum*). For the ferns, among-plot, within-stand variation was higher in MT than in ML; similarly, among-stand within-tract variability was higher in MT than ML. For *Gaultheria*, among-plot within-stand variation was similar in both tracts, and the among-stand within-tract variation was much greater in MT than in ML. In general, cover of *Gaultheria* was substantially higher in MT than in ML. For moss cover, among-plot and among-stand variabilities were similar in the two tracts, with total moss cover being much higher in the ML stands than in MT (fig. 6, A-F).

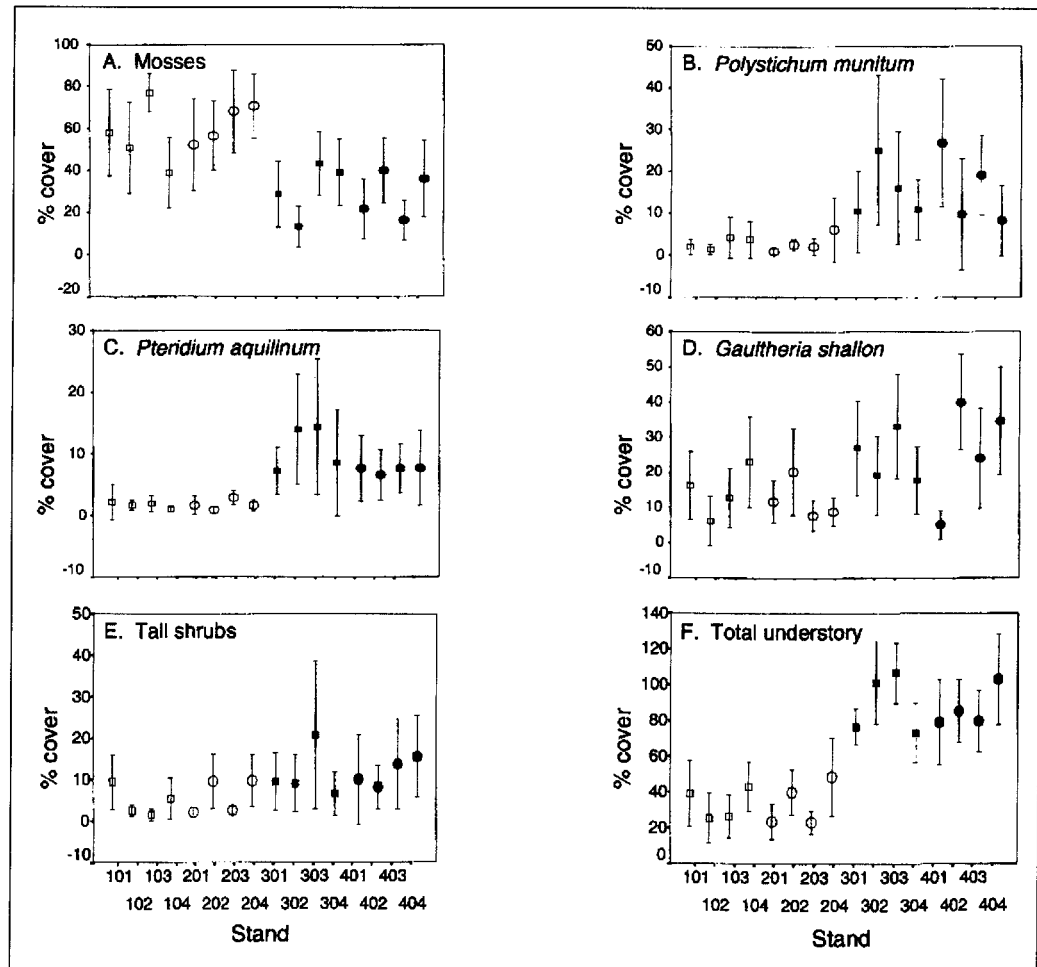


Figure 6—Stand level mean cover values in percent cover (± 95% CI) for forest floor mosses (A), *Polystichum munitum* (B), *Pteridium aquilinum* (C), *Gaultheria shallon* (D), tall shrubs (E), and the total vascular understory (F) in forests managed with legacies (stands 101-204; Star and Stellar blocks) and managed with thinning (stands 201-404; Farley and Hill Blocks), summer 1992. Star block and stands (□); Stellar block and stands (○); Farley block and stands (■); Hill block and stands (●). N = 15 plots per stand.

Table 4-Block-wise one-way ANOVA of percentage of cover for major understory species or groups^a

Species or group ^b	Block ^c				Block-wise ANOVA		
	Star	Stellar	Farley	Hill	F	df	P
GASH	14.5 ± 3.5 ¹	12.1 ± 2.8 ¹	24.2 ± 3.6 ¹	25.9 ± 7.7 ¹	1.4 ^d	3,12	0.295
POMU	2.8 ± 0.7 ¹	2.9 ± 1.1 ¹	15.6 ± 3.4 ²	16.0 ± 4.3 ²	13.7 ^d	3,12	<0.001
PTAQ	1.7 ± 0.2 ¹	1.7 ± 0.4 ¹	11.0 ± 1.8 ²	7.4 ± 0.3 ²	40.7 ^d	3,12	<0.001
MOSS	56.2 ± 8.0 ¹	61.9 ± 4.4 ¹	31.0 ± 6.7 ²	28.4 ± 5.7 ²	7.3	3,12	0.005
Total vascular understory	33.5 ± 4.5 ¹	34.0 ± 6.3 ¹	89.3 ± 8.5 ²	86.9 ± 5.6 ²	24.1	3,12	<0.001

^a Star and Stellar blocks are in the managed with legacy tract; Farley and Hill blocks are in the managed with thinning tract. Data are mean covers in percent ± 1 SE.

^b GASH = *Gaultheria shallon*; POMU = *Polystichum munitum*; PTAQ = *Pteridium aquilinum*; MOSS = all ground mosses (80-90 percent *Kindbergia oregana* (Sull.) Ochyra; the remainder primarily *Hylocomium splendens* (Hedw.) B.S.G., *Rhytidiadelphus* spp., *Dicranum scoparium* Hedw., and *Plagiothecium undulatum* (Hedw.) B.S.G.).

^c Within each species or group, blocks with different numeral superscripts differed significantly; those with the same numerals did not differ significantly (Tukey's B *post hoc* test, $p = 0.05$, Norušis 1993). N = 4 stand means per block.

^d ANOVAs for these species were based on natural log transformed values.

The two ferns, *Polystichum munitum* and *Pteridium aquilinum*, were much more abundant in MT than in ML as was total understory cover; mosses were more abundant in ML. For each of these four variables, blocks differed significantly between but not within tracts. Although *Gaultheria* was about twice as abundant in MT blocks as in ML blocks, the small number of stands and high interstand variability precluded detection of a significant difference between blocks for this species (table 4). Between-tract differences in abundance of *Gaultheria*, *Polystichum*, *Pteridium*, total moss cover, and total understory cover were highly significant (table 5).

Of the 94 vascular plant species found in MT, 51 were not found in ML. Of those 51 species, 33 were native species and 18 were nonnative. The 18 nonnative species included 1 tall shrub, 2 low shrubs, 13 herbaceous species, and 2 grass species (nonnative species are indicated by lower-case acronyms in table 5). At least one nonnative species was found in 44 of 120 plots in the MT tract. *Mycelis muralis* was the most frequently encountered nonnative plant species (found in 22 percent of MT plots), followed by *Senecio jacobaea* (8 percent) and *Ilex aquifolium* (7 percent). Though many of the non-native species were found infrequently in MT, collectively they accounted for 35 percent of the 51 species not found in ML. Of the 33 native species found only in MT, 9 were tall shrubs or understory trees, 1 was a low shrub, 18 were herbaceous, 2 were ferns, and 3 were graminoids (table 5).

Of the 47 vascular plant species found in ML, 4 were not found in MT. All four were native; two were understory shrubs or trees (*Taxus brevifolia* and *Thuja plicata*) and two were herbaceous species (*Disporum hookeri* and *Maianthemum stellatum*). Only one nonnative species, *Ilex aquifolium*, was encountered in ML and was found on only one plot. Of the 43 species found in both tracts, 21 were significantly more abundant and 23 were significantly more frequently encountered in MT than in ML. Two

Table 5-Percentage of cover and percentage of frequency of occurrence of vascular plant species and cover of mosses and vascular plant groups in forests managed with legacies versus managed with thinning in the Puget Trough, 1991-92

Functional group/species name	Species code ^a	Managed with legacies		Managed with thinning	
		Absolute cover (%) ^b	Frequency (%) ^c	Absolute cover (%) ^b	Frequency (%) ^c
Tall shrubs/understory trees:					
<i>Acer macrophyllum</i>	ACMA	T	0.8	0.5±0.3	13.3
<i>Alnus rubra</i>	ALRU2	0	0	1.2±0.7	10.00
<i>Amelanchier alnifolia</i>	AMAL2	<u>0.1±0.0</u>	9.2	T	3.3
<i>Arbutus menziesii</i>	ARME	0	0	T	0.8
<i>Cornus nuttallii</i>	CONU	0	0	T	1.7
<i>Corylus cornuta</i> var. <i>californica</i>	COCOC	2.4±0.5	45.8	3.5±1.0	45.0
<i>Frangula purshiana</i>	FRPU7	T	5.0	0.1±0.0	15.0
<i>Holodiscus discolor</i>	HODI	1.5±0.5	24.2	2.5±0.6	42.5
<i>Ilex aquifolium</i>	ilaq80	T	0.8	0.1±0.0	6.7
<i>Oemlaria cerasiformis</i>	OECE	T	0.8	0.3±0.1	17.5
<i>Philadelphus lewisii</i>	PHLE2	0	0	T	0.8
<i>Populus balsamifera</i> ssp. <i>trichocarpa</i>	POBAT	0	0	T	0.8
<i>Pseudotsuga menziesii</i>	PSME	T	2.5	0.2±0.1	20.0
<i>Rubus spectabilis</i>	RUSP	0	0	0.1±0.1	1.7
<i>Salix scouleriana</i>	SASC	0	0	0.2±0.1	4.2
<i>Sambucus racemosa</i>	SARA2	0	0	2.2±0.8	22.5
<i>Sorbus aucuparia</i>	soau	0	0	T	0.8
<i>Taxus brevifolia</i>	TABR2	T	1.7	0	0
<i>Thuja plicata</i>	THPL	0.3±0.1	7.5	0	0
<i>Tsuga heterophylla</i>	TSHE	0	0	T	2.5
<i>Vaccinium ovatum</i>	VAOV2	T	0.8	T	2.5
<i>V. parvifolium</i>	VAPA	1.0±0.2	61.7	1.0±0.2	40.8
Total, tall shrubs		5.4±0.8	-	11.7±1.7	-
Low shrubs:					
<i>Cytisus scoparius</i>	cysc4	0	0	T	0.8
<i>Gaultheria shallon</i>	GASH	13.3±1.5	92.5	25.1±2.2	86.7
<i>Mahonia nervosa</i>	MANE2	4.2±0.5	81.7	4.0±0.7	70.8
<i>Rosa gymnocarpa</i>	ROGY	0.3±0.1	25.8	0.9±0.2	35.0
<i>Rubus laciniatus</i>	rula	0	0	T	2.5
<i>R. leucodermis</i>	RULE	0	0	0.2±0.1	5.8
<i>R. parviflorus</i>	RUPA	T	2.5	T	3.3
<i>Symphoricarpus albus</i>	SYAL	T	0.8	0.1±0.1	5.8
Total, low shrubs		17.8±1.3	-	31.1±1.4	-
Trailing shrubs/vines:					
<i>Linnaea borealis</i>	LIBO3	3.3±1.3	27.5	3.1±1.0	32.5
<i>Lonicera ciliosa</i>	LOCI3	T	5.0	0.8±0.5	14.2
<i>Rubus ursinus</i>	RUUR	0.7±0.1	77.5	4.2±0.6	95.0
<i>Symphoricarpus hesperius</i>	SYHE	0.4±0.1	21.7	3.0±0.7	57.5
Total, trailing shrubs/vines		4.3±1.3	-	11.1±1.1	-
Herbs and subshrubs:					
<i>Achlys triphylla</i>	ACTR	0.3±0.1	5.8	0.8±0.4	7.5

Table 5-Percentage of cover and percentage of frequency of occurrence of vascular plant species and cover of mosses and vascular plant groups in forests managed with legacies versus managed with thinning in the Puget Trough, 1991-92 (continued)

Functional group/species name	Species code ^a	Managed with legacies		Managed with thinning	
		Absolute cover (%) ^b	Frequency (%) ^c	Absolute cover (%) ^b	Frequency (%) ^c
<i>Actaea rubra</i>	ACRU2	0	0	T	0.8
<i>Adenocaulon bicolor</i>	ADBI	T	0.8	<u>0.1±0.1</u>	10.0
<i>Anaphalis margaritacea</i>	ANMA	0	0	T	4.2
<i>Anemone deltoidea</i>	ANDE3	T	1.7	T	1.7
<i>Asarum caudatum</i>	ASCA2	0	0	T	0.8
<i>Campanula scouleri</i>	CASC7	T	1.7	<u>0.1±0.0</u>	10.8
<i>Chimaphila umbellata</i>	CHUM	0	0	T	3.3
<i>Circaea alpina</i>	CIAL	T	2.5	<u>0.4±0.2</u>	<u>20.8</u>
<i>Cirsium arvense</i>	ciar4	0	0	T	0.8
<i>C. vulgare</i>	civu	0	0	T	0.8
<i>Claytonia siberica</i> var. <i>siberica</i>	CLSIS	0	0	<u>0.2±0.0</u>	<u>26.7</u>
<i>Corallorhiza maculata</i>	COMA4	T	8.3	T	8.3
<i>Crepis capillaris</i>	crca3	0	0	T	3.3
<i>Disporum hookeri</i>	DIHO3	T	3.3	0	0
<i>Epilobium angustifolium</i>	EPAN2	0	0	T	0.8
<i>Fragaria crinita</i>	FRCR	0	0	T	1.7
<i>Galium aparine</i>	GAAP2	0	0	0.2±0.0	<u>20.8</u>
<i>G. triflorum</i>	GATR3	0.2±0.1	26.7	<u>0.6±0.1</u>	<u>78.3</u>
<i>Geum macrophyllum</i> var. <i>macrophyllum</i>	GEMAM	0	0	T	1.7
<i>Goodyera oblongifolia</i>	GOOB2	<u>0.1±0.0</u>	<u>15.8</u>	T	5.0
<i>Hieracium albiflorum</i>	HIAL2	0	0	<u>0.1±0.0</u>	<u>10.8</u>
<i>Hypochaeris radicata</i>	hyra3	0	0	T	3.3
<i>Lapsana communis</i>	laco3	0	0	T	0.8
<i>Lathyrus polyphyllus</i>	LAPO3	T	5.0	<u>0.7±0.3</u>	<u>29.2</u>
<i>Lilium columbianum</i>	LICO	0	0	T	1.7
<i>Listera caurina</i>	LICA10	T	4.2	T	2.5
<i>Maianthemum stellatum</i>	MAST4	<u>0.1±0.0</u>	2.5	0	0
<i>Monotropa uniflora</i>	MOUN3	T	1.7	T	4.2
<i>Mycelis muralis</i>	mymu	0	0	<u>0.3±0.1</u>	<u>21.7</u>
<i>Nemophila parviflora</i>	NEPA	0	0	T	10.0
<i>Osmorhiza berteroi</i>	OSBE	0	0	<u>0.1±0.0</u>	10.0
<i>Petasites frigidus</i> var. <i>palmatius</i>	PEFRP	0	0	T	0.8
<i>Prunella vulgaris</i>	prvu	0	0	T	1.7
<i>Pyrola asarifolia</i>	PYAS	T	1.7	T	0.8
<i>Ranunculus repens</i> var. <i>repens</i>	rarer	0	0	T	1.7
<i>R. uncinatus</i> var. <i>parviflorus</i>	RAUNP	0	0	T	1.7
<i>Senecio jacobaea</i>	seja	0	0	T	7.5
<i>Sonchus asper</i>	soas	0	0	T	0.8
<i>Stellaria crispa</i>	STCR2	0	0	<u>0.1±0.0</u>	10.8
<i>Taraxicum officinale</i>	taof	0	0	0.1±0.1	1.7
<i>Tiarella trifoliata</i>	TITR	T	2.5	<u>0.2±0.1</u>	<u>18.3</u>
<i>Trientalis borealis</i> ssp. <i>latifolia</i>	TRBOL	0.4±0.0	51.7	<u>0.8±0.1</u>	65.00
<i>Trifolium</i> spp. ^d	trifo	0	0	T	0.8
<i>Trillium ovatum</i>	TROV2	0.1±0.0	19.1	0.1±0.0	20.0

Table 5-Percentage of cover and percentage of frequency of occurrence of vascular plant species and cover of mosses and vascular plant groups in forests managed with legacies versus managed with thinning in the Puget Trough, 1991-92 (continued)

Functional group/species name	Species code ^a	Managed with legacies		Managed with thinning	
		Absolute cover (%) ^b	Frequency (%) ^c	Absolute cover (%) ^b	Frequency (%) ^c
<i>Urtica dioica</i>	URDI	0	0	<u>0.6±0.4</u>	<u>13.3</u>
<i>Vancouveria hexandra</i>	VAHE	0.6±0.1	44.2	<u>3.4±1.0</u>	<u>63.3</u>
<i>Veronica</i> sp.	veron	0	0	T	1.7
<i>Viola glabella</i>	VIGL	0	0	T	0.8
<i>V. sempervirens</i>	WISE	0.1±0.0	14.2	<u>0.3±0.0</u>	<u>41.7</u>
Total, herbaceous		1.6±0.2	-	<u>8.8±1.3</u>	-
Ferns:					
<i>Adiantum aleuticum</i>	ADAL	0	0	T	0.8
<i>Athyrium filix-femina</i>	ATFI	T	1.7	<u>0.5±0.1</u>	<u>29.2</u>
<i>Blechnum spicant</i>	BLSP	0	0	T	<u>5.0</u>
<i>Dryopteris campyloptera</i>	DRCA3	T	0.8	T	2.5
<i>Polypodium glycyrrhiza</i>	POGL8	T	0.8	T	1.7
<i>Polystichum munitum</i>	POMU	2.8±0.6	63.3	<u>15.8±2.0</u>	<u>88.3</u>
<i>Pteridium aquilinum</i>	PTAQ	1.7±0.2	80.8	<u>9.2±1.1</u>	<u>92.5</u>
Total, ferns		4.6±0.7	-	<u>25.6±2.5</u>	-
Graminoids:					
<i>Bromus vulgaris</i>	BRVU	T	1.7	<u>0.3±0.1</u>	<u>26.7</u>
<i>Carex deweyana</i>	CADE9	0	0	<u>0.1±0.0</u>	<u>10.8</u>
<i>Festuca occidentalis</i>	FEOC	0	0	<u>0.1±0.0</u>	<u>10.8</u>
Grass (unidentified)		0	0	T	5.8
<i>Luzula parviflora</i>	LUPA4	T	0.8	<u>0.1±0.0</u>	<u>9.2</u>
<i>Melica subulata</i>	MESU	0	0	T	<u>5.0</u>
<i>Poa pratense</i>	popr	0	0	T	2.5
Total, graminoids		T	-	<u>0.5±0.1</u>	-
Moss		<u>59.0±3.1</u>	-	29.7±2.5	-
Total, vascular plants		33.8±2.5	-	<u>88.2±3.3</u>	-

- Not calculated

^a Capital letters indicate native species. Lower-case letters indicate nonnative species.

^b Mean cover in percent (\pm 1 SE) per plot on 120 plots per tract. T indicates < 0.1 percent cover. Between-tract differences are significant at $P < 0.10$ (underline), $P < 0.01$ (bold), or $P < 0.001$ (bold plus underline) ($df = 238$, Mann-Whitney U-test, Norušis 1993).

^c Frequency of occurrence (percentage of 120 plots per tract in which plant species or group was found). Frequency values differ significantly between tracts at $P < 0.10$ (underline), $P < 0.01$ (bold), or $P < 0.001$ (bold plus underline) ($df = 1$, χ^2 -test for tract effect, Norušis 1993).

^d Both *Trifolium repens* and *T. pratense* are widespread and naturalized in managed forests in the Puget Trough. Because these plants were observed without flowers, we refer to them as *Trifolium* spp.

species, *Vaccinium parvifolium* and *Goodyera oblongifolia*, were significantly more frequent in ML than in MT. All vascular plant life forms were significantly more abundant in MT than in ML, but moss cover was significantly more abundant in ML than in MT (table 5).

**Ranked Abundance
and Species Indicator
Values**

Of the commonly encountered tall shrubs and understory tree species, all except *Corylus cornuta* var. *californica* and *Vaccinium parviflorum* were significantly more frequent and abundant in MT than in ML. *Corylus* was encountered at similar frequencies and abundances in both tracts. *Vaccinium parviflorum* was found at similar cover in both tracts but at significantly higher frequency in ML. Of the low shrubs, all except *Mahonia nervosa* were found more frequently and at higher cover in MT. *Mahonia nervosa* was found at about the same frequency and abundance in both tracts. Except for *Linnaea borealis*, all trailing shrub and vine species were significantly more frequent and abundant in MT than in ML. In particular, *Rubus ursinus* and *Symphoricarpos hesperius* were much more frequent and abundant in MT than in ML; their combined cover in MT was nearly seven times that in ML, summing to over 7 percent cover in MT. The frequency and abundance of *Linnaea borealis* was similar in the two tracts.

Herbaceous species accounted for a large portion of the increased species richness and abundance in the MT tract; herbaceous cover totaled nearly 9 percent in MT but <2 percent in ML. Thirty-one of 51 herbaceous species were found only in MT; 2 of 51 only in ML. Of the 18 herbaceous species found in both tracts, 10 were significantly more abundant in MT; only *Goodyera oblongifolia* was significantly more abundant in ML. Of the 31 herbaceous species found only in MT, 18 were native and 13 were nonnative. Nonnative herbaceous species were primarily members of the family Asteraceae and included species of such widespread and weedy genera as *Cirsium*, *Crepis*, *Hypochaeris*, *Lapsana*, *Mycelis*, *Senecio*, *Sonchus*, and *Taraxacum* (table 5).

The two fern species, *Polystichum munitum* and *Pteridium aquilinum*, were common (>60 percent frequency) in both tracts but were much more abundant in MT. Their combined cover averaged 25 percent in MT but <5 percent in ML. More graminoids occurred in MT (7 taxa) than in ML (2 taxa), and the two species common to both tracts (*Bromus vulgaris* and *Luzula parviflora*) were significantly more frequent and more abundant in MT than in ML (table 5).

The two tracts were qualitatively similar in species composition with 9 of the 10 most abundant understory species found in both tracts. *Vaccinium parviflorum*, 8th most abundant in ML, was 13th in MT and was found in similar abundance in both tracts. *Symphoricarpos hesperius*, 9th in MT, was 11th in ML but was nearly three times as abundant in MT than ML. Of the 13 vascular plant species in MT and the 9 in ML with >40 percent frequency, 8 species were in common (*Corylus cornuta* var. *californica*, *Gaultheria shallon*, *Mahonia nervosa*, *Pteridium aquilinum*, *Rubus ursinus*, *Polystichum munitum*, *Trientalis latifolia*, and *Vancouveria hexandra*). *Gaultheria shallon* was the most abundant understory species in both tracts but was nearly twice as abundant in MT than in ML. In ML, the combined cover of the 10 most abundant species was 31 percent and constituted 93 percent of total understory cover, whereas in MT the 10 most abundant species totaled 74 percent cover and accounted for 84 percent of total understory (table 6).

Many common species had high indicator value in one or both tracts. Understory species characteristic of both tracts were *Gaultheria shallon*, *Mahonia nervosa*, *Corylus cornuta* var. *californica*, and *Vaccinium parviflorum*. *Polystichum munitum*, *Pteridium aquilinum*, and *Rubus ursinus* had the highest indicator values of any species and reached their IV-max in the MT tract. Species with IV-maxima that were

Table 6-Ranked abundance (by absolute cover) for top 10 species in forests managed with legacies versus managed with thinning in the Puget Trough, 1991-92

Managed with legacies			Managed with thinning		
Frequency (%) ^a	Absolute cover (%) ^b	Species code ^c	Species code	Absolute cover (%)	Frequency (%)
92.5	13.3	GASH	GASH	25.1	87.7
81.7	4.2	MANE	POMU	15.8	88.3
27.5	3.3	LIBO	PTAQ	9.2	92.5
63.3	2.9	POMU	RUUR	4.2	95.0
45.8	2.4	COCOC	MANE	4.0	70.8
80.8	1.7	PTAQ	COCOC	3.5	45.0
24.2	1.5	HODI	VAHE	3.4	63.3
61.7	1.0	VAPA ^d	LIBO	3.1	32.5
77.5	0.7	RUUR	SYHE ^e	3.0	57.5
44.2	0.6	VAHE	HODI	2.5	42.5
Total cover for top 10 species				73.8	
% of total cover for all species				83.7	

^a Percentage of 120 plots in which the species was found.

^b Average cover for a species in all 120 plots.

^c Species codes are as follows: COCOC = *Corylus cornuta* var. *californica*; GASH = *Gaultheria shallon*; HODI = *Holodiscus discolor*; LIBO = *Linnaea borealis*; MANE = *Berberis nervosa*; POMU = *Polystichum munitum*; PTAQ = *Pteridium aquilinum*; RUUR = *Rubus ursinus*; SYHE = *Symphoricarpos mollis*; VAHE = *Vancouveria hexandra*; VAPA = *Vaccinium parviflorum*.

^d VAPA was 13th in abundance in the managed with thinning forest (1.0 percent cover).

^e SYHE was 11th in abundance in the managed with legacies forest (0.4 percent cover).

significant ($P < 0.01$) and >20 percent were all found in the MT tract and included mostly native but one nonnative (*Mycelis muralis*) species. One native species, *Goodyera oblongifolia* (a shade-tolerant orchid [Klinka and others 1989]), attained its IV-max in the ML tract. Though its IV-max was only 12 percent, this value was significant ($P < 0.05$) (table 7).

Bray-Curtis Ordination

We calculated the first three Bray-Curtis ordination axes by using the full data set of 240 plots and 98 species from both tracts. The three axes accounted for 45.3 percent of the variance (18.9 percent, 20.8 percent, and 5.6 percent, respectively, for axes 1, 2, and 3). The two tracts exhibited substantially different data swarms when graphed against axes 1 and 2 (fig. 7A) and axes 2 and 3 (fig. 7B), with the two blocks in each tract clustering similarly.

Of the most common species, abundance of *Gaultheria shallon* and *Polystichum munitum* were most highly correlated with axis 1; *Gaultheria* was negatively correlated and *Polystichum* was positively correlated. No other frequently encountered species was strongly correlated with axis 1 (table 8). Thus, we interpreted axis 1 to represent

Table 7-Indicator values for selected vascular plant species in forests managed with legacies versus managed with thinning in the Puget Trough. 1991-92

Species ^a	Managed with legacies, indicator value	Managed with thinning, indicator value	<i>P</i> ^b
<i>Athyrium filix-femina</i>	0	29	<0.001
<i>Bromus vulgaris</i>	0	26	<0.001
<i>Claytonia siberica</i> var. <i>siberica</i>	0	27	<0.001
<i>Corylus cornuta</i> var. <i>californica</i>	19	27	0.470
<i>Galium aparine</i>	0	21	<0.001
<i>Gaultheria shallon</i>	32	57	0.003
<i>Goodyera oblongifolia</i>	12	1	0.011
<i>Lathyrus polyphyllus</i>	0	28	<0.001
<i>Mahonia nervosa</i>	42	34	0.375
<u><i>Mycelis muralis</i></u>	0	22	<0.001
<i>Polystichum munitum</i>	10	75	<0.001
<i>Pteridium aquilinum</i>	13	78	<0.001
<i>Rosa gymnocarpa</i>	7	26	0.003
<i>Rubus ursinus</i>	11	82	<0.001
<i>Sambucus racemosa</i>	0	23	<0.001
<i>Symphoricarpos hesperius</i>	2	52	<0.001
<i>Trientalis latifolia</i>	16	45	<0.001
<i>Vancouveria hexandra</i>	7	54	<0.001
<i>Vaccinium parvifolium</i>	30	21	0.288
<i>Viola sempervirens</i>	3	33	<0.001

^a Underlined name indicates a nonnative species; all others are native species.

^b Using a Monte Carlo method, plots were randomly assigned to groups (tracts) 1,000 times. The *P*-value is the proportion of 1,000 times that the maximum indicator value (IV_{max}) from the randomized data set is greater than or equal to the actual IV_{max} (Dufrene and Legendre 1997, McCune and Meford 1997).

a gradient of increasing available soil moisture from left to right. Our interpretation was strengthened by other plant species concentrating in their expected locations along such a gradient. Moist-site indicators, such as *Athyrium filix-femina*, *Blechnum spicant*, and *Sambucus racemosa* (Franklin and Dyrness 1973, Klinka and others 1989, Pojar and MacKinnon 1994), were most frequent and achieved high abundances only at the right or moist end of axis 1 and were not found in plots at the left or dry end of the axis. Dry site or water-shedding-site species, such as *Amelanchier alnifolia*, *Holodiscus discolor*, and *Rosa gymnocarpa* (Klinka and others 1989), were most frequent and most abundant at the dry end of axis 1. The range of variation along axis 1 for the MT tract was much greater than for the ML tract, with ML plots concentrating from the middle or mesic portion of the illustrated range to the dry end (fig. 7A).

Axis 2 further separated ML from MT. Most ML plots clustered toward the upper end of axis 2 where these plots also had minimal variation along axis 1. Though most individual species correlated poorly with axis 2, the widespread species *Gaultheria shallon*, *Polystichum munitum*, and *Pteridium aquilinum* were negatively correlated with axis 2. Total vascular plant understory cover was negatively correlated with axis

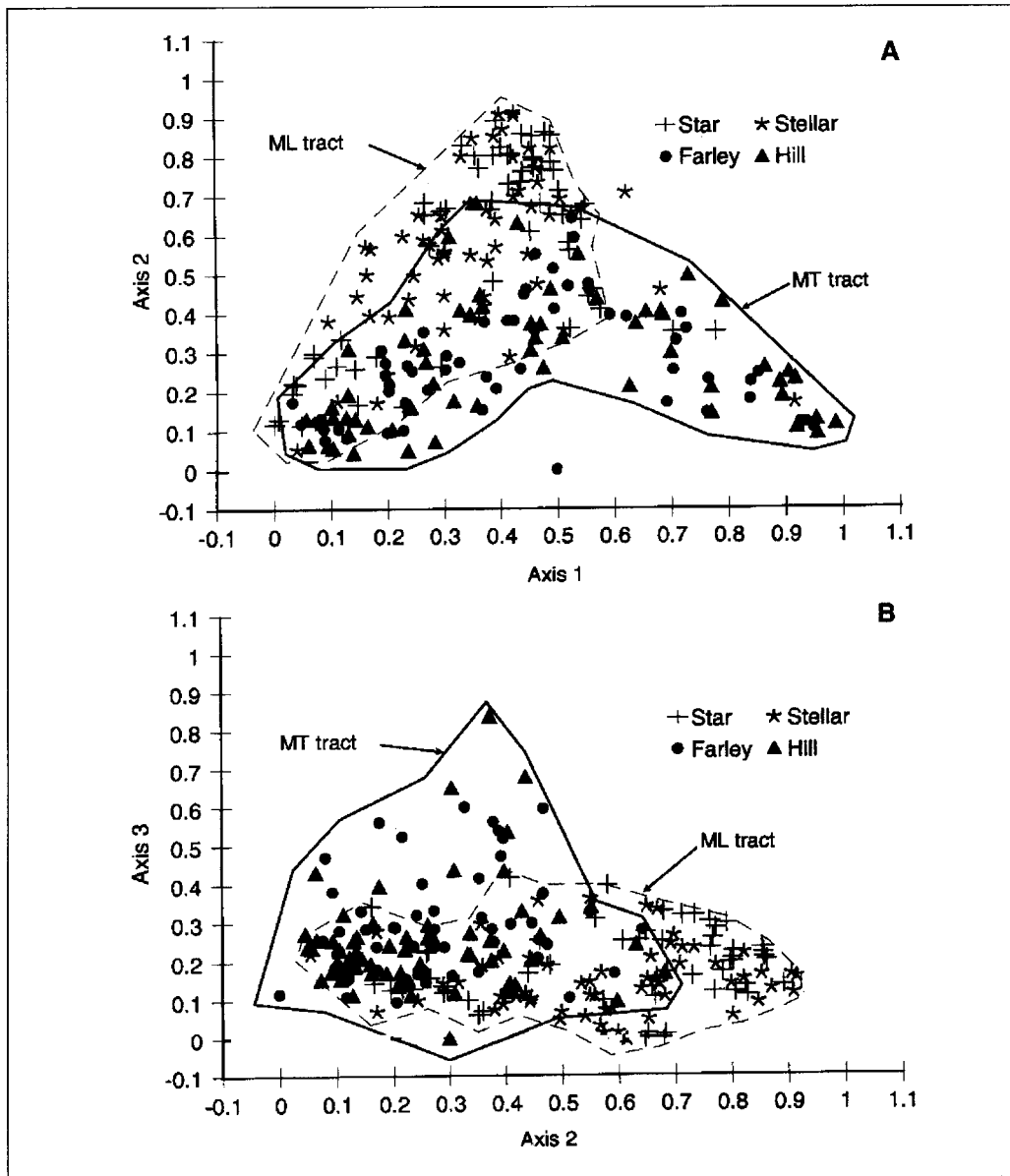


Figure 7-Bray-Curtis ordination of the managed-with-thinning (MT) and managed-with-legacies (ML) tract: and blocks along axes 1 and 2 (A) and along axes 2 and 3 (B). The Star and Stellar blocks are in the ML tract; the Farley and Hill blocks are in the MT tract. Data are from summer 1992.

2, as was the summed cover of *Gaultheria shallon*, *Polystichum munitum*, *Pteridium aquilinum*, and *Rubus ursinus* (the four most abundant species in MT). Plot-level tree density and moss cover were positively correlated with axis 2 (table 8). We interpreted axis 2 to represent a gradient of increasing tree density with associated increasing overstory canopy cover and decreasing understory--a competitive exclusion axis.

Table 8-Frequency of occurrence of selected vascular plant species; correlations (r) between species abundance or other variables with the 3 Bray-Curtis ordination axes^a for all plots in forests managed with legacies and managed with thinning in the Puget Trough, 1991-92

Species and other variables	Frequency (%) ^b	Correlation coefficient, <i>r</i>		
		Axis 1	Axis 2	Axis 3
<i>Athyrium filix-femina</i>	15.4	0.359	-0.194	0.042
<i>Bromus vulgaris</i>	14.2	0.094	-0.052	0.219
<i>Claytonia siberica</i> var. <i>siberica</i>	13.3	0.263	-0.203	0.147
<i>Corylus cornuta</i> var. <i>californica</i>	45.4	-0.067	-0.142	-0.012
<i>Galium aparine</i>	10.4	0.157	-0.096	0.214
<i>Gaultheria shallon</i>	89.6	-0.716	-0.672	-0.013
<i>Goodyera oblongifolia</i>	10.4	0.010	0.337	-0.058
<i>Lathyrus polyphyllus</i>	17.1	0.006	-0.019	0.081
<i>Mahonia nervosa</i>	76.3	-0.143	0.078	-0.150
<i>Mycelis muralis</i>	10.8	0.133	-0.038	0.281
<i>Polystichum munitum</i>	75.4	0.696	-0.422	-0.053
<i>Pteridium aquilinum</i>	86.7	0.163	-0.281	0.608
<i>Rosa gymnocarpa</i>	30.4	-0.184	-0.177	-0.017
<i>Rubus ursinus</i>	86.3	0.001	-0.225	0.244
<i>Sambucus racemosa</i>	11.3	0.290	-0.109	0.064
<i>Symphoricarpos hesperius</i>	39.6	0.072	-0.150	0.443
<i>Trientalis latifolia</i>	58.3	0.135	-0.081	0.076
<i>Vancouveria hexandra</i>	53.8	0.189	-0.051	0.534
<i>Vaccinium parviflorum</i>	51.3	-0.148	-0.051	-0.039
<i>Viola sempervirens</i>	27.9	0.104	-0.055	0.182
Other variables:				
GPPR ^c	-	-0.045	-0.858	0.197
PSV ^d	-	0.208	-0.239	0.758
Total moss cover	-	-0.155	0.511	-0.210
Total understory vascular plant cover	-	0.087	-0.781	0.404
Plot-level trees/hectare	-	-0.135	0.518	-0.304

- = not applicable

^a See figure 7.

^b Percentage of 240 plots in which species was found.

^c Combined cover of *Gaultheria shallon*, *Polystichum munitum*, *Pteridium aquilinum*, and *Rubus ursinus*.

^d Combined cover of *Pteridium aquilinum*, *Symphoricarpos hesperius*, and *Vancouveria hexandra*.

Certain plant species did, however, cluster strongly or exclusively within the distal portion of axis 2. In particular, *Goodyera oblongifolia* was nearly restricted to the closed-canopy conditions of the ML tract at the top of axis 2 and *Corallorhiza maculata* was most frequent there-both species are mycotrophs. Other widespread species, such as *Mahonia nervosa*, *Trientalis latifolia*, *Trillium ovatum*, *Vaccinium parvifolium*, and *Viola sempervirens*, were distributed evenly along axis 2.

Variation along axis 3 was associated with a positive and significant correlation with the abundance of *Pteridium aquilinum* (fig. 7B, table 8). The abundances of *Symphoricarpos hesperius* and *Vancouveria hexandra* also were correlated positively and significantly with ordination axis 3 and achieved their maxima in the distal portion

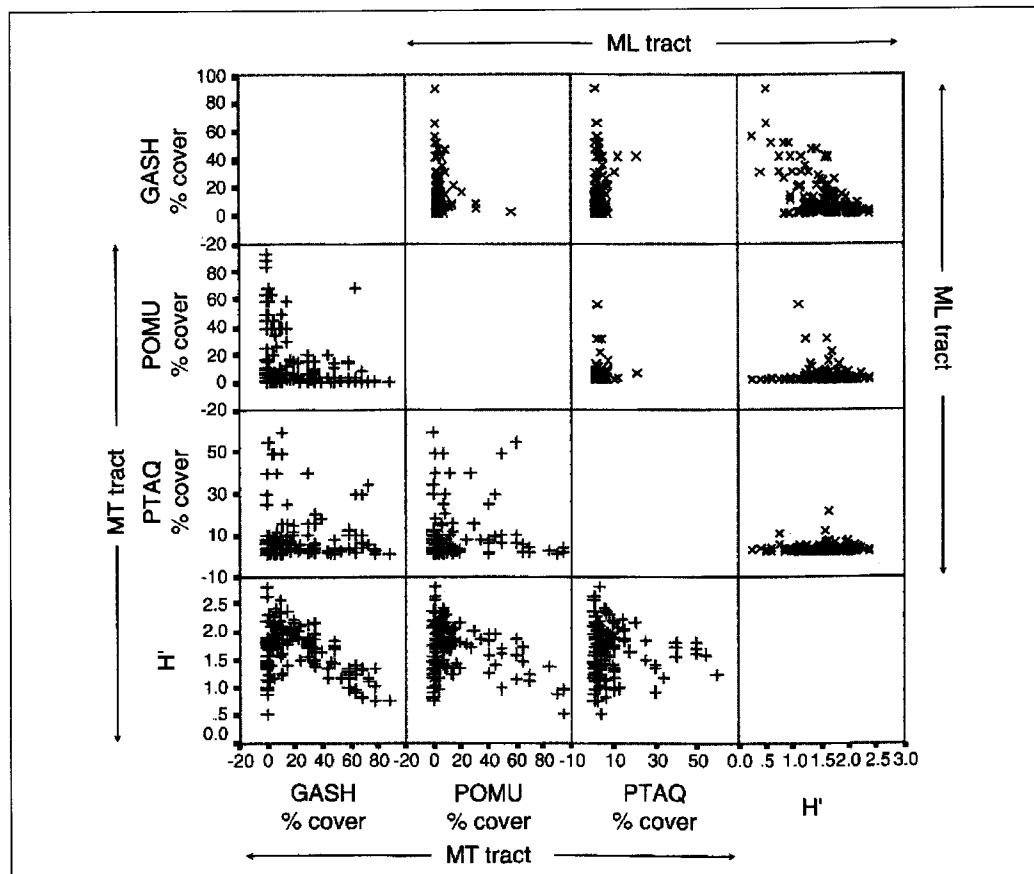


Figure 8—Bivariate plots of percentage of cover of *Gaultheria shallon* (GASH), *Polystichum munitum* (POMU), and *Pteridium aquilinum* (PTAQ), and of the value of the Shannon-Weiner diversity index (H') from forests managed with thinning (MT) and managed with legacies (ML). The graphs below and to the left of the diagonal cells (+) are from the MT tract. Those above and to the right (x) are from the ML tract. Data are from summer 1992.

of axis 3. Combined abundance of these three species was positively and significantly correlated with axis 3. The plots with high abundances of these three rhizomatous species were all located in MT and did not contain any obligate mycotrophic members of the families Pyrolaceae, Monotropaceae, and Orchidaceae (Cronquist 1981) (e.g., *Chimaphila umbellata*, *Corallorhiza maculata*, *Goodyera oblongifolia*, *Listera caurina*, *Monotropa uniflora*, and *Pyrola asarifolia*). Total understory cover was positively correlated with axis 3 and the number of trees/ha was negatively correlated with axis 3. We interpreted axis 3 to represent a gradient of increasing past ground disturbance associated with the repeated logging and yarding in MT and suggest that these plots are a legacy of previous thinning-related disturbances.

Particularly in MT, there were three understory conditions characterized by high abundance of *Gaultheria shallon*, *Polystichum munitum*, or *Pteridium aquilinum*. These taxa were by far the most abundant understory species in the MT tract, and our ordination suggests these three species attained their optima where light was not limiting and under dry, moist, or previously disturbed conditions, respectively. High abundance of any one of these three species also was associated with reduced plot-level diversity (H'). In the ML tract, similar patterns were apparent but less pronounced owing to the low cover of vascular vegetation (fig. 8).

Discussion

Limitations

Our study is retrospective and quasi-experimental (Cook and Campbell 1979). We have treatments and measured outcomes but lack random treatment assignment necessary to infer treatment-induced causality. In addition, our comparisons are confounded because the study sites differed in ways other than the treatments of interest. Thus, we strove to separate treatment effects from those due to other differences. Besides the treatments (management strategies), we recognize two potentially confounding influences on the plant community.

First, the two tracts differed slightly in measured site quality, age, and soil substrate. Because stand density may influence tree height-based site-quality estimates where substrate and climate are otherwise comparable (King 1966), we attribute observed differences in site index primarily to variation in tree density. Age as a determinant of tree size accounted for <40 percent of the observed difference in tree d.b.h.; we attribute the remaining differences to effects of tree density management. We do not feel that age difference alone is a major component of current between-tract plant community differentiation. Because of the high permeability, low-moderate water capacity, and surface-layer droughtiness characteristic of the glacially derived sandy and gravelly soils in the study area (Pringle 1990), we also do not regard variation in substrate as a major cause of between-tract differentiation.

Second, we lacked complete histories of fire intensity and frequency and data on operational (spatial, temporal, and logger variation) differences during previous harvests. We recognize that Puget Lowland Douglas-fir forests have burned frequently in the past, but there was no evidence that either tract had burned since stand initiation, and we do not attribute current between-tract differentiation to fire-related causes---the differences we observed are of the sort we would expect as a result of management. We also were aware that differences in implementation of treatments at the time of timber harvest would have been inevitable, thus we chose to contrast block- with tract-level management effects. However, our systematic sampling template allowed us to characterize plot-, stand-, and block-sources of variability, and thus to evaluate differences likely due to management strategy.

Having chosen stands on the basis of their homogeneity in areas of contiguous forest, and having used a systematic sampling template, it is unlikely that bias would have been introduced by oversampling or undersampling of canopy gaps. At 47° N. latitude and with heights-to-live-crown of 20 m, maximum mid-day summer insolation to the forest floor occurs where canopy openings are ≥ 9 m south, therefore confounding one-to-one relations between the understory and the canopy immediately overhead. Thus, though our overstory and understory plots were 5 m apart, we nonetheless chose to present plot-level correlations between ordination axes (based on understory data) and tree density (based on overstory data) while also recognizing the potential weakness of this association.

Our analyses were exploratory rather than hypothesis testing. We characterized patterns in our data set, but caution must be used in extrapolating our results beyond our study area, though most species from our study sites are common species throughout western Oregon and Washington and our findings pertaining to the dominant understory species *Gaultheria shallon*, *Polystichum munitum*, and *Pteridium aquilinum* were consistent with previous research. Thus, our study has furthered understanding of the ecology of managed stands by providing a rather unique

Community Composition and Structure

opportunity to examine influences of past forest management on (1) plant community structure and composition, (2) the autecology of some native species, and (3) the spread of exotic species and of native species favored by management. These factors, in turn, suggest how forests such as MT and ML may continue to develop after additional management.

Of the macroscopic species and species groups in conifer-dominated forests of the Pacific Northwest, vascular plants contain a large portion of total species diversity. In conifer forests of western Washington and Oregon, the understory contains, or has the potential to contain, most of the vascular plant diversity while also supporting much of the faunistic diversity (Carey and others 1996b, 1999b; Franklin and Dyrness 1973; Halpern and Spies 1995). The extremely diverse mycorrhizal fungal community (Kendrick 1992, Molina and others 1992) is chiefly associated with the Douglas-fir overstory (Carey and others 1999b; Trappe 1962, 1977), whereas most understory species are associated with the much less diverse vesicular arbuscular or endomycorrhizal fungi (Kendrick 1992, Malloch and others 1980, Perry and others 1990, Trappe 1987). Our study of two forested tracts of about the same age demonstrates some of the effects forest management can have on plant composition and structure in the space of only 55 to 70 years. Through its effects on forest plant communities, management also can affect lichen (Neitlich and McCune 1997), mycorrhizal fungi (Colgan 1997, Colgan and others 1999), avian (Carey and others 1991; Chambers and McComb 1997; Hansen and others 1995; Huff and others 1991; B. Haveri and A. Carey²), and mammal (Carey 1995; Carey and Johnson 1995; Carey and others 1999a; Corn and Bury 1991; S. Wilson and A. Carey³) communities as well, thus confirming the importance of evaluating plant community responses to forest management.

We consider current plant community structure and composition in ML and MT to be a reflection of management-induced vertical partitioning of solar energy absorption (and associated forest floor disturbances) and differences in legacy retention. In ML, insolation is primarily intercepted by the dense tree canopy. Because of the dense ML canopy, there was minimal structural and vertical vegetative development below the tree crowns. The extremely high diversity of ectomycorrhizal symbionts in these Douglas-fir forests (Carey and others 1999b, Colgan 1997, Colgan and others 1999, Trappe 1977) ensures that photosynthetically fixed carbon, in addition to contributing directly to tree girth, height, and foliage growth, also contributes to mycelial and sporocarpic growth. Because of the relatively depauperate angiosperm community in ML, vertebrate primary consumers should be skewed toward mycophagy (rather than herbivory or granivory) as we have observed, although the conifer-seed specialist, *Tamiasciurus douglasii*, was common in both ML and MT (Carey and others 1999b).

In ML, retention of some legacy trees, snags, and CWD during the previous harvest and subsequent lack of active management are now associated with a high density of small-diameter trees and a relatively sparse and species-poor understory vascular plant community. Competitive-exclusion forests such as ML often provide unfavorable conditions to most wildlife while also supporting the lowest understory vascular plant

² Haveri, B.; Carey, A. Manuscript in preparation. Authors may be contacted at the Forestry Sciences Laboratory, Olympia, WA.

³ Wilson, S.; Carey, A. Manuscript in preparation. Authors may be contacted at the Forestry Sciences Laboratory, Olympia, WA.

diversity (Brown 1985, Carey 1995, Carey and Johnson 1995, Carey and others 1999b, Ruggiero and others 1991), though remnant old trees and snags in ML and other similar forests can provide important habitat for sciurids (Carey 1995, Carey and others 1997) and other old-growth-associated organisms (Neitlich and McCune 1997). The reduced plant species richness and abundance in the ML tract understory were as expected following a lengthy competitive-exclusion phase, as was the high cover of forest floor mosses (Alaback 1982, Halpern and Spies 1995, Long 1977, Oliver and Larson 1996, Schoonmaker and McKee 1988, Turner and Long 1974). In such densely stocked stands, the sparse understory will probably persist until widespread changes occur in the now minimally differentiated canopy. A gradual increase in understory diversity and abundance may not occur until 100 or even 200 years of age without intervention (Carey and others 1999a, Franklin and others 1981). Thus, native-dominated, well-developed, botanically diverse understory stages (Carey and others 1996a, Oliver and Larson 1996) may not develop for a century or more following ecosystem initiation, especially in forests that lack shade-tolerant tree species, as did ML and MT (Carey and others 1999b).

Compared to ML, the MT tract contained fewer, but larger, trees and a greater diversity of tree sizes. Below the more open MT canopy was a diverse and abundant low vascular understory that was frequently dominated by one or more of the common and widespread species, *Gaultheria shallon*, *Polystichum munitum*, or *Pteridium aquilinum*. In our study area, as throughout much of the range of coastal Douglas-fir forests (Franklin and Dyrness 1973, Halpern 1989, Halpern and Spies 1995, Klinka and others 1989), these three species typically reach their optima under dry, moist, or previously disturbed conditions, respectively. Optimal conditions for each of the three species was most likely to be found in the MT tract, where high abundance of any one of the three was typically associated with low plot-level diversity (H'). The MT flora also contained substantial numbers of nonnative species that persist or continually establish under that type of management. The prevalence of exotic species in the MT flora was in marked contrast to ML, and substantially increased the overall MT species richness--more than one-third of the species unique to MT were exotics.

Though species richness and abundance for all vascular plant groups were greater in MT than in ML, both tracts lacked appreciable vertical differentiation (foliage height diversity). The general absence of shade-tolerant conifers or deciduous tree species contributed to the minimal structural development in both tracts making it unlikely these stands will develop high structural diversification without underplanting (Carey and others 1999b). Shade-tolerant tree species are found in surrounding areas and were present in small numbers in stands formerly occupying these sites, suggesting clearcut harvesting followed by burning and heavy natural regeneration may have contributed to producing these Douglas-fir monocultures.

The combination of widespread and evenly applied thinning activities and removal of CWD in MT was associated with an increase in low shrubs and ferns, primarily the strongly rhizomatous species *Gaultheria shallon* and *Pteridium aquilinum*, as well as *Polystichum munitum*. In addition to increasing light to the forest floor, canopy opening during thinning would be associated with localized increases in evapotranspiration, precipitation, and disturbance. We hypothesize that thinning, such as has taken place in MT, may promote development of three broad site types that are otherwise rare in densely stocked, unmanaged forests. In our study area, such site types were typified

Autecological Considerations

by high abundance of (1) *Gaultheria shallon* on well-drained sites or where evapotranspiration was elevated, (2) *Polystichum munitum* where soils were poorly drained or able to store precipitation not intercepted by the canopy, and (3) *Pteridium aquilinum* where soils were most disturbed during thinning activities. Through the use of alternative methods, such as variable-density thinning (Carey and others 1999b), we believe silviculture could promote a much wider range of vegetation site types (Carey and others 1999a) than are currently found in stands such as ML and MT.

Though the tall shrub-understory tree layer was significantly more abundant in MT than in ML, many constituents of that layer, such as the shade-intolerant and relatively short-lived *Alnus rubra*, *Populus balsamifera*, and *Salix scouleriana* (Burns and Honkala 1990), probably became established shortly after logging in the 1920s and are not expected to persist or reestablish under the current canopy. As such, their contribution to plant diversity will diminish as the stand ages, though they will then become short-lived snags and cavity trees for primary and secondary cavity dwellers (Carey and others 1997). The more shade-tolerant tall shrubs such as *Corylus cornuta* var. *californica* have not increased significantly in response to the MT thinnings, possibly due to damage during repeated thinning activities or to poor seedling survival below the strongly *Gaultheria-Polystichum-Pteridium* dominated understory.

Goodyera oblongifolia and *Vaccinium parvifolium* were more frequent in ML than in MT. *Goodyera* is often found associated with well-decayed woody debris or among mosses in decayed litter, and *V. parvifolium* is often found in decaying wood and on stumps and logs (Klinka and others 1989, Pojar and MacKinnon 1994), conditions that were more frequent in ML. Two common and widespread species, *Corylus cornuta* var. *californica* and *Mahonia nervosa*, were found at similar abundance and frequency in the two tracts.

Corylus is ectomycorrhizal (Agerer 1987-95, Molina and others 1992), and so *C. cornuta* may benefit from shared ectomycorrhizal symbionts with Douglas-fir as has been demonstrated with Douglas-fir and *Betula papyrifera* (Simard and others 1997). This association could partially explain the abundance of *C. cornuta* beneath the mostly closed ML canopy and suggests that retained *Corylus* could provide ectomycorrhizal inoculum to Douglas-fir after timber harvest as has been suggested for other hardwoods (Amaranthus and Perry 1994, Borchers and Perry 1990, Jones and others 1997, Smith and others 1995). Alternatively, the similarity in *Corylus* abundance in ML and MT could have resulted from (1) comparable establishment in the two tracts after the previous harvests and ability to persist under variable light conditions for the subsequent 55 to 70 years or (2) mediation by small-scale variation in organic and mineral soils. Nonetheless, because of the potential for shared ectomycorrhizae between *Corylus* and Douglas-fir, further research into the ecology of *Corylus* is warranted.

Unlike the dominant low shrub *Gaultheria shallon*, abundance of *Mahonia nervosa* did not differ between tracts. Though both species are rhizomatous, evergreen, perennial shrubs, *Mahonia* probably has much less potential for clonal spread (Huffman and Tappeiner 1997). Because of greater recruitment into an apparently wider range of acceptable seedling microsites for the larger-seeded *Mahonia* than for *Gaultheria* (Huffman and Tappeiner 1997, USDA 1974), *Mahonia* may be able to increase more by seedlings after further forest management in ML than in MT owing to less

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competition from *Gaultheria* and other understory species, though its subsequent clonal growth would be slower than that of *Gaultheria* (Bailey and Tappeiner 1998, Huffman and Tappeiner 1997). In MT, however, additional management could result in *Gaultheria* becoming even more widespread and dominant through its strong clonal growth. After further increase, *Gaultheria* and other clonal shrubs persist for many years, even into old growth (Bailey and Tappeiner 1998, Huffman and others 1994) providing an enduring legacy, but perhaps an unwanted homogeneity, in some intensively managed stands. In contrast, stem-exclusion conditions as in ML may be useful for suppressing those species favored by human-caused disturbance regimes that differ substantially than from historic disturbance regimes (Hobbes and Huenneke 1992, Roberts and Gilliam 1995). For example, the ML tract was almost totally lacking in nonnative plant species--*Ilex aquifolium* was the only introduced species observed there--and the clonal natives *Gaultheria shallon* and *Pteridium aquilinum* were much less abundant there than in MT. Stem-exclusion forests also may encourage seedling rather than vegetative reproduction after subsequent management (Bailey and Tappeiner 1998, Tappeiner and Zasada 1993) and may provide better habitat for some shade-tolerant or other minor species such as mycotrophs.

In the Puget Trough and in the vicinity of the MT and ML tracts, there are many well-established exotic species (e.g., *Agrostis capillaris*, *Crataegus monogyna*, *Cytisus scoparius*, *Digitalis purpurea*, *Geranium robertianum*, *Hedera helix*, *Holcus lanatus*, *Hypochaeris radicata*, *Ilex aquifolium*, *Leucanthemum vulgare*, *Polygonum cuspidatum*, *Rubus discolor*, *R. laciniatus*) (Carey and others 1999b; personal observation of the senior author). Many of these species are members of the "pan-temperate ruderal flora"--a relatively few highly invasive species attaining global distribution and dominance (Hobbs and Humphries 1995). In addition, an expanding fraction of newly introduced species in the rapidly changing Pacific Northwest flora are trees and shrubs (Toney and others 1998). Because time lags are common between initial introduction and noticeable impacts (United States Congress, Office of Technology Assessment 1993), and because woody and herbaceous exotic species have become unwanted components of forested ecosystems elsewhere (Walker and Vitousek 1991, Wisser and others 1998, Woods 1993), it is important to consider how forest management practices could affect establishment of these potentially deleterious species. Nonnative plant species on the nearby Olympic Peninsula increased from 40 in 1900 to 143 in 1936 to 333, or nearly 25 percent of the 1,452 reported plant taxa (Buckingham and others 1995) in 1995, demonstrating the potential for rapid and extensive transformation of a nearby bioregional flora. Though the effects of a rapidly expanding exotic species presence on Pacific Northwest forest ecosystem structure and function remain largely unknown, the differences we observed between ML and MT lead us to believe that in contrast to the essentially fixed native species pool, the exotic species presence will continue to increase with subsequent management entries.

Additional forest management can be expected to be accompanied by an influx of exotic species proportional to the amount of long-lasting ground-disturbing activity on the landscape and to the abundance of invasive nonnative species in the surrounding flora--such species find a ready avenue of dispersal where road density is high, as it often is in managed landscapes (Forman and Alexander 1998, Perry 1998). The

⁴Update as PNW-GTR-488 goes to press: Heckman, C.W. 1999. The encroachment of exotic herbaceous plants into the Olympic National Forest. Northwest Science. 73: 264-276.

ecological effects of the rapid (about 100 years) expansion of the exotic flora into Pacific Northwest forests are difficult to predict, but the combined effects of a high rate of exotic species introductions (Toney and others 1998) and further management and other forms of disturbance across the landscape will surely increase the nonnative component in the vascular flora and continue to homogenize ecological communities (Soule 1990) regardless of current forest conditions, while also increasing threats to the native flora and fauna from alien species (Wilcove and others 1998).

Native species also may be favored by forest management. Many of the species with high indicator value in the MT forest are characteristic of disturbed or cutover land or open-canopy Douglas-fir forests (e.g., *Galium aparine*, *Gaultheria shallon*, *Mycelis muralis*, *Polystichum munitum*, *Pteridium aquilinum*, *Rosa gymnocarpa*, *Rubus ursinus*, *Sambucus racemosa*, and *Symphoricarpos hesperius* [Klinka and others 1989, Pojar and MacKinnon 1994]). In forests such as MT where these common species are already abundant, additional systematic human-caused disturbances can be expected to promote their continued expansion, which in turn may impede forest and shade-tolerant shrub regeneration because of competition (Huffman and others 1994) or changes in the humus form and associated mycorrhizal community (Ponge and others 1998).

Rapid expansion of already-common clonal species also could reduce the chance for obligate mycotrophs or other minor or specialized species to find suitable regeneration niches (Grubb 1977). Members of the mycotrophic genera *Chimaphila*, *Corallorhiza*, *Goodyera*, *Listera*, *Monotropa*, and *Pyrola* or closely related species may be extirpated for 40 years or more following clearcutting and burning of old growth (Halpern and Spies 1995, Schoonmaker and McKee 1988)-a period of time that usually coincides with major expansion of *Gaultheria shallon*, *Polystichum munitum*, and *Pteridium aquilinum* (Halpern 1989, Long 1977, Schoonmaker and McKee 1988). Our work also suggests that high abundances of these three species are associated with low plot-level species diversity, similarly to what other studies have shown (Long 1977, Schoonmaker and McKee 1988). Because infrequently occurring herbaceous, fern, and graminoid species constituted a substantial portion of species richness in MT and ML, further expansion of the three dominant species could be accompanied by a reduction in native understory diversity. In general, however, there is a lack of research on the autecology of minor native understory species or that relates effects of management (including spread of nonnative species and dominance by clonal native ferns and shrubs) to the distribution and abundance of native understory species. Recent demographic research has shown, however, that clearcutting and site preparation can reduce seedling recruitment of the common *Trillium ovatum* and result in localized extirpations (Jules 1998). Further research will be necessary to determine management effects on other species in other areas.

Though the MT and ML stands certainly do not represent the potential range of variability in structure or biodiversity that could exist (Spies 1997), even among forests of this age, they nonetheless show some of the differences that can accrue during only one rotation cycle. We view the between-tract differences in tree size and density, legacy retention, exotic species presence, and understory composition and abundance as representing only part of a continuum of forest expression. We also suggest that the range of potential forest conditions and native-dominated vegetation site types could be even greater and more rapidly developed with active, adaptive, site-

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specific, and intentional management (Carey 1998, 2000), with deliberate efforts to reduce forest-floor disturbance, and through the use of variable-density thinning to augment site-type variation in the understory vegetation (Carey and others 1999a, 1999b).

The patterns of vegetation structure and diversity we observed in ML and MT are as would be expected under such management and stocking scenarios, and suggest hypotheses that can be tested by experiments that focus on manipulation of factors crucial to the future development of late-seral conditions in such stands. Site-specific knowledge such as we have gained about the two tracts allows refinement of hypotheses and of expected responses to management activities within each forest. Among processes that are alterable through active management (and as such allow testing of hypotheses) are crown-class differentiation, decadence, canopy stratification, gap formation, understory development, and development of habitat breadth (Carey and others 1999a). Current conditions in ML and MT have *very* different implications for future management of the two tracts and for forest-specific hypotheses concerning these factors.

In MT, past management has reduced CWD and snags to a low level while increasing both the diameter of the retained trees and their size-class diversity. The use of size-class diversity and crown volume magnitude and variability as surrogates for amount of crown differentiation indicates that the process of crown differentiation within the current cohort of trees is more advanced in MT than in ML. However, because of the near-absence of legacy trees and snags in MT, crown differentiation must take place entirely among the current cohort of about 230 trees per hectare. Because CWD is depauperate in MT, these trees are the source of future forest-floor woody debris as well as snags. Fifty trees averaging 50 cm in diameter and 40 m tall would be necessary to create 5 percent cover on the ground-removal of 22 percent of the current stand solely for woody debris augmentation would probably be unacceptable in most pragmatic management scenarios. Some habitat attributes associated with late-seral form and function may require >10 percent cover of CWD (Carey and Johnson 1995, Carey and others 1999a), thus management for increased decadence in MT is constrained by lack of woody debris and by tree densities that resulted from past management solely for optimal tree growth and periodic financial return.

Management legacies in MT also include high cover of rapidly growing and long-lived clonal shrubs and ferns such as *Gaultheria shallon* and *Pteridium aquilinum* and a well-developed exotic flora. The abundant MT understory and lack of CWD may hinder development of the shade-tolerant conifers and midstory that are currently lacking. Ground-disturbing activities associated with future thinning in MT may aggravate this condition, although a well-developed shade-tolerant strata could begin to reduce dominance of understory species with high light requirements, while also favoring other shade-tolerant taxa. This process of expanding the amount of canopy stratification and spatial partitioning should result in a greatly expanded multidimensional niche space, even if absolute vascular plant species richness does not increase.

Previous thinnings in MT have presumably obscured incipient gap formation processes--again legacies of past management complicate formulation of future management scenarios. Where natural gap-forming processes such as *Phellinus weirii* (laminated root rot) pockets could have begun to create patchiness in a forest of this

age (Thies and Sturrock 1995), thinning entries would have removed dead or dying trees that could serve as patches of decadence, crown differentiation (through lateral spread into open areas), stratification (through hardwood or root-rot resistant species recruitment into the patch), and variation in understory composition and structure.

In ML, however, lack of active density management and retention of legacy trees, snags, and CWD imply different future management alternatives. The use of size--class diversity and crown volume as surrogates for crown differentiation suggests a greater crown uniformity within the current cohort in ML. However, because of the presence of some snags and legacy trees in ML (the contribution of which to crown differentiation was not quantified because previous-stand trees were excluded from the dominant tree sampling in the prism plots) and because of the much greater density of current cohort trees, there are more opportunities for multiple-entry manipulations to increase levels of crown-class differentiation, although relatively low live-crown ratios and crown volumes suggest conservative expectations.

Opportunities for decadence management are also greater in ML than MT. ML enters the next round of management with substantial CWD and snags. In addition, the current cohort is experiencing widespread suppression mortality resulting in numerous 15- to 25-cm diameter trees becoming woody debris on the forest floor. For trees averaging 35 cm diameter and 34 m tall, 83 of the 620 per hectare could be felled to augment woody debris cover by an additional 5 percent-removal of that many trees for CWD enhancement is more likely to be acceptable to managers. Thus future management for decadence in ML will benefit from previous legacy retention and from the high tree density in the current stand.

Management legacies in ML also include a poorly developed understory, a lack of exotics, and a near-total absence of shade-tolerant conifers and midstory constituents. The depauperate ML understory may mean that shade-tolerant conifers (planted or natural), midstory species, and other understory species will more rapidly establish after future management entries (because of a wider range of regeneration niches [Grubb 1977] on the more open forest floor, more abundant nurse logs [Christie and Mack 1984], and with less competition from *Gaultheria shallon*, *Pteridium aquilinum*, and *Polystichum munitum*). Ground-disturbing activities associated with future thinning can be expected to result in a larger proportional increase in weedy plant species abundance in ML than in MT, at least in the short term, though we also expect a rapid increase in seedling establishment and clonal expansion by *Mahonia nervosa*, *Gaultheria shallon*, *Pteridium aquilinum*, *Polystichum munitum*, *Rubus ursinus*, *Vaccinium parvifolium*, *Corylus cornuta*, and other native species frequently found in or near ML. In ML as in MT, increasing the amount of canopy stratification and spatial partitioning by the plant community should result in a greatly expanded multidimensional niche space. In ML we expect a proportionately greater increase in vascular plant richness and diversity after future management than in MT, though again, the absolute numbers are probably less important than the process of niche expansion.

A lack of previous thinnings in ML has allowed the expression of incipient gap formation processes--the ML tract contained a number of gaps created by *Phellinus weirii* (laminated root rot) infection (Carey and others 1999b). Thus, natural patch-forming processes have begun in ML that otherwise would be obscured by repeated thinning.

Where such patches occur in a forest of this age, they provide opportunities to capitalize on preexisting areas of decadence, early crown differentiation, stratification, and variation in understory composition and structure. Naturally occurring patches also suggest that silvicultural management of tree density should emphasize variable relative densities on 0.2- to 0.5-ha scale to reduce homogeneity in the understory and the overstory and to stimulate the development of a wide variety of vegetation site types (Carey and others 1999a).

If forested communities are richest in species adapted to the most commonly occurring patch type (Denslow 1980, Roberts and Gilliam 1995), past management endeavors (especially "broad-brush," extensively applied techniques such as clearcutting, burning, single-species planting, subsequent density control for optimal tree growth, and short rotations) may represent both a departure from historical disturbance regimes and a shift to larger, more homogeneous, and more frequently and predictably created patch types. Widespread use of such extensive management tools creates a new and different selective filter on the landscape (Perry 1998), and it will increase abundance of species most able to establish and reproduce in such managed environments, just as we observed with invasives and abundant clonal species in MT. If natural forests serve as legacy-perpetuating systems wherein the evolutionary memory of genes, cells, species, and communities is preserved and reproduced, then a major challenge of future silvicultural management will be to retain as much of that memory as possible while minimizing the effects of exotics and of novel or unexpected human-related selective filters.

Management-induced disturbances are now the most common type of disturbance in many Pacific Northwest forests and have initial and lasting effects that differ from historical disturbance patterns. Many managed, Douglas-fir forests in the Pacific Northwest differ along continua defined by (1) amount of coarse woody debris, snags, and previous-stand trees retained after harvest and (2) initial and subsequent tree density. These two factors are typically associated with continuous variation in ground-disturbance intensity (e.g., harvest-related disturbances and site preparation). Past management that resulted in forests definable along such continua also brought about variability in the operational factors (Spomer 1972) affecting species distributional patterns. Our ordination implies that availability of water and light for understory plants (axes 1 and 2, fig. 7a) are the major operational factors affected by such management and thus affecting distribution and abundance of the understory species. Variation along the less precisely defined axis 3 (fig. 7b) may have resulted from a range of initial disturbance intensity associated with management, differences in colonization by appropriate species (particularly *Pteridium aquilinum*), and variation in subsequent disturbance during thinning entries. The *ML* and *MT* tracts represent different positions along the two management-created continua and thus along the three ordination axes. Intentional manipulation of snag, woody debris, and legacy retention, and of variation in tree density will thus directly influence the operational factors that determine patterns of understory vascular plant species distribution and abundance.

The *MT* and *ML* tracts present different conditions that we view as having developed primarily in response to two commonly applied strategies of management for wood only. The two tracts now provide distinct opportunities for hypothesis testing relative to important factors in the development of late seral forests such as crown-class differentiation, decadence, crown stratification, gap formation, and understory

development. Conditions in the two tracts are expected to affect forest development in different but quite predictable, ways after future entries. Associated with future forest management are major scientific challenges that include (1) ascertaining how best to ensure continuity of evolutionary legacy-perpetuating systems in managed forests, (2) assessing the use of management to foster development of habitat for late-seral associated species and reduce spread of exotic species, and (3) determining effects of the increasing numbers of exotics on site productivity and ecological function of managed forests. A complete randomized block experiment is now in progress in the MT and ML tracts that uses the same experimental template reported herein to begin addressing aspects of these three challenges. It incorporates variable-density thinning, underplanting of shade-tolerant conifers, direct wildlife habitat augmentation in specific tests of hypotheses concerning enhancement of species and patch-type diversity, and development of late-seral forest attributes through active, adaptive, site-specific, and intentional management (Carey and others 1999b).

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Metric Equivalents

When you know:	Multiply by:	To find:
Millimeters (mm)	0.0394	Inches
Centimeters (cm)	3.94	Inches
Meters (m)	3.281	Feet
Hectares (ha)	2.471	Acres

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