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Canopy Structure on Forest Lands in Western Oregon: Differences Among Forest Types and Stand Ages

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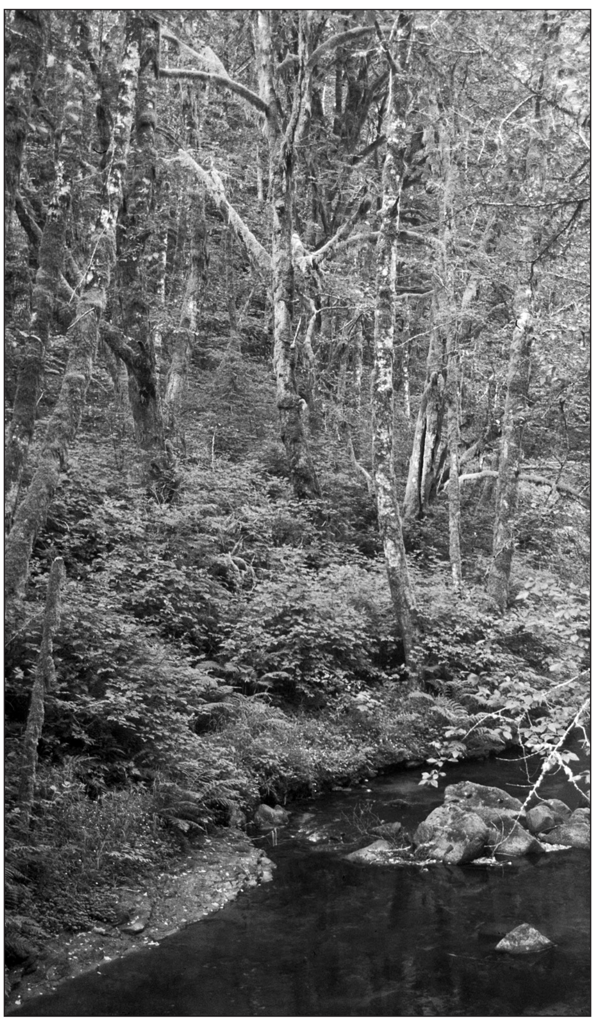

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Cover photographs by Andrew Gray.

Abstract

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Canopy structure is an important attribute affecting economic and ecological values of forests in the Pacific Northwest. However, canopy cover and vertical layering are rarely measured directly; they are usually inferred from other forest measurements. In this study, we quantified and compared vertical and horizontal patterns of tree canopy structure and understory cover along a successional gradient of forests and among stands with different thinning histories on nonfederal lands in western Oregon. Analyses focused on three dominant forest type groups: wet conifer, wet hardwood, and dry hardwood. We used data from 917 systematically located, forested Forest Inventory and Analysis plots measured between 1995 and 1997. On each plot, canopy cover by layer and species was measured on line-intercept transects, and cover of understory species was measured on five subplots. Trends in canopy structure with stand age did not always follow the patterns predicted by common successional models. Most of the cover in moist stands was in the upper tree layer, but cover in dry hardwood stands was more evenly distributed among layers. Contrary to expectations of canopy closure, mean canopy cover by age class rarely exceeded 85 percent, even in unthinned productive young conifer forests. Possibly as a result, effects of stand age on understory vegetation were minimal, except for low levels of forbs found in 20- to 40-year-old wet conifer stands. Shade-tolerant tree species rarely made up more than 20 percent of canopy cover, even in the lower canopy layers and in stands >100 years old. Although heavily thinned stands had lower total cover, canopy structure did not differ dramatically between thinned and unthinned stands. Our findings suggest potential limitations of simple stand succession models that may not account for the range of forest types, site conditions, and developmental mechanisms found across western Oregon.

Keywords: Canopy structure, Douglas-fir, succession, canopy cover, understory vegetation, forest inventory, Pacific Northwest, hardwood.

Introduction

Characterization of canopy structure is important for the management of forests in the Pacific Northwest (PNW). Amount of cover and the vertical structure of forest canopies can determine key ecological attributes: wildlife habitat (Hayes et al. 1997, Johnson and O'Neil 2001, MacArthur and MacArthur 1961, Maguire and Bennett 1996, North et al. 1999, Thomas and Verner 1986), disease and insect susceptibility (Mathiasen 1996, Winchester and Ring 1996), fire hazard (Latham et al. 1998), atmospheric fluxes of energy and gases (Rose 1996), and microclimate (Gray et al. 2002, Yang et al. 1999). Forest management goals that include conservation of wildlife, reduction of fire hazard, or control of insect/pathogen outbreaks usually set criteria for canopy structure, either implicitly or explicitly.

Canopy structure is the horizontal and vertical distribution of tree crowns in a forest stand. Vertical canopy structure is often simplified by dividing canopy cover into height layers. Horizontal canopy structure is commonly quantified as the vertically-projected percentage of cover of plant canopies, and the abundance and size of canopy gaps. Additional attributes used to describe canopy structure include the number of vertical canopy layers, heights of the vertical layers, and the proportions of cover contributed by different species groups (Fiala 2003).

It is generally understood that canopy structure changes as forests develop with age (Bond and Franklin 2002, Franklin et al. 2002, Oliver 1981, Van Pelt and North 1996), but these changes have rarely been quantified. Forest succession has nevertheless been a useful template for describing changes in canopy structure and for comparing canopies between managed and natural environments (Franklin et al. 2002, McCook 1994). Managing forests based on simple characterizations may not adequately replicate the stand structure of natural forests, including canopy structure. The challenge for forest managers and biologists is to describe canopy structure as a meaningful forest indicator that is also repeatable, efficient, and reliable across a wide range of field-tested conditions. Characterizing canopy structure attributes across a stand development gradient can help achieve this objective.

Forest succession has been a useful template for describing changes in canopy structure and for comparing canopies between managed and natural environments.

Multiple stand development models are used to describe forest succession patterns and processes (e.g., Carey and Curtis 1996, Franklin et al. 2002, Oliver 1981, Spies and Franklin 1991). The most commonly cited stand development model is Oliver's (1981) four-stage model, which comprises stand-initiation, stem-exclusion, understory-reinitiation, and old-growth phases, all of which include canopy cover criteria. Franklin et al. (2002) proposed an alternative stand development model for natural stands. Their model highlights eight commonly encountered development stages: disturbance and legacy creation, cohort establishment, canopy closure, biomass accumulation/competitive exclusion, maturation, vertical diversification, horizontal diversification, and pioneer cohort loss, with canopy attributes described for each of these stages. Quantifying canopy structure attributes across a successional gradient can aid in evaluating these stand development models.

The development of understory plant communities is usually related to changes in the overstory (Franklin et al. 2002, Henderson 1981, Naesset and Okland 2002, Oliver 1981, Stewart 1988, Zamora 1981). According to Connell and Slatyer's (1977) "tolerance" model of succession, shade-tolerant species are generally present in all stages of succession, but invade the understory and increase in abundance across the gradient of development stages. To assess successional patterns, it is crucial to understand how variance of foliage and its patterns of distribution in the forest canopy impact understory conditions (Van Pelt and Franklin 2000). Therefore, it is important to examine patterns in both overstory and understory cover across a successional gradient, including the quantities and proportions of shade-tolerant cover vertically distributed in the canopy.

The progression of forest canopy structure development among successional stages differs with forest type, species composition, disturbance history, and management practices. In the coniferous forests of the Pacific Northwest, the longevity of some tree species results in slower successional change than in forest types with more rapid seral replacement of species (e.g., red alder hardwood stands) (Ishii et al. 2000). However, the differences in canopy structure along forest succession gradients for multiple forest types have rarely been described.

Forest management has an impact on canopy structure. In western Oregon, clearcut logging, tree planting, and short stand rotation lengths have greatly reduced the structural variability of forests (Garman et al. 1992; Hansen et al. 1991, 1995; Smith et al. 1996). The vertical distribution of foliage can be altered by multiple silvicultural treatments, including pruning, fertilization, and thinning (Berg et al. 1996, Maguire and Bennett 1996, but see Gillespie 1994). With increasing awareness of the value of structural heterogeneity for multiple wildlife species, there has been a growing emphasis on silvicultural techniques that promote heterogeneity in stand structure throughout the rotation interval (Berg et al. 1996). Retention of overstory trees during even-age regeneration harvest is an effort to better represent patterns of disturbance and the structural complexity of natural forests (Hansen et al. 1995). It is not known, however, how different management regimes affect canopy structure.

Much ecological research has described similarities and differences in patterns and processes associated with succession (McCook 1994), but we are unaware of any study that examines canopy structure attributes across a large range of forest types and successional stages.

The purpose of this study was to enhance understanding of canopy structure development patterns across the forests of western Oregon using inventory data. Specifically, we quantified and compared total cover of trees and understory vegetation, vertical canopy layering, and abundance of shade-tolerant cover across seral stages and forest types, and assessed the impact of thinning on canopy structure. Our expectations were that most stands would fall along the successional trajectory for productive forests after severe disturbance: an initial period of low tree cover and moderate understory cover; an early period of rapid increase to full tree closure in a single layer and sparse understory cover; an intermediate period of slow development of multiple tree canopy layers and slow increase in understory cover; and a later period of reduced tree cover in the tallest layer, with tree cover dispersed among multiple layers, and moderate to high understory cover.

Methods

Data Collection

This study used data collected during the inventory of western Oregon forests conducted by the USDA Forest Service Forest Inventory and Analysis (FIA) Program from 1995 through 1997 (Azuma et al. 2004). Study sites were a permanent grid of systematically located plots located throughout western Oregon. Western Oregon was defined as the area west of the crest of the Cascade Mountain Range, delimited by county boundary lines. The study sites included all private and public forested lands, except for lands managed by the USDI Bureau of Land Management and the USDA Forest Service national forests. A separate inventory system was used on those federal lands in the 1990s that did not collect comparable canopy structure data. The systematic-grid design of the FIA inventory allows for statistical inferences to the population from which the grid points were sampled. Information compiled and distributed from the FIA inventory is comprehensive, has minimal bias, is scientifically sound, and has known precision (Azuma et al. 2004). The forested plots are representative of the entire population of nonfederal forest lands in western Oregon.

The study area encompassed five physiographic provinces: The Oregon Coast Range, The Willamette Valley, Oregon Western Cascades, Klamath Mountains, and High Cascades (Franklin and Dyrness 1973) (fig. 1). The forest zones included in the FIA inventory were Sitka spruce, western hemlock, Pacific silver fir, mountain hemlock, oak woodland, interior valley, mixed-evergreen, mixed-conifer, white fir, and Shasta red fir (Franklin and Dyrness 1973). A total of 1,127 FIA plots were measured for the inventory of western Oregon forests. Plots consisted of a cluster of

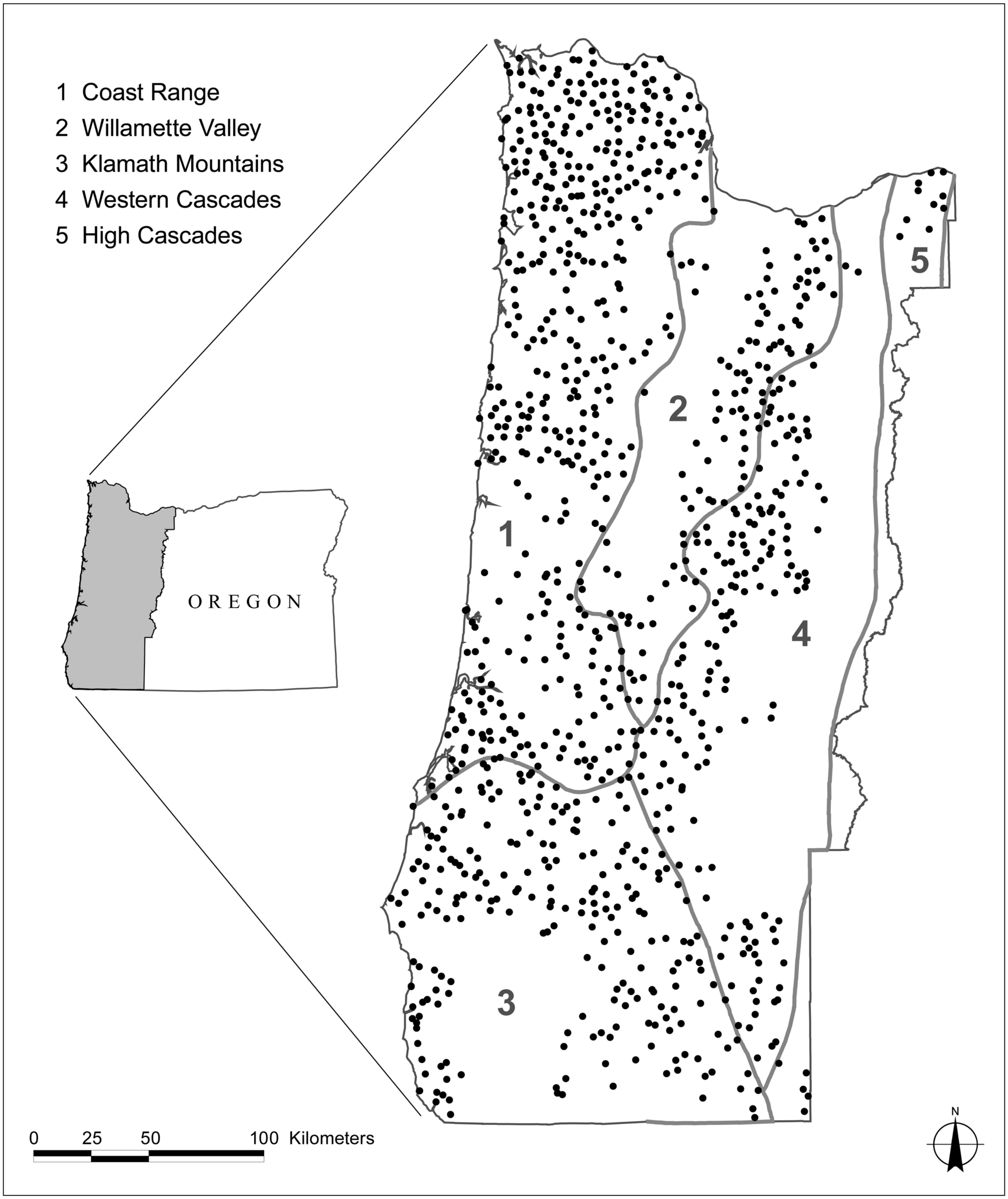

Figure 1—Locations of the 917 forested Forest Inventory and Analysis 1995–97 inventory plots analyzed in this study and the boundaries of the Franklin and Dyrness (1973) physiographic provinces.

five 0.09-ha subplots systematically placed over a 2.5-ha area. Portions of plots in different land class or stand types were delineated in the field, and all data collected identified to the type being sampled. For this study, data were only used for forested stands that were sampled by a minimum area of 0.27 ha (three subplots) to ensure an adequate sample of stand characteristics. Of the original 1,127 plots, 934 met this criterion. We eliminated another 17 plots classified as non-stocked by FIA (<10 percent stocking of trees), leaving 917 plots for this study. We refer to each FIA plot as a ”stand” throughout this paper, and treat a stand as the experimental unit.

Ground-based canopy cover estimates were made on the forested portions of each plot. Canopy cover was measured on three 17-m (horizontal distance) transects originating at subplot center and radiating out at 0, 135, and 225 degrees. Trees ≥ 1.4 m in height were assigned to as many as three canopy layers (upper, middle, lower), with discrete layers differing by a minimum of 5 m in mean height. Canopy layers were relative to conditions within a stand; actual layer heights differed among stands. The line-intercept method was used to measure canopy cover in each layer (Canfield 1941, Fiala et al. 2006, O'Brien 1989). For every tree species (see app. 1) within a canopy layer, generalized crown boundaries (i.e., ignoring minor gaps and openings) were vertically projected onto transects using a clinometer (see USDA Forest Service 1995 for detailed procedures). The distance along a transect line that the crown intercepted was recorded. The proportion of transect lengths intercepted by the crowns was the ground-estimated canopy cover for a stand.

Selected tree and understory plant attributes measured by FIA crews were also used for this study. Composition, cover, and height of all trees ≥ 0.5 m in height and < 2.5 cm diameter at breast height (d.b.h.), all shrubs, and forbs and grasses with ≥ 3 percent cover were measured on 5-m fixed-radius plots around each subplot center. Separate estimates of total shrub and forb cover were also made. Age, d.b.h., and height of trees were measured with a combination of variable- and fixed-radius plots. Trees 2.5 to 12.5 cm d.b.h. were measured on 2.35-m-radius plots, whereas trees > 12.5 cm d.b.h. were measured using a 7-m^2/ha basal area factor prism to a maximum distance of 17 m from subplot center.

Analyses

We calculated multiple cover values for each of the 917 stands. For trees, we calculated cover for individual species for each of the vertical layers (≤ 3) as the proportion of the transect lengths covered by them. Total cover of a species was the combination of its cover in each of the three layers. Combining of layers did not double-count cover from multiple layers that intercepted the same horizontal areas along each transect; cover could not exceed 100 percent. We classified tree species as either shade-tolerant or shade-intolerant, wherein Pacific silver fir, white fir, grand fir, Pacific dogwood, western redcedar, Pacific yew, western hemlock, English holly, mountain hemlock, and Sitka spruce (see appendix for species names) were classified as shade-tolerant. We then quantified canopy cover separately for shade-tolerant and shade-intolerant cover, for both individual layers and total combined cover. Finally, we combined all tree species to calculate cover by layer and total cover, accounting for overlap within and among layers so cover could not exceed 100 percent. We summarized tree cover levels at the stand level, accounting for transects and/or layers within transects that had no cover recorded by assigning them cover values of 0. We averaged total shrub and total forb cover values across the three to five subplots.

Stand age, forest type, and forest type group were classified using the tree data for each stand in the FIA inventory (Azuma et al. 2004). Stand age was based on the ages of the dominant trees in each stand (excluding residual trees from previous stands) and grouped into 10-year age classes up to age 200, lumped into a 100-year age class for ages 200 to 300 (labeled as age “250” in this study), and combined into a single age class stands >300 years old (labeled as age “400” in this study). Forest type was assigned based on the dominant tree species in the stand. We assigned each stand to a forest type group, which was defined by the dominant species type (conifer, hardwood) and relative site moisture characteristic (wet or dry). To determine site moisture characteristics, each stand was overlaid on a map of mean annual precipitation generated with the PRISM climate model (1971-2000 means, 800-m grid size; Daly et al. 1994). Four forest type groups were generated with this procedure: wet conifer, dry conifer, wet hardwood, dry hardwood (table 1). Douglas-fir was the dominant species in the wet conifer group, red alder was the dominant species in the majority of wet hardwood stands, and Oregon white oak and Pacific madrone dominated most of the dry hardwood stands. Because the FIA sample is representative of distributions on the landscape, sample sizes were not evenly distributed among forest type groups (hereafter referred to as forest groups) and age classes (table 2).

Canopy structure patterns were evaluated for all forest groups combined and separately for three forest groups. The dry conifer group had few samples (n = 33) and was not analyzed separately (see Fiala (2003) for additional analyses). Because 70 percent of the stands were in the wet conifer group (table 1), results for all forest groups combined paralleled trends of the wet conifer group. Therefore, beyond describing total canopy cover and canopy cover for the three vertical layers, we focused our analyses on cover for the three dominant forest groups in our data set.

Table 1—The four forest groups included in the 1995–97 Forest Inventory and Analysis inventory of western Oregon that met the criteria for inclusion in this study, and the number of plots in each category

Forest group[a]	Precipitation (SE)	Number	Dominant tree species in the stand
	Centimeters		
Wet conifer	185.4 (7.3)	645	Douglas-fir (n = 558), western hemlock (n = 57), Sitka spruce (n = 15), western redcedar (n = 7), noble fir (n = 4), Pacific silver fir (n = 2), Port-Orford cedar (n = 2)
Dry conifer	124.2 (21.6)	33	Grand fir (n = 9), incense-cedar (n = 9), lodgepole pine (n = 6), white pine (n = 6), ponderosa pine (n = 3)
Wet hardwood	188.4 (5.1)	137	Red alder (n = 99), bigleaf maple (n = 25), black cottonwood (n = 5), willow spp. (n = 3), California laurel (n = 3), Oregon ash (n = 2)
Dry hardwood	125.6 (12.4)	102	Oregon white oak (n = 42), Pacific madrone (n = 32), tanoak (n = 18), California black oak (n = 6), canyon live oak (n = 3), golden chinkapin (n = 1)

Note: SE = standard error.

[a] Stands were grouped by hardwood and conifer dominance and mean precipitation levels from the PRISM model (Daly et al. 1994).

Table 2—Sample sizes for each forest group and stand-age class combination in the 1995–97 Forest Inventory and Analysis inventory stands used in this study

	Sample size by forest group			
Stand-age class	Wet conifer	Wet hardwood	Dry hardwood	All forest groups
Years				
5	67	13	12	92
15	90	14	12	122
25	118	23	14	161
35	89	31	8	131
45	107	27	16	154
55	66	16	11	96
65	36	8	7	54
75	22	0	5	29
85	9	2	3	16
95	9	0	4	16
105	13	1	4	19
115	9	0	4	13
125	2	0	0	2
145	0	0	1	1
155	1	1	0	2
165	0	0	1	1
175	1	0	0	1
250[a]	4	1	0	5
400[b]	2	0	0	2
Total	645	137	102	917

[a] All stands between ages 200 and 300 were combined into the 250-year age class.

[b] All stands aged > 300 years were combined in the 400-year stand-age class.

We calculated means and standard errors of multiple canopy structure attributes by stand-age class for the forest groups. Although age is not a predictor of successional stage, it serves as a proxy for stand-development pattern (Spies and Cohen 1992). Overstory attributes were canopy cover of shade-tolerant, shade-intolerant, and all tree species combined, cover in each of the three vertical canopy layers, heights of the three vertical layers, and the number of vertical canopy layers. Mean shrub and forb cover for each stand were calculated to compare understory and overstory vegetation cover along the stand-age development gradient. For shrub and forb species present in $\geq$ 20 percent and $\geq$ 10 percent of the 917 stands, respectively, we calculated mean species cover by stand age for stands with observations of the species (“characteristic cover”). Shrub species richness also was derived by stand age for all stands combined.

Analysis of variance (General Linear Model procedure, SAS Institute Inc. 1999) were computed for selected canopy attributes by stand age, forest group, and the age × forest-group interaction. Effects with an estimated type 1 error of $p < 0.05$ were considered significant, and comparison of means for significant effects was done with the Tukey-Kramer procedure. The data were approximately normally distributed. Although an arcsin-square-root transformation of the percentage of cover data somewhat improved normality, the impact on parameter estimates and p-values for effects was minor. Thus, analyses used the untransformed cover data for greater simplicity of interpretation of results. Statistical analyses with forest group were restricted to stands <75 years old to ensure data were available for each combination of stand age × forest group ($n = 785$). We assessed patterns qualitatively for data from stands >75 years old.

Two vertical structural diversity measures were calculated for each wet conifer stand: Simpson’s Diversity Index (SDI, Simpson 1949), and the Canopy Height Diversity Index (CHDI, Spies and Cohen 1992). The indexes were not calculated for hardwood stands because the numbers of stands by age class were less evenly distributed than for wet conifer stands and because CHDI was developed for wet conifer stands, and its reliance on maximum tree height makes it less appropriate for hardwood stands. For SDI, trees $\geq$ 2.5 cm d.b.h. were grouped into 5-m vertical intervals based on their heights. Stem density weighted by basal area was used as a substitute for species to compare diversity among height intervals. Proportions of total basal area were used because the number of stems gave higher weight to smaller trees. However, we expected the larger trees to be taller with larger crowns, and thus contribute more to stand vertical diversity than smaller trees. Previous studies have also used basal area instead of density to better represent the use of resources, recognizing that larger trees will have more influence (e.g., Staudhammer and Lemay 2001). The CHDI equation requires crown area estimates, which were calculated using equations developed to estimate crown width from d.b.h. (Moeur 1985).

Effects of recent management on canopy cover were assessed by comparing Douglas-fir forests 15 to 45 years old that were unthinned, lightly thinned, or heavily thinned in the 10 years prior to measurement, as estimated or verified by FIA crews. There were 245 unthinned stands without evidence of harvest or wildfire. Twenty-one stands had evidence of light harvest levels, defined as remaining trees constituting $\geq$ 25 percent crown cover with <20 percent of live trees >12.5 cm d.b.h. harvested. Heavy partial harvest, with $\geq$ 25 percent crown cover and $\geq$ 20 percent of live trees >12.5 cm d.b.h. harvested, was identified for 20 stands.

Results

Tree Cover

Tree canopy cover differed significantly by age class and forest type group (fig. 2; $F_{6,764}$ = 118.3, $p < 0.001$ and $F_{2,764}$ = 5.47, $p = 0.004$, respectively), and for their interaction ($F_{12,764}$ = 4.76, $p < 0.001$). For all forest groups, mean total cover significantly increased with increasing stand age up to age 35 (canopy closure) and subsequently remained high (60 to 96 percent) after canopy closure was reached, although it rarely exceeded 85 percent. Mean cover of the upper layer contributed the most to total cover and thus closely mirrored trends in total canopy cover, except in stands >200 years old. Mean cover of the middle layer also increased with stand age ($F_{6,764}$ = 8.21, $p < 0.001$). Mean cover of the lowest layer was nominal (< 20 percent) except in stand ages >200 years. Canopy cover values and trends for wet conifer and wet hardwood forests paralleled those for all forest types combined, except that total canopy cover was significantly higher in 1- to 10-year-old wet hardwood stands than in wet conifer stands (as seen in the significant interaction term). In contrast, the dry hardwood forest type had the lowest total cover levels, and the upper and middle cover layers contributed similar amounts of cover across stand ages.

Mean total cover increased with increasing stand age up to age 35 and subsequently remained high, although it rarely exceeded 85 percent.

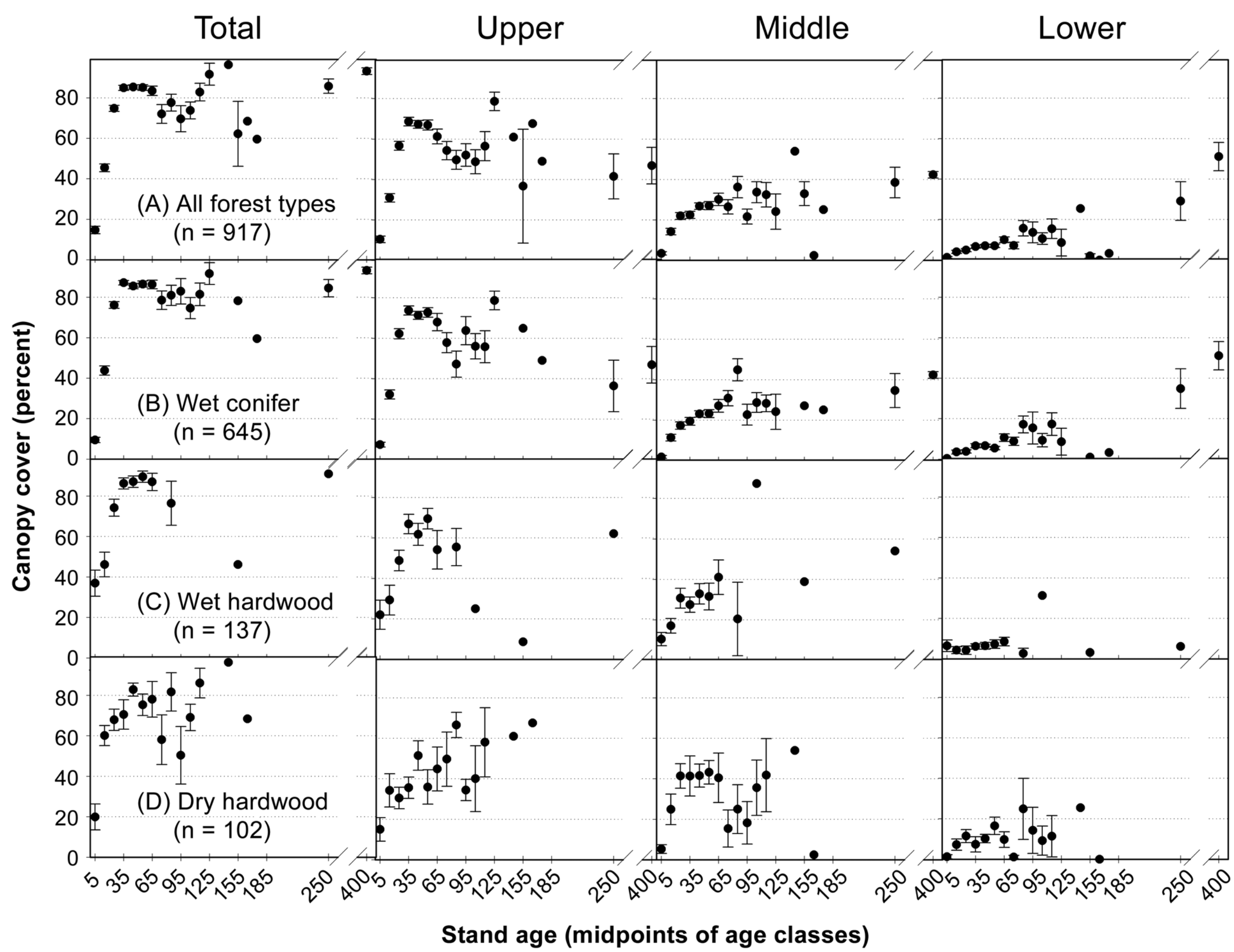

Figure 2—Mean canopy cover (±1 SE) for three tree canopy layers and all layers combined across a chronosequence of stand ages (grouped into 10-year intervals and labeled using midpoints of intervals) by forest group (see table 1) in western Oregon. Sample sizes differed among stand ages (see table 2).

Shade-tolerant canopy cover was quite low across stand age classes for all three forest groups (fig. 3). The wet conifer stands had significantly higher levels of shade-tolerant cover than the other two groups ($F_{2,764} = 17.0$, $p < 0.001$), with about 20 percent total shade-tolerant cover between stand ages 35 to 85, primarily concentrated in the upper layer. However, total shade-tolerant cover was unexpectedly low in the older wet conifer stands. The wet hardwood stands were even lower in shade-tolerant cover, with fairly consistent and similar levels for all three layers among stand ages, except in the older single samples. The dry hardwood stands had only nominal total shade-tolerant cover in all layers for all stand ages.

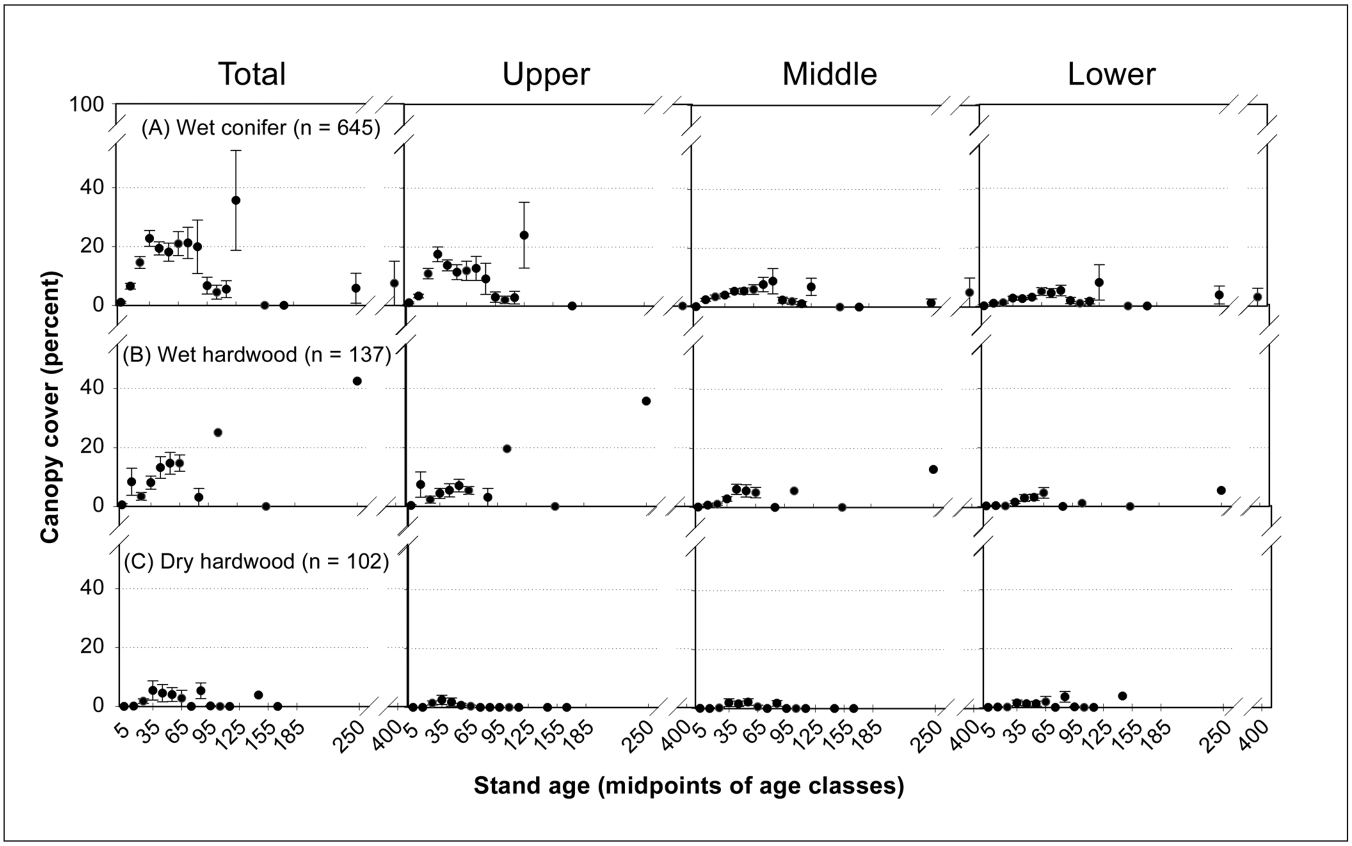

Figure 3—Mean percentage of shade-tolerant canopy cover (± 1 SE) for three tree canopy layers and all layers combined across a chronosequence of stand ages (grouped into intervals and labeled using midpoints of intervals) by forest group (see table 1) in western Oregon. Sample sizes differed among stand ages (see table 2).

In contrast with absolute abundance, the proportions of cover that were shade-tolerant were generally highest in the lower cover layer, compared with the middle and upper layers across all three forest groups (fig. 4). In the wet conifer stands, the proportions of shade-tolerant cover were consistently highest for the lower cover layer with the exception of the 5-year age class. For the wet hardwood stands, trends in the proportions of shade-tolerant cover were generally similar to wet conifer stands. The dry hardwood stands had minimal proportions of shade-tolerant cover, consistent with their nominal shade-tolerant cover levels. Across all three forest groups, the proportion of shade-tolerant cover rarely exceeded shade-intolerant cover in any of the three vertical cover layers.

Figure 4—Mean proportion (± 1 SE) of shade-tolerant canopy cover across a chronosequence of stand ages (grouped into intervals and labeled using midpoints of intervals) by forest group (see table 1) in western Oregon. Sample sizes differed among stand ages (see table 2).

Vertical Structure

Heights of canopy layers increased with increasing stand age (fig. 5; $F_{6,764} = 34.4$, $p < 0.001$). The upper and middle layer heights for wet conifer forests increased with stand age to 55 years, and then remained fairly constant in older stands. The wet hardwood forest group followed a similar pattern, except that the height of the upper layer was similar for stands aged 5- to 25-years, and heights of the upper and middle layers increased only to age 35 (forest type group by stand age interaction $F_{12,764} = 6.77$, $p < 0.001$). The lower layer heights for both wet conifer and wet hardwood forests were consistently short among stand ages. The dry hardwood group differed in that mean heights of its upper and middle canopy layers were shorter than for the other two forest groups (interaction effect for middle layer $F_{12,764} = 2.28$, $p = 0.008$), and all three canopy layer heights increased minimally across the 165-year chronosequence.

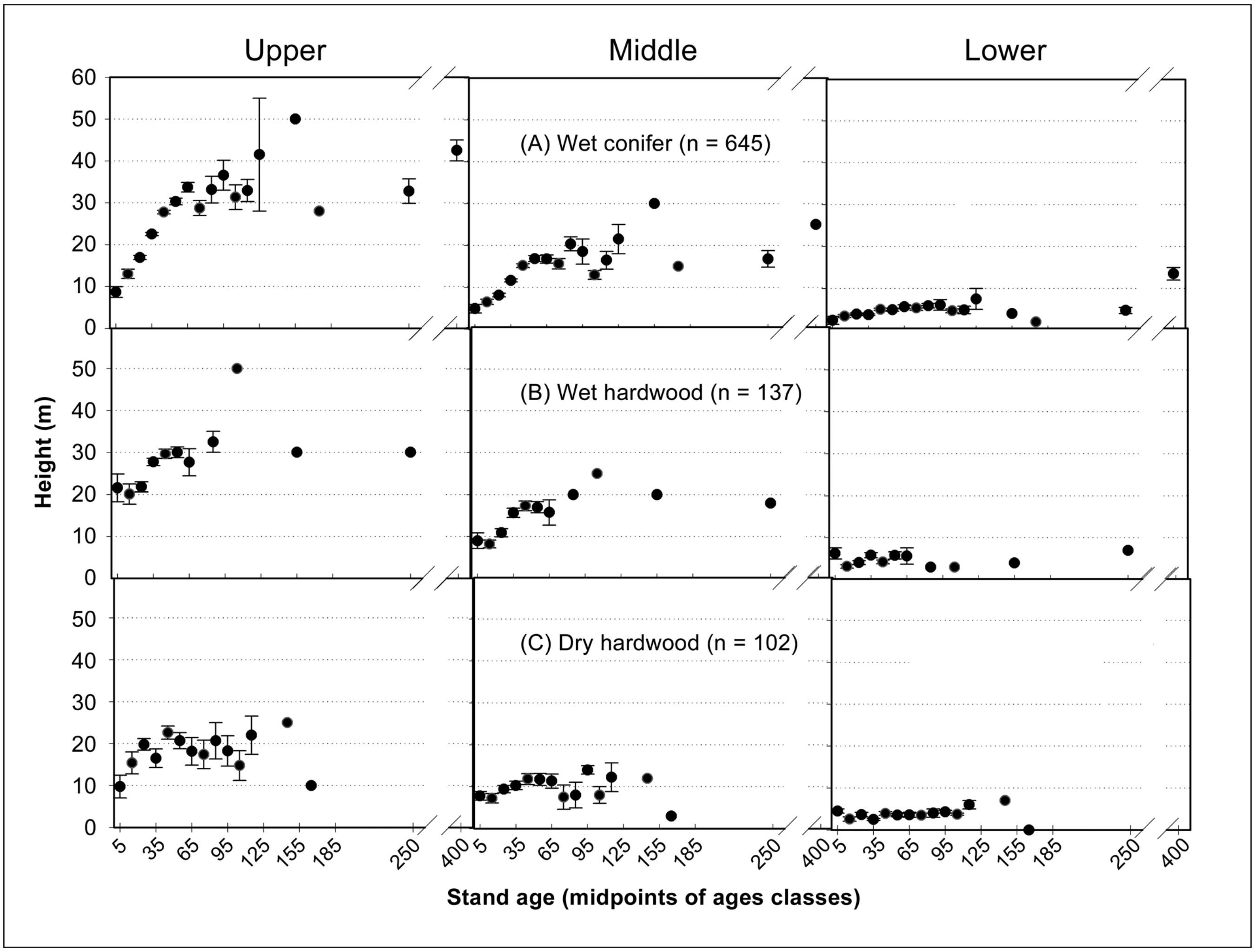

Figure 5—Mean heights (± 1 SE) for three tree canopy layers across a chronosequence of stand ages by forest group (see table 1) in western Oregon. Sample sizes differed among stand ages (see table 2).

The number of canopy layers increased with stand age in all forest groups ($F_{6,764}$ = 23.2, p < 0.001), indicating differentiation of vertical canopy structure (fig. 6). For the wet conifer stands, the mean number of layers developed from one in 5-year stands to greater than two layers for ages 15 to 55 and then leveled off at three layers. Layer development in the wet hardwood stands paralleled trends in the wet conifer stands, except that even the youngest (5- to 15-year) stands had greater than two layers of cover (group by age interaction $F_{12,764}$ = 3.56, p < 0.001). Vertical layering in the dry hardwood stands fluctuated between two and three layers for stands greater than 5 years old.

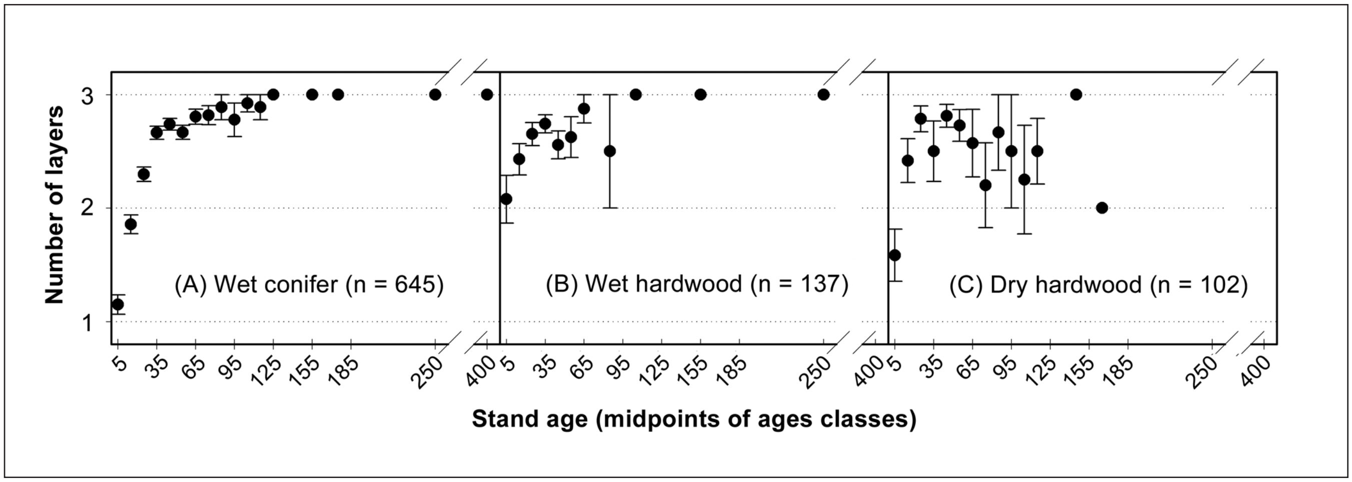

Figure 6—Mean number of canopy layers (± 1 SE) across a chronosequence of stand ages by forest group (see table 1) in western Oregon. Sample sizes differed among stand ages (see table 2).

The SDI of tree heights for wet conifer forests increased across age classes (fig. 7). Diversity increased up to age 65, and then leveled off. Similarly, CHDI for the wet conifer stands increased with stand age up to age 155, but leveled off around age 55 (fig. 8). Unlike SDI, CHDI showed lower values for stand age classes 175 and 250.

Understory Vegetation

Forb cover was negatively correlated with tree cover in the wet conifer and dry hardwood types.

Cover of shrubs and forbs differed among forest groups and stand age classes, and some of the variation was associated with overstory tree cover (fig. 9, table 3). Forb cover was lower for ages 25 to 35 than for ages 5 to 15 for the wet conifer forest type group (group by age interaction: $F_{12,764} = 2.78$, $p = 0.001$). Shrub cover was higher in the wet hardwood group than in the other types ($F_{2,764} = 5.48$, $p = 0.004$). There was no significant relationship between shrub cover and stand age ($F_{6,764} = 0.97$, $p = 0.442$), although cover levels were slightly elevated at age 15 in the wet conifer and wet hardwood types. Forb cover was negatively correlated with tree cover in the wet conifer and dry hardwood types (table 3), indicating that some of the stand-age effect may have been due to differences in tree cover. This analysis also revealed a small negative correlation between shrub cover and tree cover for the wet hardwood type.

Figure 7—Mean Simpson's Diversity Index (± 1 SE) of tree heights weighted by their proportion of total basal area, within 5-m vertical height intervals among a chronosequence of stand ages for the wet conifer stands (n = 645) in western Oregon. Sample sizes differed among stand ages (see table 2).

Figure 8—Mean Canopy Height Diversity Index (CHDI (± 1 SE)) of the wet conifer stands (n = 645) among the chronosequence of stand ages. Sample sizes differed among stand ages (see table 2).

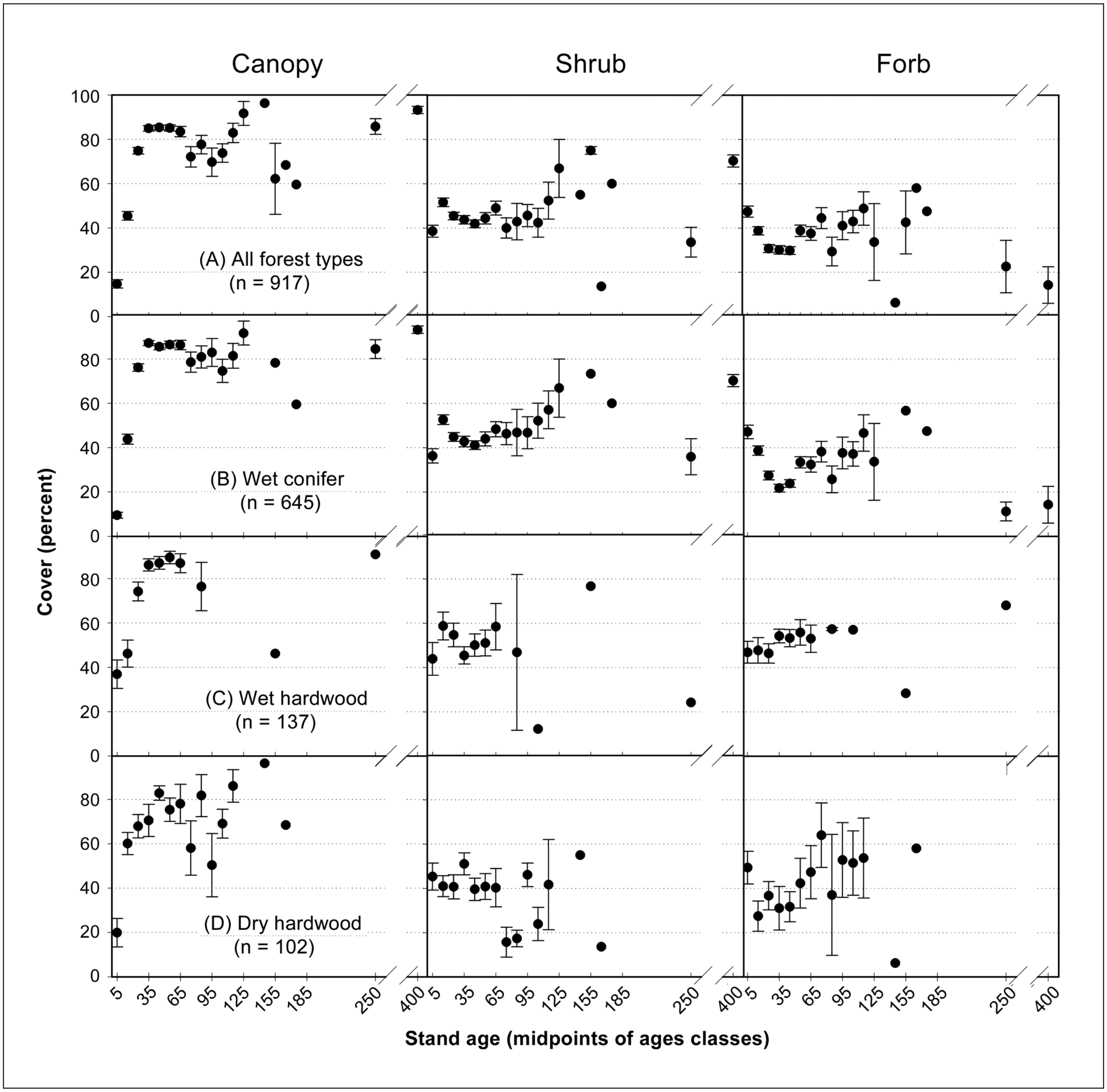

Figure 9—Mean percentage of cover (± 1 SE) for total tree canopy, shrub, and forb across a chronosequence of stand ages (grouped into intervals and labeled using midpoints of intervals) by forest group (see table 1) in western Oregon. Sample sizes differed among stand ages (see table 2).

Table 3—Pearson correlation coefficients and p-values between tree cover and forb cover, and tree cover and shrub cover, by forest group

	Forb cover		Shrub cover	
Forest group	**R**	**p**	**R**	**p**
All	-0.251	<0.0001	-0.037	0.2647
Wet conifer	-0.340	<0.0001	-0.024	0.5370
Wet hardwood	0.117	0.1745	-0.187	0.0286
Dry hardwood	-0.360	0.0002	-0.105	0.2921

There were 18 shrub species present in >20 percent of the stands and 5 forb species present in >10 percent of the stands that were analyzed for cover trends with age (figs. 10 and 11). Of the shrub species analyzed, the stand age effect was significant ($p < 0.05$) for vinemaple, red huckleberry, dwarf Oregon grape, oceanspray, trailing blackberry, and snowberry (fig. 10). For the first four shrub species, cover was lower in stands aged 5 and 15 than in stands aged 35 to 65, whereas the reverse was true for the last two species. Of the forb species analyzed, the stand age effect was significant ($p < 0.05$) for sword fern and bracken fern (fig. 11). For swordfern, cover was lower in stands aged 5 and 15 than in stands aged 35 to 65; the reverse was true for bracken fern.

Mean shrub species richness peaked just prior to crown closure (age 15) and revealed a small but significant drop in richness coincident with age of canopy closure at ages 25 to 35 (fig. 12; $F_{18,896} = 2.94$, $p < 0.001$). Shrub species richness appeared to rise somewhat with older age classes, but variability in the low sample size obscured patterns in the oldest age classes.

Mean shrub species richness peaked just prior to crown closure (age 15) and revealed a small but significant drop in richness coincident with age of canopy closure at ages 25 to 35.

Tree and Understory Cover After Thinning

Canopy cover differed significantly among the levels of thinning in the 15- to 45-year-old Douglas-fir stands (table 4; $F_{2,292} = 6.38$, $p = 0.002$). Undisturbed (ND) and lightly thinned (LT) stands had similar (78 to 79 percent) total mean canopy cover, whereas mean cover was lower (62 percent) in heavily thinned (HT) stands. Trends in canopy cover for the upper layer were similar to those of total cover. Mean canopy cover of the middle layer appeared lower in the HT stands than in the ND and LT stands, but the difference was not significant ($F_{2,292} = 1.08$, $p = 0.340$). Mean cover of the lower canopy layer was nominal for all three thinning intensities.

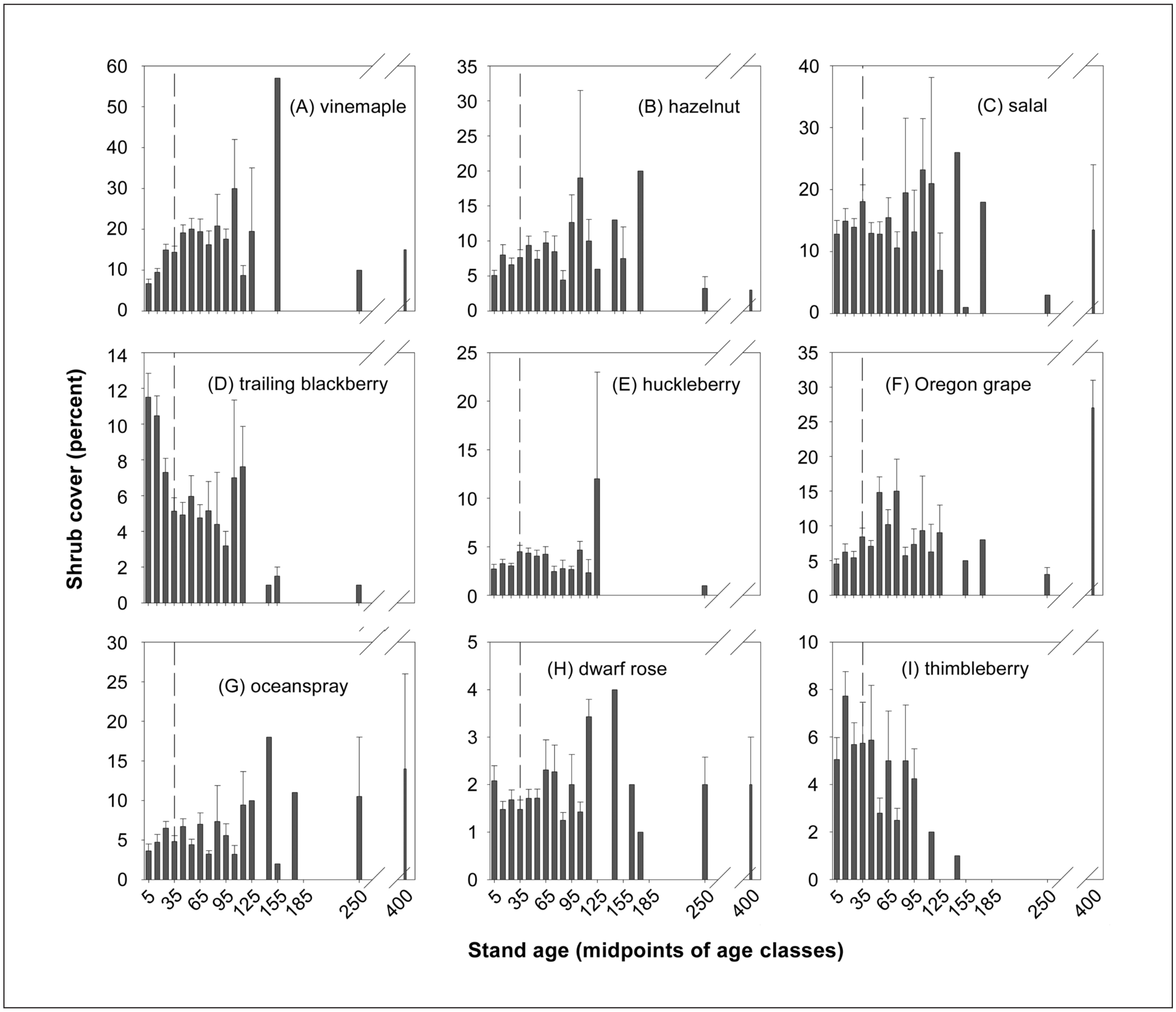

Figure 10—Mean percentage of cover (± 1 SE) of the 18 most commonly occurring shrubs in stands in which the particular species was found ("characteristic cover") from the Forest Inventory and Analysis inventory across a chronosequence of stand ages (grouped into intervals and labeled using midpoints of intervals) in western Oregon. The dashed line at age 35 represents canopy closure.

Mean layer heights also differed among the three levels of thinning. The upper layer of the ND stands was on average shorter (20 m) than for thinned stands (24 to 25 m) ($F_{2,292}$ = 5.17, p = 0.006). The heights of the middle and lower layers were consistent among thinning intensities. All three thinning levels had a mean of approximately 2.5 canopy layers. There were no evident trends between understory cover and thinning history; both shrub and forb cover were fairly similar among the three thinning intensities. The difference in mean shade-tolerant canopy cover was not significantly lower in LT and HT than in ND stands ($F_{2,292}$ = 1.54, p = 0.216).

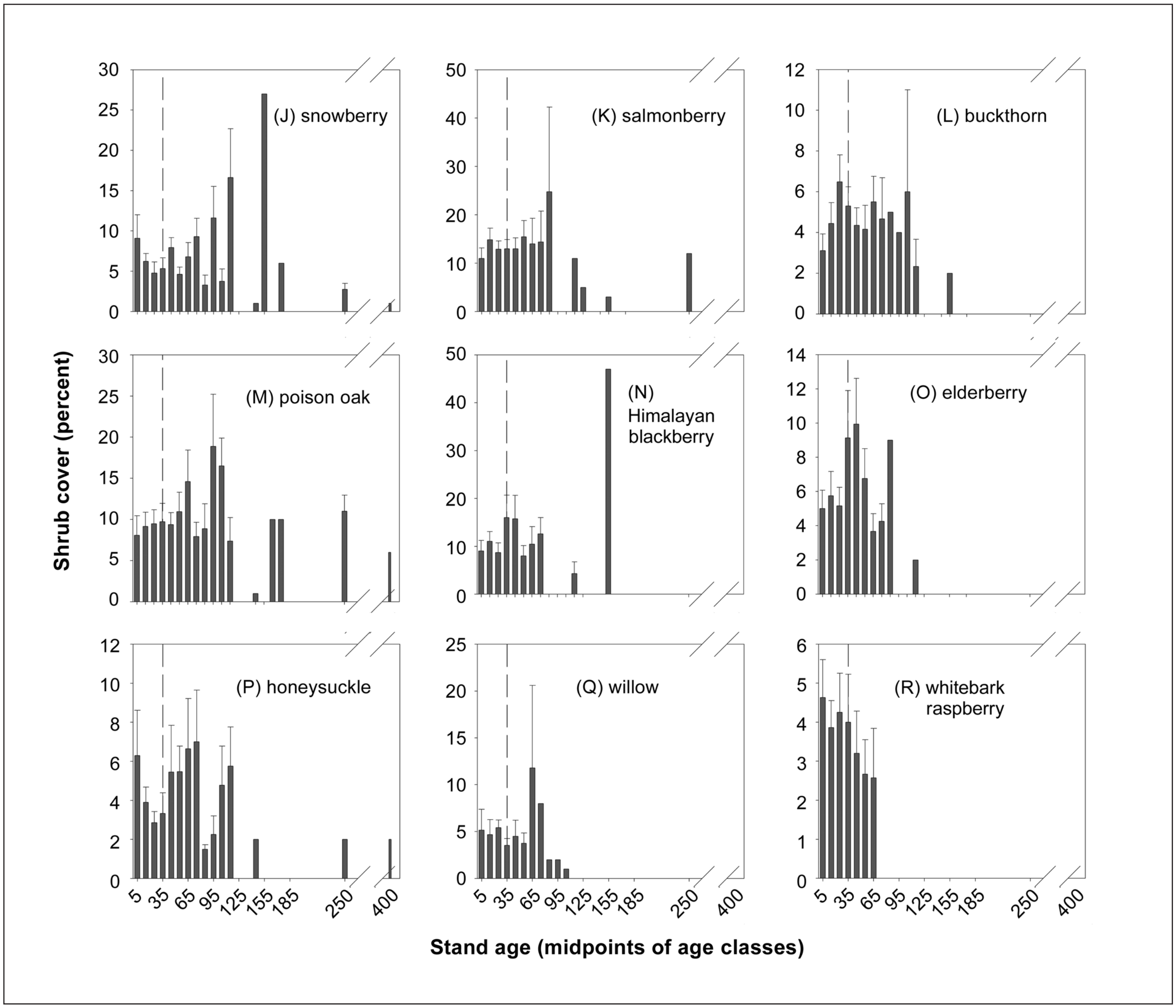

Figure 10—Continued.

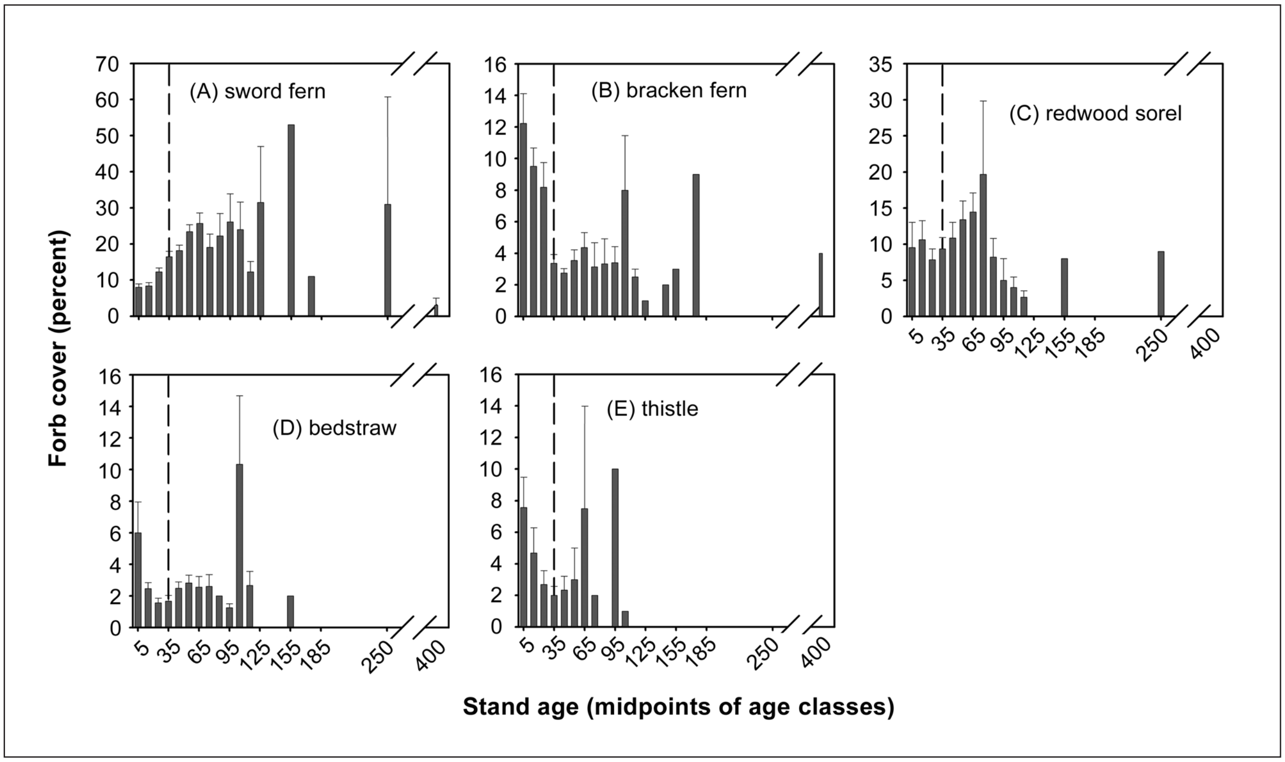

Figure 11—Mean percentage of cover (± 1 SE) of the five most commonly occurring forbs in stands in which the particular species was found ("characteristic cover") from the Forest Inventory and Analysis inventory across a chronosequence of stand ages (grouped into intervals and labeled using interval midpoints in western Oregon. Sample sizes differed among stand ages (see table 2). The dashed line at age 35 represents age of canopy closure.

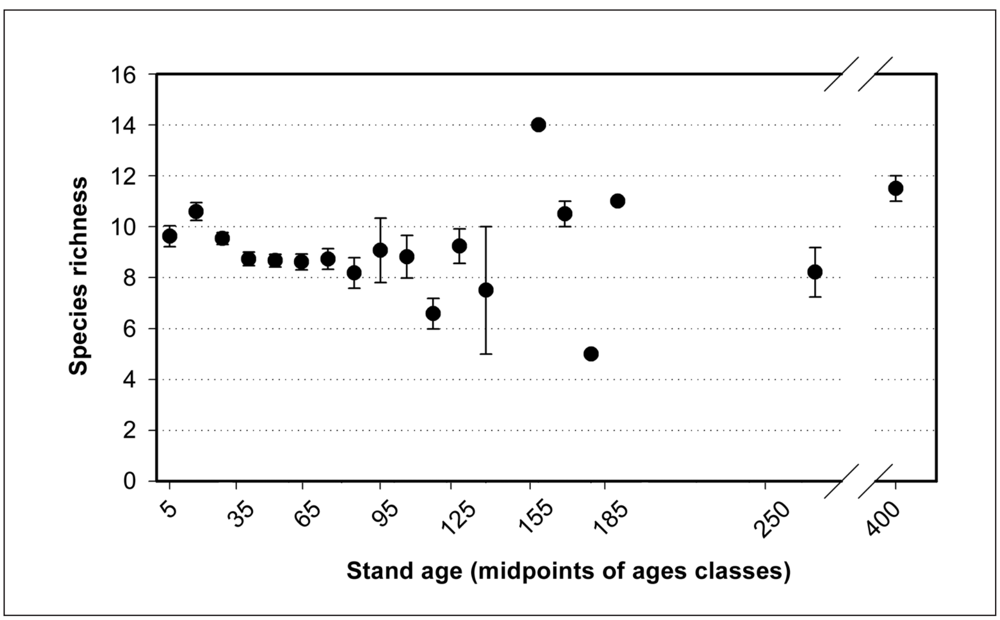

Figure 12—Mean species richness of shrubs (± 1 SE) across a chronosequence of stand ages (grouped into intervals and labeled using midpoints of intervals) in western Oregon (all forest types combined). Sample sizes differed among stand ages (see table 2).

Table 4—Mean total and shade-tolerant percentage of cover levels (± 1 SE) and mean heights of the canopy layers for three levels of thinning in 15- to 45-year-old Douglas-fir stands

Thinning intensity[a]		Canopy layer						Height of layer		
		Combined layers	Upper	Middle	Lower	Shrub	Forb	Upper	Middle	Lower
		Percent						*Meters*		
None	Total	78.3 (1.3)	64.4 (1.6)	19.4 (1.2)	5.1 (0.5)	46.4 (1.3)	27.0 (1.3)	20.5 (0.5)	11.1 (0.4)	4.2 (0.2)
(n = 254)	Shade tolerant	12.3 (1.0)	8.1 (0.8)	3.5 (0.4)	1.8 (0.3)					
Light	Total	79.1 (2.9)	61.0 (6.6)	18.5 (3.9)	8.4 (2.7)	46.5 (5.1)	22.2 (3.2)	25.3 (1.0)	12.4 (1.2)	4.1 (0.5)
(n = 21)	Shade tolerant	7.8 (2.3)	3.5 (6.4)	1.9 (0.7)	2.8 (1.3)					
Heavy	Total	61.9 (5.0)	48.7 (5.9)	14.6 (3.1)	8.3 (3.0)	42.7 (5.4)	28.4 (3.0)	24.2 (1.0)	12.6 (1.2)	4.5 (0.8)
(n = 20)	Shade tolerant	7.7 (2.4)	4.2 (1.8)	1.8 (0.5)	1.9 (0.9)					

[a] No disturbance (ND), light thin (LT), and heavy thin (HT).

Discussion

Stand Development Canopy Structure Patterns

The differences in canopy cover and layering found over the chronosequence of stand ages in western Oregon were largely consistent with the stand development models of Oliver (1981) and Franklin et al. (2002). The Oliver (1981) and Franklin et al. (2002) models proposed different starting points for the initiation of stand development. The Oliver model generally describes stand development after a "major" disturbance, whereby all living stems in an area are killed. The Franklin et al. model is more flexible as it offers a gradient of starting points for a stand, from disturbance regimes in which large remnant trees remain in the overstory, to the major stand-clearing disturbances described by Oliver. For the wet conifer stands in western Oregon, where clearcut harvesting or high-intensity stand replacement fire are the dominant stand-initiation disturbances, both models suggest a similar starting point for live trees. The wet conifer stands in the 5-year age class in our study had single layers with low levels of cover, indicating full stand replacement. However, the young hardwood stands had unexpectedly high cover levels, two layers, and tall heights of the upper canopy layer. The tree tally on many of these plots indicated postdisturbance residual overstory trees (i.e., >20 cm d.b.h.) were retained in these hardwood stands. Possible explanations for the residual hardwoods include state forest practice rules that require retention in riparian areas, which are likely to be dominated by hardwoods, and tree retention for amenity values by nonindustrial private owners that tend to be located at lower elevations where hardwood stands are most common. Also, many of the hardwood species (e.g., Pacific madrone, red alder, bigleaf maple, Oregon white oak) can vegetatively reproduce (sprout) and undergo rapid juvenile growth (Burns and

Honkala 1990), and have a broader spreading form than the upright conical conifers. Given the varied starting points for the hardwood stands included in the FIA inventory, the Franklin et al. model appears more suitable for describing the initial phases of hardwood stand development in western Oregon.

It may be an oversimplification to conclude that full use of available growing space occurs only when adjacent plant crowns are touching, as it assumes that sunlight is the limiting factor.

Canopy closure after a new cohort of trees is established is a stage proposed by both the Oliver and Franklin et al. models. In this stage, the cohort of trees is primarily within a single height class. In our study, mean canopy cover rarely exceeded 85 percent for each of the forest groups. Therefore, it may be an oversimplification to conclude that full use of available growing space occurs only when adjacent plant crowns are touching, as it assumes that sunlight is the limiting factor in stands (Oliver and Larson 1996). However, moisture and nutrients can also be limiting variables across the range of FIA sites. In addition, the average stand condition is not that of a fully stocked "normal" stand (or portion of a stand) such as those used to study growth and yield (e.g., McArdle et al. 1961). As Meyer (1930) noted for mature Douglas-fir forests (60 to 80 years old), real stands have about 85 percent of the basal area of fully stocked "normal" stands of the same site index because of patchy tree establishment, shrub-dominated openings, streams, rock outcrops, and isolated tree mortality. Our results similarly suggest that the term "closed canopy" may be misleading. Although canopy openness could be caused by previous thinning, relatively few stands had been thinned in the prior decade (between plot measurements), and the total cover of unthinned stands was below 85 percent.

Total canopy cover in young stands in the wet hardwood and wet conifer forest groups was dominated by the upper canopy layer. In contrast, dry hardwood stands were characterized by similar contributions from the upper and middle canopy cover layers across stand ages. The dry hardwood stands were dominated by Oregon white oak and Pacific madrone; although they are not generally classified as shade tolerant, they adequately reproduce under their own shade (Burns and Honkala 1990). Trees of dry hardwood stands also retain few shade leaves (Oliver and Larson 1996) allowing more light penetration to reach the forest floor. Aber (1979) proposed two potential successional pathways for hardwood stands of the Northeastern United States older than age 30: (1) the canopy would continue to grow upwards in a concentrated form; or (2) the canopy would grow taller but elongate as it grew, with a more evenly distributed canopy. In western Oregon dry hardwood stands, it appears that the second pathway is the more likely scenario given the lack of a dominant upper canopy layer and the lack of a true canopy closure stage.

Canopy cover trends in wet hardwood and wet conifer stands after canopy closure were consistent with Oliver's stem-exclusion phase and Franklin et al.'s biomass accumulation/competitive exclusion stage. As stand age increased, cover leveled off, followed by slight decreases across older stands. However, contributions from the upper canopy layer remained dominant. These changes likely resulted from the horizontal and vertical expansion of tree crowns that continues after canopy closure. Vertical tree growth would lead to differentiation of crown classes; eventually the shorter trees would be overtopped by more dominant trees, resulting in the separation of discrete layers. This process was demonstrated by the increase in number of canopy layers with increasing stand age among forest groups. Horizontal expansion of tree crowns could cause increased competition for finite light and nutrient resources and could result in tree mortality among the layers. These developments would lead to the slight decreases in total canopy cover seen in the older aged stands.

Easter and Spies (1994) documented canopies of mature stands (ages 90 to 145) in their study on the western slopes of the Cascade Range as monolayers of Douglas-fir with minimal amounts of shade-tolerant hardwoods and conifers in the lower story. This finding of a dominant single layer was expected because of the relative shade-intolerance of the dominant species (Douglas-fir and red alder), and the lack of shade-tolerants in the understory. With a dominant cohort of trees in the upper layer, the crowns of the shade-intolerant trees in the lower layers were unable to develop.

Shade-Tolerant Canopy Layers

As described in Franklin et al.'s vertical diversification and Oliver's understory-reinitiation successional stages, the number of canopy layers and the contribution from shade-tolerant tree species appeared to be greater for stands over age 45 than those under age 45. We expected the light-restricted middle and lower canopy layers to be dominated by shade-tolerant cover.

Although the lower layers had more shade-tolerant cover than the upper layer, the mean shade-tolerant proportion of total cover rarely exceeded 40 percent. The contribution by shade-tolerant species appeared to be even lower in the oldest stands than in those 30 to 75 years old. However, the systematically placed inventory plots fell in relatively few stands over 75 years of age, and the estimated annual precipitation at those plots (132 cm, SE = 7.0) was significantly lower than the precipitation at stands ≤75 years of age (174 cm, SE = 2.2; $t_{915} = 5.47$, $p < 0.001$). Nevertheless, it is possible that shade-tolerant cover does not greatly increase in naturally developing stands until substantial loss of the initial shade-intolerant cohort, which might not occur until age 200 or more without intermediate disturbance (Van Pelt and Nadkarni 2004). Because most of the species classified as shade tolerant also have higher optimum moisture levels than the shade-intolerant species (Minore 1979), the differences in shade-tolerant cover between stands ≤75 and >75 years old are probably more related to moisture availability than to stand age. A more robust analysis of canopy structure and composition would only be possible if comparable data were available for older forests that are more typical of federal lands.

Understory Vegetation

Trends in understory shrub and forb cover levels among stand ages were not consistent with the expectation that understory cover would dramatically decrease during stem exclusion (e.g., Alaback 1982). Although forb cover was lower in 25- to 45-year-old wet conifer stands than in younger and older stands, mean forb cover was 20 percent, and shrub cover did not display much of a pattern with stand age. There were no apparent patterns of understory cover in the other forest type groups. The lack of a strong effect of crown closure on understory cover may be related to our finding that mean crown cover did not exceed 85 percent. Similarly, Hanley (2005) found that few stands in southeastern Alaska are uniformly dense and depauperate of understory plants, but young hardwood stands had much greater cover of understory vegetation than did young conifer stands.

Changes in vertical structure with stand age may also play a role in understanding our results. Shrub levels in old-growth stands are highly correlated with horizontal and vertical variation in canopy cover (Van Pelt and Franklin 2000). Although the leaf-area-index values of wet conifer forests of the PNW are among the highest in the world, this cover is spread out over the vertical dimension of the stand (Van Pelt and Franklin 2000), as shown by the frequency of more than two vertical layers early in stand development in our study. Brown and Parker (1994) found that photosynthetically active radiation (PAR) was not strongly correlated with many simple measures of canopy structure, including canopy cover. Instead, PAR was highly correlated with variables that described the vertical distribution of foliage, and PAR transmittance increased during the first 50 years of stand development. These findings again suggest it is the vertical arrangement of foliage in a stand that influences light levels, rather than percentage of cover. In our study, the heights many of the stands attained, canopy closure at 85 percent cover, and the layering of tree cover appeared to allow sufficient light penetration to sustain understory shrubs and forbs.

Plants adapted to shaded habitats are less responsive to changes in light quality than those adapted to open habitats (Ross et al. 1986). Although the composition of shrubs and forbs may change from shade-intolerant to shade-tolerant species during early stand development, the absolute levels of understory cover differed little during stem exclusion. Several understory species displayed either increased or decreased cover with increasing age and corresponding high tree canopy cover. Although a few studies documented the shade tolerance of understory species, trends in cover of understory species here indicated that with 85 percent canopy closure many species were still shade tolerant enough to remain at consistent levels of cover under these reduced light conditions. However, cover is a relatively coarse measure of plant abundance; it is possible for plants to maintain similar cover in shaded environments yet have less leaf area (canopy density) and productivity than in more open environments. An analysis of invasive plants (Gray 2005) found that presence and absence of Himalayan blackberry and thistle were strongly correlated with canopy cover and stand density, whereas our analysis of cover found few relationships. Both cover and presence/absence metrics would appear to be useful in understanding the distribution and abundance of understory species.

Total cover of shrubs remained relatively consistent with age, but species richness peaked and then decreased slightly with canopy closure (age 35). This finding may have been a result of a shift in species composition with the reduction in light levels, suggested by the lower cover of vine maple, red huckleberry, dwarf Oregon grape, and oceanspray, and higher cover of trailing blackberry and snowberry with increasing stand age.

Tree and Understory Cover After Thinning

Cover in the upper tree canopy layer of young (15- to 45-year-old) Douglas-fir stands was lower in those that had been heavily thinned than in those that were unthinned or lightly thinned within 10 years prior to measurement. Commercial thinning generally coincides with crown closure to ensure steady radial log growth (Berg et al. 1996). With large gaps between trees in the heavy-thin stands, remaining trees were probably not able to extend their foliage into the newly available area in the time since thinning. In contrast, for lightly thinned stands, the remaining trees could probably quickly fill in the newly available space through lateral branch development.

Tree heights were greater in the light- and heavy-thin stands than in the unthinned stands. Although the unthinned stands were 3 years younger on average than the thinned stands, the 4- to 5-m difference in height suggests that thinning tended to occur on the more productive sites in this region. The difference in productivity among thinning treatments could also reflect a difference in ownership, because productivity tends to be higher and active stand management more common on forest industry lands than on other private or public lands (Azuma et al. 2004). Differences in shade-tolerant cover with thinning levels were inconclusive, but suggested that thinning favors more commercially desirable shade-intolerant species (e.g., Douglas-fir) over shade-tolerant species.

We expected greater cover of understory vegetation in thinned than in unthinned stands but did not detect significant differences in this analysis. It is possible that light levels did not differ sufficiently among thinning levels to have a dramatic effect. Nevertheless, thinning has been found to have significant effects on individual species, particularly weedy invasive plants (Bailey et al. 1998, Gray 2005).

Limitations

The FIA inventory design provides an unbiased representative sample of the population (i.e., nonfederal forests in western Oregon). However, the plots were not part of an experiment designed to control for variation to test the effects of a few factors. As a result, the number of plots in different age classes and forest types differed, and site attributes like species composition, site productivity, and disturbance history likely differed among plots within a forest type. The lack of balance in plot numbers has the potential to confound statistical comparisons of trends among groups, so statistical results are primarily descriptive and do not imply cause and effect.

A noticeable limitation of our analyses was the paucity of plots in older forests. Given the population of nonfederal lands sampled by this FIA inventory and the land use history of western Oregon, fewer older forests were available in the data set. Detailed canopy measurements were not collected for inventories of federal lands, where the majority of older stands in this region are located (Campbell et al. 2002). Therefore, results for the few measured stands greater than 75 years of age should not be interpreted as representative of western Oregon as a whole, rather of nonfederal forest lands in western Oregon.

Conclusions

Canopy cover and layering differed by stand age and forest type across 917 forested inventory plots representative of nonfederal lands in western Oregon. Our results support both Oliver's (1981) and Franklin et al.'s (2002) models of stand succession in wet conifer forest types, but the Franklin et al. model better represented the effects of residual trees in regenerating stands found in hardwood forests. Although both models predict a period of canopy closure in young stands, mean canopy cover in 20- to 50-year-old stands rarely exceeded 85 percent, even in productive, unthinned conifer forests. Cover of shade-tolerant tree species was also lower than expected, even in the lowest canopy layer and in mature (50- to 100-year-old) stands. As expected, the wet conifer and wet hardwood stands were dominated by cover in the upper layer in most stand age classes, but the dry hardwood stands had a more even vertical distribution of canopy cover. Although most successional models associate the period of crown closure in young stands with suppression of understory plants, there was little evidence for this in our study, except for forbs in wet conifer forest types. Further assessment of the patterns of canopy structure and underlying mechanisms on representative samples of our forest lands will enhance our understanding of forest-canopy development, and aid in the construction of realistic models of forest succession.

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English Equivalents

When you know:	Multiply by:	To get:
Centimeters (cm)	0.394	Inches
Meters (m)	3.28	Feet
Hectares (ha)	2.47	Acres
Square meters per hectare (m^2/ha)	4.37	Square feet per acre

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Appendix: List of All the Species Included in This Paper

Common name	Scientific name
Trees:	
bigleaf maple	*Acer macrophyllum* Pursh.
black cottonwood	*Populus balsamifera* L. ssp. *trichocarpa* (Torr. & Gray ex Hook.) Brayshaw
California black oak	*Quercus kellogii* Newb.
California laurel	*Umbeullularia californica* (Hook. & Arn.) Nutt.
canyon live oak	*Quercus chrysolepis* Liebm.
Douglas-fir	*Pseudotsuga menziesii* (Mirb.) Franco
English holly	*Ilex aquifolium* L.
golden chinkapin	*Chrysolepis chrysophylla* (Dougl. ex Hook.) Hjelmqvist
grand fir	*Abies grandis* (Dougl. ex D. Don) Lindl.
incense-cedar	*Calocedrus decurrens* (Torr.) Florin
lodgepole pine	*Pinus contorta* Dougl. ex Loud.
mountain hemlock	*Tsuga mertensiana* (Bong.) Carriere
noble fir	*Abies procera* Rehd.
Oregon ash	*Fraxinus latifolia* Benth.
Oregon white oak	*Quercus garryana* Dougl. ex Hook
Pacific dogwood	*Cornus nuttallii* Audubon ex Torr. & Gray
Pacific madrone	*Arbutus menziesii* Pursh
Pacific silver fir	*Abies amabilis* (Dougl. ex Loud.) Dougl. ex Forbes
Pacific yew	*Taxus brevifolia* Nutt.
Ponderosa pine	*Pinus ponderosa* Dougl. ex Laws.
Port-Orford cedar	*Chamaecyparis lawsoniana* (A. Murr.) Parl.
red alder	*Alnus rubra* Bong.
Shasta red fir	*Abies magnifica shastensis* (Lemmon) Lemmon
Sitka spruce	*Picea sitchensis* (Bongard) Carriere
tanoak	*Lithocarpus densiflorus* (Hook. & Arn.) Rehd.
western hemlock	*Tsuga heterophylla* (Raf.) Sarg.
western redcedar	*Thuja plicata* Donn ex D. Don
western white pine	*Pinus monticola* Dougl. ex D. Don
white fir	*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.
willow	*Salix* spp.
Shrubs:	
beaked hazelnut	*Corylus cornuta* Marsh
California laurel	*Umbellularia californica* (Hook. & Arn.) Nutt.
dwarf Oregon grape	*Mahonia nervosa* (Pursh) Nutt.
dwarf rose	*Rosa gymnocarpa* Nutt.
Himalayan blackberry	*Rubus discolor* Weihe & Nees
Honeysuckle	*Lonicera* spp.
oceanspray	*Holodiscus discolor* (Pursh) Maxim.
Pacific poison oak	*Toxicodendron diversilobum* (Torr. & Gray) Greene
Pursh's buckthorn	*Frangula purshiana* (DC.) Cooper
red elderberry	*Sambucus racemosa* L.
red huckleberry	*Vaccinium parvifolium* Sm.
salal	*Gaultheria shallon* Pursh
salmonberry	*Rubus spectabilis* Pursh
snowberry	*Symphoricarpos* spp.

Common name	Scientific name
thimbleberry	*Rubus parviflorus* Nutt.
trailing blackberry	*Rubus* spp.
vinemaple	*Acer circinatum* Pursh
whitebark raspberry	*Rubus leucodermis* Dougl. ex Torr. & Gray
Forbs:	
bedstraw	*Galium* spp.
bracken fern	*Pteridium aquilinum* (L.) Kuhn
redwood sorrel	*Oxalis oregana* Nutt.
swordfern	*Polystichum munitum* (Kaulf.) C. Presl
thistle	*Cirsium* spp.

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