Manipulation of density of *Pseudotsuga menziesii* canopies: preliminary effects on understory vegetation

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Abstract: Managing second-growth forests to conserve biodiversity has been proposed by both foresters and conservation biologists. Management, however, can have unintended consequences, including reduction in native species diversity and increased invasion by exotic species. Our goal was to determine if inducing heterogeneity in managed forest canopies could promote a diversity of native species without contributing markedly to invasion by exotic species. We examined 1- and 3-year responses of understory plants to variable-density thinning of 55- to 65-year-old stands of *Pseudotsuga menziesii* (Mirb.) Franco. Our study stands had been managed either with retention of old-growth legacies (large live trees, dead trees, and fallen trees) and no thinning or with removal of legacies and twice-repeated conventional thinning. Variable-density thinning initially resulted in decreased understory cover but increased importance of 20 native species, including 2 species of trees. Two native species, however, decreased in importance, and 11 exotic species increased in importance. Within 3 years, understory cover recovered, species richness increased by >150%, only four exotic species persisted with increased importance, eight native species (including four graminoids) increased in importance, and seven native species decreased in importance. Variable-density thinning shows promise as part of holistic silvicultural systems applied across landscapes throughout stand rotations and as a technique to restore vegetative complexity to closed-canopy second-growth forests.

Resume : Les forestiers autant que les biologistes qui pronent la conservation proposent d'amenager les forets de seconde venue avec l'objectif de conserver la biodiversite. L'amenagement peut cependant avoir des consequences non souhaitees, incluant la reduction de la diversite des especes indigenes et une augmentation de l'invasion par les especes exotiques. L'objectif de cette etude consistait a determiner si le fait de favoriser l'heterogeneite dans le couvert de forets amenagees pouvait encourager la diversite des especes indigenes sans contribuer de facon appreciable a l'invasion par des especes exotiques. Nous avons examine la reponse des plantes de sous-etage 1 an et 3 ans apres une eclaircie a densite variable dans des peuplements de *Pseudotsuga menziesii* (Mirb.) Franco ages de 55 a 65 ans. Les peuplements choisis daps le cadre de 1'etude avaient ete amenages en conservant des legs biologiques de la foret originale (gros arbres vivants, arbres morts et arbres tombes) sans eclaircie on en eliminant ces legs biologiques et en procedant a deux eclaircies conventionnelles. L'eclaircie a densite variable a initialement entraine une diminution du couvert en sousetage mais une augmentation de l'importance de 20 especes indigenes, incluant deux especes d'arbre. Deux especes indigenes ont cependant diminue en importance et 11 especes exotiques ont augmente en importance. Apres 3 ans, la couverture en sous-etage s'etait retablie, la richesse en especes avait augmente de plus de 150%, seulement quatre especes exotiques persistaient avec une importance accrue, huit especes indigenes (incluant quatre graminees) avaient augmente en importance et sept especes indigenes avaient diminue en importance. L'eclaircie a densite variable s'avere interessante dans un systeme sylvicole holistique applicable a 1'ensemble des paysages au cours de la periode de revolution des peuplements et comme technique pour restaurer la complexite de la vegetation dans les forets de seconde venue a couvert ferme.

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Introduction

Worldwide changes in land use to meet the needs of rapidly expanding human populations present a biodiversity crisis

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(Soule and Terbogh 1999). The need to move beyond biodiversity reserves into managing intervening agricultural and forestry lands to conserve biodiversity has been long recognized (di Castri and Younes 1990; Franklin 1993; Goodland 1995; Hunter 1999). However, there is growing concern that management often simplifies vegetation structure and composition, e.g., through overwhelming dominance of understory vegetation by clonal, native plants (e.g., Tappeiner and Zasada 1993; Carey et al. 1999c; Heckman 1999; Thysell and Carey 2000); decreased plant species richness under closed, often single-species, canopies (Thomas et al. 1999; Wikstrom and Eriksson 2000); persistent seed banks of weedy species that may germinate in

response to thinning (Halpern et al. 1999); and invasion by exotic plants following disturbance of soil and vegetation (e.g., Toney et al. 1998; Heckman 1999; Thysell and Carey 2000; Peltzer et al. 2000).

In the Pacific Northwest of the United States, secondgrowth forests are widespread, and there is considerable debate about how to manage these forests to meet societal demands (McComb et al. 1993; Kohm and Franklin 1997; Carey et al. 1999c) and as the matrix for biological reserves (FEMAT 1993; Hunter 1999; Soule and Terbogh 1999). Commonly used management strategies of legacy retention (retaining large live trees, dead trees, and fallen trees from the preceding forest, without further management or until final harvest) and management for large trees with repeated commercial thinning (removing subordinate and codominant trees, often with salvage of dead and dying trees, and leaving retained trees evenly spaced) have failed to meet diverse demands on forests, particularly demands for maintaining the species composition of biotic communities (e.g., vascular plants, Thysell and Carey 2000; fungi, Colgan et al. 1999; birds, Haveri and Carey 2000; mice, voles, and shrews, Wilson and Carey 2000; squirrels, Carey 2000), sustainability (Carey et al. 1999c; Carey and Harrington 2001), and social acceptability (Ray 1996; Kennett 1998). Computer simulations, however, suggest that ecosystem management emphasizing spatial heterogeneity potentially can meet such diverse needs in a sustainable fashion (Carey et al. 1999c).

We designed an experiment to determine whether manipulation of spatial heterogeneity in the distribution of canopy trees in second-growth *Pseudotsuga menziesii* (Mirb.) Franco, at a similar scale as observed in natural old forests, would contribute to the development of a diverse and patchy understory similar to that found in old forests (Carey et al. 1999b, 1999d). Such intermediate-scale disturbances are thought to optimize native diversity in forests by precluding dominance of the flora by a few native species while minimizing opportunities for invasion and establishment of exotic species (Denslow 1980; Hobbs and Huenneke 1992; Roberts and Gilliam 1995; Tilman 1999). We used variable-density thinning (VDT) (Carey and Johnson 1995; Carey et al. 1999b) to create 13-ha mosaics of 0.16-ha patches of widely varying relative densities of *Pseudotsuga menziesii* in 55- to 65-year-old stands previously managed either with legacy retention or with twice repeated conventional commercial thinning. We hypothesized that VDT would produce understories characterized by (i) diverse species in the short term, say ≤5 years (Halpern and Spies 1995; Roberts and Gilliam 1995); *(ii)* diverse repeating vegetation site types (patches differing in species composition, growth-form variety, and foliage-height diversity) (Whittaker 1975; Carey et al. 1999b) in the long term, say ≥20 years; *(iii)* moderate proportions (=40%) of patches dominated by ericaceous shrubs (e.g., *Gaultheria shallon* Push) or ferns (e.g., *Pteridium aquilinum (L.)* Kuhn in the short term and *Polystichum munitum* (Kaulf.) K. Presl. in the long term) intermixed with patches of low herbaceous cover or moss (Carey 1995); (iv) patches of high foliage-height diversity connecting the forest floor to the overstory canopy through tall shrubs and shade-tolerant trees in the long term (Carey et al. 1992); and (v) transient occupancy by non-native species in the short term, which increase initially in response to

soil disturbance but then decrease in the face of competition from native species in a patchy environment (Thysell and Carey 2000; but see Stohlgren et al. (1999) for an alternative view). We hypothesized that no management (legacy controls) would produce less diverse understories than VDT and that past management by thinning with even spacing would produce less diverse understories more dominated by clonal natives with a larger component of exotic species than understories following VDT.

In our stands, as in many other second-growth stands, historical management produced undesirable understory conditions that could prove difficult to alter (Thysell and Carey 2000). These include *(i)* non-native plant species adapted to disturbance were introduced and could be promoted by additional silviculture (U.S. Congress Office of Technology Assessment 1993; Weber 1997; Toney et al. 1998; Peltzer et al. 2000); *(ii)* clonal natives increased in abundance more so than other native species and could respond strongly to further manipulations to the exclusion of some native species (Tappeiner et al. 1991; Huffman et al. 1994); and *(iii)* clearcutting resulted in densely stocked tree monocultures, maintenance of the competitive exclusion stage for several decades, and concomitant elimination of desirable native species, especially shade-tolerant trees (Halpern et al. 1999).

Although it will take ≥20 years before all our hypotheses can be tested, examining the short-term responses of understory plants to experimental manipulation of canopy heterogeneity in second-growth forests managed under different strategies can help evaluate the rationality of the suite of hypotheses. In this paper we examine stand-level responses of the understory during the first 3 years after inducing canopy heterogeneity using VDT. We examine effects on the composition and abundance of native and exotic understory species and species groups, evaluate the relative contributions of exotic and native species to overall species richness, and assess the relationship between native and exotic species richness.

Methods

Study sites

We sought second-growth forests with histories of management common in the Pacific Northwest that were large enough for replication of experimental treatments in a block design that incorporated four 13-ha stands/block. Most of the Pacific Northwest is mountainous and detailed examination of topography and vegetation in large landscapes has revealed mean stand sizes of 15-18 ha for young forests (Carey and Peeler 1995); thus, our stand size of 13 ha was considered to be realistic. We found four suitable study sites on Fort Lewis Military Reservation in the Puget Trough Physiographic Province, Washington, U.S.A. (Table 1; Carey et al. 1999d). The study sites were at 46°55'42"-46°59'00"N and 122°40'-122°42'W. Elevation ranged from 120 to 165 m, and relief was flat to rolling on glacial uplands, terminal moraines, and glacial till and outwash plains. Soils were coarse-textured gravelly and gravelly-sandy loams. Annual precipitation averaged 800-900 mm with 10-15% falling during the peak growing months of summer. The forests resembled the Pseudotsuga menziesii - Holodiscus discolor association of the Tsuga heterophylla Zone of Franklin and Dyrness (1973). Baseline conditions, e.g., tree heights, heights to live crown, crown widths, diameter at breast height (DBH), densities, and basal areas, were documented by Carey et al. (1999d). Thysell and Carey (2000) reported pre-

Table 1. Pretreatment characteristics (mean ± SE, *n* = 4 stands/block) of four even-aged blocks of *Pseudotsuga menziesii* forest, Puget Trough, Washington, U.S.A; percentages of trees removed during variable-density thinning; and the post-treatment relative density index for the four blocks (from Carey et al. 1999d; Thysell and Carey 2000).

	Block			
	Legacy 1	Legacy 2	Thinned 1	Thinned 2
1992 age at 1.5 m (years)	47±0.3	47±0.3	60±0.4	60±0.4
Tree DBH (cm)	35±2	33±4	54±5	51±5
Density of trees >15 cm DBH (no./ha)	598±33	641±45	225±16	236±22
Relative density index	7.2±0.2	7.2±0.2	6.5±0.2	6.4±0.2
Cover of *Gaultheria shallon* (%)	15±4	12±3	24±4	26±8
Cover of *Mahonia nervosa* (%)	4±1	4±1	4±1	4±1
Cover of *Polystichum munitum* (%)	3±1	3±1	16±3	16±4
Cover of *Pteridium aquilinum* (%)	2±0	2±0	11±2	7±0
Cover of moss (%)	56±8	62±4	31±7	28±6
Total vascular understory cover (%)	34±5	34±6	89±9	87±6
No. of vascular plant species/25-m^2 plot	8±1	9±1	15±1	15±1
Cover of fallen trees (%)	7±0	8±0	2±0	3±0
Percent stems removed	32±2	34±2	24±3	22±3
Post-treatment relative density index	4.9±0.2	4.9±0.2	4.8±0.2	5.0±0.2

experimental percent covers and frequencies for common species and total species richness per stand.

Two of the four areas had been clear-cut ca. 1927 and conventionally thinned twice >10 years prior to our study (initiated in 1991) to final residual densities of about 200 trees/ha (ca. 7 m between trees, Table 1); <1 live tree/ha remained standing from the preceding stand. Standing and fallen dead trees were removed during thinning; thus, coarse woody debris was scarce. The areas were well stocked with *Pseudotsuga menziesii* averaging 53 cm DBH (Table 1). Cover of understory vascular plants was high (87–89%) and dominated by *G. shallon*. Vascular plant species totaled 96 (jackknife estimated mean ± SE of 64.3 ± 3.8 species/13-ha stand based on fifteen 25-m^2 plots), including 19 non-native species (Thysell and Carey 2000). Regeneration of shade-tolerant conifers was relatively low (Carey et al. 1999d).

The other two areas had been clear-cut ca. 1937, with 2.7 live trees/ha and 3.5 dead trees/ha retained from the preceding old-growth forest (Carey et al. 1999d). A few retained trees that were hazardous to helicopters were felled and left on the forest floor 10 years prior to our study, but no further silvicultural manipulations had been undertaken. Coarse woody debris included tall stumps of old-growth trees (averaging 48/ha), old well-decayed, fallen trees (8% cover), a few lightly to moderately decayed felled old-growth trees, and abundant (3% cover) fallen small-diameter trees that had died from suppression or root rot *(Phellinus weirii* (Murr.) Gilbn.). Hereafter, we refer to these conditions as legacy conditions. Cover of understory vascular plants averaged 34% and was dominated by *G. shallon* of relatively low stature; understory cover was higher in pockets of root-rot infestation where most trees were dead or had reduced foliage (Carey et al. 1999d). Vascular plant species totaled 47 (32.0 ± 1.4 species/13-ha stand), one of which was an exotic, *Ilex aquifolium L.* (Thysell and Carey 2000). Canopy *Pseudotsuga menziesii* (Table 1) were small (=34 cm DBH) and crowded (=600 stems/ha, 4 m between trees). No regeneration of shade-tolerant conifers was observed (Carey et al. 1999d) .

The study areas exemplified two types of conditions presently found in Pacific Northwest forested landscapes managed under long (>60 years) rotations: *(i)* intensive management for high-quality timber (thinned) and *(ii)* extensive management with biological legacies retained from preceding stands (legacy). Both types were past the common harvest age for industrial forest lands

(40–50 years) and approaching the age (>70 years) at which forests are commonly harvested on public lands (Carey et al. 1999c; Carey 2000).

Experimental design

Our study was part of a larger complete randomized blocks experiment consisting of four treatments: control, addition of nest boxes for squirrels (Sciuridae), VDT, and nest box addition combined with VDT (Carey et al. 1999d). We demarcated one cluster of four 13-ha stands, with boundaries ≥ 80 m apart, in each of the four study areas. We designated these clusters experimental blocks. We randomly assigned the four treatments to the four stands within each block. The nest-box treatment, however, was irrelevant to our study of vegetation. Thus, even though 8 of the 16 stands, two in each block, were randomly assigned either VDT or no treatment for this study, the two similarly treated stands per block are repeat samples of the block, not experimental replicates; thus, we combined sampling plots from similarly treated stands within blocks. In addition we sampled vegetation in two different time periods after thinning. Thus, the design evolved into a split-plot analysis of variance (ANOVA) design with VDT as the whole-plot factor and year sampled (time) as the split-plot factor. As conditions necessary to meet assumptions of explicit hypothesis testing in ecological studies are rarely met (Anderson et al. 2000), we used ANOVA as an exploratory tool to examine the preliminary effects of treatment on understory species. We used P < 0.05 as the cut-off point for statistical significance in the ANOVA and P < 0.10 as the significance level in the analysis of indicator values.

Experimental treatment

Variable-density thinning has been hypothesized to create spatial heterogeneity in canopies of second-growth stands that could lead to vegetative vertical structure and understory heterogeneity similar to that in old growth (Carey and Johnson 1995; Carey et al. 1999b). By removing subordinate trees (and if necessary, codominant trees), VDT results in small patches such that light, water, nutrients, and space become available spatially in various amounts to other vegetation (Carey et al. 1999b, 1999d). Effects go beyond conditions immediately below the altered canopy, however, as low sun angles in the Pacific Northwest combined with finescale heterogeneity create a diverse mosaic of environmental conditions

Fig. 1. Spatial heterogeneity in forest canopies. (A) Densities of trees >50 cm DBH in a 280-year-old Pseudotsuga menziesii oldgrowth forest; shading (light to dark) represents densities that range from 3 to 45 trees/ha, based on 225 sampling points (data from Carey et al. 1999b). A grid from Fig. lB is superimposed to provide scale. (B) Relative densities of Pseudotsuga menziesii >20 cm DBH following VDT of a 56-year old second-growth stand; shading (light to dark) shows relative density classes of <3.25, 3.25-4.75, 4.75-6.75, and >6.75 as measured in the cells of the sampling grid (data from Carey et al. 1999c)

(A)

(B)
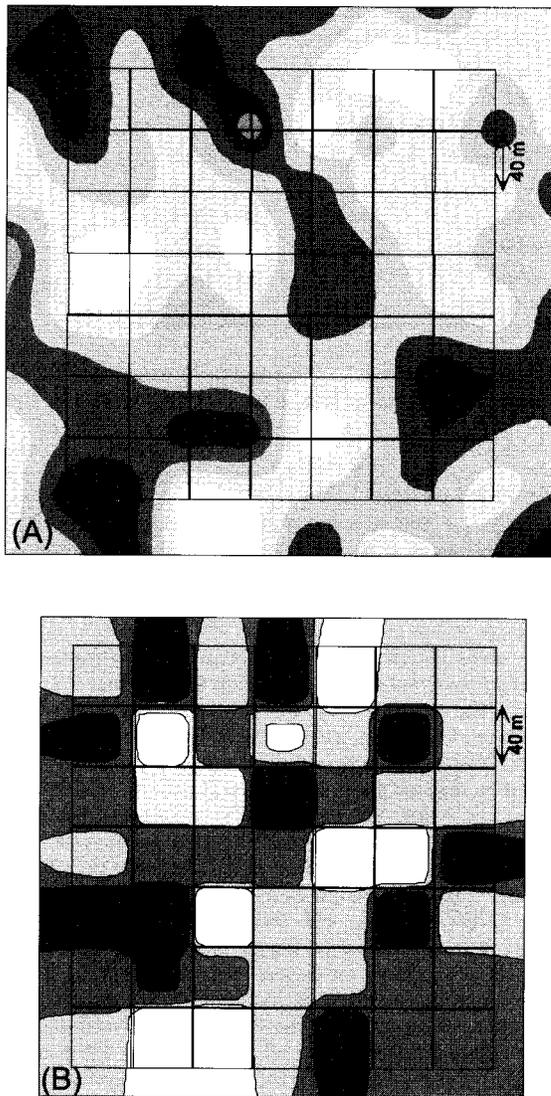
and numerous patch types (Canham et al. 1990). Carey et al. (1999b) mapped tree densities (Fig. IA), canopy cover, understory vegetation site types, and understory covers in numerous old-growth forests in a study of the effects of spatial heterogeneity on plants and wildlife. They suggested that thinning to produce a mosaic of 0.1- to 0.5-ha patches with a 2:1 ratio of patches with high relative densities (RD = 5.0) of canopy trees to patches of low RD (RD = 3.5) would help accelerate development of stand structure and heterogeneity characteristic of late-seral forests. Relative density is the ratio of basal area to the square root of quadratic mean DBH and is an index of relationships among quadratic mean DBH, stem density, basal area, and intercrown competition of Pseudotsuga menziesii (Curtis 1982). Relative density ranges from 0

(no trees) to a species-specific biological maximum of 14; excessive crown restriction leading to suppression mortality occurs with RD > 7. We designed our VDT following Carey et al. (1999b) but tailored it to on-the-ground conditions in our study areas (Carey et al. 1999d). First, we subdivided each stand with a 8 x 8 surveyed grid with grid points 40 m apart and with a 40-m buffer around the grid. We conducted a reconnaissance survey of the resulting grid cells and found root rot (*Phellinus weirii*) forming small gaps; 0-15% of the area of each stand had reduced canopy density because of root rot. We designed a root-rot treatment that produced an RD = 2 and assigned that treatment to 15% of the area of all treated stands (using random assignment to cells when root rot was not evident). Given the low-density root-rot treatment, high densities of small trees in legacy stands susceptible to windthrow upon thinning, and relatively low densities of large *Pseudotsuga menziesii* in thinned stands that were beginning to have separated crowns, we took a more conservative course than suggested by Carey et al. (1999b). We randomly treated the remaining cells to achieve a ratio of 2:1 of moderately closed (RD = 6) and moderately open (RD = 4) 0.16-ha patches of canopy, well interspersed across the stands. Buffers between treated stands were lightly thinned. Implementation of this design produced a 2:1 ratio of lightly thinned (RD > 4.75) to heavily thinned (RD < 4.75) grid cells (Fig. 1B).

Experimental thinning was completed during January-April, 1993 and removed 36% of trees >20 cm DBH and 30% of basal area from legacy stands, and 27% of trees >20 cm DBH and 24% of basal area from thinned stands. Mean relative density was reduced from 7.2 to 4.9 in legacy stands and from 6.5 to 4.9 in previously thinned stands (Carey et al. 1999d). Vegetation sampling following thinning was based on stratified random sampling of RD classes assigned to cells. Subsequently, a silvicultural assessment discovered operational errors during thinning (areas skipped by loggers or areas thinned too much or too little) that did not affect the ratio of light to heavy thinning but that did require us to use weights based on proportions of RD classes sampled when calculating stand means of vegetation variables (Carey et al. 1999d). Hereafter, we refer to experimentally treated stands as legacy VDT (from legacy blocks) or thinned VDT (from thinned blocks) and experimentally untreated stands as legacy controls and thinned controls.

Vegetation sampling

Prior to our experiment, Thysell and Carey (2000) sampled the vegetation using 25-m² plots at 15, systematically selected, grid points in each of the 16 stands (240 plots total). Because all stands had fine-scale heterogeneity and legacy stands had low understory cover, we found that plots tended to have either high or low cover values and few species; thus, in this study we used larger, 100-m² plots that were small enough for accurate estimates of cover (Gauch 1982) but large enough to represent conditions in a cell. We placed 100-m² plots in the centers of 191 grid cells: 6 in each control stand and 18 in each VDT stand (6 plots/thinning intensity), except one stand that had 17 plots. We sampled vegetation in July-August 1994, which was 14-18 months after VDT, and again in July-August 1996, which was 38-42 months after VDT. We visually estimated the percent cover for each species (mosses as group) on an octave scale modified from Gauch (1982): (1) >01%; (2) >1-3%; (4) >3-6%; (8) >6-12%; (16) >12-24%; (32) >24-48%; and (64) >48-100%. Subsequently, species were assigned to categories based on their life histories and growth habit: forest-floor mosses, graminoids (grasses, sedges, and rushes), ferns, herbs, trailing shrubs and vines, low shrubs (<2.0 m tall), and tall shrubs or understory trees, typically ≥2 m in height but below the forest canopy. Where we assigned ≥2 species to a group for analysis, we summed individual species cover estimates to arrive at a group estimate. Nomenclature follows Kartesz (1994), and

identifications of species and their origins (e.g., native or exotic) were based on regional guides (Hitchcock and Cronquist *1973;* Klinka et al. *1989;* Pojar and MacKinnon *1994).*

Data analysis

Diversity was assessed as species richness (number of species per 100 m^2 for plot-level richness and jackknife estimates (Palmer *1990)* of number of species per *600* m^2 for stand-level richness); the Shannon diversity index (H'), which incorporates both species richness and abundance; and evenness (E), which is the ratio of observed *H'* to the maximum *H'* that would occur if all species were equally abundant (Magurran *1988).* We used cover-class midpoint percentage as the measure of species abundance in calculating *H'* and E. We generated species-area curves for native and exotic species for each treatment and year, where the number of species per unit area was the average number of species based on subsampling up to *500* times (McCune and Mefford *1999).* We compared species accumulation among groups based on all *48* control-stand plots *(4800* m^2) and 48 of *143* VDT-stand plots *(4800* m^2). Hereafter, we refer to the scales of measurement of diversity as plot(mean of 100-m^2 plots), stand- (jackknife estimates based on six 100-m^2 plots), block- (Palmer *(1990)* jackknife estimates based on twelve 100-m^2 plots), and treatment-level (total species on plots totaling *4800* m^2) species richness.

We used split-plot univariate ANOVA to test for differences in species richness, percent cover, and diversity due to VDT, year, block, and VDT by year interaction. Our ANOVA was a balanced design based on 2 years and two values (one control and one VDT) in each of the four blocks. All response variables in our analysis were means for each combination of sampling year, treatment, and block, thus meeting the requirements of normality under the central limit theorem. Replicates were too few for realistic statistical tests of assumptions of normality and homoscedasticity. Means were based on twelve 100-m^2 plots from two control stands per block (arithmetic mean) and *35* or *36* plots from the two VDT stands per block (weighted mean), where weights were calculated as the actual proportions of RD classes in the total number of VDT cells per block.

To identify species characteristic of VDT or control stands in *1994* and *1996,* we calculated indicator values (IV) as defined by Dufrene and Legendre *(1997).* A species IV, in percent, is its relative abundance times its relative frequency. Relative abundance, for this purpose, is defined as the average cover of a species in a group of plots divided by its average cover in all plots; relative frequency, for this purpose, is defined as the percentage of plots within a group in which a species is present. We evaluated the statistical significance of the maximum IV (IV_{max}) for the four groups using a Monte Carlo method with 1000 permutations to produce randomized IV_{max} values. The P values were calculated as proportions of permutations in which the IV_{max} from the randomized data equaled or exceeded the observed IV_{max} (Dufrene and Legendre *1997;* McCune and Mefford *1999).* For heuristic reasons, species with P values $\leq$ 0.10 were considered to be statistically significant. All calculations were made with the Statistical Package for the Social Sciences (SPSS) version *9.0* for Windows or with PC-ORD, a program for multivariate analysis of ecological data (McCune and Mefford *1999).*

Results

Block differences

Blocks with a history of conventional thinning had greater total understory cover and greater cover of dominant perennials than legacy blocks prior to VDT (Table 1). Conventionally

thinned blocks had more total species (96 vs. 47), more species per stand (64.3 ± 3.8 vs. 32.0 ± 1.4), more species per 25-m^2 plot (15 ± 1 vs. 8.5 ± 1), and a higher percentage of exotics (20 vs. 2%) than legacy blocks. Prior to VDT, we found only one nonnative species in the legacy blocks but 19 non-native species in the thinned blocks.

Experimental effects on plant species diversity

Plant species richness was greater in VDT than in controls, including total species per plot, native species per plot, native shrub species per plot, and species per block (Tables 2 and 3, Fig. 2). Percent exotic species was significantly greater in VDT than in controls, markedly in year 1 with differences decreasing somewhat by year 3 (Tables 2 and 3). On a plot level, richness and percent exotics were strongly and positively correlated *(r =* 0.94). Shannon diversity (H') and Shannon evenness (E) were greater in VDT stands than in controls in 1994, but the differences decreased somewhat with time as exotic-species cover and richness declined (Tables 2 and 3). Richness of mycotrophs (Pyrolaceae, Monotropaceae, and Orchidaceae; sensu Cronquist (1981)) in plots was less in VDT than in controls.

We recorded a total of 170 species of vascular plants (vs. a jackknife estimate of 114 species reported prior to treatment); most (111 species) had frequencies of occurrence $\leq$10%; fifty-five species were exotic (vs. 19 species prior to treatment). In control plots *(n =* 48 plots, 4800 m^2), we found 77 and 78 species, 16 and 13% exotic, in 1994 and 1996, respectively. In VDT plots (4800-m^2 basis), we found an average of 117 and 120 species (40 more species than in controls), 30 and 26% exotic, in 1994 and 1996, respectively; VDT had three times the number of exotics as controls. Similarly, VDT had more exotic species per plot (3.8/plot in 1994 and 2.6/plot in 1996, with a significant decrease between years) than controls (0.4/plot in 1994 and 0.3/plot in 1996).

Graphical analysis of the combined effects of management history and experimental treatment revealed that, in 1996, greatest richness (number of species per stand) and lowest variance in richness for both native (Fig. 3A) and exotic (Fig. 3B) species occurred in the thinned VDT condition. Native species richness in legacy VDT stands reached thinned control levels; native species richness in thinned VDT stands was greater than in thinned controls. Exotic species richness was greater in both legacy VDT and thinned VDT stands than in controls.

Experimental effects on understory cover

Variable-density thinning did not have significant effects on cover of understory plants, but year and year x treatment interactions were significant (Table 2). Cover was less in VDT than in controls immediately after treatment but increased in VDT (but not controls) during the next 2 years. Covers of native shrubs and dominant perennials were reduced in VDT compared with controls but recovered to equivalent or greater covers than in controls. Differences were largely due to changes in the cover of *G. shallon* (Table 2). Cover of exotic species was substantially greater in VDT than in controls 1 year after VDT (10.2 vs. 0.8%), but the difference declined over the next 2 years along with a decline in percentage of species that were exotic (Tables 2 and 3). Of the 170 species found during sampling, only four were recorded with >5% cover: one evergreen shrub variable

Table 2. Variables (mean ± SE from 100-m² plots) showing statistically significant effects of variable-density thinning (VDT) 1 year (1994) and 3 years (1996) after treatment compared with untreated control stands in the Puget Trough, Washington, U.S.A.

Response variable	Treatment and year				Effect[a]
	Control 1994	VDT 1994	Control 1996	VDT 1996	
Cover of native woody species (%)[b]	47.3±10.5	32.1±6.3	45.8±11.7	41.9±13.4	2, 3
Cover of exotic species (%)	0.8±0.4	10.2±2.8	0.6±0.3	7.1±1.4	1
Cover of dominant perennials (%)[c]	55.1±13.8	40.5±11.3	53.5±15.3	60.5±17.3	2, 3
Cover of *Gaultheria shallon* (%)	34.8±8.7	17.9±4.4	31.2±8.6	25.7±3.8	2, 3
Total species richness/100-m² plot	15.7±1.3	27.5±2.6	17.2±1.4	24.9±1.9	1, 3
Native species richness/100-m² plot	15.3±1.1	22.1±1.5	16.9±1.2	21.3±1.4	1, 3
Percent exotic species/100-m² plot[d]	2.3±1.0	17.0±2.2	1.7±1.0	12.4±1.1	1, 2, 3
Native woody species richness/100-m² plot	4.8±0.5	6.7±0.5	5.0±0.4	6.7±0.6	1
Mycotroph richness/100-m² plot[e]	0.6±0.2	0.5±0.2	1.0±0.3	0.6±0.2	1
Total species/treatment per block[f]	45.3±6.3	76.9±7.6	48.0±6.7	76.9±5.0	1
Shannon diversity index (*H'*)	1.9±0.1	2.7±0.0	2.0±0.1	2.5±0.0	1, 2, 3
Shannon evenness (*E*)	0.7±0.0	0.8±0.0	0.7±0.0	0.8±0.0	1, 2, 3

[a]Significant effects at $P \leq 0.05$ resulting from treatment (1), year (2), or treatment × year (3). [b]
Combined cover of all native, woody, understory species.
[c]Combined cover of *Gaultheria shallon, Polystichum munitum, Pteridium aquilinum,* and *Rubus ursinus.* [d]
Percentage of all vascular plant species per plot that were exotic.
[e]Obligate mycotrophic members of the families Pyrolaceae, Monotropaceae, and Orchidaceae (Cronquist 1981), including the genera *Chimaphila, Pyrola, Monotropa, Corallorhiza, Goodyera,* and *Listera.*
[f]The total number of species in twelve 100-m² control plots per block was compared with an equal number of VDT plots by randomly subsampling 12 of 36 VDT plots in the same block 500 times to arrive at a mean value for 12 plots (McCune and Mefford 1999).

Table 3. Analysis of variance of block, treatment, year, and year × treatment effects 1 year (1994) and 3 years (1996) after variable-density thinning, Puget Trough, Washington, U.S.A.

Response variable	Block (df = 3,15)		Treatment (df = 1,15)		Year (df = 1,15)		Treatment × year (df = 1,15)	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Total understory cover (%)[a]	27.11	0.011	2.00	0.252	2.99	0.134	2.60	0.157
Cover of native woody species (%)[a]	4.32	0.130	1.46	0.313	10.96	0.016	20.60	0.004
Cover of exotic species (%)[a]	2.10	0.279	22.45	0.018	4.46	0.079	3.24	0.122
Cover of dominant perennials (%)[b]	109.06	0.001	1.99	0.253	6.60	0.042	9.19	0.023
Gaultheria shallon (%)	1.58	0.358	1.77	0.275	8.75	0.025	66.91	0.000
Polystichum munitum (%)	2.54	0.232	0.13	0.740	5.27	0.062	0.11	0.750
Pteridium aquilinum (%)	12.65	0.033	5.54	0.100	3.30	0.119	4.41	0.081
Rubus ursinus (%)	2.83	0.208	3.37	0.164	4.36	0.082	4.96	0.068
Species richness/100-m² plot	4.92	0.112	41.90	0.007	1.43	0.277	18.85	0.005
Native species richness/100-m² plot	6.42	0.081	33.75	0.010	3.18	0.125	26.96	0.002
Percent exotic species/100-m² plot (%)[c]	9.81	0.046	246.11	0.001	15.81	0.007	10.00	0.020
Native woody species richness/100-m² plot	2.98	0.197	13.24	0.036	0.97	0.363	0.52	0.498
Mycotroph richness/100-m² plot[d]	59.32	0.004	16.00	0.028	3.00	0.134	1.98	0.209
Total species/treatment per block[e]	34.51	0.008	195.35	0.001	0.92	0.374	0.99	0.358
Shannon diversity index (*H'*)	0.66	0.628	32.61	0.011	7.20	0.036	53.44	0.000
Shannon evenness (*E*)	9.32	0.050	20.69	0.020	7.63	0.033	31.11	0.001

[a]Combined cover of all species in the respective groups.
[b]Combined cover of *Gaultheria shallon, Polystichum munitum, Polystichum aquilinum,* and *Rubus ursinus.*
[c]Percentage of all vascular plant species per plot that were exotic.
[d]Obligate mycotrophic members of the families Pyrolaceae, Monotropaceae, and Orchidaceae (Cronquist 1981), including the genera *Chimaphila, Pyrola, Monotropa, Corallorhiza, Goodyera,* and *Listera.*
[d]The total number of species in 12 control plots per block were compared with an equal number of VDT plots by randomly subsampling 12 of 36 VDT plots in the same block 500 times to arrive at a mean value for 12 plots (McCune and Mefford 1999).

in height (0.2-5 m) and creeping to erect in form *(G. shallon,* 26% cover), one deciduous trailing shrub *(Rubus ursinus* Cham. & Schldl., 8% cover), one evergreen fern *(Polystichum munitum,* 10% cover), and one deciduous rhizomatous fern *(Pteridium aquilinum, 10%* cover). After these four, the next most abundant species (across all plots and both years) were a short (<10 cm), erect, semiwoody evergreen shrub *(Linnaea borealis,* 5% cover); a taller

Fig. 2. Species area curves for native (squares) and exotic (circles) species in variably thinned (open symbols) and control (solid symbols) plots 1 year (solid lines) and 3 years (broken lines) after thinning in the Puget Trough, Washington, U.S.A. Number of species per unit area was calculated as the average number of species based on subsampling 48 control plots and 48 of 143 experimental plots 500 times (McCune and Mefford 1999).
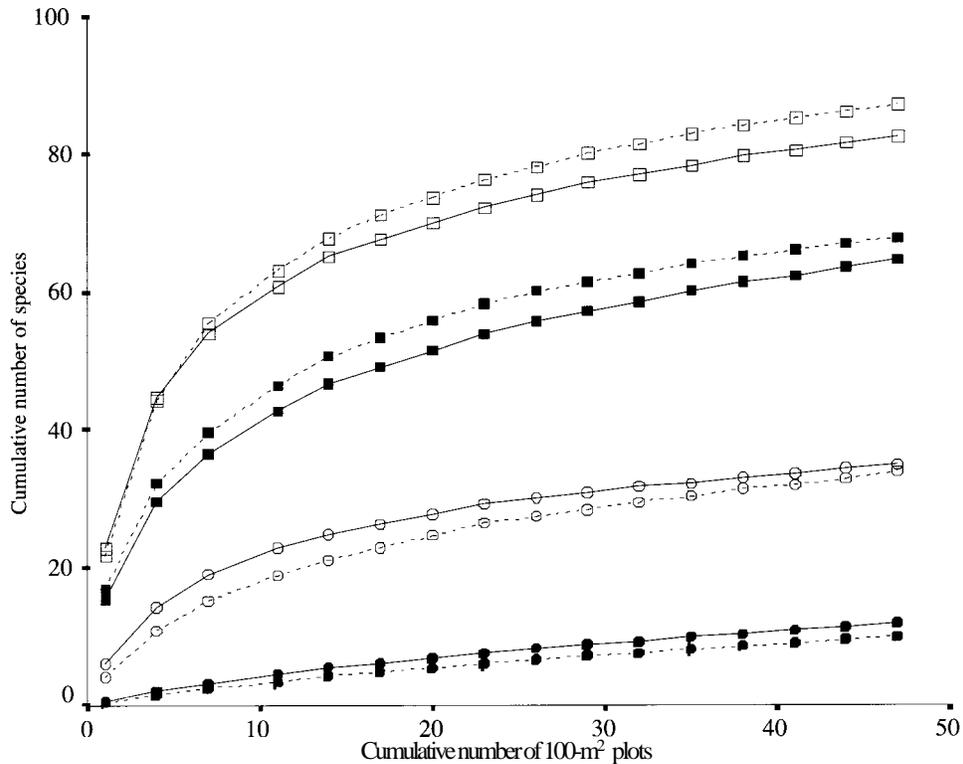
(<60 cm), stiff-branched, evergreen shrub *(Mahonia nervosa* (Pursh) Nutt., 4% cover); and two tall deciduous shrubs, *Corylus cornuta* (4% cover) and *Holodiscus discolor* (Pursh) Maxim. (2% cover).

Graphical analysis of the combined effects of management history and VDT suggested that, by 1996, cover of dominant perennials in legacy VDT increased only in areas of low cover; the variance in perennial cover was lower, but the mean only slightly larger, compared with controls (Fig. 4A). In contrast, variance in perennial cover increased in thinned VDT concomitant with an increase in mean cover (Fig. 4A). Thinned stands maintained higher covers of dominant perennials than developed in legacy VDT. Herbaceous plant cover increased markedly in legacy VDT to a level such that total vascular plant cover there exceeded that in thinned controls (Fig. 4B). Total vascular plant cover in thinned VDT was higher than in any other stand condition in 1996.

Native species with significant indicator values included two species *(Anemone deltoidea* and *Corallorhiza maculata)* characteristic of controls and 18 species indicative of VDT (Table 4). All but 2 of these 18 were herbaceous (11) or graminoid (5) species. The maximum indicator values for 7 of the 11 herbs occurred in 1994, whereas the maxima for four of the five graminoids and for two tree species *(Alnus rubra* Bong. and *Populus balsaminifera L.* var. *trichocarpa* (Tory. & A. Gray) Brayshaw) occurred in 1996. None of the dominant perennials were indicative of year or treatment. Of the other 35 species showing significant IV maxima (P <

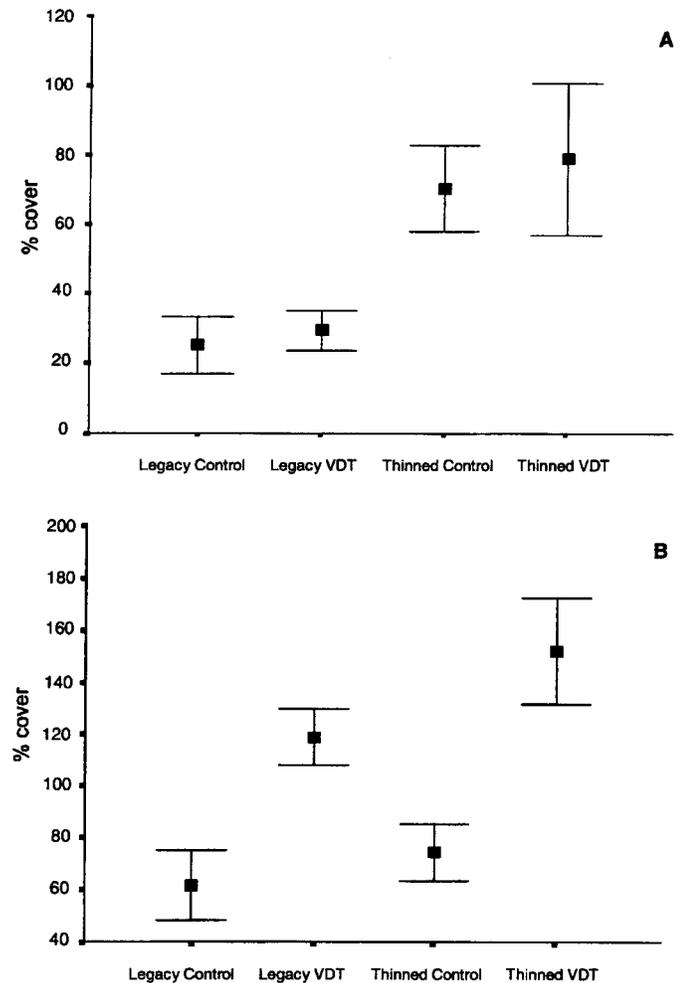0.10), 15 were exotics indicative of VDT treatments (11 in 1994 and 4 in 1996).

Discussion

Variable-density thinning dramatically affected the diversity of understory plants in the first 3 years after thinning. As expected, most effects seemed to be short-term disturbance effects due to removal of trees as opposed to hypothesized long-term effects of changes in the spatial pattern imposed on the canopy. We hypothesized that VDT would result in increased species diversity (first hypothesis) and transient occupancy by additional non-native species (fifth hypothesis) in the short term. Before treatment, legacy stands had abundant moss, sparse ferns and shrubs (M. *nervosa* and G. *shallon)* interspersed with patches of denser and taller G. *shallon* and *Alnus rubra* near root-rot pockets, and relatively low vascular plant diversity (47 species). Three years after VDT, species diversity and vascular plant cover had increased markedly supporting our first hypothesis. Before VDT, thinned stands had dense understories dominated by moderate covers of moss, ferns, and robust G. *shallon* (Carey et al. 1999d); species richness was high (96 species). Three years after VDT, species richness and vascular plant cover had increased. Thus, as hypothesized and without regard to management history, the number of species increased markedly following VDT (by 173%); however, 65% of species were rare. Only four species, all perennials, had average covers >5%. Mycotrophs were

Fig. 3. Mean vascular plant species richness per 600-m² sample per stand *(n = 4 stands/condition)* in untreated legacy stands (legacy control), legacy stands treated with variable-density thinning (legacy VDT), conventionally thinned stands (thinned control), and 3 years after VDT (thinned VDT): (A) native species; (B) exotic species. Error bars are 95% confidence intervals.

Fig. 4. Mean total vascular plant cover *(n = 4 stands/condition)* in untreated legacy stands (legacy controls), legacy stands treated with variable-density thinning (legacy VDT), conventionally thinned stands (thinned control), and 3 years after VDT (thinned VDT): (A) native species; (B) exotic species. Error bars are 95% confidence intervals.
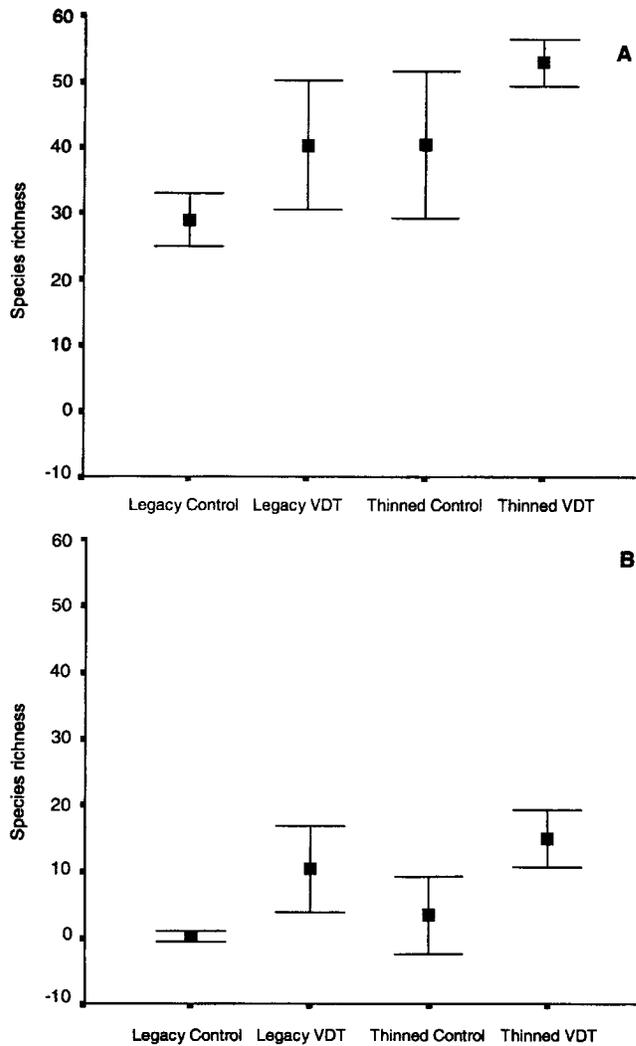
reduced in abundance, an unexpected finding signaling potential long-term loss of diversity with continued VDT. The number of exotic species increased initially (by 280%) but decreased in abundance (by 30%), number (by 27%), and importance value (11 of 15 species) from the first year to the third year after VDT, supporting our fifth hypothesis of transient occupancy by non-native species. Thinned VDT, however, retained more exotic species than thinned controls, and it is too early to tell if newly established exotic species will persist through time. Indicator species for control conditions were one mycotrophic and one herbaceous species; indicators of VDT included 5 graminoids, 11 herbs, and 2 trees (*Alnus rubra* and *Populus balsaminifera).* Indicator species confirmed the results of species richness; VDT leads to increased species diversity, growth-form variety, and foliage-height diversity supporting the long-term second hypothesis but suggesting a potential reduction in number of species in the mycotrophic life form contrary to the second hypothesis.

Variable-density thinning dramatically affected abundance of understory plants in the first 3 years after thinning. We predicted that legacy controls would have understories with lower cover and fewer life forms than legacy VDT and that thinned controls would have understories more dominated by clonal natives and exotics than thinned VDT. As predicted, understory cover, especially herbaceous cover, increased markedly in legacy stands, even well beyond herbaceous cover in conventionally thinned controls. Clonal natives continued to dominate the understories in thinned controls, but herbaceous cover in legacy VDT and thinned VDT was greater than or equivalent to the cover of the dominant perennials. A variety of perennial life forms benefited from VDT, supporting the third hypothesis, which predicted an intermixing of patches of shrubs and ferns with herbaceous species. Shade-tolerant trees, however, remained rare. The rarity of shade-tolerant regeneration suggests that hypothesized long-term effects of increased site-type diversity, growth-form variety, and foliage-height diversity (the second and fourth hypotheses) may not materialize without addi

Table 4. Indicator values for vascular plant species in control and variably thinned (VDT) stands 1 year (1994) and 3 years (1996) after treatment in the Puget Trough, Washington, U.S.A.

Species	Control 1994	Control 1996	VDT 1994	VDT 1996	P
*Agrostis capillaris**	0	0	25	67	0.043
Alnus rubra Bong.	3	5	20	64	0.067
Anaphalis margaritacea (L.) Benth. & Hook	1	5	37	51	0.004
Anemone deltoidea Hook.	15	54	0	0	0.083
Campanula scouleri Hook. ex A. DC.	7	14	40	31	0.090
Cirsium arvense (L.) Scop.*	0	0	60	40	0.016
Cirsium brevistylum Cronq.	0	0	75	19	0.010
Cirsium vulgare (Savi) Tenore*	0	0	77	23	0.004
Corallorhiza maculata Raf.	18	42	19	15	0.010
Crepis capillaris (L.) Wallr.*	1	1	51	42	0.044
Deschampsia elongata (Hook.) Munro	0	0	64	4	0.052
Epilobium angustifolium L.	2	2	38	45	0.089
Epilobium glaberrimum ssp. *glaberrimum* Barbery	0	0	69	29	0.004
*Erechtites minima** (Poir.) DC.	0	0	90	7	0.016
Festuca occidentalis Hook.	7	7	38	43	0.050
Festuca subulata Trin.	4	4	8	51	0.066
Fragaria crinita Rydb.	0	0	0	75	0.035
Gnaphalium purpureum L.*	0	0	70	2	0.030
Holcus lanatus L.*	0	2	36	59	0.030
Hypericum perforatum L.*	0	0	28	72	0.014
Hypochaeris radicata L.*	2	0	48	45	0.092
Juncus effusus var. *gracilis* L.	0	0	4	63	0.037
Lactuca biennis (Moench) Fern.	0	0	75	0	0.034
Lathyrus polyphyllus Nutt.	12	8	31	43	0.024
Lotus micranthus Benth.	1	0	59	27	0.036
Lupinus rivularis Dougl. ex Lindl.	0	0	66	34	0.015
Luzula parviflora (Ehrh.) Desv.	2	2	0	83	0.003
Populus balsamifera ssp. *trichocarpa* Torr. & A. Gray) Brayshaw	0	0	9	81	0.006
Senecio jacobea L.*	8	0	60	24	0.033
Senecio sylvaticus L.*	1	1	82	4	0.004
Sonchus asper (L.) Hill*	0	0	84	16	0.004
Trifolium arvense L.*	0	0	0	75	0.037
Trifolium campestre Schreb.*	0	0	75	0	0.030
Trifolium repens L.*	0	0	74	0	0.061
Vicia americana Mühl.	0	8	66	13	0.019

Note: Plots were randomly assigned to groups 1000 times in a Monte Carlo simulation. The P value is the proportion of 1000 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 Mefford 1999).

*Non-native species.

tional treatments; e.g., underplanting of shade-tolerant species.

Exotic species

Of the exotic species indicative of VDT, many were annuals or biennials, and as expected, they declined from 1994 to 1996. However, some exotic species, notably the sod-forming grasses *Agrostis capillaris* and *Holcus lanatus,* increased from 1994 to 1996, suggesting novel life forms could become increasingly abundant in *Pseudotsuga menziesii* forests in response to frequent and widespread managerial disturbance. Grasses that form dense sods are not

normal components of these forests (Franklin and Dyrness 1973) and may compete with native grasses and herbs.

The rate of introduction of new species is high in the Pacific Northwest (Toney et al. 1998). Exotic species are regularly found in managed forests, and traditional silviculture (e.g., clear-cutting, burning, and conventional thinning) creates opportunities for exotic species to become established and to grow in some areas at the expense of herbaceous natives (Deferrari and Naiman 1994; Heckman 1999; Thysell and Carey 2000). Similar phenomena have been reported for boreal forests (e.g., Peltzer et al. 2000). Our study has not been long enough to determine whether or not increasing

spatial heterogeneity in stands historically managed as monocultures with conventional thinning can subvert established non-natives, including *I. aquifolium, Hedera helix,* exotic species of *Prunus* and *Rubus,* and the sod-forming grasses. The exotic shade-tolerant *I. aquifolium* and *Prunus* spp. have the potential to become a midstory stratum now missing in Puget Trough forests. *Hedera helix L.* inhabits many urban, suburban, and managed lowland forests already and has the potential to impede regeneration of both *Pseudotsuga menziesii* and native shade-tolerant tree species (Thysell and Carey 2000; D. Peters, unpublished data). Certainly, these species portend forested associations of the future that differ from those of the present. Although we found that VDT increases numbers of exotics, we hypothesize that most exotics will decline as aggressive natives increase in response to VDT. However, conventional thinnings maintained 19 species of exotics on our sites for >15 years beyond thinning, even in the face of robust growth of *G. shallon, Polystichum munitum,* and *Pteridium aquilinum.* Shade-tolerant conifers in the understory might be necessary to create the kind of patchy, competitive environment that promotes native species diversity at the expense of exotics (Carey et al. 1999b; Thysell and Carey 2000).

Invasion by exotic plant species depends on the type of disturbance, frequency of disturbance, and existing diversity in the plant community (Elton 1958; Fox 1990; Hobbes and Huenneke 1992). For example, understory composition in managed forests of the Pacific Northwest varies with type of disturbance soon after disturbance (Halpern 1988, 1989; North et al. 1996; Bailey and Tappeiner 1998; Thysell and Carey 2000) and disturbance effects may persist for centuries (Alaback 1982; Alaback and Herman 1988). Silviculture may change relationships among native and exotic species and has the capacity to alter ecosystem composition, structure, and development in the near- and long-term in various ways (Carey et al. 1999c). Intense, stand-replacing disturbance results in massive invasion by ruderal species; subsequent freedom from disturbance can result in rapid canopy closure, failure to develop understories of native species, and maintenance of the seeds of ruderal species in soil seed banks (Halpern et al. 1999; Carey and Harrington 2001). Intense disturbance followed by relatively open stand conditions maintained by conventional thinning can maintain numerous exotic species and dominance by native perennials, such as in our thinned stands. With such conventional forest management, increases in exotics may be accompanied by a loss of native herbaceous species, few of which have the ability to expand or reproduce as rapidly as the exotics (Halpern et al. 1999; Lezberg et al. 1999). It has yet to be determined if increasing heterogeneity in within-stand environmental conditions will promote a diversity of vegetation site types, including shade-tolerant trees, that will promote resistance to invasion by exotics, even in the face of minor to moderate disturbances.

Native species

The nature, frequency, and intensity of disturbance also influences the development of native understories (Spies and Franklin 1989; Tappeiner and Zasada 1993; Huffman et al. 1994; Gray and Spies 1996; North et al. 1996; Bailey and Tappeiner 1998). The nature of the disturbance determines the variety of regeneration niches for understory plants and how quickly some understory or overstory species outcompete (shade out) other species. Site characteristics and seed or seedling sources are important (Tappeiner and Zasada 1993; Huffman et al. 1994; Gray and Spies 1996). For example, conventional thinning may promote *(i)* one or more clonal natives (e.g., *Rubus spectabilis* Pursh, G. *shallon, Acer circinatum* Pursh, *Acer macrophyllum* Pursh) that may delay or prevent regeneration of even shade-tolerant conifers or *(ii)* dense conifer regeneration that shades out shrubs and herbs. Theoretically, then, VDT has the potential to promote a diversity of vegetation site types when seeds or seedlings of native plants are present. Native species richness increased in response to VDT in 1994 but, unlike exotic richness, did not decline from 1994 to 1996. Richness and lifeform diversity of native shrubs and trees was promoted by VDT, thus building our confidence in effects of VDT on hastening structural diversification. Structural diversification, however, requires growth of shade-tolerant conifers (North et al. 1999; Carey et al. 1999b). Frequent disturbance can lead to dense, homogeneous understories, including overwhelming dominance by clonal natives as in our thinned stands (Tappeiner and Zasada 1993; Bailey and Tappeiner 1998). On mesic to xeric sites, disturbance can favor clonal shrubs and *Alnus rubra* and *Pseudotsuga menziesii* over shade-tolerant species (e.g., *Tsuga heterophylla* (Raf.) Sarg.), as in our thinned stands (see Curtis et al. 1998 for a review). Clonal natives are normal and desirable components of Pacific Northwest managed and unmanaged forests, become established early on, and persist into old growth (e.g., Franklin and Dyrness 1973; Huffman et al. 1994; Carey 1995; Carey and Johnson 1995; Huffman and Tappeiner 1997; Bailey and Tappeiner 1998). Our concerns lie in the abilities of these species, in conjunction with certain exotic species, to create unwanted homogeneity and dominance by a few species to the extent that they reduce vegetation site type diversity and preclude regeneration of shade-tolerant trees. So far, conditions in our thinned stands have precluded establishment of the shade-tolerant conifers so important in the function of late-seral forests (Franklin and Dyrness 1973; Carey et al. 1992, 1999b; North et al. 1999), even with underplanting (Carey et al. 1999d). On sites where shade-tolerant seedlings are present, thinning can release shade-tolerant trees to form a continuous understory tree layer, again at the expense of overall species and vegetation site type diversity (Alaback 1982; Gray and Spies 1996; Bailey and Tappeiner 1998).

Most native species were relatively infrequent, in the tails of rank-abundance curves. Such species, although locally rare and often highly variable spatially, are a major component of overall species richness (Stohlgren et al. 1999). Around 90% of the species in the tails of rank-abundance curves are abundant somewhere (Murray et al. 1999). However, rarity and local abundance implies that these species could be subject to local extirpation by broad-brush homogeneous management. Natural forest development leads to contrasts of high-light and low-light patches compared with homogeneous second-growth forests (Canham et al. 1990) and also to fine-scale heterogeneity that promotes vegetation site type diversity (Carey et al. 1999b), which in turn, should protect those species restricted to the tails of the rank-

abundance curves. Variable-density thinning also increases the complexity through a wide variety of patch types, thus potentially increasing vegetation site-type diversity. Thus, VDT also should provide niches for rare species that are not abundant elsewhere. Mycotroph species, however, were more abundant in legacy controls than in stands that had been thinned. This suggests that VDT should be modified to incorporate a no-disturbance subtreatment, perhaps 10-15% of the stand in 0.2-ha patches. Retaining some minimally disturbed areas could conserve native species that might be eliminated by thinning. In contrast, promoting vascular plant diversity through conventional thinnings may fail to meet conservation goals because of increased homogeneity, dominance by a few aggressive clonal natives, increased exotics, and, perhaps, extirpation of native species with restricted distributions (Thysell and Carey 2000).

Plant species diversity

Increases in species diversity may lead to increased community stability and resilience (Tilman 1999) and increased vegetation site type diversity that contributes to niche diversification and taxonomic diversity in birds and mammals (Carey et al. 1999b, 1999c; Haveri and Carey 2000; Wilson and Carey 2000; Carey and Harrington 2001). However, increases in vascular plant species richness in Pacific Northwest forests are generally accompanied by substantial increases in numbers of exotic species (Deferrari and Naiman 1994; Thysell and Carey 2000; this study). The effects of exotic species on community stability are as yet unknown. The trend of increasing numbers of exotic species in forests will probably continue because of the continually expanding exotic species load in the Pacific Northwest flora (Toney et al. 1998). Thus, management for environmental sustainability (Goodland 1995) and biotic integrity (Carey et al. 1999c) should emphasize maintaining native-species-diverse ecosystems that maintain native species with re stricted distributions but not necessarily maximally diverse ecosystems (which may mean large numbers of exotic species). Species composition, then, should be more important in ecosystem management than diversity per se (Peltzer et al. 2000).

Management implications

The concept of VDT (Carey 1995) was developed to be part of a complex ecosystem management system that incorporates *(i)* variable-retention harvest systems (Franklin et al. 1997) that retain biological legacies from the preceding forest, including understory plants, and that reduce site disturbance, including burning, in preparation for planting; *(ii)* planting trees to ensure a mix of trees species; *(iii)* precommercial thinning to maintain vascular plant diversity, including tree species diversity; *(iv)* series of VDTs to promote spatial heterogeneity and vegetation site type diversity; *(v)* management of decadence (e.g, decay in live trees, snags, and coarse woody debris); and *(vi)* long rotations in conjunction with large-scale landscape management (Carey 1995; Carey and Johnson 1995; Carey et al. 1999a, 1999b, 1999c). Our experimental results support this kind of management. Experienced managers in western Washington find this approach pragmatic and operational (Carey et al. 1999a).

Variable-density thinning has also been suggested as an ecological restoration tool, in conjunction with decadence management and other techniques (Carey et al. 1999c). Our experimental results are more equivocal here; historical management provides a multitude of confounding factors, including lack of seed sources for shade-tolerant regeneration, hidden seed banks of exotic species, reduced tree species diversity (often monocultures), firmly established exotic plants, and dense covers of a few native perennials (Thysell and Carey 2000; this study). In particular, shade-tolerant trees exert much more control over ambient light conditions of the understory in mature and old stands than widely spaced *Pseudotsuga menziesii,* because mature *Pseudotsuga menziesii* are relatively restricted by growth form in crown width (J.F. Franklin, personal communication). The size of our treatment subplots (1600 m^2) was well within the 1000-2000 m^2 range that Coates (2000) found adequate to promote regeneration and growth of both shade-tolerant and shade-intolerant conifers in northern temperate forests; however, it is too early to tell if tree seedlings can compete successfully with densely established shrubs and ferns in conventionally thinned blocks. Vegetation control may be a necessary adjunct in efforts to restore full ecological function in conventionally thinned stands. Time will tell if manual control of aggressive clonal species will be required to establish shade-tolerant regeneration on our study sites or if canopy closure in the light-thin subtreatment of VDT and low-angle light interception in our fine-scale mosaics will reduce the homogeneous stands of G. *shallon, Polystichum munitum,* and *Pteridium aquifolium* that resulted from conventional thinning.

Hardwood species such as *Acer circinatum, Acer macrophyllum, Arbutus menziesii, Sambucus racemosa L.,* and *Frangula [Rhamnus] purshiana (DC.)* Cooper, which variously have high value to epiphytic plants, lichens, mycorrhizal fungi, or wildlife are uncommon in many second-growth plant communities (Neitlich and McCune 1997; Carey et al. 1999c), including our stands. In large areas with histories of homogeneous management, special management may be necessary to restore these species to the plant community. Certainly, other forest components could be missing also, depending on historical management. Such components include coarse woody debris as nurse logs for shade-tolerant trees (as in our thinned stands); other plants; fungi; and certain mycotrophs, mosses, and lichens. Potential for VDT to minimize spread of exotics while accelerating forest development may be poor without restoration of missing habitat elements.

To maintain native species diversity and to limit invasion by exotic species, changes in present silvicultural systems are warranted. Short-rotation extensive management (e.g., clearcut, burn, precommercial thinning, and harvest at 40-50 years; see Carey et al. 1999c) will promote establishment of exotics in managed forest landscapes. Conventional thinning in competitive exclusion stages originating after clearcutting may revive ruderal plants stored in soil seed banks (Halpern et al. 1999). Given that our Pacific Northwest native flora is generally lacking ruderals and that the established exotic flora is full of them, native herbaceous species requiring mineral substrate to establish probably may be threatened with extirpation by quick invasion of exposed

mineral soil by aggressive exotics. However, we have insufficient data to predict effects of increasing exotics on native plant communities and forest ecosystem function.

Acknowledgments

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