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The Structure of Natural Young, Mature, and Old-Growth Douglas-Fir Forests in Oregon and Washington

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Abstract

Structural characteristics of forest overstories, understories, and forest floor and coarse woody litter accumulations were related to stand age, geography, and relative site moisture in 196 Douglas-fir stands in western Oregon and Washington. Stands ranged in age from 40 to 900 years and typically originated after wildfire. A series of multivariate analyses was used to identify structural attributes that distinguished old-growth (>195 years old) from mature (80-195 years old) and young (40-80 years old) age-classes. Separate analyses of four attribute sets—overstory, stand condition (degree of damage and disease), understory vegetation, and forest floor and coarse woody litter indicated that the age-classes differed in numerous attributes. Discriminant models that used overstory characteristics, such as tree density, density of large Douglas-firs, and variation in tree diameter, and models combining variables from the four different attribute sets were most successful in distinguishing the age-classes. Age-classes represent portions of a continuous gradient of structural

variation associated with age, based on ordinations with canonical discriminant analysis. Old-growth stands from different geographic provinces and relative site moisture-classes differ considerably in structure. Much of this variation in old-growth structure was associated with variation in densities of shade-tolerant trees and characteristics of the understory vegetation. Variation in old-growth-forest structure strongly suggests that low to moderate disturbance during the life of the stands has had an important influence on stand structure. The study provides a basis for defining and taking inventory of old-growth conditions as well as for managing the natural diversity of old-growth and earlier successional Douglas-fir forests in western Oregon and Washington.

Introduction

Douglas-fir forms dense, long-lived coniferous forests that dominate the mountainous landscapes of western Oregon and Washington. The structure and habitat quality of these forests varies greatly as a consequence of forest succession, disturbance, and plant community and environmental factors. The loss of the habitat structure associated with natural and old-growth Douglas-fir forests is a matter of intense public debate. The range of variability in the ecological structure of these forests is becoming more and more limited as the majority of forest lands are committed to short rotations for wood products. Information about natural Douglas-fir forest structure, its variability, and the processes that determine it are needed to identify wildlife habitat relationships, to

inventory critical habitat conditions, and to provide management targets for silvicultural manipulations, habitat reserve areas, and the maintenance of biological diversity.

Little quantitative information has been available on variation in natural Douglas-fir forests over a wide range of ages. Franklin and others (1981) describe the general ecological characteristics of old-growth Douglas-fir forests. They identify large live trees, large snags, and large logs as major distinctive features of these old ecosystems. Juday (1976) examines the species composition and some structural attributes in old-growth forests in the Oregon Coast Range. Alaback (1984) compares the structure of old-growth and second-growth western hemlock-Sitka spruce forests in southeastern Alaska. Most quantitative studies in Douglas-fir forests have focused on woody-debris components (Agee and Huff 1987, Graham and Cromack 1982, Sollins 1982, Spies and others 1988) or live tree components (Grier and Logan 1977; Franklin and DeBell 1988; Spies and others, unpubl. manuscript) in detailed studies of relatively few stands.

The major objectives of this study were to identify distinctive attributes and contrast the ecological structures of old-growth, mature, and young Douglas-fir forests; and to contrast the old-growth forest structure of different physiographic provinces and relative site moisture-classes in western Oregon and Washington. Several general questions were addressed: Are overstory, understory, and debris components equally distinctive among age-classes? Do different structural components change at the same rate and in the same manner with stand development and succession? How similar is old-growth forest structure among site moisture-classes from different physiographic provinces?

Study Area

Douglas-fir-dominated forests were studied in Washington and Oregon in three physiographic provinces: the southern Washington Cascade Range, the Oregon Cascade Range, and the southern half of the Coast Ranges of Oregon (Franklin and Dymess 1973). These provinces are characterized by steep, deeply dissected terrain with well-developed soil. Parent materials are Tertiary basalts and andesites in the Cascade Range, and early Tertiary sedimentary rocks in the Coast Range. The climate is wet in winter and dry in summer. Annual precipitation is heavy, ranging from 800 to over 3000 mm. Highest amounts of precipitation occur near the upper western slopes of the Coast Range and in the Cascade Range in Washington and northern Oregon (Franklin and Dymess 1973). Lowest precipitation occurs on the eastern slopes of the Coast Range and in the southern Oregon Cascades.

The study area encompasses two major vegetation zones: the Western Hemlock Zone and the lower elevational portion of the Pacific Silver Fir Zone (Franklin and Dymess 1973). Western hemlock and Pacific silver fir are the climax species on most sites in these zones; on dry sites, Douglas-fir may be climax. In southern Oregon, the northern margin of the Mixed Conifer Zone was sampled. In the Coast Range, the eastern margin of the Sitka Spruce Zone was sampled.

Most Douglas-fir stands in the region originated after catastrophic wildfire (Franklin and Hemstrom 1981); see Franklin and Dymess (1973) for a generalized, natural successional sequence. Young stands originating from wildfires are typically dominated by Douglas-fir, although western hemlock or red alder may dominate in some areas. By 200 years, many stands exhibit old-growth characteristics (Franklin and others 1981, Spies and Franklin 1988), such as codominance of western hemlock in the overstory, diverse vertical distribution of foliage, and large accumulations of woody debris (Spies and others 1988). True climax forests are rare because pioneer Douglas-fir can persist in stands for over 1000 years (Franklin and DeBell 1988; Franklin and others 1988; Spies and others, unpubl. manuscript), and wildfires occur more frequently than 1000 years on most sites.

Methods

General Design

A total of 196 Douglas-fir stands in Washington and Oregon representing different ages (40 to 900 years) and site conditions were sampled during 1983 and 1984 (see frontispiece). All stands originated after wildfires, which killed all or nearly all the overstory trees. We sampled along two gradients: a chronosequence of Douglas-fir stands on sites with moderate moisture, and a full range of site-moisture conditions for old-growth Douglas-fir stands (≥ 200 years old). Resources were not available to sample extremes of site moisture for stands < 200 years old. Consequently, the results of the Chronosequence analyses are based only on moderate or mesic sites (from young through old growth), and site-moisture analyses are based only on old-growth stands. To maintain a similar geographic distribution among ages of sampled stands, sampling was concentrated in areas in each province that contained all three of the following broad age-classes: young (< 80 years), mature (80-195 years), and old growth (2195 years).

Site Moisture Classification

Stands > 200 years were tentatively assigned during field reconnaissance into three broad moisture-classes-dry, moderate, and moist-based on observations of vegetation composition (Franklin 1979, Zobel and others 1976), physiography, and soils. Dry sites occur on steep upper slopes of southerly aspects, commonly with skeletal soils. Plant communities of

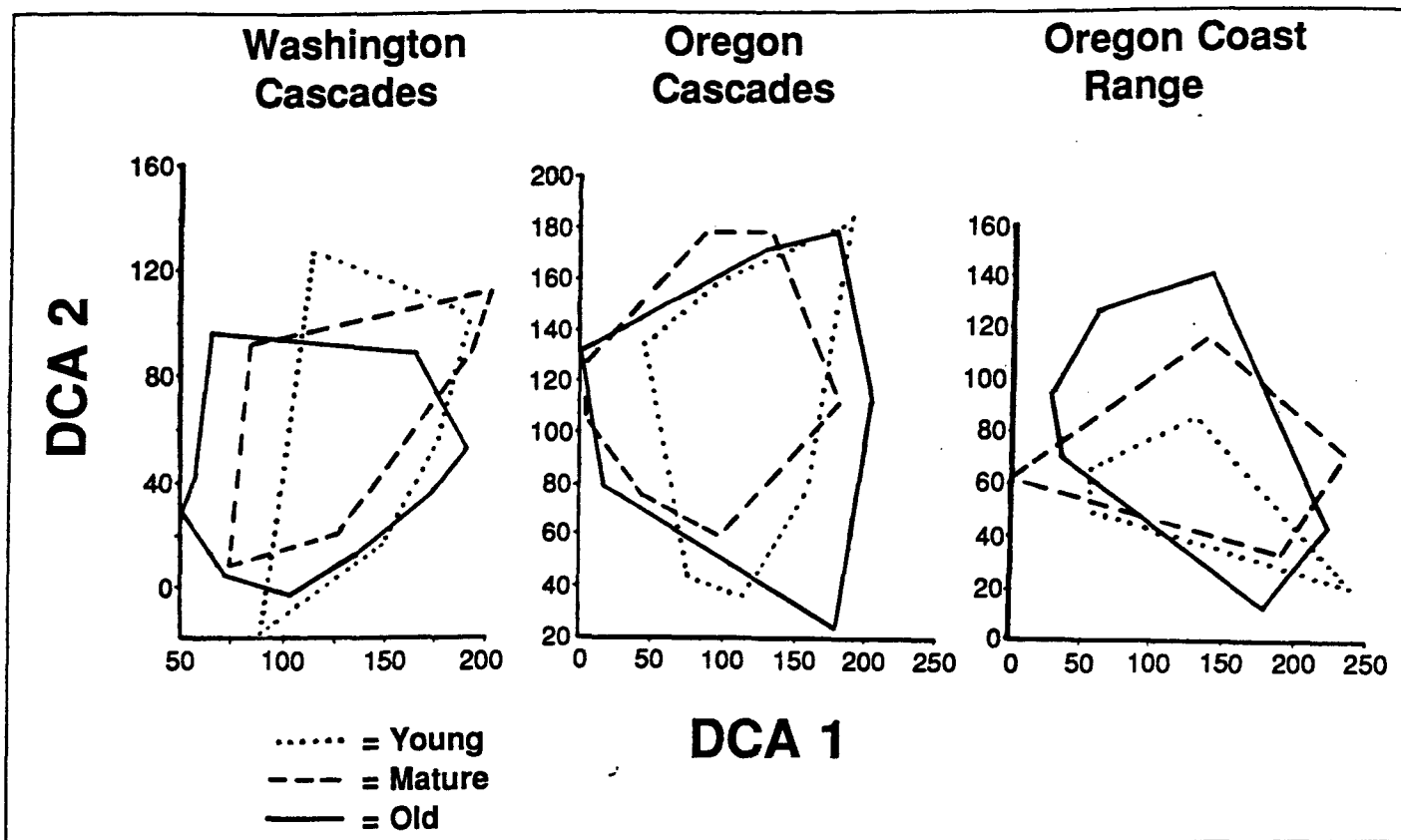


Figure 1—Ordination of old-growth, mature, and young stands along first two axes from a detrended correspondence analysis (DCA) of understory vegetation.

this moisture-class are characterized by Douglas-fir/*Holodiscus discolor*¹ and western hemlock/*Gaultheria shallon* plant associations (Franklin 1979). Moderate sites are on deeper soils of mid to low topographic position. Plant communities of this moisture-class were characterized by western hemlock/*Berberis nervosa*, western hemlock/*Berberis nervosa*/*Polystichum munitum* and related associations. Moist sites occur on lower northerly slopes, wet benches, and river terraces where plant communities include western hemlock/*Polystichum munitum*, western hemlock/*Oxalis oregana*, and western hemlock/*Oplopanax horridum* and other related types.

After field sampling was completed, the site-moisture classifications were refined for each province using detrended correspondence analysis (DECORANA) (Gauch 1982), a multivariate data-reduction and ordination program for ecological data. Moisture classifications also were done separately for

each of three subprovinces (north, central, and south) in the Oregon Cascade province, because it spanned a very large and diverse area. The moisture classifications consequently relate to specific provinces or subprovinces. Refinements to the classification were made subjectively, based on the environmental interpretation of the ordination axes.

DECORANA was also used to help reduce differences in environment among the age-classes. Analysis of understory vegetation data from all stands indicated that young and mature stands sampled a broader range of environment than originally intended. Scatter plots of the DECORANA stand scores were used as a guide for deleting stands within an age-class that were outliers from the general range of stands of the other age-classes. This editing procedure, which was done subjectively, based on both the DECORANA analyses and knowledge of the site conditions, resulted in selection of 177 stands from the 196 for comparing age-classes. Although the distributions of the stands differed somewhat with respect to the ordination scores, the stand scores of the age-classes still overlapped considerably (fig. 1).

¹ In this botanical chapter herbaceous plants and lichens are referred to by their scientific names for accuracy and the convenience of the reader.

Stand Selection and Plot Measurements

Stand size ranged from about 4 to 20 ha. Within each stand, five circular plots were systematically located. In some of the very small stands, only three or four plots were established. Plots were spaced either 100 or 150 m apart, depending on stand size, with wider spacing in large stands. The locations of the plots were determined before the field sampling by the size and shape of the stand as seen on aerial photographs.

Each plot was a nested set of circular plots of six sizes: 0.002 ha, 0.02 ha, 0.05 ha, 0.1 ha, and 0.2 ha. In the 0.1-ha plot, trees over 50 cm in d.b.h. and snags over 0.1 m tall with upper diameters >10 cm were measured (10 cm in d.b.h. for snags >1.4 m tall) and recorded by species, diameter, height-class, and decay-class using the five-class system of Cline and others (1980). Trees were classified into one of the following height-classes: 1 to 2 m; 2 to 4 m; 4 to 8 m; 8 to 16 m; 16 to 32 m; 32 to 48 m; 48 to 64 m; >64 m. Additional measurements on trees included coding of condition of crowns and boles, presence of disease and disturbance indicators, and presence of natural and excavated cavities on the readily visible lower third of the bole. Additional measurements on snags included the presence of natural cavities and excavations, and heights that were estimated visually after heights of a few snags or trees on each plot were measured with a clinometer and tape. The 0.2-ha plot was used during the second field season to record information on snags >50 cm in d.b.h. and >15 m tall, which occurred with low densities in most forests. The 0.05-ha plot was used to record the information described above for trees 50 cm in d.b.h. All logs >10 cm in diameter (large end) that projected into the 0.05-ha plot were measured. Log measurements included length (within plot), horizontal diameter at both ends, species and decay-class using a five-class scheme developed for Douglas-fir logs (Fogel and others 1973, modified by Sollins 1982). The decay-classes were used for all species because no classification was available for the other species.

Understory vegetation information was recorded by species in the three smallest plots. The number, species, and height by class of all tree seedlings and saplings 1 m tall to 5 cm in d.b.h. was recorded in the 0.05-ha plot. The percentage cover of tall shrubs was estimated by species over the 0.05-ha plot. The percentage cover of all vascular plants, mosses, and lichens (including foliose lichens from the canopy that had fallen to the forest floor) was estimated by species in the 0.02-ha plot. All vascular plants were identified to species or genus, but only selected mosses and lichens were identified to species. The number, species, and height-class of all tree seedlings <1 m tall were recorded in four 0.002-ha plots systematically located in the 0.05-ha plot. The depth of the L, F, and H litter layers was recorded to the nearest millimeter at three points in each 0.002-ha plot (12 points in each 0.05-ha plot) by use of a trowel and ruler.

Data on slope, aspect, topographic position, and shape of topographic cross section were collected from the 0.1-ha plot. The heights of two to four trees on each plot were measured with a clinometer and tape. Tree ages were determined for young and mature stands by increment coring at breast height of at least one dominant Douglas-fir per plot, adding 5 to 7 years for growth to breast height (depending on site), and averaging the plot estimates to obtain an age estimate for the stand. For old-growth stands, age estimates were made from stumps in nearby clearcuts, along trails or roads, or, sometimes, from increment cores on dominant trees. Data collected by Hemstrom (1979) were used to estimate ages of the stands in Mount Rainier National Park.

Calculations and Analyses

The density of trees, and volume and number of logs and snags, were computed by species, decay-class, and various size-classes for each plot in a stand. Diversity of tree heights (H') (Pielou 1977) was calculated for the height-classes, based on either density of trees or basal area of trees in each class. Volume was computed by using the formula for a cone. Stand values were then calculated as the means and variances of the plot values. Logs in decay-classes 1 to 4 were considered round in cross section. For decay-class 5 logs, which are flattened in cross section, vertical diameters were estimated by multiplying the horizontal diameter by 0.439, a ratio determined from a sample of 20 logs (J. Means, unpubl. data). We estimated the upper diameters of snags by using a taper value of 0.12 cm/dm, determined from diameters and lengths of class 1 to 3 logs. Plot areas were not area-corrected for slope because such corrections result in an overestimate of stand characteristics as compared with level ground (Mueller-Dombois and Ellenberg 1974).

The potential number of variables available to characterize the forest stands is extremely large—perhaps over 2000 if characteristics of species are included. Therefore, the analysis began with a multi-step process of variable selection and data reduction, with aggregation of species information into life-form-group variables (appendix table 10) to reduce the number of variables. The only exception was Douglas-fir, which retained its species identity for several tree characteristics. Variables were then divided subjectively into four attribute-sets: overstory, stand condition (tree and snag characteristics related to vigor, damage, disease, or animal use), understory, and debris. In each of these sets, 15 to 30 variables were subjectively chosen, based on documented or hypothesized importance to wildlife habitat, ecosystem function, and successional development (appendix table 11).

Four separate but related analyses were used for each attribute-set and the combination of all attributes. First, a stepwise discriminant analysis (SAS 1987) was conducted on each set with either the three age-classes for the entire study area, or nine province/site moisture-classes. A significance

level of $P < 0.15$ was used to include or exclude a variable from the model. The distributions of all variables were examined before analyses, and square-root or logarithmic transformations were used where appropriate to produce normal or close-to-normal distributions. The stepwise analyses typically selected 8 to 12 variables for each attribute-set with significant discriminatory power for the particular class models. These new smaller attribute-sets were then used in the next three analytic steps.

Canonical discriminant analysis (SAS 1987), a data-reduction technique, was the next step, which extracted a small set of new variates that maximized differences between the classes. The correlations of the original variables with the new variates was used to evaluate the dependence structure of the variables associated with differences in the classes. The stand scores of the variates were plotted to evaluate the relative distinctness or degree of overlap among the age- or old-growth province/moisture-classes.

Discriminant analysis was then used to determine the classification error rate by a jackknife procedure based on the variables selected in the stepwise analysis (Lachenbruch and Mickey 1968). This procedure generates a relatively unbiased estimate of the error or success rate of the discriminant models. Within-class covariate matrices were used in the discriminant analysis of the age-classes, and pooled covariate matrices were used in the analysis of the province/moisture-classes.

The fourth and last analysis on the variables from the stepwise analysis consisted of combining the best variables from each of the four attribute-sets and conducting another series of stepwise discriminant analyses, canonical discriminant analyses, and error-rate analyses.

Results

How Do Old-Growth Forests Differ From Younger Forests?

Overstory (trees >5 cm in d.b.h.)—Tree density, mean stand diameter, and basal area were most important in discriminating among age-classes (table 1). Tree density was about twice as high in young stands as it was in mature and old-growth stands (table 2). Basal area increased with age-class, and mean tree diameter was highest in mature stands, which lacked the smaller diameter, shade-tolerant trees common in the old growth (table 2). The high variability in old-growth stand structure was evidenced by old growth's having the highest standard deviation of tree diameter at breast height (table 2). Diversity of tree heights (H'), which had weak discriminating power, was actually highest in mature stands, probably because tree densities were more evenly

distributed across the height-classes in mature stands than in young or old-growth stands, where tree densities are concentrated in the shortest height-classes.

Most of the variance between age-classes could be reduced to a single canonical variate related to the standard deviation of tree diameter and the density of large trees (>100 cm in d.b.h.) (table 3). A second minor variate was related to mean tree diameter and tree density. Ordination of the stands, based on their canonical variate scores, revealed relatively distinct age-class means but considerable within-age-class variation and moderate overlap between the mature stands and the old-growth and young stands (fig. 2a).

Stand condition—Percentage of snags with natural cavities, percentage of Douglas-fir boles with resinosis, and percentage of tree crowns with broken tops were important in the discriminant model (table 1). Nearly all measures of tree decadence were much higher in old growth than in the younger age-classes (table 2). The percentage of Douglas-firs with broken-topped crowns was nearly 10, and it was nearly 3 times higher in old growth than in young and mature stands. The percentage of broken tops in old growth is probably much higher than we measured because many smaller breaks or older, obscured breaks were not counted. The percentage of trees with excavated cavities was <1 in all age-classes, although the percentage in old growth was several times that of the other age-classes. Both old-growth and young stands had similar percentages of fall scars. The bark of small, shade-intolerant trees in young stands is easily scarred; in old-growth, thin-barked, shade-tolerant species also scar relatively easily, and falling trees and large limbs can cause scarring even on thick-barked shade-intolerant trees.

Most of the between-class variation could be accounted for by the first canonical variate, which is related to tree crowns with broken and dead tops (table 3). The second, minor variate was related to fall scars and dead tops. Age-class means were not well separated, and considerable overlap occurred between the mature stands and the old and young stands, although the distributions of the old and young age-classes overlapped only slightly (fig. 2b).

Understory vegetation—Cover of herbs, density of shade-tolerant saplings, and cover of deciduous shrubs were important in the discriminant model (table 1). Herb and deciduous-shrub cover increased with stand age-class. As expected, the density of shade-tolerant saplings was highest in old growth, but, unexpectedly, shade-tolerant saplings were lowest in mature stands and intermediate in young ones (table 2).

Table 1—Variables and their *F* values in final models selected by stepwise discriminant analyses of forest age-classes based on different subsets of variables (all variables significant at *P* ≤ 0.05)

Overstory	Variable set									
	<i>F</i>	Stand condition ^a	<i>F</i>	Understory	<i>F</i>	Debris	<i>F</i>	Combined set	<i>F</i>	
Tree density	22.7	Snags with natural cavities	7.6	Percentage herb cover	8.6	5- to 15-m-tall snag density	22.2	Shade-intolerant tree species density	14.8	
Tree d.b.h. mean	20.3	Resinosis, Douglas-fir	6.4	Density shade-tolerant saplings	7.7	Decay class 2 log volume	14.3	100-cm-d.b.h. Douglas-fir density	7.4	
Total basal area >100-cm-d.b.h. Douglas-fir density	18.4	Broken-topped crowns	6.4	Percentage cover deciduous shrubs	6.1	>5-m-tall and >50-cm-d.b.h. snag density	9.8	>5-m-tall and >50-cm-d.b.h. snag density	7.1	
Tree spp. richness in stand	10.3	Sweeping boles, all spp.	4.6	Density of sub-canopy saplings	4.7	50-cm-d.b.h. snag density	6.7	1.5- to 5-m-tall snag density	5.7	
Shade-tolerant species density	7.5	Trees with excavated cavities	4.1	Percentage total vegetation cover	4.0	Snag volume	6.3	Decay-class 2 log volume	5.5	
Tree d.b.h. standard deviation	5.2	Snags >50-cm-d.b.h. with natural cavities	3.9	Coefficient of variation of herb cover	3.4	Decay class 4 snag volume	5.9	Tree d.b.h. standard deviation	5.1	
Broad-leaved species basal area	5.0	Broken-topped crowns, Douglas-fir	3.6			1.5- to 5-m-tall snag density	5.1	Snag volume	5.0	
Shade-intolerant species density	4.8	Trees with root-collar cavities	3.4			Decay class 5 snag volume	4.5	Decay class 5 snag volume	4.9	
Diversity of tree heights (H) based on density	4.0	Douglas-firs with fall scars	3.4			Log volume	3.7	Percentage herb cover	4.3	
	3.6	Trees with leaning boles	3.2					Broken-topped tree crowns	4.2	
	3.6	Snags >50-cm-d.b.h. with excavated cavities	3.2					Decay class 4 snag volume	4.0	
								Broad-leaved tree species basal area	3.6	
								>50-cm-d.b.h. snag density	3.6	

^a All variables are percentages.

The first canonical variate, which explained most of the variation, was related to the density of shade-tolerant saplings, density of subcanopy saplings, and density of herb cover (table 3). The second, minor variate was related to graminoid cover and herb cover. All of the age-class distributions overlapped in the ordination (fig. 2c). Only a portion of the old-growth distribution was distinct from the young and mature stands; these old-growth stands had high densities of shade-tolerant saplings and high cover of herbs.

Debris—Density of snags 5 to 15 m tall, decay-class 2 log-volume, and density of large snags were important variables in the discriminant model (table 1). The density of snags 5 to 15 tall decreased with age-class (table 2), but decay-class 2 log-volume and density of large snags increased with age-class. In general, small snags and logs were more numerous in young stands and large ones were most numerous in old growth. Although not selected by the stepwise discriminant

analysis, the combined depth of the F and H litter layers was deeper in old growth (\bar{x} = 21 mm) than in young (\bar{x} = 15 mm) or mature stands (\bar{x} = 14 mm).

The density of snags less than 15 m tall was related to the first canonical variate, which explained most of the between-group variation (table 3). The ordination along this variate separated the old-growth from young and mature forest, which overlapped almost entirely (fig. 2d). The second, minor variate, which was related to log volume and the coefficient of variation of numbers of large logs per ha (table 3), distinguished mature stands from both old-growth and young stands, although the overlap among classes was high (fig. 2d). The high coefficient of variation for large logs in mature stands may result from the scarcity amounts of logs of this size and the patchy mortality in these stands from root pathogens and bark beetles, or from an occasional remnant old-growth tree or a large snag that falls to the forest floor.

Table 2—Means^a and confidence limits^b of characteristics selected in stepwise discriminant analyses of young, mature, and old-growth forests

Characteristic ^c	Age-class			Characteristic ^c	Age-class		
	Young	Mature	Old-growth		Young	Mature	Old-growth
Overstory:				Boles with lean (%)	11 (8-14)	12 (9-15)	15 (13-17)
Tree density	935 (758-1154)	452 (373-548)	448 (394-511)	Snags >50-cm-d.b.h. with excavated cavities (%)	19 (8-35)	24 (12-40)	8.9 (4.1-15.7)
Tree d.b.h. mean	21 (19-25)	34 (30-39)	31 (28-34)	Understory:			
Total basal area	44 (39-50)	59 (53-65)	69 (64-74)	Herb cover (%)	2.5 (1.5-4.1)	5.1 (3.3-8.1)	6.4 (4.7-8.7)
>100-cm-d.b.h. Douglas-fir density	0.5 (0.2-0.73)	2.5 (0.99-4.73)	19 (16-23)	Shade-tolerant saplings density	228 (104-400)	84 (22-186)	335 (233-456)
Tree spp. richness (no./stand)	5.6 (4.7-6.6)	5.1 (4.3-5.9)	5.5 (4.9-6.0)	Deciduous shrub cover (%)	6.8 (4.1-11.2)	8.9 (5.6-14.1)	12 (9-16)
Shade-intolerant spp. density	490 (333-719)	243 (171-346)	63 (49-79)	Subcanopy tree saplings density	14 (1-46)	11 (0-37)	53 (29-84)
Shade-tolerant spp. density	277 (165-416)	132 (64-223)	270 (199-353)	Total understory cover (%)	46 (33-62)	57 (44-72)	52 (43-62)
Tree d.b.h. standard deviation	12 (10-14)	22 (20-24)	32 (30-34)	C.V. herb cover	81 (66-97)	80 (66-94)	75 (66-84)
Broad-leaved spp. basal area	0.01 (0.0-0.08)	0.01 (0.0-0.08)	0.001 (0.0-0.004)	Debris:			
Diversity (H') of tree heights based on density	2.6 (2.4-2.9)	2.8 (2.5-3.0)	2.6 (2.5-2.8)	5- to 15-m-tall snag density	80 (59-103)	60 (44-79)	12 (8-18)
Stand condition:				Decay-class 2 log volume	2.0 (0.9-4.5)	8.3 (3.9-17.8)	16 (9.6-26.9)
Boles with fall scars (%)	5.5 (3.5-7.9)	4.3 (2.7-6.3)	6.6 (5.3-8.3)	>50-cm-d.b.h. and >5-m-tall snag density	5.6 (3.1-8.9)	6.1 (3.6-9.3)	12 (10-15)
Resinosis, Douglas-fir (%)	0.3 (0-1.2)	1.0 (0.2-2.3)	2.2 (1.2-3.4)	>50-cm-d.b.h. snag density	25 (18-32)	14 (10-20)	24 (20-28)
Broken-topped crowns, all spp. (%)	1.7 (0.8-2.9)	4.6 (3.2-6.4)	6.3 (5.2-7.7)	Snag volume	132 (92-189)	85 (62-119)	159 (128-199)
Sweeping boles, all spp. (%)	12 (9-16)	15 (12-20)	13 (11-16)	Decay-class 4 snag volume	57 (36-83)	25 (13-42)	33 (23-45)
Trees with excavated cavities (%)	<0.001 (0-0)	0.06 (0-0.2)	0.1 (0.06-0.3)	1.5- to 5-m-tall snag density	54 (41-72)	40 (31-52)	24 (20-28)
Snags >50-cm-d.b.h. with natural cavities (%)	21 (9-36)	7.8 (2.0-17.4)	7.0 (3.0-12.8)	Decay-class 5 snag volume	26 (14-41)	13 (6-23)	15 (9-22)
Broken-topped crowns, Douglas-fir (%)	1.3 (0.1-3.8)	4.2 (1.6-7.9)	11 (8-15)	Log volume	223 (163-305)	124 (93-165)	266 (219-324)
Root-collar cavities (%)	3.4 (1.0-7.3)	6.7 (3.3-11.3)	12 (9-17)				
Boles with fall scars, Douglas-fir (%)	3.7 (1.6-6.5)	2.4 (0.9-4.6)	3.0 (1.8-4.5)				

^a Means are back-transformed to linear values from either a logarithmic or square root transformation.

^b 95% confidence limits of the mean; Scheffe's procedure. Limits are asymmetrical about the mean because of transformations.

^c Units: basal area in square meters per hectare density in number/percent hectare; volume in cubic meters per hectare and diameter in centimeters.

Table 3—Percentage explained variance and correlation coefficients of the first two canonical variates of analyses of age-classes based on different sets of characteristics (only the 2 highest correlations are shown for each canonical variate, except for the combined analysis where the variables with the 4 highest correlations are shown)

Characteristic	Variate 1	Variate 2
Overstory:		
Percentage of variance explained	91	9
Correlation coefficients		
Tree d.b.h. standard deviation	0.89	0.20
>100-cm-d.b.h. Douglas-fir density	0.85	-0.12
Tree diameter mean	0.33	0.63
Tree density	-0.50	0.63
Stand condition:		
Percentage of variance explained	85	15
Correlation coefficients		
Broken-topped crowns, all spp. (%)	0.56	0.40
Broken-topped crowns, Douglas-fir (%)	0.56	0.04
Trees with conks on lower bole (%)	0.19	0.37
Dead-topped crowns, all spp. (%)	0.54	-0.34
Understory:		
Percentage of variance explained	74	26
Correlation coefficients		
Shade-tolerant tree sapling density	0.54	-0.56
Subcanopy tree sapling density	0.53	-0.09
Graminoid cover (%)	-0.11	0.70
Herb cover (%)	0.50	0.60
Debris:		
Percentage of variance explained	82	18
Correlation coefficients		
5- to 15-m-tall snag density	0.83	-0.10
<5-m-tall snag density	0.61	0.04
Log volume	-0.32	0.63
>60-cm-diameter log C.V. density	0.09	-0.60
Combined:		
Percentage of variance explained	89	11
Correlation coefficients		
Tree d.b.h. standard deviation	0.88	0.18
>100-cm-d.b.h. Douglas-fir density	0.85	-0.10
Shade-intolerant tree spp. density	-0.79	0.08
>5-m-tall snag density	-0.54	0.04
Tree d.b.h. mean	0.33	0.55
>60-cm-diameter log density	0.04	0.50
>50-cm-d.b.h. snag density	0.08	-0.43
Snag volume	0.20	-0.39

Combined variable set—When all classes of variables are considered together, overstory and debris variables are the most important in the discriminant model (table 1). Density of shade-intolerant overstory trees appeared to separate the age-classes (table 2). The density of large-diameter Douglas-firs increased dramatically with age-class; snag volume distinguished mature stands, which had the lowest volume, from young and old-growth stands, which had relatively high snag volumes (table 2).

A high percentage of between-class variation was accounted for by the first canonical variate, which was positively correlated with the standard deviation of tree diameter and density of large Douglas-firs and negatively correlated with density of shade-intolerant trees (table 3). The second variate was related to log and snag volume. The age-classes were relatively distinct when the stands were ordinated along the two variates, although overlap still occurred (fig. 2e).

The scores of the first canonical variate were closely related to stand age in an approximately logistic relation (fig. 3a) illustrating the continuous nature of habitat variation. The changes with stand age begin to level-off by 400 to 500 years, reflecting changes in variation in tree diameter and density of large Douglas-fir. The scores of the second canonical variate followed a different pattern with stand age, rising to a peak between 100 and 200 years, and then declining (fig. 3b). This pattern reflects changes in both average tree diameter, which is high between 100 and 200 years, and amounts of coarse woody debris which are high both early and late in succession.

Classification error among attribute types—The variable sets differed in their capacity to distinguish among the age-classes (table 4). The highest classification success was achieved by overstory- and combined-attribute sets. Tree condition- and understory-attribute sets had the lowest success percentages. The overstory discriminant model achieved a slightly higher classification success for old-growth stands than did the combined-attribute model. In the combined-attribute model, however, no young stands were classified as old-growth; in the overstory model, 5 percent of the young stands were classified as old growth. In all but the understory- and debris-attribute models, mature stands were the least successfully classified age-class, which is not surprising because mature stands are intermediate in the more or less continuous process of stand development and succession.

How Does Old-Growth Structure Differ Among Geographic Provinces and Site Moisture-Classes?

Overstory—Basal area of shade-tolerant tree species and basal area of broad-leaved tree species were most important in the discriminant model (table 5). Old-growth stands in the Washington Cascades generally had the highest basal areas of shade-tolerant trees of all provinces, although old growth on moderate sites in the Oregon Cascades had the highest total basal area of any single province moisture-class (table 6). In general, moist sites had higher basal areas of shade-tolerant tree species than did moderate or dry sites. The basal area of broad-leaved tree species, although typically less than 0.1 m² per ha, was highest in the Coast Range. The broad-leaved trees in old growth in the Coast Range primarily are bigleaf maple, which is most common on the east side of the mountain range. The density of large-diameter Douglas-firs

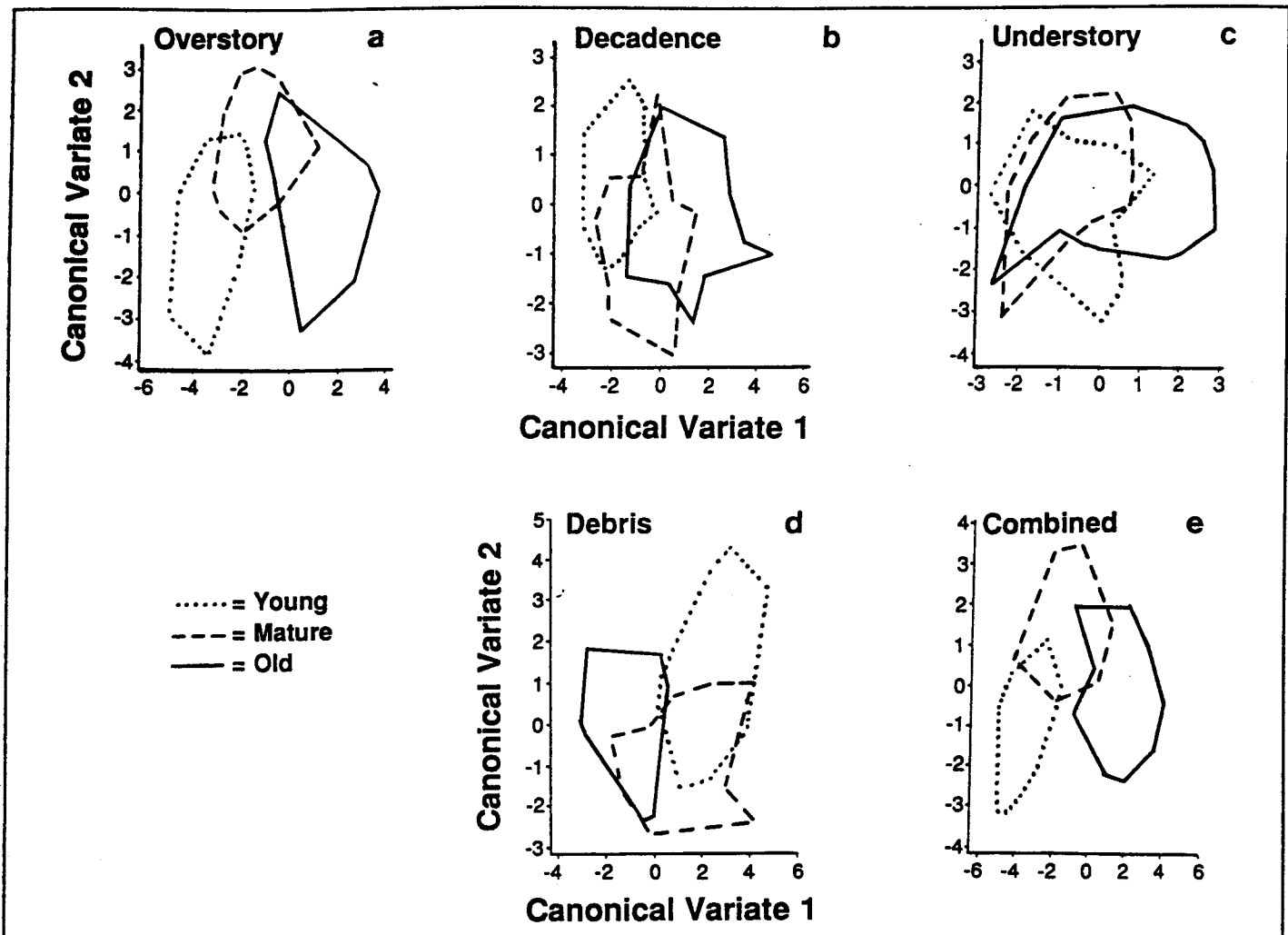


Figure 2—Ordinations of old-growth, mature, and young stands along first two canonical variates from analyses of overstory attributes (a), stand condition attributes (b), understory attributes (c), debris attributes (d), and a combination of all attribute sets (e).

was typically lowest in the Washington Cascades and did not exhibit a strong pattern related to moisture-class, except for a decrease in density with increasing moisture in the Coast Range. The density of subcanopy trees generally decreased with increasing site moisture, probably as a result of increasing basal area of shade-tolerant trees in the upper canopy that creates low-light conditions unfavorable to understory trees.

Basal area of shade-tolerant species and density of shade-intolerant species were related to the first canonical variate, which accounted for 49 percent of the variation (table 7). This variate essentially distinguished dry sites of the Oregon Cascades and Coast Range from all other old-growth sites (fig. 4a). The second variate was related to variation in tree diameter, density of subcanopy trees, and basal area of broad-leaved trees (table 7). Stands positioned along this

variate ranged from moist Washington and Oregon stands with high standard deviations of tree diameter to dry Washington stands with lower variation in tree diameter and high densities of subcanopy trees (table 7).

Stand condition—Percentages of natural root-collar cavities, of trees with arching boles, and of trees with fungal conks on the lower bole were important in the discriminant model (table 5). Natural root-collar cavities were most abundant in stands in the Washington Cascades, where western hemlock—which often roots on rotten wood and forms stilted roots—was very common; root-collar cavities were least common in the Coast Range stands (table 7). The percentage of arching boles, perhaps an indicator of steep slopes and soil creep or disease-weakened stems, was highest in the Coast Range. The percentage of trees with fungal conks in

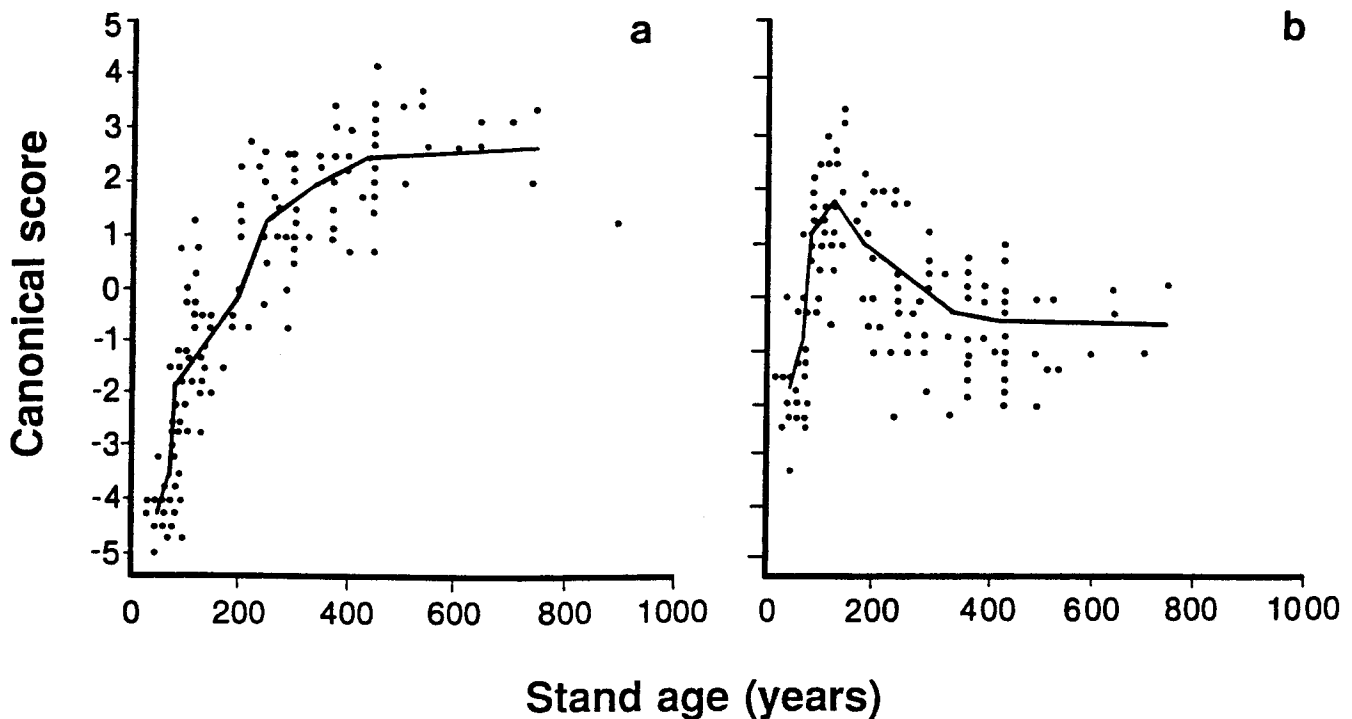


Figure 3—Relation of canonical variates 1 (a) and 2 (b) from combined-attribute set to stand age. Curves are fit to variate means from age-classes (years): <60; 60-80; 80-120; 120-160; 160-200; 200-300; 300-400; 400-600; >600.

Table 4—Summary of discriminant classifications of age-classes based on different sets of characteristics^a

From age-class	Percentage classified into age-class by discriminant function														
	Variable set														
	Overstory			Tree condition			Understory			Debris			Combined		
	Y	M	O	Y	M	O	Y	M	O	Y	M	O	Y	M	O
Young (n = 37)	81	14	5	68	27	5	54	32	5	65	30	5	84	16	0
Mature (n = 44)	16	73	11	32	43	25	23	64	14	18	68	14	11	73	16
Old-growth (n = 96)	0	6	94	6	17	77	18	27	55	5	13	82	0	10	90

^a Values in bold indicate correctly classified percentages.

the stands, an indicator of disease incidence, was highest in the Coast Range on all sites, and generally highest on dry sites in all provinces.

The percentages of trees with arching boles and fungal conks were related to the first canonical variate, which explained 51 percent of the variance (table 7). The second variate was related to the percentage of large snags with excavated cavities and Douglas-fir boles with sweep. Coast Range stands and the dry Oregon stands were separate from all

other classes when plotted against the two variates (fig. 4b), although considerable variation was found within groups and overlap among groups.

Understory vegetation—Important variables in the discriminant model included percentage cover of graminoids, total vegetation, evergreen shrubs, and deciduous shrubs (table 5). Coast Range stands had the highest cover of graminoids on all sites (table 6). Total cover by understory vegetation also tended to be higher in the Coast Range and did not exhibit a strong relation to site moisture, except perhaps in the Oregon

Table 5—Variables and their *F* values in final models selected by stepwise discriminant analyses of province-moisture classes based on different subsets of variables (all variables significant at $P \leq 0.05$)

Overstory	Variable set								
	<i>F</i>	Stand condition ^a	<i>F</i>	Understory	<i>F</i>	Debris	<i>F</i>	Combined set	<i>F</i>
Shade-tolerant tree spp. basal area	7.6	Trees with root-collar cavities	6.0	Graminoid cover (%)	11.0	F and H litter layer depth	8.7	Shade-tolerant tree spp. basal area	7.5
Broad-leaved tree spp. basal area	4.3	Arching boles	4.8	Total vegetation cover(%)	9.8	30- to 60-cm-diameter log density	4.9	Deciduous shrub cover (%)	6.1
>100-cm-d.b.h. Douglas-fir density	3.1	Conks on lower bole	3.8	Evergreen shrub cover (%)	8.3	Snag volume	3.9	100-cm-d.b.h. tree density (%)	5.3
Subcanopy tree spp. density	3.1	Dead-topped crowns	3.8	Deciduous shrub cover(%)	7.6	Decay class 5 snag volume	2.7	Total vegetation cover (%)	4.9
Total basal area	2.9	Snags with natural cavities	3.3	Herb cover (%)	5.8			Subcanopy tree spp. density	4.5
>100-cm-d.b.h. tree		Broken-topped crowns	2.9	Subcanopy tree spp. sapling density	3.1			>100-cm-d.b.h. Douglas-fir density	4.3
Shade-intolerant tree spp. basal area	2.1	Resinosis, Douglas-fir	2.6	Evergreen shrub cover C.V.	2.8			F and H litter layer depth	3.8
		Multiple-stem crowns	2.6					Sweeping boles, Douglas-fir (%)	3.7
		Snags with excavated cavities	2.4					Evergreen shrub cover (%)	3.6
		>50-cm-d.b.h. snags with excavated cavities	2.8					Herb cover (%)	3.2
		Sweeping boles, Douglas-fir	2.1					Broken-topped crowns (%)	3.2
								Conks on lower bole (%)	3.0
								Dead-topped crowns(%)	2.9
								Broad-leaved tree spp. basal area (%)	2.5
								>60-cm-diameter logs C.V. density	2.4
								Snag volume	2.1

^a All variables are percentages.

Cascades, where it increased with site moisture. Evergreen shrub cover tended to be higher on dry sites in all provinces. Canonical variates analysis indicated that two variates were required to account for most of the variation between the classes (table 7). Cover of graminoids was most closely related to the first canonical variate, and cover of evergreen shrubs was related to the second variate. Ordination of the stands along the first two variates separated the Coast Range stands from the Cascade stands and suggested a gradient of increasing moisture from top to bottom (fig. 4c).

Debris—The combined depth of the F and H litter layers and the density of medium-diameter logs were important in the discriminant model (table 5). The litter layers were generally thinnest in the Coast Range and thickest in the Washington Cascades, except on moist sites, where the litter layers of the

Oregon Cascades were thickest (table 6). The forest floor depth was typically highest on moist sites and lowest on dry sites, except in the Coast Range. Snag volumes were highest in the Washington Cascades on all sites and highest on moist sites in all provinces.

Depth of the F and H litter layers and the density of medium-diameter logs were related to the first and second canonical variate (table 7). Ordinations of stands along the first canonical variate (fig. 4d) separated Coast Range stands and dry Oregon stands, which had relatively thin litter layers and low amounts of coarse woody debris, from all other classes. As with the other discriminant models, dry old growth in the Washington Cascades was more similar to moderate sites in Washington and Oregon than to dry sites in the other provinces.

Table 6—Means^a and confidence limits^b for characteristics selected in stepwise discriminant analyses of province-moisture-classes of old-growth forests

Characteristic ^c	Moisture-class								
	Dry			Moderate			Moist		
	Washington	Oregon	Coast	Washington	Oregon	Coast	Washington	Oregon	Coast
Overstory:									
Shade-tolerant tree spp. basal area	29 (13-51)	23 (0-11.0)	2.2 (0-10.9)	35 (25-53)	20 (11-33)	15 (6-32)	60 (38-86)	39 (26-55)	31 (10-63)
Broad-leaved tree spp. basal area	<0.1 (0-0.1)	<0.1 (0-0.1)	0.3 (0-36.1)	<0.1 (0-0)	<0.1 (0-0)	0.1 (0-0)	<0.1 (0-0.1)	<0.1 (0-0.1)	0.1 (0-30.1)
>100-cm-d.b.h. Douglas-fir density	5.6 (0.05-20.4)	18 (5-41)	20 (11-57)	13 (0-30)	21 (10-46)	34 (1-63)	15 (1.6-24.9)	20 (10-34)	18 (2-25)
Density subcanopy trees	56 (14-218)	67 (6.9-187)	43 (1-145)	38 (3-91)	28 (13-51)	21 (0-11)	0.6 (0-31)	23 (2-70)	0
Total basal area	56 (35-79)	61 (43-87)	65 (46-93)	36 (25-50)	23 (14-31)	20 (11-30)	90 (66-124)	81 (63-101)	72 (45-115)
>100-cm-d.b.h. tree density	7.6 (0.4-23.7)	22 (7-46)	30 (11-58)	25 (0-57)	34 (13-61)	37 (11-57)	32 (15-56)	32 (19-49)	25 (5-62)
Shade-intolerant tree spp. basal area	25 (0-52)	58 (32-84)	60 (34-85)	35 (15-50)	33 (16-70)	25 (2-79)	30 (8-52)	43 (26-59)	39 (4-73)
Stand condition:									
Root-collar cavities (%)	24 (7-52)	3.6 (0-17.9)	2.9 (0-16.2)	23 (10-39)	13.1 (4-29)	14 (0-23.5)	27 (10-52)	14 (5-28)	19 (2-57)
Arching boles (%)	2.4 (0-9.4)	1.5 (0-7.7)	11 (1-24)	1.8 (0-13.0)	2.1 (0-6.5)	10.4 (2.8-18.0)	2.3 (0-8.2)	1.8 (0.1-5.4)	4.8 (0-18)
Conks on lower bole (%)	0.5 (0-2.9)	2.4 (0.3-6.5)	5.9 (2.0-11.8)	0.4 (0-1.0)	0.1 (0-0.1)	0.1 (0-0.1)	0.2 (0-1.8)	1.0 (0.1-2.7)	0.8 (0-5.0)
Dead-topped crowns (%)	4.0 (0.9-9.4)	2.0 (0.1-6.2)	1.9 (0.1-6.1)	2.4 (1.1-4.6)	2.0 (0.8-5.7)	2.2 (0.1-4.1)	2.5 (0.5-6.3)	3.9 (1.7-7.0)	0.3 (0-3.7)
Snags with natural cavities (%)	11 (0-37)	13 (1-40)	22 (4-54)	19 (0-39)	12 (0-21)	14 (0-30)	20 (5-50)	13 (3-28)	20 (1-66)
Broken-topped crowns (%)	4.2 (0.8-10.4)	4.8 (1.0-11.3)	6.1 (1.7-13.3)	3.1 (1.4-5.6)	3.2 (1.6-5.9)	3.4 (1.4-10.0)	5.9 (2.0-11.8)	9.7 (5.6-14.9)	8.4 (1.8-20.0)
Resinosis, Douglas-fir (%)	0.3 (0-6.8)	2.2 (0-12.1)	5.7 (0.1-19.5)	0.9 (0-1.2)	1.0 (0-7.7)	3.9 (0.1-13.9)	0.1 (0-4.4)	3.6 (0.4-10.1)	0.7 (0-12.5)
Multiple-stemmed crowns (%)	5.5 (0.6-14.8)	1.4 (0-7.4)	10 (3-23)	2.0 (0.4-5.0)	0.7 (0-1.9)	0.4 (0-1.4)	4.2 (0.5-11.4)	2.7 (1.8-10.8)	5.8 (0.1-20.0)
Snags with excavated cavities (%)	10 (0-33)	15 (1-38)	19 (0-48)	12 (0-27)	14 (0-31)	10 (0-30)	5.5 (0-21.0)	3.0 (0-11.5)	16 (0-57)
Snags >50-cm-d.b.h. with excavated cavities (%)	16 (0-69)	15 (0-64.5)	11 (0-57)	13 (0-28)	23 (0-47)	15 (0-36)	8.9 (0-43.9)	2.6 (0-18.6)	28 (0-120)
Sweeping boles, Douglas-fir (%)	24 (3-62)	16 (1-50)	20 (2-57)	21 (6-44)	12 (0-25)	23 (4-51)	12 (1-37)	5.0 (0.2-18)	23 (1-78)

See footnotes on next page.

Table 6—continued

Characteristic ^c	Moisture-class								
	Dry			Intermediate			Moist		
	Washington	Oregon	Coast	Washington	Oregon	Coast	Washington	Oregon	Coast
Understory:									
Graminoid cover (%)	<0.01 (0-0.01)	0.5 (0-16.8)	0.7 (0-36.0)	0.01 (0-0.01)	0.01 (0-0.01)	0.01 (0-0.01)	0.04 (0-1.3)	<0.01 TO 1 (0-0.01)	(0-26.2)
Total vegetation cover (%)	49 (21-91)	43 (16-89)	72 (34-122)	49 (21-91)	43 (16-89)	72 (34-122)	44 (20-78)	64 (41-93)	66 (22-134)
Evergreen shrubs cover (%)	21 (5-49)	19 (3-43)	54 (12-89)	2.3 (0-12.6)	16 (7-31)	1.2 (0-18.3)	2.3 (0-12.6)	16 (7-31)	1.2 (0-18.3)
Deciduous shrub cover (%)	14 (4-50)	11 (3-31)	21 (6-73)	13 (4-37)	15 (7-33)	8.0 (2.0-49.0)	13 (4-37)	15 (7-33)	8.0 (2.0-49.0)
Herb cover (%)	4.3 (1.7-11.1)	4.9 (1.5-16.4)	4.5 (1.1-11.7)	11 (3.9-31.3)	17 (7.3-36.0)	5.0 (0-25.1)	11 (3.9-31.3)	17 (7.3-36.0)	5.0 (0-25.1)
Subcanopy tree sapling density	160 (74-404)	194 (21-540)	19 (0-100)	4.4 (0-103.1)	61 (3-190)	0.8 (0-168.0)	4.4 (0-103.1)	61 (3-190)	0.8 (0-168.0)
C.V. evergreen shrub cover (%)	78 (34-136)	73 (32-129)	63 (25-115)	148 (94-215)	79 (50-115)	133 (59-236)	148 (94-215)	79 (50-115)	133 (59-236)
Debris:									
F and H litter layer depth	78 (33-121)	14 (0-33)	1.7 (0.2-22.0)	37 (14-58)	35 (23-45)	7.0 (0-27.0)	37 (14-58)	35 (23-45)	7.0 (0-27.0)
30- to 60-cm-diameter log density	148 (87-230)	79 (29-164)	41 (13-75)	226 (123-423)	180 (104-277)	136 (53-362)	226 (123-423)	180 (104-277)	136 (53-362)
Snag volume	270 (121-617)	64 (24-170)	91 (37-181)	293 (123-679)	207 (132-282)	288 (154-764)	293 (123-679)	207 (132-282)	288 (154-764)
Decay-class 5 snag volume	18 (0-43.5)	1.1 (0-22.4)	1.7 (0-22.9)	8.1 (0-33.9)	24 (8-31)	17 (1-66)	8.1 (0-33.9)	24 (8-31)	17 (1-66)

^a Means are back-transformed to linear values from either a logarithmic or square root transformation.

^b 95% confidence limits of the mean, Scheffe's procedure. Limits are asymmetrical about the mean because of transformations.

^c Units: basal area in square meters per hectare; density in number per hectare; volume in cubic meters per hectare; litter depth in millimeters.

Combined variable set—Basal area of shade-tolerant trees, cover of deciduous shrubs, and density of large-diameter trees were important in the discriminant model (table 5). The first canonical variate, which explained only 37 percent of the variance between classes, was related to basal area of shade-tolerant trees, depth of the F and H litter layer, and basal area of broad-leaved trees (table 7). The second canonical variate was related to basal area of shade-tolerant trees, density of subcanopy trees, and cover of evergreen shrubs. Ordinations of stands along the two variates again resulted in relatively good separation of Coast Range stands and dry Oregon stands from the other classes, as well as better separation of the other classes, than had been achieved by the models that used individual variable sets (fig. 4e). Site moisture appears to increase from upper left to lower right.

Classification error among attribute sets—Analysis of total error rates of classification indicated that the province-site moisture types were not easily distinguishable (table 8). The combined-attribute set and the overstory set provide the best discriminant models, although the successful percentages were relatively low. When just the three province-classes were considered, the success of the discriminant models was considerably better, especially for the combined-attribute and stand-condition models (table 8). When the three site moisture-classes were considered alone the models were not very successful in discriminating these classes, even for the combined-attribute model. These results suggest that differences in old-growth habitat structure are driven more by geographic variation than by variation associated with local-site moisture and that combinations of several different attribute types are needed to resolve the differences. The

Table 7—Percentage of explained variance and correlation coefficients (*r*) of the first 3 canonical variates of analyses of province-moisture-classes based on different sets of characteristics (only the 2 highest correlations are shown for each canonical variate except for the combined analysis sets where variables with the 4 highest correlations are shown)

Characteristic	Variate 1	Variate 2	Variate 3
Overstory:			
Percentage of variance explained	49	25	11
Correlation coefficients			
Shade-tolerant tree spp. basal area	0.97	0.09	-0.06
Shade-intolerant tree spp. density	0.50	0.16	0.14
Tree d.b.h. standard deviation	0.16	0.53	0.29
Subcanopy tree spp. density	-0.34	-0.53	0.07
Broad-leaved tree spp. basal area	-0.44	0.48	0.45
>100-cm-d.b.h. Douglas-fir density	-0.31	0.20	0.29
Stand condition:			
Percentage of variance explained	51	18	11
Correlation coefficients			
Conks on lower boles (%)	0.63	-0.26	0.23
Arching boles (%)	0.56	0.33	0.003
Snags 50-cm-d.b.h. with excavated cavities (%)	0.27	0.47	0.02
Sweeping boles, Douglas-fir (%)	0.11	0.45	0.15
Snags with natural cavities (%)	0.11	0.23	0.52
Trees with swollen knots (%)	0.27	-0.10	-0.46
Understory:			
Percentage of variance explained	44	30	13
Correlation coefficients			
Graminoid cover (%)	0.82	0.08	-0.30
Herb cover (%)	-0.46	-0.24	0.21
Evergreen shrub cover (%)	0.11	0.69	0.47
Total vegetation cover (%)	0.15	-0.02	0.44
Evergreen shrub cover C.V. (%)	0.02	-0.55	-0.61
Debris:			
Percentage of variance explained	48	30	12
Correlation coefficients			
F and H litter layer depth	0.83	-0.54	-0.03
30- to 60-cm-d.b.h. log density	0.80	0.25	0.14
Snag volume	0.68	0.32	0.07
Decay class 5 snag volume	0.44	0.10	-0.64
>60-cm-diameter log density C.V.	-0.55	-0.03	0.46
Combined set:			
-Percentage of variance explained	37	22	16
Correlation coefficients			
Shade tolerant spp. basal area	0.72	-0.58	0.14
F and H litter layer depth	0.70	0.04	0.42
Broad-leaved tree spp. basal area	-0.63	-0.14	-0.13
Conks on lower bole (%)	-0.53	0.34	0.13
Subcanopy tree density	0.06	0.50	-0.24
Evergreen shrub cover (%)	-0.25	0.47	0.03
Snag volume	0.43	-0.44	0.03
Sweeping boles (%)	0.10	0.53	-0.48
Herb cover (%)	0.36	-0.13	0.47
Broken-topped crowns (%)	0.02	-0.16	0.42
>100-cm-d.b.h. tree density	-0.17	-0.22	0.41

results also suggest that the broad moisture-classes developed in each province are not comparable across provinces or even within large provinces, such as the Oregon Cascades.

Of the three provinces, the Coast Range old-growth types were most successfully identified in the discriminant model based on combined attributes (table 9). The Washington Cascade old-growth types were the next most-successfully classified types—except for Washington dry old-growth types, which were often classified as dry or moderate Oregon Cascade types. The moderate and moist Oregon Cascade types were not distinctive in the models; the moderate types often were classified as other Cascade moisture types or Coast Range types, and the moist types often were classified as other Oregon Cascade types or Washington Cascade types. These results suggest that the Oregon old-growth types are somewhat intermediate in habitat structure between the Washington types to the north and the Coast Range types to the south and west.

Discussion

Limitations of the Chronosequence

In characterizing habitat structure in relation to stand age, the assumption has been that space can be substituted for time—an assumption that is violated to different degrees in most chronosequence studies because of differences in site and stand history. In this study, the effects of site differences were controlled somewhat by maintaining similar levels and ranges of site characteristics across the age-classes. Stand history could not be controlled except by restricting the stands primarily to those that regenerated naturally after stand-replacing wildfire. Differences in climate, establishment, and subsequent minor and moderate rates of disturbance also could not be controlled and can leave a strong imprint on stand structure (Spies and others, unpubl. manuscript). Given these caveats, successional interpretation of differences in age-classes must be made with caution.

Differences Among Age-classes

Multivariate analyses indicated that forest habitat structure differs among age-classes in numerous ways. The variables selected by stepwise discriminant analyses were not the only variables that exhibited significant differences among age-classes. They have high discriminating power, but are not necessarily the most discriminating set (Legendre and Legendre 1983). Other variable sets that were not selected may have equal or possibly somewhat greater discriminating power, and the subset of variables selected by the stepwise process is not stable against small changes in the data set (SAS 1987). Variables with the highest *F* values, however, typically stable against small changes in the sample set, and the general kind of variables selected were very stable against changes in sample sets. Several different stepwise analyses run on different subsets of the data, for example,

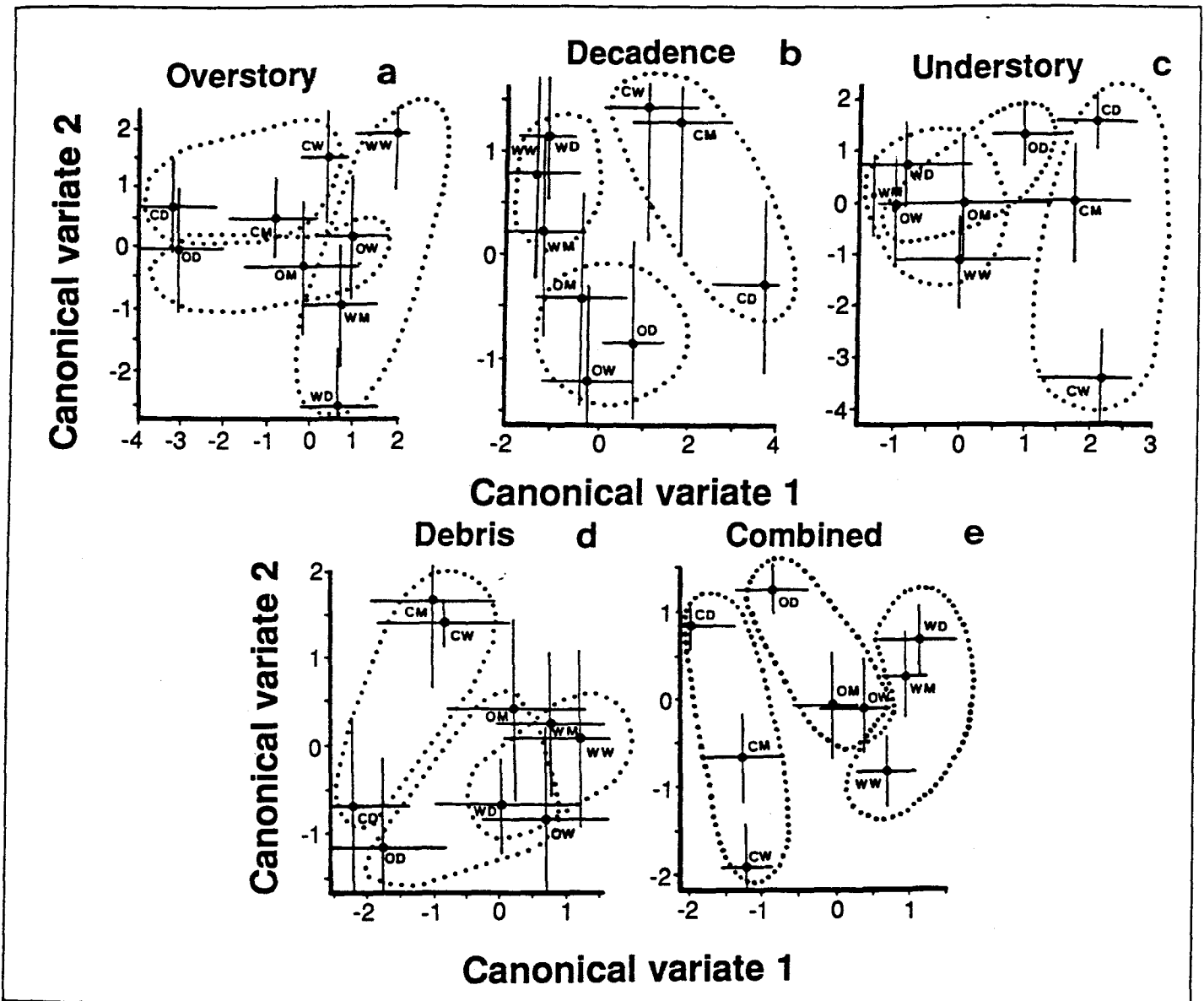


Figure 4—Ordinations of province-moisture class means (with standard deviations) of old-growth stands along first two canonical variates from analyses of overstory attributes (a), stand-condition attributes (b), understory attributes (c), debris attributes (d), and a combination of all attribute-sets (e). First letter indicates province: Oregon Cascades (O); Washington Cascades (W); Coast Range (C). Second letter indicates moisture class: Dry (D), Moderate (M), Moist (W). Dotted lines encompass province distributions.

still indicated that overstory attributes had the highest discriminating power. These characteristics of the analyses suggest generalizing the results not on the basis of the discriminating power of a single specific structural attribute or exact size-class of attributes, but rather on the general type or gross features of the attributes.

The high discriminating power of overstory attributes for age-classes is not surprising because the age-classes were based on the age of overstory trees. Within the overstory set,

two general processes contribute to the structural changes. The first is associated with stand development: the decline in stand density and the increase in tree size. The second is more related to successional changes: the increase in variation in tree diameter as the density of large-diameter Douglas-firs increases and the density of smaller-diameter, shade-tolerant trees increases. Variation in tree diameter increased strongly with succession, but diversity of tree heights (H') did not, which probably reflects the fact that the height-classes were too broad to be sensitive to height diversity.

Table 8—Summary of discriminant classifications of province-moisture-classes based on different sets of attributes

From classes	Percentage classified into class by discriminant function				
	Variable set				
	Overstory	Stand condition	Understory	Debris	Combined
Nine province- and moisture-classes	44	33	42	30	56
Three province-classes alone	66	71	61	56	81
Three moisture-classes alone	57	43	58	55	65

Table 9—Summary of discriminant classifications of province- and moisture-classes based on combined sets of attributes^a

From class		Percentage classified into class by discriminant function								
		Dry			Moderate			Moist		
		Washington	Oregon	Coast	Washington	Oregon	Coast	Washington	Oregon	Coast
Moist	Province									
Dry	Washington	44	44	0	0	11	0	0	0	0
Dry	Oregon	0	67	33	0	0	0	0	0	0
Dry	Coast	0	11	67	0	0	22	0	0	0
Moderate	Washington	20	5	0	50	10	0	10	5	0
Moderate	Oregon	0	15	0	0	35	10	0	30	10
Moderate	Coast	0	0	0	0	0	91	0	0	9
Moist	Washington	0	0	0	17	8	8	58	8	0
Moist	Oregon	5	5	0	5	14	5	14	55	0
Moist	Coast	0	0	0	0	20	0	0	0	80

^a Values in bold type indicate correctly classified percentages.

The developmental and successional changes of stands, which are described above, account for most of the variation in overstory structure associated with stand age.

Debris attributes were not as powerful in discriminating the age-classes. This difference is probably because the time since disturbance provides a better measure of debris amounts than does stand age (Spies and others 1988). Woody debris attributes operate with a different cycle than overstory attributes. Woody debris amounts actually are highest early in succession and lowest in mid-succession for many Douglas-fir ecosystems. This difference produces a more U-shaped pattern of development with stand age, which tends to reduce the discriminating power of these characteristics for natural forest age-classes. Because natural disturbances typically do not destroy much of the debris biomass in large pieces of wood, these features are present in natural stands of all ages to some degree (Spies and others 1988).

Stand-condition attributes alone did not exhibit good discriminatory power, probably because of high variability associated with non-age-related factors. Characteristics such as percentage of broken-topped crowns increased with stand age; however, topography and the history of windstorms at a

site are likely to play an equally important role. The difficulty of observing tall canopies from the ground may also have contributed to the poor discrimination.

Understory characteristics exhibited the lowest discriminatory power for age-classes. Although forest understories are likely to be strongly controlled by the overstory, the important overstory characteristics are not necessarily closely linked to stand age. Overstories casting dense shade, for example, may occur in dense, young Douglas-fir stands and in old-growth stands with dense hemlock canopies. Despite their low discriminatory power, many of the understory characteristics exhibited trends associated with the age-classes.

Among the strongest trends in understory characteristics was the increase in percentage of herb cover with stand age-class. An increase in herb cover in late-successional forests has been observed in Sitka spruce-western hemlock forest in southeastern Alaska (Alaback 1982). Higher herbaceous cover in old growth might be explained by changes in understory light intensity and microclimate. Light intensity under old-growth forest canopies dominated by western hemlock is lower than under mature or young forest canopies dominated by Douglas-fir (Spies and others 1990). Low light might

favor more shade-tolerant herbs over evergreen shrubs such as salal that often form dense clonal patches in mature- and young-forest understories. The more competitive, light-demanding shrubs such as salal could limit the development of herbaceous plants in the understories of younger forests (Long and Turner 1974). In addition, a more moderated microclimate in old-growth understories might favor more mesic understory species.

The high discriminatory power of overstory attributes does not mean that other attributes are unimportant in characterizing the habitat structure of natural young, mature, and old-growth forests. Other attributes with more subtle changes or greater variability can play important roles in the habitat and ecosystem function of these forests. These characteristics must be considered along with the characteristics of the overstory when habitat relations and land-management objectives are identified. The discriminatory power of the overstory attributes, however, can be used advantageously when simple indicators of forest habitat condition are sought, such as when aerial-photo inventories of habitat conditions over large areas are needed. We can infer that overstory characteristics such as densities and sizes of trees might be reasonably successful in identifying old-growth habitat from aerial photographs.

Regional and Site Differences in Old-Growth Forests

The study indicates that regional gradients exist in the structure of old-growth forest habitat, and to a lesser degree, gradients in structure occur within provinces in relation to site moisture. Given the large geographic area covered in the study, finding regional patterns stronger than within-region site differences is not surprising.

One of the prime drivers of habitat differences among the provinces was the basal area of shade-tolerant trees, primarily western hemlock. The study area ranged from near the southern limit of the species toward the middle part of its range (Harlow and Harrar 1969). This area encompasses relatively steep gradients in species composition and stand structure (Franklin and Dyrness 1973).

Disturbance history also plays a role in the regional differences. The southern and eastern Coast Range, where most of the Coast Range stands were located, probably has experienced more fires in the last several hundred years than the two Cascade provinces (Juday 1976). Fire disturbance is evidenced by the fact that fire-sensitive subcanopy trees and shade-tolerant trees such as western hemlock are less common in the Coast Range than in the Cascades; forest floor layers are much thinner there, and the percentage of Douglas-firs with fire scars on moderate sites in the Coast Range was 1.6 but only 0.4 and 0 on similar sites in the Oregon and

Washington Cascades. Stand ages of old growth in the Coast Range are younger, averaging 330 years compared with over 420 years for the Cascade Range stands (Spies and others 1988).

Differences in climate and site productivity also played a role in the regional patterns that were observed. Coast Range stands averaged almost 400 meters lower in elevation than Cascade stands, and winter minimum temperatures are 2 to 5 °C higher than in the Cascades (Franklin and Dyrness 1973). Trees can grow faster in the Coast Range than in the Cascades, which is evidenced by the relatively high densities of large-diameter (>100 cm in d.b.h.) trees in the Coast Range, despite the younger average stand age.

Differences in the moisture-related habitat structure of sites were not as great as regional patterns, but several general trends were apparent. The understories on dry sites generally have a low abundance of shade-tolerant species, which probably reflects drier conditions, greater fire frequencies, and younger stand ages. The low density of shade-tolerant species on these sites suggests that canopies are more open, which allows greater understory development. The greater density of subcanopy trees such as chinkapin or possibly Pacific dogwood on these sites, and the relatively high cover of total understory vegetation and graminoids supports this conclusion. Moist old-growth sites, by contrast, have relatively high cover of herbaceous species. The relatively high cover of evergreen shrubs on drier sites follows a similar finding by Zobel and others (1976) for the central Oregon Cascades, although they primarily associated the higher evergreen understory cover with low nitrogen availability.

Differences in debris characteristics associated with moisture conditions of sites have been identified by Spies and others (1988). Amounts of debris and numbers and sizes of debris pieces generally increase with site moisture, probably as a result of higher site productivity, lower fire frequencies (which can consume some of the wood), and possibly because of lower rates of decay resulting from excessively high moisture in the wood (Harmon and others 1986). Thicker litter layers on moist sites probably reflect the infrequency of fire and higher litter-fall rates associated with dense canopies of western hemlock and other shade-tolerant species.

Differences in stand condition across moisture-classes were associated with either species-composition differences, age/disturbance factors, disease, or tree vigor. The higher percentage of root-collar cavities on moderate and moist sites is related to the higher abundance of western hemlock on these sites. The higher incidence of broken tops on moderate and moist sites, which contain the oldest trees, may be related to the fact that with increasing age, trees are more likely to experience wind storms that cause crown damage. The higher incidence of fungal conks on dry sites, which are

characterized by steep south and west-facing slopes, is similar to the findings of Boyce and Wagg (1953) who observed a higher incidence of conk rot in old-growth Douglas-fir on steep slopes and southerly aspects. Our percentages of fungal conk incidence (1 to 6 percent) are much lower than the percentage incidence of conk rot (Boyce and Wagg 1953), but we surveyed only the lower one-third of the tree boles for fungal conks, which are only one indicator of the disease.

Conclusions and Management Implications

The structure of natural Douglas-fir forests in western Oregon and Washington is extremely diverse because of numerous processes operating at different spatial and temporal scales. Stand development and succession are important processes that determine forest habitat; however, regional flora, disturbance, local site potential, and climatic patterns are also important. We should not assume that the old-growth forest structure will be the same at one location or area as at another until we have a better understanding of how these processes interact and affect structure. Nor should we assume that the young and mature forests of today will produce the same old-growth forest structure in the future as the one that we see today. Management of old growth in western Oregon and Washington should be sensitive to the regional diversity of old-growth conditions. It should recognize the fact that natural young and mature forests have also provided important habitat and ecosystem functions that may be lost if only old-growth forest areas are used to provide habitat diversity for an entire landscape.

These results indicate that differences in forest structure associated with stand age and regional and local geography are numerous; they are characterized by multiple continua in forest structure rather than discrete classes. Changes in forest habitat structure do not stop when stands become 200 years old, the age often used for the onset of old-growth conditions. The results of this study suggest that structural changes continue until stands are at least 400 to 500 years. Additional changes likely happen after this time, but they may be more gradual and may move toward less structural diversity as stands become dominated by western hemlock and other shade-tolerant species.

The variability in old-growth forest structure strongly suggests varied developmental histories. Many, if not most, old-growth stands have been affected by low to moderate

amounts of disturbance during their histories. Such disturbances have contributed to the development of multiple size- and age-classes. Structurally distinguishing old-growth stands with continuous age-class distributions from those composed primarily of a few (3 to 5) tree cohorts may be difficult, but this difficulty suggests that one method for creating stands that resemble old growth is to leave an overstory of dominant green trees at the time of final cutting.

The young and mature stands examined in this study are not the equivalent of intensively managed, even-aged plantations. Many natural young and mature stands have some of the attributes of old-growth stands that may not be present in young, managed stands. Perhaps the greatest difference between natural and managed stands is the lower number and volume of large snags and logs in managed plantations (Spies and Cline 1988). Many young natural forests less than 80 years old have high amounts of carry-over of woody debris, although some young natural stands have little carry-over (Spies and others 1988). Other structural differences between young and mature natural forests and their managed equivalents are less well known. Managed plantations, however, generally will have fewer tree species, more uniform tree sizes and spacing, and no large remnant overstory trees. Understories of young natural and managed stands may be less spatially heterogeneous if overstory density is controlled. Over several rotations, a decline in the population of some understory species may occur if those species are sensitive to the short interval between major canopy and forest-floor disturbances in short-rotation plantations.

The concept of the "intensively managed stand" is, however, an ideal that has not yet been realized in many forests. It is also subject to change if management objectives are broadened to include a greater array of ecological values. Lessons from the natural forests in this study will be useful as our concept of forest management evolves with society's needs.

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Appendix

Table 10—Tree life form groups used in analysis

Shade-intolerant dominant trees:

Subalpine fir
California red fir
Noble fir
Incense-cedar
Engelmann spruce
Sitka spruce
Sugar pine
Western white pine
Douglas-fir

Shade-tolerant dominant trees:

Pacific silver fir
White fir
Grand fir
Port-Orford-cedar
Alaska-cedar
Western redcedar
Western hemlock
Mountain hemlock

Table 10—continued

Subcanopy trees:

Pacific madrone
Golden chinkapin
Pacific dogwood
Western hemlock

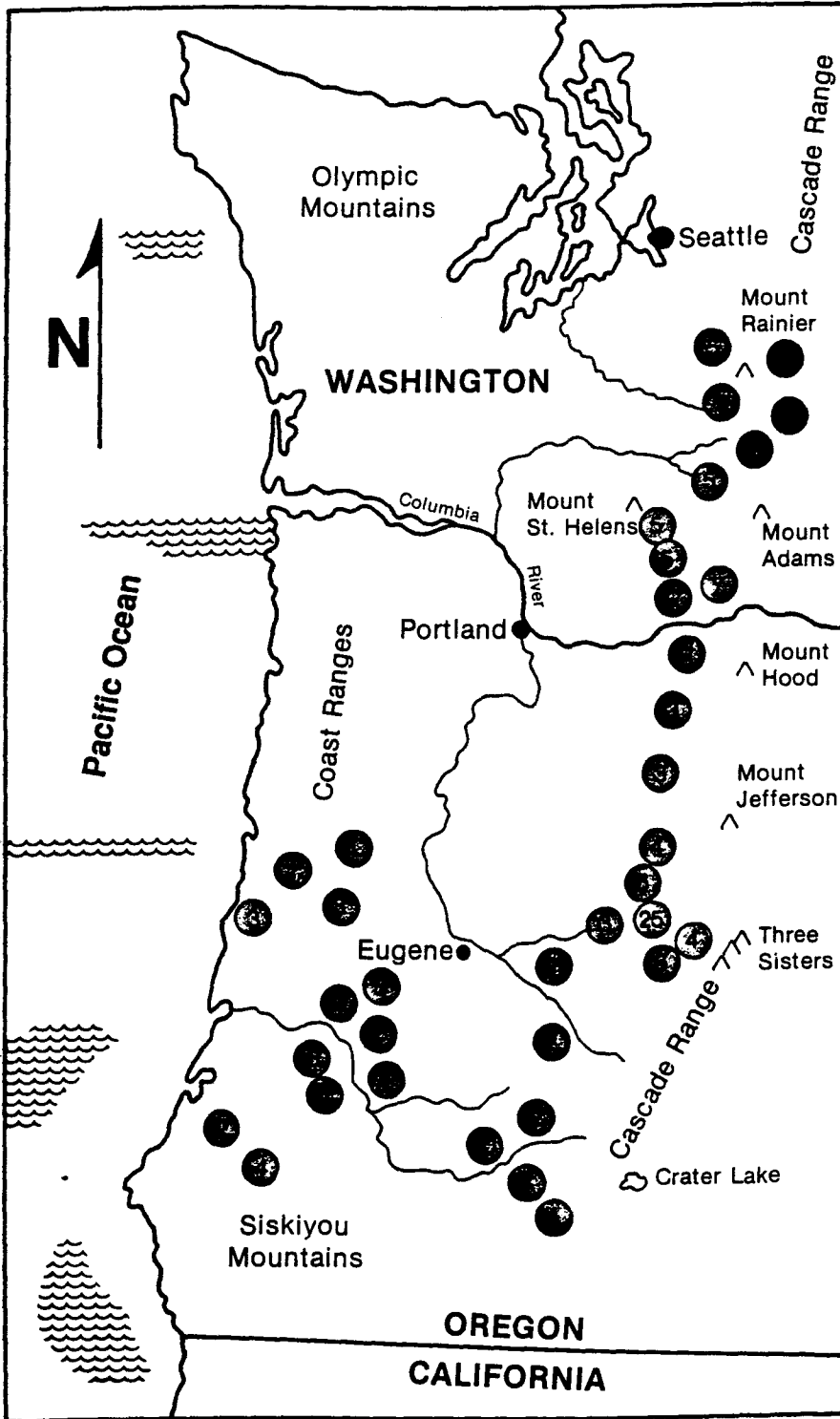
Broad-leaved dominant trees:

Bigleaf maple
Red alder
Oregon ash
Tanoak
Bitter cherry
Oregon white oak
Willow
California-laurel

Table 11—Variables used in stepwise discriminant analyses

Overstory (>5-cm-d.b.h.)	Stand condition ^a	Understory	Debris
Total basal area	Broken-topped crowns, Douglas-fir	Shade-tolerant sapling density	F and H litter layer depth
Tree density	Broken-topped crowns, all spp.	Subcanopy sapling density	Snags 50-m-tall density
Basal area, standard deviation	Sweeping boles, Douglas-fir	Cover vegetation <2 m tall (%)	10- to 30-cm-diameter log C.V. density
Tree density, standard deviation	Sweeping boles, all spp.	C.V. herb cover	30- to 60-cm-diameter log C.V. density
Tree d.b.h. mean	Multiple-stemmed crowns, all spp.	Lichen cover (%)	Snag >5-m-tall and 50-cm-d.b.h. density
Tree d.b.h. standard deviation	Multiple-stemmed crowns, Douglas-fir	Moss cover (%)	5- to 15-m-tall snag density
Number of overstory trees	Dead-topped crowns, Douglas-fir	Fern cover (%)	50-cm-d.b.h. snag density
Trees >100-cm-d.b.h. density	Dead-topped crowns, all spp.	Herb cover (%)	Snags >50-cm-d.b.h. density
Tree height diversity (H') based on basal area	Broken-topped crowns with upturned leaders, Douglas-fir	Evergreen shrub cover (%)	10- to 30-cm-diameter logs density
Tree height diversity (H') based on stem density	Broken-topped crowns with upturned leaders, all spp.	Deciduous shrub cover (%)	30- to 60-cm-diameter log density
Douglas-fir basal area	Forked bole	Total understory cover (%)	60-cm-diameter log density
Douglas-fir >100-cm-d.b.h. density	Arching boles.	C.V. evergreen shrub cover	Decay-class 1 log volume
Shade-tolerant tree spp. basal area	Boles with fall scars, Douglas-fir	C.V. deciduous shrub cover	Decay-class 2 log volume
Shade-intolerant tree spp. basal area	Boles with fall scars, all spp.	C.V. <2-m-tall vegetation cover	Decay-class 3 log volume
Subcanopy tree spp. basal area	Trees with swollen knots, Douglas-fir		Decay-class 4 log volume
Broad-leaved tree spp. basal area	Conks on lower boles, Douglas-fir		Decay-class 5 log volume
Shade-intolerant tree spp. density	Conks on lower bole, all spp.		Decay-class 1 snag volume
Shade-tolerant tree spp. density	Resinosis, Douglas-fir		Decay-class 2 snag volume
Subcanopy tree spp. density	Resinosis, all spp.		Decay-class 3 snag volume
Trees with root-collar cavities	Trees with excavated cavities		Decay-class 4 snag volume
Trees with natural cavities	Snags with natural cavities		Decay-class 5 snag volume
Snags with excavated cavities	Snags >50-cm-d.b.h. with excavated cavities		Ratio log-volume decay-class 4 + 5 to total log volume
	Snags >50-cm-d.b.h. with natural cavities		Log volume
			Snag volume
			Snag volume (C.V.)

^a All variables are percentages.



Location of stands in western Oregon and Washington. Numbers indicate total number of stands in an area.

WILDLIFE AND VEGETATION OF UNMANAGED DOUGLAS-FIR FORESTS

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