Plant community attributes 12 to 14 years following precommercial thinning in a young lodgepole pine forest

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Abstract: We investigated plant community responses (abundance, species diversity, and structural diversity) to a range of precommercial thinning densities in young lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) stands 12 to 14 years after thinning, with both unthinned and old-growth stands for comparison. Abundance of understory plants, especially herbs, appeared to increase dramatically in the thinned stands. The moss layer was significantly more abundant in old-growth stands than in the young pine stands. Of a total of 108 species sampled, only three were introduced species, all of which occurred more frequently in the low-density stands than in any of the other stands. Thinning treatments appeared to increase the abundance of late-seral species. Our results suggest that by disrupting canopy closure, thinning decreased the dominance of tall trees and increased the abundance of herbs, shrubs, and trees in the understory height classes. As a result, thinning to low densities significantly increased the structural richness of the tree layer and caused an increase in total structural diversity, which, although only marginally significant ($p = 0.06$), was likely biologically important. Our results suggest that thinning will enhance the abundance, species diversity, and structural diversity of the plant community 12 to 14 years postthinning.

Résumé : Les auteurs ont étudié les réactions des communautés végétales (abondance, diversité d'espèces et diversité structurale) à une gamme de densités d'éclaircie précommerciale dans de jeunes peuplements de pin lodgepole (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) 12 à 14 ans après l'éclaircie en les comparant à des peuplements non éclaircis et à des peuplements de forêt ancienne. L'abondance des plantes de sous-étage, particulièrement des herbacées, a semblé augmenter considérablement dans les peuplements éclaircis. La strate de mousse était significativement plus abondante dans les peuplements de forêt ancienne de pin que dans les jeunes peuplements de pin. Sur un total de 108 espèces échantillonnées, seulement trois étaient des espèces introduites, toutes présentes plus fréquemment dans les peuplements à faible densité que dans n'importe quel autre peuplement. L'éclaircie a semblé augmenter l'abondance des espèces de fin de succession. Les résultats indiquent qu'en perturbant la fermeture de la canopée, l'éclaircie diminue la dominance des grands arbres et augmente l'abondance des herbacées, des arbustes et des arbres dans les classes de hauteur de sous-étage. Par conséquent, l'éclaircie forte a significativement augmenté la richesse structurale de la strate arbustive et causé une augmentation de la diversité structurale totale qui, bien que seulement marginalement significative ($p = 0,06$), était probablement importante du point de vue biologique. Les résultats indiquent qu'une éclaircie va augmenter l'abondance, la diversité des espèces et la diversité structurale de la communauté végétale 12 à 14 ans après l'éclaircie.

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Introduction

Management of forest ecosystems for biological diversity must include a wide range of tree species, successional stages since harvesting or natural disturbance, stand structures, edges, and riparian zones across a landscape (Hunter 1990, 1999). Conservation of natural levels of biodiversity may be achieved where a mosaic of ecosystems includes forest reserves and a managed "landscape matrix" (Hunter 1999; Lindenmayer and Franklin 2002). Much of the landscape matrix in temperate and boreal forests of North America consists of vast areas of young second-growth stands. It is in these largely productive ecosystems that perhaps most of forest biological diversity resides (Franklin 1993).

Second-growth stands are highly responsive to forestry practices that can provide a wide variety of vegetative composition and related stand structure attributes important to wildlife and biodiversity (Carey et al. 1999*a*; Sullivan et al. 2001). Various stand thinning regimes, including precommercial and commercial thinning, as well as variable-density thinning, are silvicultural practices that could diversify young forests. Precommercial thinning is designed to increase both the volume and quality of wood fiber of those crop trees selected for superior growth and form during the thinning operation (Johnstone 1985). Commercial thinning also has the goal of enhancing growth of standing trees, but all, or part, of the felled trees are extracted for useful products. Variable-density

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thinning manipulates the distribution of canopy trees to enhance spatial heterogeneity to a scale similar to that observed in natural old forests (Carey et al. 1999*b*; Thysell and Carey 2001). Because these practices can dramatically alter stand structure and the rate and direction of ecological succession, a diverse array of prescriptions should help diversify second-growth stands in the landscape matrix.

The major coniferous tree species in inland areas of the Pacific Northwest is lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.), which constitutes the majority of second-growth forests having regenerated after wildfire and harvesting (Koch 1996). Lodgepole pine reaches its greatest areal extent in Canada, where it occupies ~20 × 10^6 ha, mostly in British Columbia and Alberta. This pine species occurs in about 6 × 10^6 ha in the western United States (Koch 1996). Because of its favorable responses to silvicultural practices, lodgepole pine is a strong candidate for focusing efforts at accelerating ecosystem development and late-seral conditions.

Old-growth structural attributes (trees with large diameters and crowns, multilayered canopies, smaller shade-tolerant trees, patches of herb and shrub communities, snags, and coarse woody debris on the forest floor; Kneeshaw and Burton 1998; Wells et al. 1998) may develop in young thinned stands over time, particularly if stand densities are relatively low. Our stand development project began in 1988 with precommercial thinning of 17- to 27-year-old lodgepole pine stands to three densities compared with unthinned and old-growth stands. This design provides a measure of the effectiveness of these variously managed stands to provide habitat, increase the effective area of reserves, and provide connectivity across the landscape matrix as stipulated by Franklin (1993). To date, Sullivan et al. (2001) reported that 10 years after thinning, crop tree size and architecture, coniferous stand structure, and diversity of vegetation and forest floor small mammals were enhanced by heavy thinning of lodgepole pine stands to ≤1000 trees/ha.

Conventional thinning prescribes a single target density to an entire stand. Managing for a wide range of densities among stands would therefore provide a range of successional patterns for development of understory vegetation and coniferous stand structure in the landscape mosaic. In general, thinning stands leads to positive responses in biomass of understory vegetation (Thomas et al. 1999; Sullivan et al. 2001). Thysell and Carey (2001) argue that variable-density thinning, instead of conventional thinning, is required to induce spatial heterogeneity in second-growth stands and stimulate the development of complex vegetative understories. However, conventional precommercial thinnings seldom appear to yield homogeneous stands because of the natural variability of openings caused by site heterogeneity, uncontrolled natural disturbances, poor regeneration, and later tree mortality (Hansen et al. 1991). To date, 3-year (Thysell and Carey 2001) and 5-year (Sullivan et al. 2002) responses of vegetation abundance and diversity to variable-density thinning are equivocal. A range of stand densities across a landscape matrix, including a substantial area of heavy (<1000 stems/ha) precommercial thinning, may provide the range of spatial heterogeneity for development of dynamic forest mosaics and hence conservation of biodiversity.

This study was designed to compare the plant community abundance (amount of vegetation) and diversity (species diversity and structural diversity of herb, shrub, and tree layers) among young pine stands treated with three levels of precommercial thinning, untreated pine stands of the same age, and old-growth pine forests, 12 to 14 years after treatment.

Study areas and methods

Study areas

Lodgepole pine stands within each of the three study areas had relatively uniform tree cover and comparable diameter, height, and density of trees prior to stand thinning (Sullivan et al. 2001). The Penticton Creek study area was located in south-central British Columbia, Canada, 15 km northeast of Penticton (49°34′N; 119°27′W). This area is in the Interior Douglas-fir biogeoclimatic zone (Meidinger and Pojar 1991). Topography in the area is hilly with sandy loam soil at 1340 to 1500 m elevation and southeastern aspect, with an average slope of 10%. The climate is characterized by warm, dry summers and cool winters. The average temperature is below 0 °C for 2–5 months, and above 10 °C for 3–5 months, with mean annual precipitation ranging from 30 to 75 cm. Open- to closed-canopy forests of mature Douglas-fir (*Pseudotsuga menziesii* var *glauca* (Beissn.) Franco) cover much of this zone, with even-aged postfire lodgepole pine stands at higher elevations. This area (several thousand hectares) was burned by wildfire in 1970, salvage logged in 1971, and planted with lodgepole pine in 1972. Natural regeneration increased the density of pine to a range of 18 500 – 30 000 stems/ha. Minor components of the stands included Douglas-fir, Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), western larch (*Larix occidentalis* Nutt), willow (*Salix* spp.), Sitka alder (*Alnus sinuata* (Regel) Rydb.), and trembling aspen (*Populus tremuloides* Michx.).

Precommercial thinning was conducted in 1978, leaving ~1000–2000 stems/ha. Additional ingress of pine during the 10-year postthinning period up to 1988 resulted in the need to conduct further thinning. In 1988 the mean stand age was 17 years. In 1998 mean (±1 SE) DBH (diameter at breast height, 1.3 m above the soil surface) among thinned stands ranged from 12.7 ± 0.2 cm to 14.8 ± 0.2 cm, and mean stand height ranged from 8.9 ± 0.1 m to 9.8 ± 0.1 m. All stands were 0.2–2.3 km apart and ranged in area from 20 (each of the thinned stands) to 100+ ha (unthinned stand).

The Kamloops study area was located 30 km south of Kamloops, British Columbia (50°28′N; 120°32′W), within the Montane Spruce biogeoclimatic zone (Meidinger and Pojar 1991). Engelmann spruce, and hybrid Engelmann spruce × white spruce (*Picea engelmannii* × *Picea glauca* (Moench) Voss), and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), in varying amounts, are the characteristic tree species. Because of past wildfires, successional forests of lodgepole pine, Douglas-fir, and trembling aspen are common. This zone has a cool continental climate characterized by cold winters and moderately short, warm summers. The mean temperature is below 0 °C for 5 months and above 10 °C for 2–4 months, with mean annual precipitation ranging from 38 to 90 cm. The topography is hilly at 1400 to 1500 m elevation, with northerly aspects. This area (~15 000 ha) was burned by wildfire in 1960 and regenerated naturally to lodgepole pine with a mean density of 20 000 stems/ha. Minor components

of the stands included Engelmann spruce, subalpine fir, willow, Sitka alder, and trembling aspen.

Precommercial thinning was conducted from 1975 to 1978, leaving 1100–1600 stems/ha over ~200 ha. However, additional ingress of pine up to 1989 suggested that further thinning was warranted. In 1989 stand age ranged from 23 to 27 years. In 1998 mean (±1 SE) DBH among thinned stands ranged from 12.2 ± 0.2 cm to 16.5 ± 0.2 cm, and mean stand height ranged from 11.0 ± 0.1 m to 12.5 ± 0.1 m. These stands were 0.5–5.0 km apart, the area of thinned stands ranged from 15 to 22 ha, while the area of the unthinned stand was 100+ ha.

The Prince George study area was located 60 km west of Prince George, British Columbia (53°52′N; 123°32′W), in the Sub-Boreal Spruce biogeoclimatic zone (Meidinger and Pojar 1991). The general topography is gently rolling at 800 m elevation, with variable aspects. In mature stands, hybrid Engelmann spruce × white spruce and subalpine fir are mixed with extensive stands of lodgepole pine, which regenerated after wildfires. Stands of young lodgepole pine covered ~1000 ha; this area was harvested during 1966–1972 and left to natural regeneration of pine. Stand densities ranged from 2700 to 4700 stems/ha. Minor components of the stands included white spruce, black spruce (*Picea mariana* (Mill.) BSP), Douglas-fir, willow, alder, and aspen. In 1988 the age of trees ranged from 15 to 20 years. In 1998 mean DBH (±1 SE) among thinned stands ranged from 13.5 ± 0.3 cm to 17.8 ± 0.3 cm, and mean stand height ranged from 11.3 ± 0.2 m to 13.0 ± 0.2 m. The area of stands ranged from 30 to 39 ha (thinned stands) to 41 ha (unthinned stand). These stands were 0.5–1.7 km apart.

The old-growth stands at the three study areas were all in the age range of 160 to 250 years. The Penticton stand was dominated by lodgepole pine with a relative abundance of 64.6% followed by spruce (14.6%) and subalpine fir (20.8%) for overstory trees. The Kamloops stand was dominated by subalpine fir (68.4%) with lesser proportions of somewhat larger diameter pine and spruce. The Prince George stand had similar abundance of lodgepole pine (57.5%) and spruce (42.5%) trees. Heights of overstory trees ranged from 19.5 m to 23.9 m and were similar in all stands. Overall stand density was 2330, 1930, and 1960 stems/ha for the Penticton, Kamloops, and Prince George stands, respectively. Overstory snag densities ranged from 90 snags/ha at Penticton and Prince George to 140 snags/ha at Kamloops. Additional details of these study areas are described in Sullivan et al. (2001).

Experimental design

Our experiment included three thinning densities (low, medium, and high) as well as unthinned young lodgepole pine and old-growth stands at each study area in the following design: stand A was low density, target 500 stems/ha; stand B was medium density, target 1000 stems/ha; stand C was high density, target 2000 stems/ha; stand D was unthinned, >2000 stems/ha; and stand E was old growth. Treatments were assigned to stands in a randomized block design. Each of the three study areas was considered a regional replicate (block).

Operational thinning was conducted after the growing season in the fall of 1988 at the Penticton and Prince George

study areas, and after the growing season in the fall of 1989 at the Kamloops study area. Trees in the low-density stands were pruned to a 2.8 m lift (above ground level) at Penticton (October 1992), Kamloops (September 1992), and Prince George (November 1991). Densities of pine in the unthinned stands were 4755 stems/ha at Penticton, 7665 stems/ha at Kamloops, and 4300 stems/ha at Prince George in 1998.

Vegetation

Three 25 m transects, consisting of five contiguous 5 m × 5 m plots, were randomly located in each of the five stands at each of the study areas. Each plot contained three sizes of nested subplots: a 5 m × 5 m plot for sampling trees, a 3 m × 3 m subplot for sampling shrubs, and a 1 m × 1 m subplot for sampling herbs, mosses, and ground lichens. Tree, shrub, and herb layers were subdivided into height classes: 0–0.25, 0.25–0.5, 0.5–1.0, 1.0–2.0, 2.0–3.0, and 3.0–5.0 m (Walmsley et al. 1980). A visual estimate of percent cover of the ground was made for each species – height class combination within the appropriate nested subplot. Total percent cover for each layer was also estimated for each subplot. These data were then used to calculate a crown volume index (m^3/0.01 ha) for each plant species (Stickney 1985). The product of percent cover and corresponding height gives the volume of a cylindroid, which represents the space occupied by the plant in the community. Crown volume index values were then averaged by species for each plot size and converted to a 0.01 ha base to produce the values given for species and layer (mosses, lichens, herbs, shrubs, and trees). Sampling was carried out during July–August 2000, 2001, and 2002. Sampling was carried over three consecutive years to ensure that vegetation differences were well documented and to provide insight into any temporal changes that may still be occurring 12 to 14 years posttreatment, particularly within the very open, low-density stands. Plant species were identified in accordance with Hitchcock and Cronquist (1973), Parish et al. (1996), and MacKinnon et al. (1992). Grasses, mosses, and lichens were not identified to species.

All understory species (herbs and shrubs) were divided into a priori categories according to species origins (native vs. introduced) and seral association (early-seral vs. late-seral association), as indicated by Hitchcock and Cronquist (1973), Klinka et al. (1989), Parish et al. (1996), and MacKinnon et al. (1992). Species that did not have any clear association with either early-seral or late-seral habitats were not included in analyses.

Diversity measures

Plant communities were described by species richness, species turnover, species diversity, and structural diversity. All diversity measures were calculated separately for herb, shrub, and tree layers, as well as for a combined total layer, which included all species. Species richness was the total number of species sampled. Estimates of total species richness were calculated as the sum of the species richness from three different sized subplots (herb, shrub, and tree plots). Because of species–area relationships, it would have been preferable to have subplots of equal size; however, estimates of total species richness still provide a valuable measure for comparing plant communities among different sites. Species turnover was defined as the sum of the number of species

lost and gained during the course of the study, divided by the total number of species sampled during the same period (Schoonmaker and McKee 1988). In this way, species turnover is a measure of compositional change expressed as a proportion of the total number of species within a community.

Species diversity was described using the Shannon–Wiener index (Pielou 1966), which is based on information theory and the degree of difficulty in correctly predicting the next species sampled. This diversity index is sensitive to changes in rare species, has good discriminant ability, and is well represented in the ecological literature (Burton et al. 1992). Species diversity was calculated using the crown volume index for each plant species averaged across the three transects, each of which was an average of five subplots, in a given stand. Species diversity was calculated separately for herbs, shrubs, and trees, as well as for a combined total layer.

Structural diversity (foliage height diversity; MacArthur and MacArthur 1961) was also described using the Shannon–Wiener index. Structural diversity index was calculated with height classes acting as "species". Thus, structural richness was the total number of height classes occupied by the various vegetative layers.

Statistical analysis

Transect means were handled as subsamples of each experimental unit (stand), which was replicated within three regional study areas, resulting in a randomized complete-block design with $n = 3$. A repeated measures analysis of variance (RM-ANOVA) (SPSS Institute Inc., Chicago, Illinois, 1997) was conducted to determine the effects of treatment and time (12 to 14 years postthinning) on mean crown volume index of the moss, lichen, herb, shrub, and tree layers, as well as a combined total layer. Mean species richness and diversity as well as mean structural diversity of the herb, shrub, tree, and combined layers were also compared using this RM-ANOVA model. In addition, this model was used to compare mean species richness and mean crown volume index between native and introduced species, as well as between early- and late-seral species. Finally, a univariate ANOVA was conducted to determine treatment effects on mean species turnover 12 to 14 years postthinning.

Before performing any analyses, data not conforming to properties of normality and equal variance were subjected to various transformations to best approximate the assumptions required by any ANOVA (Zar 1999). Mauchly's W test statistic was used to test for sphericity (independence of data among repeated measures) (Littel 1989; Kuehl 1994). For data found to be correlated among years, the Huynh–Feldt correction (Huynh and Feldt 1976) was used to adjust the degrees of freedom of the within-subjects F ratio. Duncan's multiple range test (DMRT) was used to compare mean values based on ANOVA results. In all analyses, the level of significance was at least $p = 0.05$.

Results

Abundance

A total of 108 species of vascular plants were sampled during this study, which included 66 species of herbs, 34 species of shrubs, and 8 species of trees. Grasses dominated the herb layer of all the young pine stands and contributed 31% to 62% of the total mean crown volume index of herbs. Fireweed (*Epilobium angustifolium* L.) was also a commonly encountered herb in the young pine stands, as well as in the old-growth stands. Arctic lupine (*Lupinus arcticus* S. Wats.) was the dominant herb species in the old-growth stands and was also common in the thinned stands. This shade-intolerant herb (Klinka et al. 1989) was rarely encountered in the shaded understory of the unthinned stands. Bunchberry (*Cornus canadensis* L.) and heart-leaved arnica (*Arnica cordifolia* Hook.) were also widespread throughout all of the stands.

Sitka alder dominated the shrub layer in all stands, contributing 54% to 67% of the total mean crown volume index of the shrub layer in the young pine stands and 26% in the old-growth stands. Willow and wild rose (*Rosa acicularis* Lindl.) were also common, particularly in the young pine stands, but also in the old-growth stands. Soapberry (*Shepherdia canadensis* (L.) Nutt.) was very common in the low-density, medium-density, and old-growth stands; however, it contributed little to the shrub volume of the high-density and unthinned stands. Despite the trailing nature of twinflower (*Linnaea borealis* L.) and the dwarf size of grouseberry (*Vaccinium scoparium* Leiberg), both of these short-statured shrubs made up a considerable volume of the shrub layer of all stands.

Lodgepole pine contributed 71% to 90% of the mean total crown volume index of the tree layers in the young stands. This seral species was less prevalent within the old-growth stands, contributing only 20% of the mean total crown volume index of the tree layer. Spruce and subalpine fir were the two dominant tree species in the old-growth stands and were also sampled in the young pine stands. Trembling aspen and Douglas-fir were also common in the young pine stands.

The mean crown volume index of the herb layer was significantly different ($F_{[4,8]} = 10.23$, $p < 0.01$) among stands, with higher (DMRT, $p = 0.05$) herb volume in all of the thinned stands (high-, medium-, and low-density) than in either of the unthinned or old-growth stands (Table 1).

The mean crown volume index of the moss layer was significantly different ($F_{[4,8]} = 7.75$, $p < 0.01$) among stands, with a higher (DMRT, $p = 0.05$) volume of moss in the old-growth stands than in any of the young pine stands (Table 1). There was no significant difference ($F_{[4,8]} = 0.82$, $p = 0.55$) in mean crown volume index of the lichen layer among the stands (Table 1).

The mean crown volume index of the shrub layer was approximately five times greater in the thinned stands than in the old-growth stands. However, differences in shrub volume were not significant ($F_{[4,8]} = 1.60$, $p = 0.26$; Table 1). The mean crown volume index of trees increased with increasing stand density and age and was highest in the unthinned and old-growth stands. However, differences in tree volume were only marginally significant ($F_{[4,8]} = 3.14$, $p = 0.08$; Table 1).

Species diversity

Although mean species richness tended to be greater in the thinned stands than in both the unthinned and old-growth stands, differences were not significant ($p > 0.05$) for the herb, shrub, and tree layers and only marginally significant ($F_{[4,8]} = 2.94$, $p = 0.09$) for the combined total layer (Ta-

Table 1. Mean (n = 3 replicate stands) (±1 SE) crown volume index (m³/0.01 ha) in each sample year and results of RM-ANOVA.

Vegetation layer and year	Treatment					Overall analysis					
	Low density	Medium density	High density	Unthinned	Old growth	Treatment		Time		Treatment × time	
						$F_{[4,8]}$	p	$F_{[2,20]}$	p	$F_{[8,20]}$	p
Herb	A	A	A	B	B	10.23	<0.01	0.66	0.53	0.11	1.00
2000	11.05±2.57	12.14±4.63	16.81±6.70	5.76±3.50	4.19±2.70						
2001	11.14±3.04	10.84±3.62	11.21±3.60	4.20±1.65	4.08±2.65						
2002	8.17±1.68	7.43±1.64	8.93±3.32	3.12±1.53	3.47±2.20						
Moss	B	B	B	B	A	7.75	<0.01	0.69	0.51	0.36	0.93
2000	5.49±3.73	5.45±3.11	3.73±2.22	5.05±3.95	12.74±3.87						
2001	4.91±3.48	6.45±4.16	3.64±2.80	5.34±4.58	12.76±4.19						
2002	5.64±4.16	5.17±3.07	3.75±2.86	4.91±4.20	10.85±4.62						
Lichen						0.82	0.55	4.59	0.02	0.12	1.00
2000	0.53±0.18	0.36±0.13	0.30±0.09	0.56±0.23	0.59±0.20						
2001	0.52±0.15	0.42±0.12	0.44±0.13	0.60±0.28	0.53±0.16						
2002	0.46±0.14	0.36±0.13	0.30±0.10	0.39±0.17	0.40±0.16						
Shrub						1.60	0.26	2.32	0.12	0.65	0.72
2000	50.44±13.12	53.79±15.41	50.92±37.69	47.41±19.03	10.68±5.57						
2001	59.81±17.46	72.19±28.18	60.27±49.52	37.09±13.43	12.44±5.71						
2002	57.49±15.65	59.22±20.58	55.92±44.71	45.35±15.53	10.37±4.80						
Tree						3.14	0.08	0.97	0.40	0.16	0.99
2000	115.11±32.61	146.96±14.77	122.49±21.04	187.45±25.15	178.70±53.27						
2001	130.74±32.40	136.91±31.15	148.53±27.40	181.04±31.94	181.64±47.45						
2002	122.09±23.63	126.62±7.91	139.65±20.89	189.09±27.53	195.41±53.63						

Note: Column of mean values with different letters were significantly different according to Duncan's multiple range test, adjusted for multiple contrasts. Mauchly's tests for sphericity determined that there was no correlation of data among repeated measures (years) for these data.

ble 2). Mean species diversity of the herb, shrub, and tree layers were similar ($p > 0.05$) among all stands. Total species diversity tended to be greatest within the low-density stands (Table 2); however, this difference was only marginally significant ($F_{[4,8]} = 2.80$, $p = 0.10$).

During the 12- to 14-year posttreatment period, changes in plant community composition were very similar among thinned, unthinned, and old-growth stands. Mean species turnover was statistically similar among all stands for the herb ($F_{[4,8]} = 0.22$, $p = 0.92$), shrub ($F_{[4,8]} = 0.58$, $p = 0.69$), and combined total layers ($F_{[4,8]} = 1.60$, $p = 0.26$; Table 3). Mean species turnover of trees, however, was significantly different ($F_{[4,8]} = 12.85$, $p < 0.01$) among stands, with higher (DMRT; $p = 0.05$) species turnover in the high-density stands than in any of the other stands (Table 3). Means of 1.3 and 0.7 species were gained and lost, respectively, in the high-density stands, whereas a mean of only 0.3 species was gained (no species lost) in the medium-density and unthinned stands, and no species were gained or lost in either the low-density or old-growth stands.

Native and introduced species

Of the 100 species of understory plants, only three were classified as introduced: white sweet-clover (*Melilotus alba* Desr.), common dandelion (*Taraxacum officinale* Weber), and red clover (*Trifolium pratense* L.). Mean native species richness tended to be lowest within the old-growth stands; however, this difference was only marginally significant ($F_{[4,8]} = 3.30$, $p = 0.07$; Table 4). Mean crown volume index of native species was noticeably less in the old-growth stands than in any of the young stands, but again, differences were only marginally significant ($F_{[4,8]} = 3.20$, $p = 0.08$; Table 4). Mean introduced species richness was significantly different ($F_{[4,8]} = 4.40$, $p = 0.04$) among stands, with the low-density stands having greater (DMRT, $p = 0.05$) species richness than the medium-density, unthinned, and old-growth stands (Table 4).

Mean crown volume index of native species was similar ($F_{[4,8]} = 3.20$, $p = 0.08$) among stands (Table 4). There were no significant differences ($F_{[4,8]} = 2.25$, $p = 0.15$) in mean crown volume index of introduced species among stands (Table 4).

Seral associations

Of the 100 species of understory plants (herb and shrub layers combined) sampled during this study, 17 species (12 herbs and 5 shrubs) were associated with early-seral habitats, and 50 species (32 herbs and 18 shrubs) were associated with late-seral (forest) habitats. The remaining 33 species (22 herbs and 11 shrubs) did not have any clear seral associations and, therefore, were not included in the following comparisons. The mean species richness of understory plants associated with early-seral habitat was significantly different ($F_{[4,8]} = 4.32$, $p = 0.04$) among stands, with the old-growth stands having fewer (DMRT, $p = 0.05$) early-seral species than any of the thinned young pine stands (Table 4). The mean species richness of understory plants associated with late-seral habitat was similar ($F_{[4,8]} = 1.23$, $p = 0.37$) among stands (Table 4).

The mean crown volume index of early-seral species was at least five times higher in the young pine stands than in the old-growth stands; however, these differences were not sig-

nificant ($F_{[4,8]} = 1.55$, $p = 0.28$; Table 4). The mean crown volume index of late-seral species appeared highest in the thinned stands and lowest in the unthinned and old-growth stands, but these differences were not significant ($F_{[4,8]} = 0.64$, $p = 0.65$; Table 4).

Structural diversity

The mean structural richness of the herb layer was similar ($F_{[4,8]} = 2.51$, $p = 0.12$) among stands (Table 5). The mean structural richness of the shrub layer was significantly different ($F_{[4,8]} = 6.30$, $p = 0.01$) among stands, with higher (DMRT, $p = 0.05$) structural richness in the thinned and unthinned stands than in the old-growth stands (Table 5). The mean structural richness of the tree layer was also significantly different ($F_{[4,8]} = 3.72$, $p = 0.05$) among stands, with higher (DMRT, $p = 0.05$) structural richness in low-density and old-growth stands than in unthinned stands (Table 5). The mean structural richness of the combined layer was statistically similar ($F_{[4,8]} = 0.96$, $p = 0.48$) among all stands (Table 5).

The mean structural diversity of the herb and shrub layers were similar ($p > 0.05$) among stands (Table 5). Mean structural diversity of the tree layer tended to be greatest within the low-density and old-growth stands; however, differences were only marginally significant ($F_{[4,8]} = 2.88$, $p = 0.09$; Table 5). Total structural diversity was greatest within the low-density stands; however, differences were only marginally significant ($F_{[4,8]} = 3.61$, $p = 0.06$; Table 5).

Discussion

Experimental design

Our study is the first detailed investigation of relatively long-term plant community response (abundance, composition, species diversity, and structural diversity) to various precommercial thinning densities of lodgepole pine within interior forests of western North America. This study addressed the perception that forest management activities, such as thinning, decreases plant diversity relative to the diversity in old-growth plant communities (Gilliam and Roberts 1995) by comparing vegetation attributes of young thinned stands with those of nearby unthinned and old-growth stands. Investigating both thinned and unthinned stands of equal age provided insight into how thinning may have influenced plant community development relative to the more natural conditions observed in unthinned stands (Roberts and Gilliam 1995). Our study was conducted in operational-sized units (15 to 39 ha), was replicated within three different ecological zones, and was based on three consecutive years of detailed vegetation data. Therefore, the results provide an accurate description of plant community conditions observed 12 to 14 years postthinning as well as insight into the influence that thinning treatments have had on plant community development. Consequently, these results have meaningful implications for the management of lodgepole pine stands across the interior of British Columbia.

This study employed an intensive sampling design; however, as with any investigation of natural processes, limited resources and logistics precluded collecting some data that might have been relevant to testing our hypotheses. In particular, future studies of plant community response to forest management should include several data that would have im-

Table 2. Mean (*n* = 3 replicate stands) (±1 SE) species richness and species diversity of vegetation layers in each sample year and results of RM-ANOVA.

Vegetation layer and year	Treatment					Overall analysis					
	Low density	Medium density	High density	Unthinned	Old growth	Treatment		Time		Treatment × time	
						$F_{[4,8]}$	p	$F_{[2,20]}$	p	$F_{[8,20]}$	p
Species richness											
Herb											
2000	10.11±2.05	8.11±2.47	12.11±3.31	7.33±1.91	7.22±3.61	2.08	0.18	0.52	0.60	0.28	0.97
2001	10.89±2.88	8.44±2.65	11.67±2.74	7.11±1.69	7.56±3.88						
2002	10.78±1.82	7.67±2.55	10.67±2.72	6.78±1.80	7.56±3.80						
Shrub											
2000	8.89±1.37	8.11±1.02	8.67±1.35	7.78±0.95	6.44±1.39	2.18	0.16	0.39	0.69	0.87	0.56
2001	9.22±1.44	8.56±1.19	7.89±0.98	7.44±1.12	6.56±1.48						
2002	8.67±1.47	8.11±0.84	8.56±1.23	7.78±1.07	6.22±1.68						
Tree											
2000	3.44±0.82	3.00±0.41	2.89±0.67	2.33±0.65	2.44±0.30	0.75	0.58	0.67	0.52	1.11	0.40
2001	3.44±1.00	2.67±0.41	2.78±0.56	2.44±0.77	2.56±0.42						
2002	3.33±0.91	2.78±0.38	3.33±0.87	2.56±0.87	2.44±0.30						
Total											
2000	24.44±3.22	21.22±3.41	25.67±4.33	19.44±1.58	18.11±4.22	2.94	0.09	0.54	0.59	0.31	0.95
2001	25.56±3.90	21.67±3.61	24.33±3.45	19.00±1.35	18.67±4.38						
2002	24.78±3.02	20.56±3.33	24.56±3.62	19.11±1.77	18.22±4.81						
Species diversity											
Herb											
2000	1.38±0.44	1.27±0.34	1.76±0.53	1.51±0.19	1.53±0.57	0.24	0.91	0.68	0.52	0.07	1.00
2001	1.36±0.46	1.24±0.44	1.56±0.51	1.45±0.17	1.56±0.56						
2002	1.45±0.42	1.36±0.46	1.84±0.67	1.58±0.34	1.64±0.61						
Shrub											
2000	1.33±0.23	1.33±0.29	1.81±0.27	1.43±0.43	1.46±0.40	0.60	0.67	0.65	0.53	0.36	0.93
2001	1.26±0.23	1.21±0.37	1.76±0.36	1.42±0.38	1.41±0.42						
2002	1.25±0.25	1.21±0.33	1.71±0.36	1.38±0.39	1.57±0.47						
Tree											
2000	0.85±0.26	0.27±0.23	0.55±0.27	0.35±0.25	0.70±0.25	1.26	0.36	0.02	0.98	0.29	0.96
2001	0.81±0.31	0.29±0.23	0.58±0.27	0.38±0.25	0.69±0.25						
2002	0.79±0.31	0.27±0.22	0.60±0.27	0.38±0.27	0.71±0.25						
Total											
2000	2.28±0.24	1.71±0.26	2.07±0.31	1.42±0.21	1.58±0.33	2.80	0.10	0.62	0.55	0.24	0.98
2001	2.19±0.22	1.76±0.28	1.76±0.27	1.43±0.27	1.57±0.30						
2002	2.19±0.17	1.67±0.28	1.74±0.35	1.40±0.30	1.52±0.40						

Note: Mauchly's tests for sphericity determined that there was no correlation of data among repeated measures (years) for these data.

Table 3. Overall mean species turnover ($n = 9$; 3 replicate stands × 3 years) (±1 SE) during a period of 12 to 14 years postthinning (2000–2002) and results from univariate ANOVA.

Vegetation layer	Treatment					ANOVA	
	Low density	Medium density	High density	Unthinned	Old growth	$F_{[4,8]}$	p
Herb	0.20±0.02	0.18±0.02	0.22±0.01	0.25±0.10	0.22±0.03	0.22	0.92
Shrub	0.11±0.04	0.03±0.03	0.09±0.05	0.09±0.02	0.12±0.09	0.58	0.69
Tree	0.00±0.00b	0.05±0.05b	0.22±0.04a	0.03±0.03a	0.00±0.00b	12.85	<0.01
Total	0.14±0.00	0.10±0.02	0.18±0.02	0.14±0.03	0.16±0.03	1.60	0.26

Note: Mean values followed by different letters were significantly different by Duncan's multiple range test, adjusted for multiple contrasts.

proved our study, namely collecting pretreatment data, sampling of spring ephemeral plants (Elliott et al. 1997; Fredericksen et al. 1999) and vascular epiphytes, identifying grasses and mosses to species, and collecting site data such as litter depth, soil moisture, soil nutrients, temperature, and understory light conditions (Graae and Heskjaer 1997; Gray et al. 2002).

Abundance

The dramatic impact that thinning treatments appear to have had on understory abundance was not surprising, as several studies have documented the positive response of both herb and shrub layers to increased resources (particularly light, but also moisture and nutrients) resulting from canopy disturbance (e.g., Thomas et al. 1999; Thysell and Carey 2000). That all three of the thinned stands had significantly greater herb abundance than both the unthinned and old-growth stands clearly suggests that thinning enhances the abundance of understory vegetation. Differences in shrub abundance among stands may increase with time, as shrubs have been shown to be much slower than herbs to respond to increased resources following disturbance (Halpern 1989; Thomas et al. 1999). An abundant and well-developed herb and shrub layer is, in and of itself, a valuable habitat for maintaining a diverse community of plants and animals (Hansen et al. 1991; Graae and Heskjaer 1997) and is also a distinctive attribute of old-growth forests (Halpern and Spies 1995; Cole 1996).

The similar abundance of moss among thinned and unthinned stands suggested that thinning did not have any effect on this group of plants 12 to 14 years postthinning. This result is consistent with that of Thomas et al. (1999), who also reported no difference in moss abundance among a similar range of thinning densities, 12 to 16 years postthinning. Abundance of moss was significantly greater in the old-growth stands than in any of the young pine stands. Halpern and Spies (1995) suggested that one of the reasons that a species may be associated with old growth is because of the buffered temperature and moisture conditions provided by the multilayered canopy of large trees. Abundance of ground lichens was similar among thinned, unthinned, and old-growth stands, suggesting that abundance of this group may not be affected by stand age or thinning treatments in these stands.

Even though the removal of trees during precommercial thinning must have had a dramatic effect on the abundance of the tree layer, a difference in tree volume among stands was only weakly indicated ($p = 0.08$) 12 to 14 years postthinning, and tree volume will likely become even more similar among stands as the canopies of the thinned stands continue to close. Similar volume of trees among stands with very

different densities implies that average tree crown volume index must have been much larger in the low-density stands than in the more densely stocked stands. The suggestion that thinning, particularly to low densities, accelerated the development of large trees was directly supported by Sullivan et al. (2001). These authors noted that 10 years after thinning of these same stands, mean diameter increment in the low-density stands was significantly higher than that of the medium- and high-density stands and was almost twice that of unthinned stands. In addition, low- and medium-density stands had significantly wider and deeper crowns than unthinned stands (Sullivan et al. 2001). Because large diameter trees with well-developed crowns are often associated with old-growth forests and are absent in managed forests, accelerated growth of trees is often cited as one of the most important steps for enhancing the diversity of both plant and animal communities (e.g., Thysell and Carey 2000; Busing and Garman 2002). As a result, thinning, particularly to low densities (Vora 1994), has the potential to enhance diversity and accelerate the development of old-growth characteristics and is consistent with production forest objectives (Cole 1996; Acker et al. 1998), although some reduction in timber outputs may occur if stands are thinned to very low densities (Hansen et al. 1991).

Species diversity and composition

Plant community response to forest practices is often expressed using index-based descriptors such as species richness and species diversity. While these descriptors do provide useful data for comparisons, many, if not most, of the details of a plant community's response to treatments are missed without also considering the changes in species composition. This study investigated changes in species composition by comparing species richness and abundance between species groups such as early-seral versus late-seral species and introduced versus native plants (Halpern and Spies 1995; Roberts and Gilliam 1995).

Differences in total species richness among stands were marginally significant (an increase from 19 to 25 species in unthinned and low-density stands, respectively; $p = 0.09$), which suggested a biologically important response to thinning. Thomas et al. (1999) performed thinning treatments in young Douglas-fir stands that were similar to the treatments in this study and reported an increase in total species richness 12 to 16 years postthinning that was nearly identical to the increase observed in this study (an increase from 20 to 26 species in unthinned and low-density stands, respectively); however, their treatment effect was highly significant ($p = 0.006$). Species richness was also found to increase dramati-

Table 4. Mean ($n = 3$ replicate stands) (±1 SE) species richness and crown volume index ($m^3/0.01$ ha) of understory species (herbs and shrubs combined) in each year by species origin (native and introduced) and seral association (early-seral and late-seral habitats) with results of RM-ANOVA.

| Vegetation layer and year | Treatment | | | | | Overall analysis | | | | | |
	Low density	Medium density	High density	Unthinned	Old growth	Treatment $F_{[4,8]}$	p	Time $F_{[2,20]}$	p	Treatment × time $F_{[8,20]}$	p
Species origins											
Native species											
Species richness											
2000	18.33±2.96	16.11±3.37	20.33±1.69	15.11±1.69	13.67±4.32	3.30	0.07	0.92	0.41	0.42	0.89
2001	19.78±3.53	16.89±3.41	19.33±3.55	14.56±1.53	14.11±4.58						
2002	19.11±2.78	15.78±3.19	18.89±3.86	14.56±2.00	13.78±4.89						
Crown volume index											
2000	61.44±13.27	65.93±12.78	67.70±39.92	53.17±17.71	14.87±7.58	3.20	0.08	0.33	0.72	0.29	0.96
2001	70.94±70.94	83.03±26.06	71.47±51.74	41.29±12.33	16.52±6.91						
2002	65.59±16.20	66.64±20.29	64.83±43.87	48.47±15.81	13.84±5.74						
Introduced species											
Species richness	A	B	AB	B	B						
2000	0.67±0.41	0.11±0.19	0.44±0.42	0.00±0.00	0.00±0.00	4.40	0.04	1.68	0.21	0.73	0.66
2001	0.33±0.41	0.11±0.19	0.22±0.25	0.00±0.00	0.00±0.00						
2002	0.33±0.29	0.00±0.00	0.33±0.29	0.00±0.00	0.00±0.00						
Crown volume index											
2000	0.04±0.05	0.00±0.00	0.03±0.05	0.00±0.00	0.00±0.00	2.25	0.15	1.07	0.36	0.74	0.66
2001	0.02±0.02	0.00±0.00	0.01±0.01	0.00±0.00	0.00±0.00						
2002	0.07±0.10	0.00±0.00	0.02±0.02	0.00±0.00	0.00±0.00						
Seral association											
Early-seral species											
Species richness	A	A	A	AB	B						
2000	6.00±1.19	5.33±0.58	6.00±1.15	4.33±0.29	2.56±1.08	4.32	0.04	1.47	0.25	0.48	0.85
2001	5.67±1.29	5.33±0.58	5.44±0.77	4.00±0.29	2.67±1.08						
2002	5.56±1.39	4.44±0.77	5.89±0.73	3.89±0.67	2.56±1.16						
Crown volume index											
2000	36.15±16.59	41.80±16.23	49.68±38.95	43.59±19.35	5.03±2.21	1.55	0.28	0.22*	0.64	0.28*	0.95
2001	43.58±21.42	57.39±30.41	56.88±50.33	32.66±13.39	6.31±3.37						
2002	39.90±19.40	46.11±22.15	51.98±43.67	39.42±15.85	4.50±2.59						
Late-seral species											
Species richness											
2000	8.11±1.67	7.33±2.10	9.89±2.76	7.78±1.55	8.22±2.53	1.23	0.37	0.39	0.68	0.44	0.88
2001	8.78±2.45	7.44±2.31	9.89±2.95	7.22±1.35	8.22±2.72						
2002	9.00±1.80	7.89±2.15	9.33±2.75	7.56±1.61	8.22±2.67						
Crown volume index											
2000	14.99±10.22	11.71±9.82	9.23±4.49	5.56±2.52	6.48±5.26	0.64	0.65	0.47	0.63	0.50	0.84
2001	17.72±12.06	14.59±14.17	7.86±3.64	4.50±1.66	7.16±5.22						
2002	16.71±10.85	11.94±10.14	6.39±2.54	5.03±2.31	5.79±3.84						

Note: Columns of mean values with different letters were significantly different by Duncan's multiple range test, adjusted for multiple contrasts. F values identified by an asterisk were calculated using the H–F correction factor, which decreased the stated degrees of freedom because of correlation of data among repeated measures (years).

Table 5. Mean (n = 3 replicate stands) (±1 SE) structural richness and diversity in each sample year and results of RM-ANOVA.

Vegetation layer and year	Treatment					Overall analysis					
	Low density	Medium density	High density	Unthinned	Old growth	Treatment $F_{[4,8]}$	p	Time $F_{[2,20]}$	p	Treatment × time $F_{[8,20]}$	p
Structural richness											
Herb											
2000	2.89±0.19	3.00±0.29	2.89±0.45	2.56±0.30	2.00±0.58	2.51	0.12	3.38	0.05	0.22	0.98
2001	3.33±0.29	3.22±0.25	3.44±0.30	3.00±0.41	2.22±0.69						
2002	3.00±0.41	2.56±0.30	3.00±0.41	2.44±0.51	2.00±0.65						
Shrub	A	A	A	A	B						
2000	5.22±0.48	5.11±0.67	4.89±0.67	5.44±0.51	3.56±0.65	6.30	0.01	0.93	0.41	0.77	0.64
2001	5.44±0.51	5.22±0.69	5.00±0.58	5.56±0.51	3.78±0.81						
2002	5.11±0.45	5.22±0.69	5.11±0.61	5.56±0.51	3.11±0.67						
Tree	A	AB	AB	B	A						
2000	5.56±0.51	4.67±0.65	3.67±0.91	3.78±1.15	5.33±0.58	3.72	0.05	0.04	0.96	0.11	1.00
2001	5.44±0.51	4.22±0.38	3.67±0.96	3.33±1.04	5.67±0.41						
2002	5.44±0.51	4.33±0.65	4.00±0.91	3.33±1.00	5.33±0.76						
Total											
2000	6.00±0.00	5.78±0.25	5.67±0.41	5.67±0.29	5.89±0.19	0.96	0.48	0.19	0.83	0.22	0.98
2001	6.00±0.00	5.78±0.25	5.67±0.29	5.78±0.25	6.00±0.00						
2002	6.00±0.00	5.67±0.29	5.78±0.25	5.78±0.25	5.89±0.19						
Structural diversity (H')											
Herb											
2000	1.27±0.17	1.26±0.20	1.36±0.25	1.09±0.21	0.65±0.40	1.73	0.24	4.14	0.03	0.33	0.95
2001	1.42±0.17	1.35±0.17	1.35±0.21	1.35±0.26	0.84±0.48						
2002	1.28±0.21	0.92±0.25	1.02±0.26	0.99±0.33	0.63±0.41						
Shrub											
2000	1.69±0.17	1.59±0.22	1.54±0.25	1.52±0.31	1.28±0.43	1.38	0.32	0.51	0.61	0.58	0.78
2001	1.71±0.30	1.28±0.24	1.61±0.23	1.70±0.26	1.32±0.43						
2002	1.79±0.20	1.32±0.20	1.46±0.32	1.53±0.35	1.10±0.43						
Tree											
2000	0.44±0.16	0.08±0.03	0.13±0.11	0.15±0.13	0.26±0.11	2.88	0.09	0.29	0.75	0.50	0.84
2001	0.44±0.15	0.10±0.04	0.13±0.10	0.15±0.12	0.31±0.13						
2002	0.39±0.14	0.12±0.06	0.14±0.13	0.11±0.10	0.34±0.15						
Total											
2000	1.78±0.13	1.31±0.20	1.25±0.28	0.92±0.22	0.94±0.28	3.61	0.06	3.02	0.07	0.40	0.91
2001	1.65±0.13	1.14±0.25	1.02±0.22	0.91±0.24	0.99±0.24						
2002	1.66±0.12	1.06±0.23	0.96±0.20	0.77±0.24	0.93±0.26						

Note: Column of mean values with different letters were significantly different by Duncan's multiple range test, adjusted for multiple contrasts. Mauchly's tests for sphericity determined that there was no correlation of data among repeated measures (years) for these data.

cally with thinning treatments reported by Thysell and Carey (2001), who observed >150% increase in species richness 3 years after thinning in older (ca. 60-year-old) Douglas-fir stands.

Increased species richness following canopy disturbance is largely attributed to early-seral, shade-intolerant herbs and shrubs invading sites to take advantage of increased light conditions (Fredericksen et al. 1999; Thysell and Carey 2000). However, we observed early-seral species richness to be statistically similar between thinned and unthinned stands and to be significantly lower in old-growth stands than in any of the young pine stands. Therefore, our results support the findings of Thomas et al. (1999), who reported that species richness of early-seral plants was not affected by thinning treatments, but rather was a function of stand age. It should be noted that many invasive, early-seral species are often only temporary occupants of disturbed sites, surviving as little as 5 to 10 years after disturbance (Halpern and Spies 1995), and that both Thomas et al. (1999) and this study began sampling 12 years postthinning. Therefore, thinning could have significantly increased the species richness of early-seral plants immediately following treatment; however, this effect was not evident 12 to 14 years postthinning.

While forest management activities often increase the abundance and species richness of the understory plant community, these increases are often thought to take place at the expense of late-seral species (Battles et al. 2001). Our results indicated that richness of late-seral species was similar among thinned, unthinned, and old-growth stands. Although not statistically significant, the volume of late-seral species appeared to be greater in thinned stands, particularly the low- and medium-density stands, suggesting that thinning may have increased the abundance of late-seral species. Our data were consistent with reports that late-seral species were often resilient and recovered quickly from disturbance (Halpern and Spies 1995; Graae and Heskjaer 1997). These results suggested that thinning, even to low densities, did not result in loss of late-seral species.

While many species of forest plants may be resilient to management, some species are particularly sensitive to disturbance. For example, Prince's pine (*Chimaphila umbellata* (L.) Bart.) and rattlesnake plantain (*Goodyera oblongifolia* Raf.) were described by Halpern (1989) as "…characteristic forest species that show minimal recovery after disturbance". Our results indicated that rattlesnake plantain was more abundant in thinned and unthinned stands than in old-growth stands, and that Prince's pine, while more abundant in old-growth stands, was common in our young stands (thinned and unthinned). Another vulnerable late-seral species was twinflower, which was noted to be very sensitive to fire (Halpern 1989), not recovering to old-growth abundance for at least 20 years (Spies 1991). Our results indicated that twinflower was more abundant within young pine stands than old-growth stands, despite the fact that two of our replicate blocks originated from wildfire. In addition, thinning did not appear to delay the recovery of twinflower, as volume of this late-seral species was higher in the thinned than unthinned stands. These data supported the observations of Halpern and Spies (1995), who reported that twinflower can increase in response to release from competition. Finally, Queen's cup (*Clintonia uniflora* (Schult.) Kunth.), pink win-

tergreen (*Pyrola asarifolia* Michx.), heart-leaved twayblade (*Listera cordata* (L.) R.Br.), and one-leaved foamflower (*Tiarella trifoliata* L. var. *unifoliata* (Hook.) Kurtz.) disappeared from at least some sample plots following harvest (Halpern and Spies 1995). Our data indicated that one-leaved foamflower was absent from young stands, heart-leaved twayblade was less abundant in young stands than old-growth stands, Queen's cup was only found in young stands, and pink wintergreen was far more abundant in young stands than in old-growth stands.

Of the seven late-seral species noted to be particularly sensitive to disturbance, our data indicated that only one species (one-leaved foamflower) was absent from the young stands. Interestingly, even in old-growth stands, one-leaved foamflower was rare, being sampled in only one sample plot during 1 of the 3 years of this study. Of the six species present in the young stands, two (Prince's pine and heart-leaved twayblade) were found in low abundance and assumed to be recovering, and the remaining four species (rattlesnake plantain, Queen's cup, pink wintergreen, and twinflower) were more abundant in thinned and unthinned stands than in old-growth stands. Therefore, our results suggest that thinning treatments may not delay the recovery of these sensitive late-seral species, and in the case of twinflower, they may have even accelerated recovery.

A major concern associated with the management of natural areas is the spread of introduced plants (Heckman 1999). The perception is that forest management promotes the establishment and spread of introduced plants at the expense of native flora, and in many cases, this concern appears to be well founded (Battles et al. 2001; Thysell and Carey 2001). The issues surrounding introduced plants and their effects on the environment have been particularly well studied in the Pacific Northwest of the United States, where in some areas (e.g., Olympic Peninsula, Washington) as many as 52 species (23% of the flora) are nonnative (DeFerrari and Naiman 1994). Because the vast majority of introduced plants are early-seral herbs, there is a concern that thinning treatments will significantly increase the number and abundance of introduced species (Thysell and Carey 2001), although some studies have contradicted this premise (e.g., Thomas et al. 1999). Of the 100 species of understory plants that were sampled during this study, only three were introduced (white sweet-clover, common dandelion, and red clover); all three were early-seral herbs, and the two species of clover were likely intentionally introduced as a forage crop for grazing cattle. All three introduced plants occurred in the thinned stands only, but at very low abundance. Therefore, thinning, particularly to low densities, may have slightly increased numbers of introduced species. Species richness and abundance of native plants did not appear to be affected by these few introduced species.

Response of species diversity to forest management is often assumed to be negative (Gilliam and Roberts 1995); however, observations range from increased diversity (Thysell and Carey 2000; Battles et al. 2001), to decreased diversity (Hansen et al. 1991; Elliott et al. 1997), to similar levels of diversity (Thomas et al. 1999), compared with unmanaged stands. Our results supported the observations of Thomas et al. (1999), as we found no difference in species diversity among thinned, unthinned, or old-growth stands. Similar spe-

cies diversity and richness among stands indicated that even though many plants were noticeably more abundant in the thinned stands than in unthinned and old-growth stands (e.g., grasses, fireweed, and Sitka alder), this increase in dominance did not cause a decrease in species diversity.

Structural diversity

A structurally diverse habitat is consistently noted as a defining feature of old-growth forests (Wells et al. 1998; Thysell and Carey 2000) and is the most important habitat attribute to manage for when striving to maintain or enhance biodiversity (Acker et al. 1998; Fredericksen et al. 1999). Our results for mean structural richness (number of height classes occupied by vegetation) indicated that the shrub layer had significantly greater structural richness in the young stands than in the old-growth stands. Low structural richness in the old-growth shrub layer is believed to be a function of the very low volume and patchy distribution of shrubs beneath the well-developed canopy of these old forests. Sample plots with few shrubs invariably had several empty height classes, which resulted in a lower mean structural richness than in the abundant shrub layers of the young stands. Not surprisingly, the structural richness of the tree layer in unthinned stands was very low, which can be explained by the dense cover of lodgepole pine, nearly all of which was in the >3.0 m height class. The low levels of light beneath the closed canopy of the unthinned stands may have decreased the structural richness of the trees in the lower height classes, as shade-tolerant tree species, such as subalpine fir, were not well established in these young stands.

Differences in structural diversity among stands, although not statistically significant, were likely biologically important and deserve comment. The structural diversity of the shrub layer was similar among stands; however, the distribution of shrubs among the six height classes was quite different. The low abundance of shrubs in the old-growth stands was spread evenly among all six height classes, whereas the shrub volume in the medium-density, high-density, and unthinned stands was almost entirely in the tallest height class (>3.0 m). In all of these stands, the high volume of tall shrubs is explained by the dominance of two shade-intolerant plants, Sitka alder and willow. In contrast, the low-density stands had maximum shrub volume from 1.0 to 3.0 m, with relatively little volume above 3.0 m. The fewer tall shrubs observed in the low-density stands than in the other young stands may be related to physical damage inflicted on tall shrubs during the thinning treatments or from browsing by moose (*Alces alces* L.). This explanation was supported by observations of relatively low volumes of alder and willow in the low-density stands and was also supported by Thomas et al. (1999), who suspected physical damage to be the cause of reduced volumes of herbs and shrubs in stands receiving the heaviest thinning treatments. In addition, competition with an abundant shrub layer of intermediate height (1.0–3.0 m) may have contributed to the lack of tall shrubs in the low-density stands.

Differences in structural diversity of the tree layer, while only marginally significant ($p = 0.09$), were noticeably higher in the low-density stands than in the other young stands. Not surprisingly, for all stands, the distribution of tree volume was heavily dominated by the tallest height class. However,

the openness of the low-density stands is believed to provide enough understory light to enhance the growth, and therefore structure, of the understory trees. Interestingly, we also observed that the volume of subalpine fir in low-density stands was 18 times that in all other young stands (mean crown volume index of 1.99 compared with 0.11 m^3/0.01 ha), which suggests that thinning to low densities may have encouraged the growth of this shade-tolerant conifer. Shade-tolerant conifers are a defining component of old-growth structure (Elliott et al. 1997; Thysell and Carey 2000) and are very often absent from the understories of managed stands (Acker et al. 1998; Vora 1994). Consequently, an understory that included shade-tolerant conifers would represent a significant improvement to stand structure as these low-density stands develop.

Total structural diversity was higher in the low-density stands than in all other stands, although this difference was marginally significant ($p = 0.06$). We suggest that the higher total structural diversity in the low-density stands was due to the decreased dominance of tall trees and shrubs, which, in turn, increased understory light levels and stimulated the development of an abundant understory of herbs, shrubs, and trees. Our results indicated that structural diversity in thinned stands was either equal to or greater than that observed within the understory (<4 m) of old-growth stands.

Thysell and Carey (2000) cautioned that improved understory conditions resulting from thinning treatments might be short-lived, as overstory canopies soon close. However, our results suggested that there are many attributes of the plant community that appear to remain enhanced, at least 12 to 14 years after thinning, and that these improvements will likely last longer in stands that received the heaviest thinning treatments. In addition, the effects of thinning on understory vegetation have been shown to persist after canopies have closed. Thomas et al. (1999) reported significantly greater understory abundance in thinned stands than in unthinned stands, even after canopy closure and understory light conditions had returned to control levels.

Importance of herb–shrub stage

Often, biodiversity conservation efforts focus on late-seral species and on maintaining or promoting other old-growth-related species or attributes (Cole 1996; Acker et al. 1998). Although old-growth forests provide important habitat for many plants and animals, they represent only one of several important stages of succession (Hansen et al. 1991). The herb–shrub stage can last from 20 to 30 years in natural stands (up until canopy closure), is the most dynamic of all successional stages (Schoonmaker and McKee 1988), and provides unique structure and composition that make it distinct from all later tree-dominated stages (Hansen et al. 1991).

The herb–shrub stage has recently become limited, primarily because of effective fire suppression and conventional forest management practices. Since the 1950s, effective fire suppression has resulted in fewer large stand-initiating and stand-maintaining fires and in an increase in density of trees, all of which have led to a decrease in the herb–shrub stage (Hansen et al. 1991; Fiedler and Carlson 1992). In addition, conventional forest management, which strives to replant cutblocks with a homogeneous cover of crop trees soon after harvest, has also abbreviated the herb–shrub stage (Schoonmaker

and McKee 1988; Cole 1996). By removing trees, thinning, especially to low densities, delays canopy closure and increases the duration of the herb–shrub stage and the unique community of plants that live there. We observed 39 species of plants found only in the young stands (i.e., not in the old-growth stands), 28 of which were unique to the thinned stands. Old-growth stands included 13 unique species. While the species unique to the young stands included both early- and late-seral species, the species unique to old-growth stands were nearly all late-seral species.

Caution should be used when interpreting these comparisons, as species–area relationships suggest that one would expect to find more species (and therefore more unique species) in the young stands because of the combined sample size of the low-density, medium-density, high-density, and unthinned stands (Connor and McCoy 1979). However, a conservative interpretation of our data would still suggest that the young stands, especially young thinned stands, support many unique early- and late-seral species, and that old-growth stands support many unique late-seral species.

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