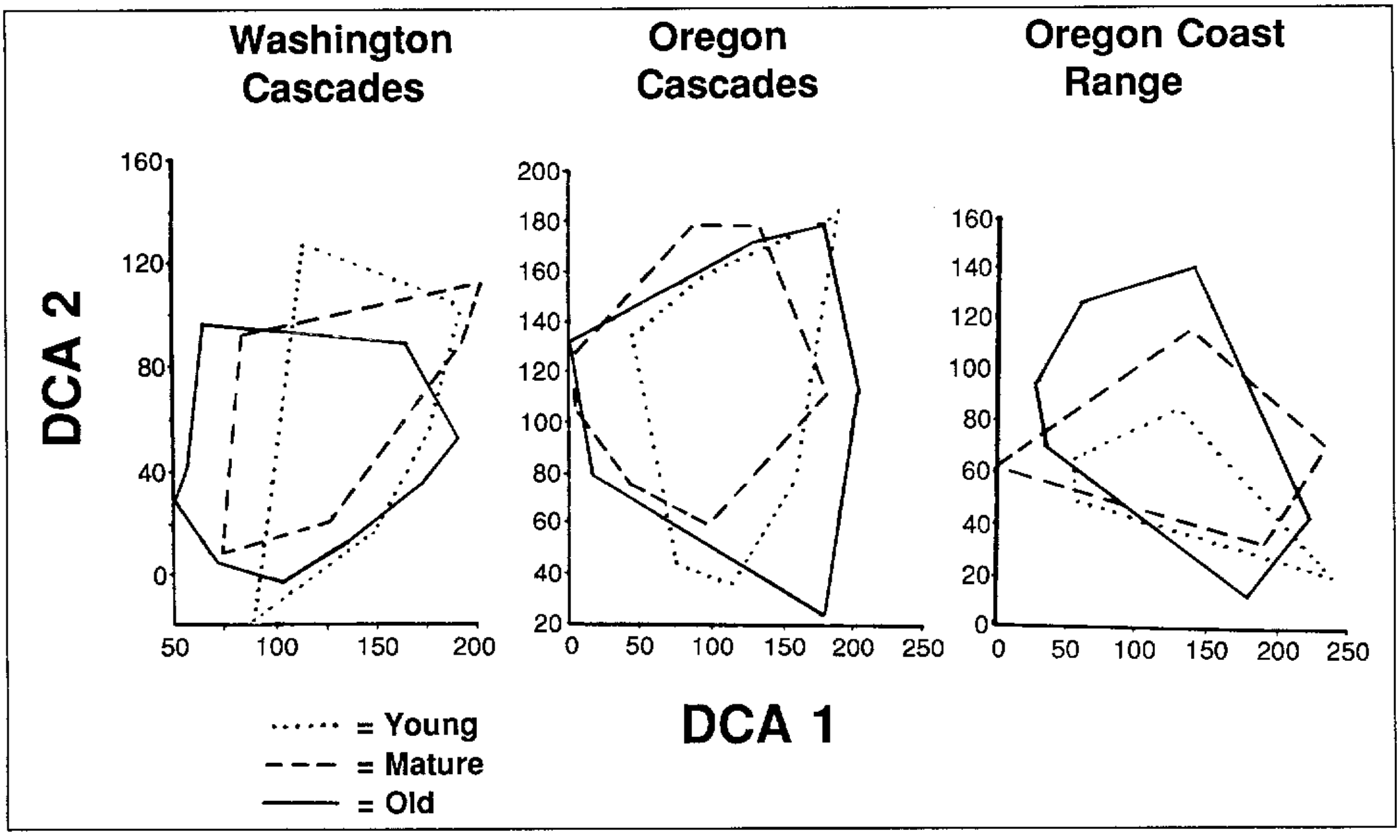

Figure 1—Ordination of old-growth, mature, and young stands along first two axes from a detrended correspondence analysis (DCA) of understory vegetation.

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).

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[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 >l0 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.l-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 (>lOO 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 $P \leq 0.05$)

Variable set									
Overstory	*F*	Stand condition[a]	*F*	Understory	*F*	Debris	*F*	Combined set	*F*
Tree density	22.1	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-fii density	7.4
Total basal area	18.4	Broken-topped croyts	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
>100-cm-d.b.h. Douglas-fii density	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
Tree spp. richness in stand	1.5	Trees with excavated cavities	4.1	Percentage total vegetation cover	4.0	Snag volume	6.3	Decay-class 2 log volume	5.5
Shade-tolerant species density	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
Tree d.b.h. standard deviation	5.0	Broken-topped crowns, Douglas-fir	3.6			1.5- to S-m-tall snag density	5.1	Snag volume	5.0
Broad-leaved species basal area	4.8	Trees with root-collar cavities	3.4			Decay class 5 snag volume	4.5	Decay class 5 snag volume	4.9
Shade-intolerant species density	4.0	Douglas-firs with fall scars	3.4			Log volume	3.7	Percentage herb cover	4.3
Diversity of tree heights (*H'*) based on density	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 (x = 15 mm) or mature stands (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. 26). 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’ and confidence limits[b] of characteristics selected in stepwise discriminant analyses of young, mature, and old-growth forests

	Age-class		
Characteristic’	Young	Mature	Old-growth
Overstory:			
Tree density	935 (758-l 154)	452 (373-548)	448 (394-5 11)
Tree d.b.h. mean	**21** **(19-25)**	**34** **(30-39)**	**31** **(28-34)**
Total basal area	**44** **(39-50)**	**59** **(53-65)**	**69** **(64-74)**
>lOO-cm-d.b.h. Douglas-fir density	**0.5** **(0.2-0.73)**	**2.5** **(0.99-4.73)**	**19** **(16-23)**
Tree spp. richness (no./stand)	**5.6** **(4.7-6.6)**	5.1 (4.3-5.9)	**5.5** **(4.9-6.0)**
Shade-intolerant spp. density	490 (333-719)	243 (171-346)	**63** **(49-79)**
Shade-tolerant spp. density	277 (165-416)	132 (64-223)	270 (199-353)
Tree d.b.h. standard deviation	**12** **(10-14)**	**22** **(20-24)**	**32** **(30-34)**
Broad-leaved spp. basal area	0.01 (0.0-0.08)	0.01 (0.0-0.08)	0.001 (0.0-0.004)
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)**
Stand condition:			
Boles with fall scars (%)	**5.5** **(3.5-7.9)**	4.3 (2.7-6.3)	6.6 (5.3-8.3)
Resinosis, Douglas-fir (%)	0.3 (O-1.2)	1.0 (0.2-2.3)	2.2 (1.2-3.4)
Broken-topped crowns, all spp. (%)	**1.7** **(0.8-2.9)**	**4.6** **(3.2-6.4)**	6.3 (5.2-7.7)
Sweeping boles, all spp. (%)	**.12** **(9-16)**	**15** **(12-20)**	(11-16)
Trees with excavated cavities (%)	co.001 **(0-0)**	0.06 (O-0.2)	0.1 **(0.06-0.3)**
Snags >50-cm-d.b.h. with natural cavities (%)	**21** **(9-36)**	7.8 (2.0-17.4)	**7.0** **(3.0-12.8)**
Broken-topped crowns, Douglas-fir (%)	1.3 (0.1-3.8)	4.2 (1.6-7.9)	**11** **(8-15)**
Root-collar cavities (%)	3.4 (1 .0-7.3)	(3.3Yl.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)

	Age-class		
Characteristic[C]	Young	Mature	Old-growth
Boles with lean (%)	**11** **(8-14)**	**12** **(9-15)**	**15** **(13-17)**
Snags >50-cm-d.b.h. with excavated cavities (%)	**19** **(8-35)**	**24** **(12-40)**	8.9 (4.1-15.7)
Understory:			
Herb cover (%)	(1.5-4.1)	**5.1** **(3.3-8.1)**	6.4 (4.7-8.7)
Shade-tolerant saplings density	228 **(104-400)**	**84** **(22-186)**	335 (233-456)
Deciduous shrub cover (%)	**6.8** **(4.1-11.2)**	(5.6Y4.1)	**12** **(9-16)**
Subcanopy tree saplings density	**14** **(1-46)**	**11** **(0-37)**	**53** **(29-84)**
Total understory cover (%)	**46** **(33-62)**	**57** **(44-72)**	**52** **(43-62)**
C.V. herb cover	**81** **(66-97)**	**80** **(66-94)**	**75** **(66-84)**
Debris:			
5- to 15-m-tall snag density	(59-1O3)	**60** **(44-79)**	(8-18)
Decay-class 2 log volume	2.0 (0.9-4.5)	**8.3** **(3.9-17.8)**	**16** **(9.6-26.9)**
>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)**
>50-cm-d.b.h. snag density	**25** **(18-32)**	**14** **(10-20)**	**24** **(20-28)**
Snag volume	132 (92-189)	**85** **(62-119)**	159 (128-199)
Decay-class 4 snag volume	(36-83)	(13-42)	(23-45)
1.5- to 5-m-tall snag density	(41-72)	(31-5s2)	**24** **(20-28)**
Decay-class 5 snag volume	(14-41)	(6-23)	(9-22)
Log volume	223 (163-305)	124 (93-165)	**266** **(219-324)**

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[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 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
d-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 m^2 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

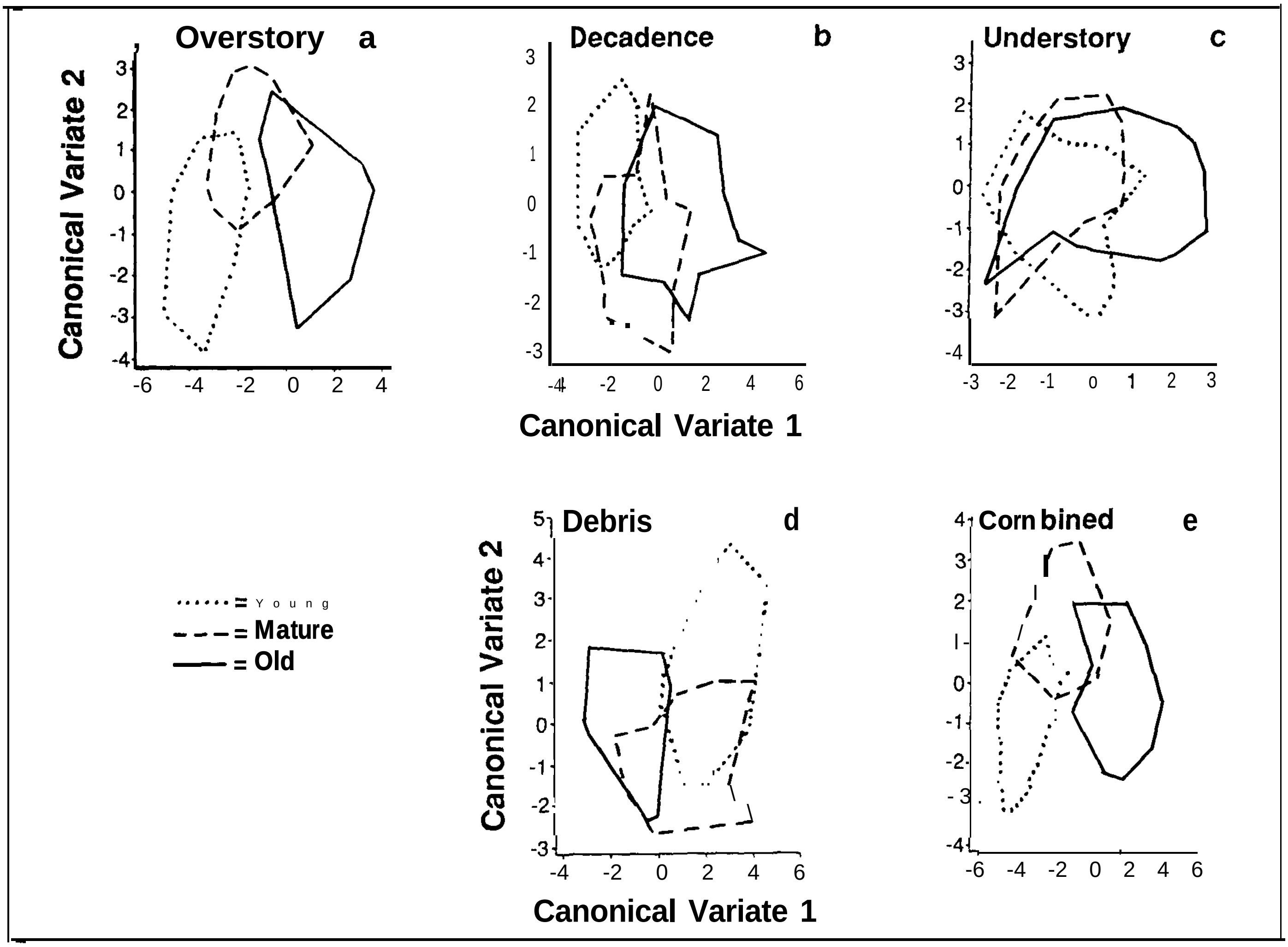

Figure 2—Ordinations of old-growth, mature, and young stands along first two canonical variates from analyses of overstory attributes (a), stand condition attributes (b), understory attributes (c), debris attributes (d), and a combination of all attribute sets (e).

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

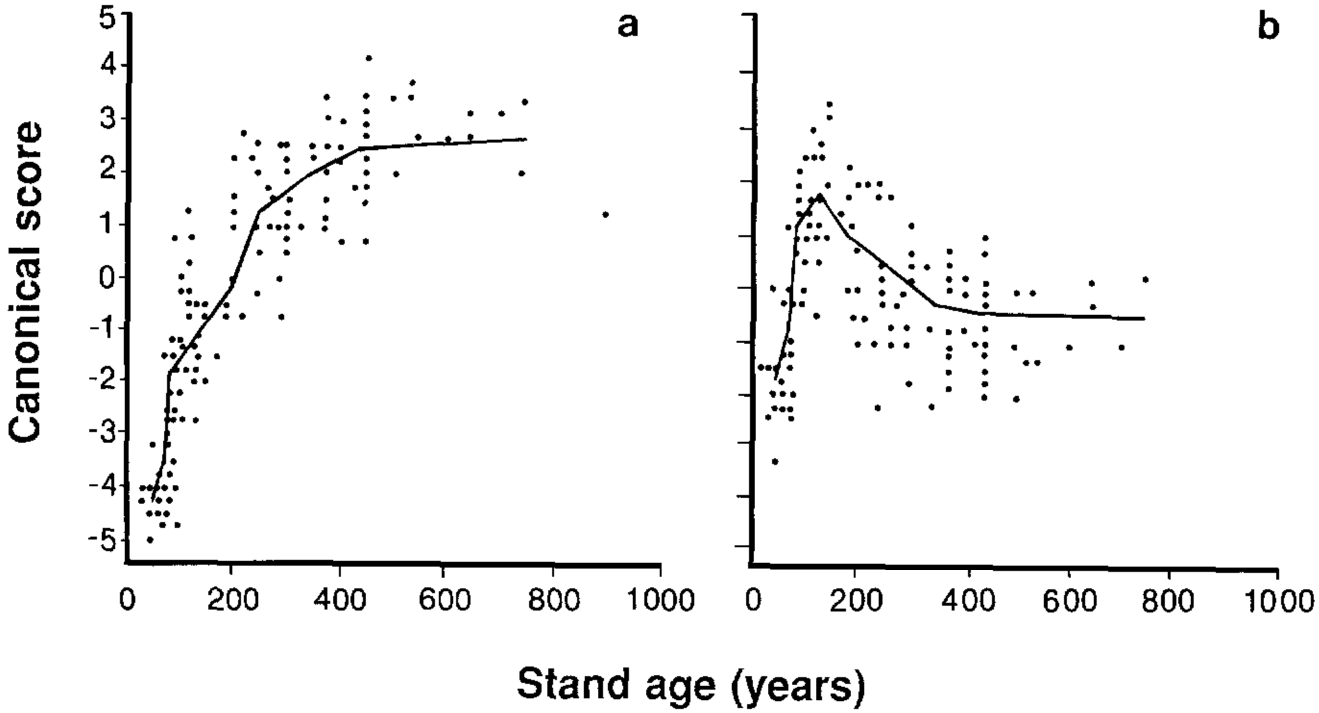

Figure 3—Relation of canonical variates 1 (a) and 2 (b) from combined-attribute set to stand age. Curves are fit to variate means from age-classes (years): <60; 60-80; 80-120; 120-160; 160-200; 200-300; 300-400; 400-600; >600.

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

	Percentage classified into age-class by discriminant function														
	Variable set														
	Overstory			Tree condition			Understory			Debris			Combined		
From age-class	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 S-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 <0.05)

		Variable set							
Overstory	*F*	Stand condition[a]	*F*	Understory	*F*	Debris	*F*	Combined set	*F*
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	Decidous 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
								&Q-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

	Moisture-class								
	Dry			Moderate			Moist		
Characteristic[c]	Washington	Oregon	Coast	Washington	Oregon	Coast	Washington	Oregon	Coast
Overstory:									
Shade-tolerant tree spp. basal area	29 (13-51)	2.3 (0-11.0)	2.2 (0-10.9)	36 (23-53)	20 (11-33)	16 (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 (0-8.0)	<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)	29 (11-57)	15 (6-29)	21 (10-36)	24 (9-46)	15 (1.6-24.9)	20 (10-34)	18 (2-25)
Density subcanopy trees	86 (14-218)	67 (6.9-187)	43 (1-145)	36 (5-94)	29 (3-83)	53 (5-151)	0.6 (0-31)	23 (2-70)	0
Total basal area	56 (39-79)	61 (43-87)	65 (46-93)	70 (56-89)	73 (58-93)	70 (51-96)	90 (66-124)	81 (65-101)	72 (45-115)
>100-cm-d.b.h. tree density	7.6 (0.4-23.7)	22 (7-46)	30 (11-58)	22 (11-37)	25 (13-41)	27 (11-51)	32 (15-56)	32 (19-49)	25 (5-62)
Shade-intolerant tree spp. basal area	26 (0-52)	58 (32-84)	60 (34-85)	33 (15-50)	53 (36-70)	51 (27-74)	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)	22 (10-39)	13 (4-26)	8.6 (0.7-25.5)	27 (10-52)	14 (5-28)	19 (2-57)
Arching boles (%)	2.4 (0-9.4)	1.5 (0-7.7)	11 (3-24)	1.8 (0.1-5.6)	2.3 (0.2-6.4)	9.4 (2.8-19.9)	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 (0-1.6)	0.6 (0-2.1)	1.0 (0-3.8)	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)	3.4 (1.3-6.6)	2.6 (0.8-5.4)	1.0 (0-3.8)	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)	18 (6-36)	2.8 (0-12.1)	14 (2-39)	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)	5.5 (2.4-10.0)	8.3 (4.4-13.4)	4.4 (1.1-10.0)	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 (0-5.2)	1.0 (0-5.5)	6.3 (0.5-18.9)	0.1 (0-4.4)	3.6 (0.4-10.1)	0.7 (0-12.5)
Multiple-stemmed crowns (%)	5.3 (0.6-14.8)	1.4 (0-7.4)	10 (3-23)	3.6 (0.8-8.6)	4.3 (1.1-9.6)	8.4 (2.3-18.4)	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)	13 (1-38)	19 (3-48)	5.9 (0.5-17.3)	3.6 (0-13.2)	10 (1-30)	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)	3.9 (0-22.9)	2.7 (0-20.1)	35 (4-94)	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)	11 (2-29)	23 (4-57)	12 (1-37)	5.0 (0.2-18)	23 (1-78)

See footnotes on next page.

Table 6—continued

	Moisture-class								
	Dry			Moderate			Moist		
Characteristic[c]	Washington	Oregon	Coast	Washington	Oregon	Coast	Washington	Oregon	Coast
Understory:									
Graminoid cover (%)	<0.01 (0-0.01)	0.3 (0-16.8)	0.7 (0-36.6)	<0.01 (0-0.01)	<0.01 (0-0.01)	0.1 (0-26.2)	0.04 (0-1.3)	<0.01T0.1 (0-0.01)	(0-26.2)
Total vegetation cover (%)	49 (20-91)	43 (16-83)	72 (36-122)	42 (23-67)	54 (32-82)	51 (24-90)	44 (20-78)	64 (41-93)	66 (22-134)
Evergreen shrubs cover (%)	21 (5-49)	17 (3-43)	34 (12-68)	12 (3-25)	18 (7-34)	21 (6-45)	2.3 (0-12.8)	16 (7-31)	1.2 (0-18.3)
Deciduous shrub cover (%)	14 (4-50)	11 (3-38)	21 (6-73)	16 (7-37)	9.5 (4-22)	6.7 (2.0-21.0)	13 (4-37)	15 (7-33)	9.0 (2.0-49.0)
Herb cover (%)	6.3 (1.9-21.1)	4.9 (1.5-16.4)	3.5 (1.1-11.7)	6.8 (3.0-15.2)	7.3 (3.3-16.5)	3.9 (1.3-11.5)	11 (3.9-31.3)	17 (7.8-36.6)	5.0 (0-25.1)
Subcanopy tree sapling density	169 (14-498)	194 (21-540)	13 (0-169)	25 (0-127)	30 (0-138)	7.1 (0-123.1)	4.4 (0-103.3)	61 (3-190)	0.8 (0-168.6)
C.V. evergreen shrub cover (%)	78 (36-136)	72 (32-129)	62 (25-115)	97 (63-139)	65 (38-99)	102 (56-161)	148 (94-215)	79 (50-115)	133 (59-236)
Debris:									
F and H litter layer depth	28 (11-52)	14 (4-33)	7.7 (0.7-22.0)	29 (17-45)	22 (12-36)	5.2 (0.3-16.2)	35 (18-58)	39 (25-55)	7.0 (0-27.0)
30- to 60-cm-diameter log density	163 (80-335)	70 (34-144)	61 (30-125)	225 (139-365)	152 (94-247)	124 (65-238)	226 (122-422)	162 (102-257)	138 (53-362)
Snag volume	170 (64-447)	64 (25-170)	71 (27-188)	232 (121-145)	202 (105-387)	166 (69-393)	290 (125-670)	207 (112-385)	208 (56-764)
Decay-class 5 snag volume	5.9 (0-34.5)	5.2 (0-32.6)	1.7 (0-22.5)	24 (7-52)	23 (6-61)	10 (0-39)	8.1 (0-33.9)	24 (8-51)	12 (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 ‘I-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	2s	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 SO-cmd.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
>6O-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 Amcmg Age-classes

Multivariate analyses indicated that forest habitat structure differs among age-&asses 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,

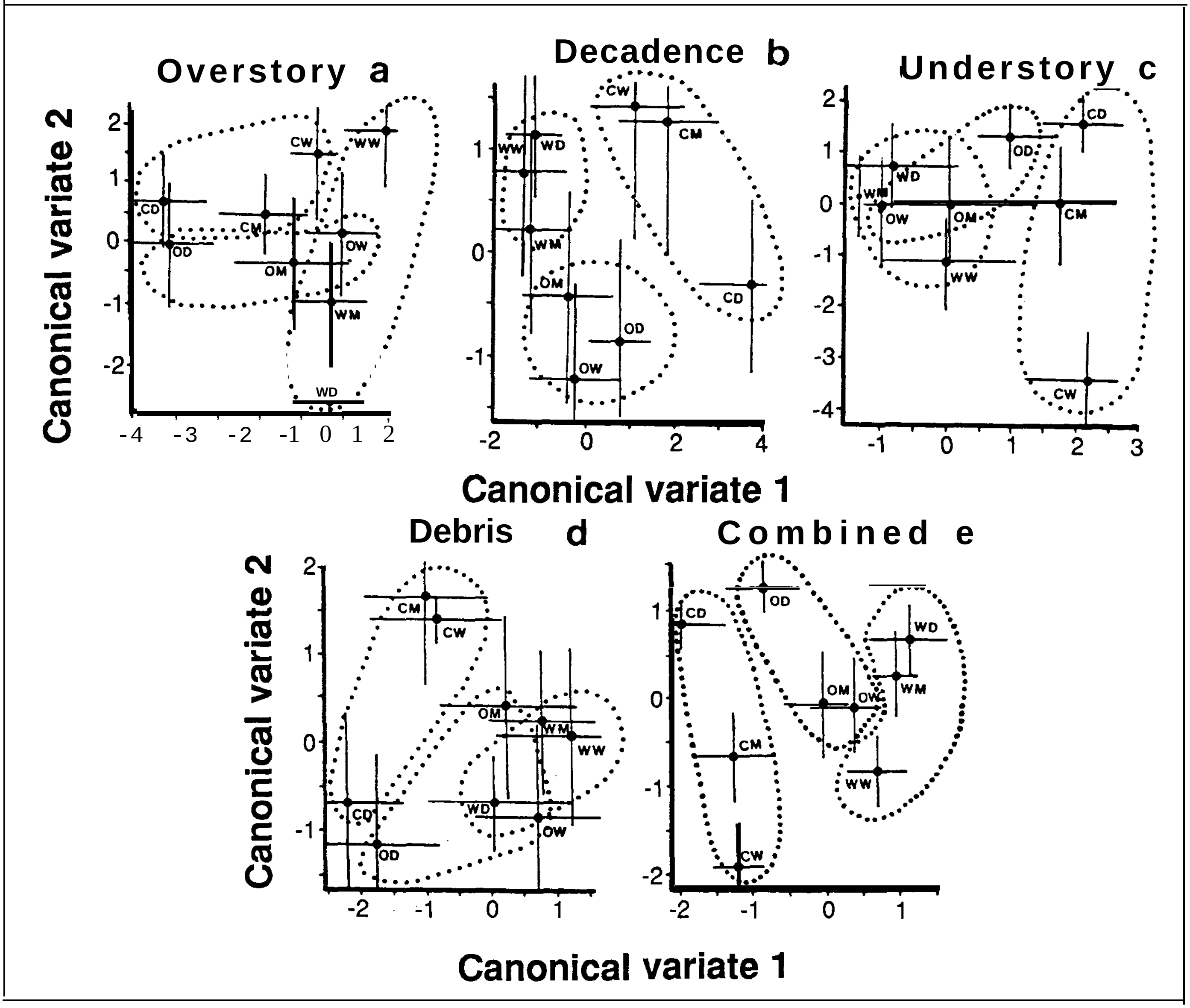

Figure 4-Ordinations of province-moisture class means (with standard deviations) of old-growth stands along first two canonical variates from analyses of overstory attributes (a), stand-condition attributes (b), understory attributes (c), debris attributes (d), and a combination of all attribute-sets (e). First letter indicates province: Oregon Cascades (0); 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 S-Summary of discriminant classifications of province-moisture-classes based on different sets of attributes

	Percentage classified into class by discriminant function				
	Variable set				
From classes	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”

From class		Percentage classified into class by discriminant function								
		Dry			Moderate			Moist		
Moist	Province	Washington	Oregon	Coast	Washington	Oregon	Coast	Washington	Oregon	Coast
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 Dymess 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 Dymess 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 overstories 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 sixes 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.

Acknowledgements

Field work could not have been completed without the efforts of several dedicated field crews. Gody Spycher, Diane Chung, and Janice Harmon provided valuable assistance in managing and analyzing of the large data set. We thank Jim Agee, Paul Alaback, and an anonymous reviewer for their helpful comments.

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 fii
- 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 ll-Variables used in stepwse discriminant analyses

Overstory (>5-cm-d.b.h.)
- Total basal area
- Tree density
- Basal area, standard deviation
- Tree density, standard deviation
- Tree d.b.h. mean
- Tree d.b.h. standard deviation
- Number of overstory trees
- Trees >100-cm-d.b.h. density
- Tree height diversity (H') based on basal area
- Tree height diversity (H') based on stem density
- Douglas-fir basal area
- Douglas-fir >100-cm-d.b.h. density
- Shade-tolerant tree spp. basal area
- Shade-intolerant tree spp. basal area
- Subcanopy tree spp. basal area
- Broad-leaved tree spp. basal area
- Shade-intolerant tree spp. density
- Shade-tolerant tree spp. density
- Subcanopy tree spp. density
- Trees with root-collar cavities
- Trees with natural cavities
- Snags with excavated cavities

Stand condition[a]
- Broken-topped crowns, Douglas-fir
- Broken-topped crowns, all spp.
- Sweeping boles, Douglas-fir
- Sweeping boles, all spp.
- Multiple-stemmed crowns, all spp.
- Multiple-stemmed crowns, Douglas-fir
- Dead-topped crowns, Douglas-fir
- Dead-topped crowns, all spp.
- Broken-topped crowns with upturned leaders, Douglas-fir
- Broken-topped crowns with upturneds leaders, all spp.
- Forked bole
- Arching boles.
- Boles with fall scars, Douglas-fir
- Boles with fall scars, all spp.
- Trees with swollen knots, Douglas-fir
- Conks on lower boles, Douglas-fir
- Conks on lower bole, all spp.
- Resinosis, Douglas-fir
- Resinosis, all spp.
- Trees with excavated cavities
- Snags with natural cavities
- Snags >50-cm-d.b.h. with excavated cavities
- Snags >50-cm-d.b.h. with natural cavities

Understory
- Shade-tolerant sapling density
- Subcanopy sapling density
- Cover vegetation c2 m tall (%)
- C.V. herb cover
- Lichen cover (%)
- Moss cover (%)
- Fern cover (%)
- Herb cover (%)
- Evergreen shrub cover (%)
- Deciduous shrub cover (%)
- Total understory cover (%)
- C.V. evergreen shrub cover
- C.V. deciduous shrub cover
- C.V. >2-m-tall vegetation cover

Debris
- F and H litter layer depth
- Snags SO-m-tall density
- 10- to 30-cm-diameter log C.V. density
- 30- to 60-cm-diameter log C.V. density
- Snag >5-m-tall and 50-cm-d.b.h. density
- 5-to 15-m-tall snag density
- SO-cm-d.b.h. snag density
- Snags >50-cm-d.b.h. density
- 10- to 30-cm-diameter logs density
- 30- to 60-cm-diameter log density
- 60-cm-diameter log density
- Decay-class 1 log volume
- Decay-class 2 log volume
- Decay-class 3 log volume
- Decay-class 4 log volume
- Decay-class 5 log volume
- Decay-class 1 snag volume
- Decay-class 2 snag volume
- Decay-class 3 snag volume
- Decay-class 4 snag volume
- Decay-class 5 snag volume
- Ratio log-volume decay-class 4 + 5 to total log volume
- Log volume
- Snag volume
- Snag volume (C.V.)

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[a] All variables are percentages.

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Plant Species Diversity and Occurrence in Young, Mature, and Old-Growth Douglas-Fir Stands in Western Oregon and Washington

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Abstract

The objective of the study was to characterize differences in vascular plant diversity and species abundance among young (30-80 years old), mature (80-195 years old), and old-growth (195-900 years old) Douglas-fir forests. A chronosequence of Douglas-fir stands was sampled in each of three physiographic provinces: southern Washington Cascade Range; Oregon Cascade Range; and southern Oregon Coast Range. The cover of all vascular plants was recorded in 177 stands, each consisting of 4 to 5200 m^2 plots. Measures of species diversity were calculated for the overstory and understory strata of each stand. Species diversity in the three provinces showed an age-class effect ($P < 0.1$) in 6 of the 12 tests performed. Diversity tended to remain constant or increase slowly with age-class. The frequency of occurrence of species showed an age-class effect ($P < 0.1$) in 15 to 20 percent of understory species tested in the three provinces. Similar results were obtained in analyses based on species cover, although relative differences between old growth and the other age-classes were greater. Species occurring with greatest frequency and abundance in old growth included Pacific yew, an understory *tree;* Cornus *canadensis*[1] and *Tiarella trifoliata var unifoliata,* understory herbs; and *Lobaria* spp., foliose canopy lichens. Four factors contributing to late-successional change in these communities are hypothesized: changes in resources, changes in horizontal heterogeneity, changes in vertical heterogeneity, and long periods without intense fire.

Introduction

The plant compositional changes during the middle to late stages of succession in Douglas-fir forests are poorly known. Most research has concentrated on early successional changes after catastrophic disturbances (Dyrness 1973, Halpern 1987, Isaac 1940, Long 1977). These studies have focused on the first 50 years of a potentially 1000-year-long ecological process-less than a twentieth of the sere!

Plant species diversity within stands appears to be highest in the early stages of succession in western coniferous forests (Habeck 1968, Schoonmaker and McKee 1988), and plant community changes are rapid during the early stages of succession (Long 1977). After canopy closure, less dramatic

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

but distinct changes may continue for many centuries. For example, in Sitka spruce-hemlock forests, where stand development requires hundreds of years, understory communities continue to change for at least 300 years (Alaback 1982). Stewart (1986a, in press) reported that canopy structure and composition influenced understory development in several mature and old-growth Douglas-fir stands in the Oregon Cascades.

Few examples of plants that are restricted to old-growth Douglas-fir forests or find optimal habitat in old growth have been reported. Franklin and others (1981) suggest that some mycotrophic plants, such as pinesap, and lichens, such as *Lobaria oregana* find optimal habitat in old growth, but they do not present any data. Moir and others (1979) reported that *Tiarella unifoliata* had higher cover in old than in young growth in a chronosequence of stands on similar sites from Mount Rainier National Park. No plant community studies have reported how diversity measures change with time in the later stages of Douglas-fir forest succession.

The objective of this study was to contrast the composition of natural young, mature, and old-growth Douglas-fir stands in western Oregon and Washington, emphasizing distinctive features of old growth. The specific objectives were to characterize the species diversity in overstories (tree stratum) and understories (herb, shrub, and seedling stratum) of the three forest age-classes, and to identify plant species that differ in frequency of occurrence and abundance among the forest age-classes.

Study Area

The study was conducted in Douglas-fir-dominated stands in Washington and Oregon in three physiogmphic provinces: the southern Washington Cascade Range, the Oregon Cascade Range, and the southern half of the Oregon Coast Ranges (Franklin and Dymess 1973). These provinces are all 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 mild and wet in winter and cool 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 primarily encompasses 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 fringes of the Mixed Conifer Zone (Franklin and Dymess 1973) were 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, this volume), such as codominance of western hemlock in the overstory, diverse vertical foliage distribution, and large accumulations of woody debris (Spies and others 1988). True "climax" forests composed entirely of shade-tolerant species are rare because pioneer Douglas-fir can persist in stands for over 1000 years (Franklin and DeBell 1988), and wildfires have occurred more frequently than this on most sites.

Methods

General Design

A total of 196 Douglas-fii stands in Washington and Oregon representing different ages (40 to 900 years) and site conditions were sampled during 1983 and 1984 (for a map of the stand locations, see Spies and Franklin, this volume). All stands originated after wildfires, which killed most or all of the overstory trees. Where remnant old-growth trees occurred in young and mature stands, their densities were typically less than 1 per 10 ha. Similar geographic distribution among ages of sampled stands was maintained by sampling 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 (≥195 years). These age-classes were then used in the analyses.

To control site variation across the age-classes, a subset of 177 stands were selected based on field observations, site data, and DECORANA ordinations (Spies and Franklin, this volume). In general, the age-classes in a province had similar means and ranges of site conditions (table 1). Drier and wetter plant associations were sampled in old-growth stands (Spies and Franklin, this volume) but were not included in the chronosequence analysis. Old-growth stands occurred on slightly drier aspects than mature or young stands in the Washington Cascades and were intermediate to young and mature stands in the other provinces. Old growth did tend to occur at slightly lower topographic positions, but elevations and slope percentages were intermediate to young and mature stands. Plots from DECORANA ordinations (fig. 2, in Spies and Franklin, this volume) indicated that the overall vegetation composition was similar among the age-classes.

Table 1—Means and ranges of age and site characteristics for young (Y), mature (M), and old-growth (O) stands in 3 physiographic provinces

	Washington			Oregon			Coast		
Characteristic	Y	M	O	Y	M	O	Y	M	O
Stand age (yr)									
mean	65	130	425	60	115	395	55	100	315
range	42-75	80-190	210-900	30-79	84-180	195-750	40-70	80-120	130-525
Aspect[a]									
mean	1.2	1.1	0.9	1.1	0.7	0.9	0.9	1.0	0.9
range	0.3-2.0	0.1-2.0	0.0-2.0	0.1-1.9	0.0-1.8	0.0-2.0	0.1-1.4	0.4-1.7	0.1-1.9
Slope %									
mean	40	45	35	37	44	40	40	53	50
range	13-66	19-73	9-80	8-71	3-90	2-92	16-70	26-75	19-85
Elevation (m)									
mean	709	747	730	844	808	808	302	487	403
range	472-1167	483-1124	378-1049	474-1428	326-1478	437-1284	86-473	260-1022	153-909
Latitude (deg)									
mean	46.3	46.2	46.2	44.2	43.9	44.1	43.6	43.9	43.8
range	45.8-46.9	45.1-46.8	45.8-46.9	42.8-45.5	42.9-45.4	42.8-45.6	43.2-44.3	43.0-44.5	43.1-44.5
Topographic[b] position									
mean	2.9	2.8	2.2	2.5	2.7	2.6	3.3	3.3	2.8
range	2-4	2-4	1-4	2-4	1-4	1-4	2-4	2-4	2-4

[a] Cosine transformation: northeast = 2.0, southwest = 0.

[b] 1 = valley bottom; 2 = lower 1/3 slope; 3 = middle 1/3 of slope; and 4 = upper 1/3 of slope.

Given the large geographic area of the study and the large size of sample stands (see below), the analysis could not be stratified by individual plant associations (Hall 1988). Each age-class in the chronosequence, however, encompassed a similar range of mesic to dry-mesic plant-association groups of the Western Hemlock Series (Hall 1988). The major association groups were: Western Hemlock/Rhododendron-Salal (CHS3); Western Hemlock/Salal-Oregongrape (CHS1); Western Hemlock/Rhododendron, Cool (CHSC); Western Hemlock/Forb, Dry (CHF2); Western Hemlock/Rhododendron, Mesic (CHSM); Western Hemlock/Salal-Oregongrape, Dry (CHSD); and Western Hemlock/Shrub, Dry (CHC2). In addition, no significant difference among age-classes was found in the percentage cover ($P < 0.05$) of the following key plant association indicator species: *Gaultheria shallon*; *Xerophyllum tenax*; *Rhododendron macrophyllum*; *Holodiscus discolor*; *Berberis nervosa*; *Athyrium felix-femina*; *Rubus spectabilis*; *Oplopanax horridum*; *Oxalis oreganum*; and *Polystichum munitum*.

Every effort was made to control site variation. True chronosequences should have similar soils, sites, climates, climate histories, and disturbance and establishment histories (Oliver 1982), but these assumptions are violated to various degrees in most chronosequence studies. Given the wide geographic range of this study, the inferences about successional change should be viewed with caution, and more as working hypotheses than as established facts.

Stand selection and plot measurements

Stand size ranged from about 4 to 20 ha. Within each stand, five circular plots were established systematically. In a some very small stands, only three or four plots were established. Plots were spaced either 100 or 150 m apart, depending on stand size, with the wider spacing used 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 consisted of a set of nested circular plots of four sizes: 0.002 ha, 0.02 ha, 0.05 ha, and 0.1 ha. Each plot size sampled different aspects of forest structure (see Spies and Franklin, this volume). Within the 0.1-ha plot, trees over 50 cm in diameter at breast height (d.b.h.) were measured and recorded by species, d.b.h., and height. The 0.05-ha plot was used to record the information described above for trees 5 to 50 cm d.b.h.

Information on understory vegetation was recorded by species in the three smallest plots. The percentage cover of tall shrub species and trees less than 8 m tall was estimated by species over the 0.05ha plot. The percentage cover of all vascular plants, mosses, and lichens (including canopy foliose lichens, Lobaria *oregana* and *L. pulmonaria,* that had fallen to the forest floor) was estimated by species in the 0.02-ha plot. Species occurring in the 0.05-ha plot were also recorded and used in presence/absence analyses. All vascular plants were keyed to species or genus. For mosses and lichens, only a selected subset were identified to species or genus.

Data on slope, aspect, topographic position, and shape of topographic cross section were collected from the 0.1-ha plot. Tree ages were determined for young and mature stands by increment coring of 1 to 4 dominant Douglas-fir per plot (5 20 per stand) at breast height, adding 5-7 years for growth to that 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

Species richness and diversity were calculated separately for the overstory (trees >5 cm d.b.h.) based on basal area, and for the understory vascular plants based on percentage cover. Because about 25 percent of the stands were sampled with fewer than 5 plots, a smaller subset, 144 stands, was used to calculate mean species richness and diversity for each age-class. Stands were selected for each age-class so that the mean number of plots per stand or area was the same for each age-class in a province. Species diversity was calculated as No and N_2 (Hill **1973),** the reciprocal of Simpson's index. No is simply the total number of species in a stand. $N2$ is calculated as:

$$1/p_i2$$

where p_i is the proportional abundance of the ith species.

Analyses of species frequency and abundance in the age-classes were conducted for overstory and understory species occurring at least five times within a province. Preliminary analyses of species distributions by latitude and elevation were conducted in each province. Many species were elevationally and latitudinally restricted in the provinces. Consequently, each province was divided into ecological zones (table 2), based on inspections of sample and species distributions. The zones were typically large enough to include several stands of different age-classes. If a species did not occur in any stands within a zone, then none of the sample stands from that zone were used in the age-class analyses for that species. Consequently, sample sizes differ among species. The objective of the stratification was to restrict the analysis of species to age-class relationships within zones where the species could occur, based on their ranges and environmental conditions. It had the effect of reducing the number of zero values for some species and increasing the power of the statistical analyses. Chi-square analyses were used to test for an age-class effect in the frequency of occurrence of each species. Kruskal-Wallis nonparameteric analyses were used to test for differences in species abundance (either percentage cover or basal area) among the age-classes. All analyses were conducted using SAS (SAS Institute Inc. 1987).

Table 2-Latitudinal-elevation zones used in determining species distributions for age-class analyses

Province	Zone	Elevational range (meters)	Latitudinal range (degrees)
Oregon Cascades	1	1000-1500	42.5-43.5
	2	400-1000	42.5-43.5
	3	950-1200	43.6-44.8
	4	400-950	43.6-44.8
	5	300-950	44.9-45.6
Oregon Coast Range	1	50-800	43.0-44.0
	2	100-800	44.1-44.5
	3	800-100	44.1-44.5
Washington Cascades	1	350-1100	45.8-46.6
	2	600-1200	46.6-47.0

Results

Species Diversity

Overstory-Species richness (No) was significantly different ($P < 0.05$) among the age-classes only in the Coast Range, where old-growth stands had the highest numbers of overstory species, and mature stands the lowest numbers (fig. 1). Overstory species diversity (N_2), on the other hand, showed an age-class effect only in the Cascade provinces, where old growth had the highest diversity.

Understory-Species richness was marginally significant ($P < 0.09$) among age-classes in the Coast Range (fig. 2); old growth had the highest number of species and young stands had the lowest. Understory species diversity (N_2) showed a significant age-class effect in the Washington Cascades and the Coast Range. Old growth had the highest values in both provinces; young stands had the lowest values in the Washington Cascades, and mature stands had the lowest values in the Coast Range.

Species Occurrence

Overstory-Species differing significantly ($P < 0.1$) in basal area among the age-classes were either shade-tolerant species that had highest basal areas in old-growth stands or shade-intolerant species with highest basal area in young stands (table 3). Western hemlock, Pacific yew, and bigleaf maple

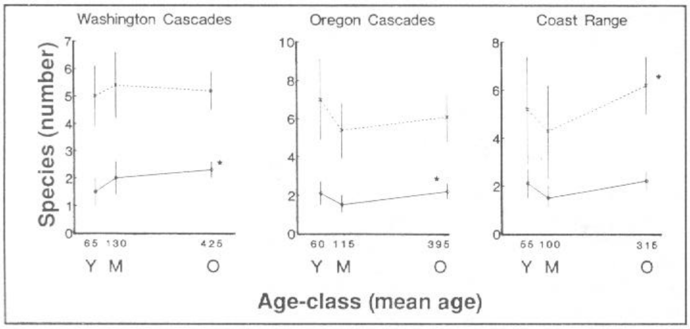

Figure 1—Species diversity of the overstory stratum in relation to age-class in Douglas-fir stands from three physiographic provinces. Dotted line is N_o and solid line is N_2. Vertical bars are Scheffe's 95 percent confidence intervals. Significant age-class effect of ANOVA is indicated by '*' ($P < 0.05$).

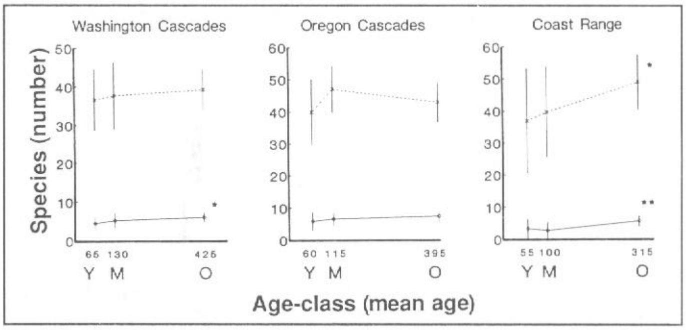

Figure 2—Species diversity of the understory stratum in relation to age-class in Douglas-fir stands from three physiographic provinces. Dotted line is N_o and solid line is N_2. Vertical bars are Scheffe's 95 percent confidence intervals. Significant age-class effect in ANOVA is indicated by '*' ($P < 0.1$) or '**' ($P < 0.05$).

Table 3—Basal area (m^2/ha) of trees species (>5 cm d.b.h.) in young (Y), mature (M), and old-growth (O) Douglas-fir stands in 3 physiographic provinces

Species	Washington			Age-class[a] effect	Oregon			Age-class[a] effect	Coast			Age-class[a] effect
	Y	M	O		Y	M	O		Y	M	O	
Pacific silver fir	0.4	0.2	5.4	***	<0.1	0.1	0.9		0	0	0	
White fir	0	0	0		9.8	11.8	3.3		0	0	0	
Grand fir	<0.1	<0.1	<0.1		0.4	1.2	0.5		<0.1	0	1.6	
Noble fir	<0. 1	0.3	0.4		0	0	0		0	0	0	
Bigleaf maple	0.1	0.2	<0.1	**	0.7	0.5	<0.1	*	0.5	0.4	1.6	+
Red alder	<0.1	0.3	0		0.6	0.3	0.0	*	1.6	2.1	0.1	*
Pacific madrone	0	0	0		<0.1	0.2	0.1		2.2	0.1	0.4	+
Incense-cedar	0	0	0		0.5	3.2	2.0		0	0.1	1.7	
Golden chinkapin	0	0	0		1.0	0.3	0.3		0.4	0.2	0.2	
Pacific dogwood	<0.1	0.2	<0.1		0.3	0.1	0.1		0.2	0.1	0.4	
Sugar pine	0	0	0		0.4	1.4	2.0		0	0	0	
Western white pine	0	<0.1	0.1		0.1	<0.1	<0.1		0	0	0	
Douglas-fir	38.5	36.0	31.3		28.6	48.8	47.8	***	36.4	47.1	49.8	
Pacific yew	<0.1	<0.1	0.7	***	0.2	0.1	0.67	**	0	0	0.4	*
Western redcedar	1.0	4.4	6.3		2.1	1.3	7.4		<0.1	2.8	2.9	+
Western hemlock	7.4	15.0	24.0	***	7.9	1.5	14.0	***	4.2	6.1	9.9	+

[a] *P* values in Kruskal-Wallis test: + = <0.10; * = <0.05; ** = <0.01; *** = <0.001.

were the only species with significant differences among age-classes in all three provinces. The basal area of Pacific yew, an understory tree, typically was 5 to 74 times higher in old growth than in the younger age-classes in the two Cascade provinces. In the Coast Range, no overstory-size stems (that is 5 cm d.b.h.) of yew were encountered in any stands younger than 200 years. The basal area of Douglas-fir was significantly different among age-classes only in the Oregon Cascades. Bigleaf maple, an early to mid-successional species in the Cascade provinces, had highest basal area in old growth in the Coast Range.

Understory—A total of 26 of 129, 35 of 171, and 13 of 98 species were found to differ in percentage frequency among the age-classes ($P < 0.1$) in the Washington, Oregon, and Coast provinces, respectively (table 4). Most species attained their maximal age-class frequency in old-growth or mature stands. Only two plants, Pacific yew and *Lobaria* spp., were significant in all provinces; they both reached their highest frequency of occurrence in old growth. Other species with maximal frequency of occurrence in old growth included: *Cornus canadensis*, *Linnaea borealis* var *longiflora*, and *Tiarella trifoliata* var *unifoliata* in the Cascade provinces, and *Synthyris reniformis* in the Coast Range province. Species occurring more frequently in mature and young stands than in old-growth stands included: *Holodiscus discolor*, *Anemone lyallii*, and *Pteridium aquilinum*. Although differences were significant for many species, most species were relatively common, occurring 25 percent or more of the time in at least two of the age-classes. This overlap includes the old-growth-associated species mentioned above, except for Pacific yew and *S. reniformis* in the Coast Range province, where these species either did not occur or occurred infrequently in mature and young stands.

Table 4—Percent frequency of occurrence of species showing an age-class effect ($P < 0.1$) in old-growth, mature, and young stands in 3 physiographic provinces (species are listed from top to bottom in order of decreasing frequency in old growth)

Species	O	M	Y	Sig.[a]
	Washington			
Trees				
Pacific yew	90	70	46	**
Pacific silver fir	90	60	62	*
Douglas-fir	27	30	69	*
Bigleaf maple	9	67	40	+
Grand fir	0	30	0	***
Shrubs				
Vaccinium membranaceum	80	50	15	***
Rubus lasiococcus	60	40	23	+
Gaultheria ovatifolia	43	20	8	*
Holodiscus discolor	10	50	39	*
Rubus parviflorus	3	30	39	**
Lonicera spp.	0	10	23	*
Herbs				
Achlys triphylla	100	100	77	**
Clintonia uniflora	87	70	54	+
Cornus canadensis	87	60	54	*
Tiarella trifoliata unifoliata	80	70	39	*
Trientalis latifolia	40	70	77	*
Campanula scouleri	33	40	69	+
Pyrola picta	20	80	62	***
Galium triflorum	16	60	61	**
Osmorhiza chilensis	7	50	31	**
Anemone lyallii	3	20	0	+
Grass				
Melica harfordii	0	20	0	**
Ferns and club mosses				
Polystichum munitum	73	100	100	*
Pteridium aquilinum	57	80	100	**
Lycopodium clavatum	30	10	0	*
Lichen				
Lobaria spp.	80	30	23	***
	Oregon			
Trees				
Pacific yew	79	44	61	**
Douglas-fir	49	68	78	+
Bigleaf maple	29	59	54	*
Noble fir	0	17	20	*
Shrubs				
Chimaphila umbellata	84	64	50	*
Chimaphila menziesii	74	80	100	+
Holodiscus discolor	26	52	33	+
Amelanchier alnifolia	21	44	17	+
Gaultheria ovatifolia	5	5	24	+
Oemleria cerasiformis	3	23	27	*
Salix spp.	0	0	17	*
Herbs				
Linnaea borealis longiflora	98	80	89	*
Goodyera oblongifolia	98	80	89	+
Coptis laciniata	62	46	20	*
Tiarella trifoliata unifoliata	58	36	33	+
Cornus canadensis	58	28	56	*
Monotropa uniflora	30	23	0	+
Vancouveria hexandra	81	100	56	***
Galium triflorum	63	92	56	**
Fragaria vesca	24	55	53	*
Disporum hookeri	58	72	39	+
Galium oreganum	18	29	0	+
Collomia heterophylla	11	32	7	+
Montia sibirica	9	36	22	*
Arenaria macrophylla	6	36	0	***
Anemone lyallii	7	33	25	+
Pyrola aphylla	5	23	40	**
Galium aparine	4	27	8	+
Plagiobothrys figuratus	4	27	17	+
Senecio bolanderi	2	20	6	*
Hypericum perforatum	0	0	17	*
Ferns				
Blechnum spicant	49	22	20	+
Pteridium aquilinum	43	88	100	***
Polypodium glycyrrhiza	17	38	0	+
Lichen				
Lobaria spp.	91	64	39	***
	Coast			
Trees				
Western hemlock	91	78	33	**
Pacific yew	55	0	0	**
Shrubs				
Berberis nervosa	100	78	67	*
Acer circinatum	91	56	50	*
Herbs				
Disporum hookeri	91	67	50	*
Anemone deltoidea	87	56	50	+
Adenocaulon bicolor	86	57	33	*
Linnaea borealis longiflora	74	56	17	*
Achlys triphylla	78	67	17	**
Synthyris reniformis	64	14	0	**
Smilacina racemosa	64	29	17	+
Goodyera oblongifolia	68	14	83	**
Lichen				
Lobaria spp.	87	33	17	***

[a] Significance level (P) in chi-square test for age-class effect: + = <0.1, * = <0.05, ** = <0.01, *** = <0.001.

The cover of many understory species also differed among the age-classes, with at least marginal significance ($P < 0.1$) (table 5). Thirty species, 45 species, and 14 species differed among the age-classes ($P < 0.1$) in the Washington, Oregon, and Coast provinces (table 5). Mean species cover was highest in old-growth 37 times, highest in mature 30 times, and highest in young stands 22 times in the three provinces. Eight species differed significantly in all three provinces. Five of these, Pacific yew, *Goodyera oblongifolia*, *Linnaea borealis* var *longiflora*, *Achlys triphylla*, and *Lobaria* spp. had highest cover in old growth; the remaining three, *Adenocaulon bicolor*, *Anemone lyallii*, and *Pteridium aquilinum* had higher cover primarily in mature stands. The cover by Pacific yew and *Lobaria* spp. in young and mature stands was typically less than one-tenth of the cover in old-growth stands (table 4). Other species with highest cover in old growth included: *Chimaphilla umbellata*, *Berberis nervosa*, *Cornus canadensis*, and *Tiarella trifoliata* var *unifoliata*.

Table 5—Ratios of mean species cover in mature (M) and young (Y) stands to mean species cover in old growth for species showing an age-class effect ($P < 0.1$) (species are listed from top to bottom in order of decreasing mean cover in old growth)

Species	M	Y	Sig.[a]
	Washington		
Trees			
Silver fir	0.05	0.03	***
Pacific yew	0.06	0.04	***
Cascara	>100	8	*
Douglas-fir	7.9	13	*
Bigleaf maple	86	15	**
Grand fir	>100	0	***
Shrubs			
Vaccinium membranaceum	0.09	0.03	***
Vaccinium alaskaense	0.10	0.05	**
Vaccinium parvifolium	0.24	0.37	**
Chimaphila umbellata	0.48	0.11	***
Holodiscus discolor	3.8	1.3	+
Rubus parviflorus	>100	>100	**
Herbs			
Tiarella trifoliata unifoliata	0.09	1.00	+
Corallorhiza mertensiana	0.13	<0.01	*
Clintonia uniflora	0.13	0.14	*
Cornus canadensis	0.36	0.24	***
Linnaea borealis longiflora	0.50	0.30	***
Goodyera oblongifolia	0.85	0.11	*
Trientalis latifolia	1.6	1.7	*
Achlys triphylla	1.7	0.63	+
Anemone deltoidea	3.5	2.5	*
Pyrola picta	4.9	2.8	*
Adenocaulon bicolor	6	7	*
Galium triflorum	12	16	**
Anemone lyallii	19	<0.01	+
Aster canescens	0.03	63	*
Osmorhiza chilensis	>100	>100	**
Ferns			
Pteridium aquilinum	3.0	17	***
Grass			
Melica harfordii	>100	0	
Lichen			
Lobaria spp.	0.01	0.02	***
	Oregon		
Trees			
Pacific yew	0.02	0.10	***
Western hemlock	0.33	0.54	**
Western redcedar	0.63	2.3	*
Cascara	7	9.8	*
Bigleaf maple	12	22	*
Noble fir	>100	>100	*
Shrubs			
Rubus nivalis	0.22	0.27	+
Chimaphila umbellata	0.95	0.24	*
Berberis nervosa	1.7	0.95	*
Chimaphila menziesii	1.7	4	**
Rosa gymnocarpa	2.7	0.85	*
Gaultheria ovatifolia	<0.01	18	*
Amelanchier alnifolia	44	44	+
Oemleria cerasiformis	66	16	+
Salix spp.	0	>100	*
Herbs			
Tiarella trifoliata trifoliata	<0.01	<0.01	*
Tiarella trifoliata unifoliata	0.10	0.01	**
Pyrola asarifolia	0.11	0.31	*
Coptis laciniata	0.28	0.03	**
Cornus canadensis	0.33	0.27	+
Linnaea borealis longiflora	0.34	0.41	***
Vancouveria hexandra	0.61	0.09	**
Goodyera oblongifolia	0.79	0.14	**
Achlys triphylla	0.8	0.04	***
Pyrola aphylla	0.72	2.47	**
Pyrola picta	1.3	4.2	**
Anemone deltoidea	2.1	0.59	*
Hieracium albiflorum	3.0	0.24	+
Galium oreganum	3.2	<0.01	*
Adenocaulon bicolor	3.3	0.99	**
Campanula scouleri	4.6	0.37	*
Galium triflorum	5.2	0.95	***
Montia sibirica	5.0	14	*
Collomia heterophylla	6.9	<0.01	*
Fragaria vesca	6.7	0.93	*
Arenaria macrophylla	24	<0.01	***
Senecio bolanderi	27	2.4	+
Anemone lyallii	32	2.3	*
Stachys rigida	>100	0	+
Plagiobothrys figuratus	0	>100	*
Ferns			
Pteridium aquilinum	9.1	18	***

See footnote on next page.

Table 5—continued

Species	M	Y	Sig.[a]
Grasses and rushes			
Festuca occidentalis	3.0	0.11	*
Bromus vulgaris	5.7	0.28	+
Luzula parviflora	>100	>100	+
Lichen			
Lobaria spp.	0.39	0.02	***
	Coast		
Trees			
Pacific yew	<0.01	<0.01	**
Western hemlock	0.25	0.02	**
Golden chinkapin	0.57	0.08	+
Shrubs			
Acer circinatum	0.02	1.08	**
Berberis nervosa	0.18	0.18	**
Herbs			
Synthyris reniformis	<0.01	0.01	*
Goodyera oblongifolia	<0.01	0.35	*
Linnaea borealis longiflora	0.06	0.07	**
Achlys triphylla	0.40	0.08	*
Anemone deltoidea	1.6	0.13	*
Adenocaulon bicolor	1.25	0.1	+
Corallorhiza maculata	4.4	1.4	+
Ferns			
Pteridium aquilinum	1.3	1.4	*
Lichen			
Lobaria spp.	0.03	0.009	***

[a] Significance level (P) in chi-square test for age-class effect: + = <0.1, * = <0.05, ** = <0.01, *** = <0.001.

Several species differed in cover among age-classes ($P < 0.1$) only in one province (table 5). For example, in the Washington Cascades, *Vaccinium* spp. and *Clintonia uniflora* had many times more cover in old growth than in mature or young stands. In the Oregon Cascades, *Coptis laciniata* and *Pyrola asarifolia* had much higher cover in old growth relative to the younger age-classes. In the Coast Range, *Acer circinatum* and *Synthyris reniformis* had highest cover in old growth.

The analyses based on percentage cover differed in two ways from the analyses based on percentage occurrence. First, more species showed significant differences among the age-classes in tests based on cover (90 species) than in tests based on occurrence (76 species). Second, for many species, such as Pacific yew and *Tiarella trifoliata* var *unifoliata*, relative differences among age-classes were greater for percentage cover than for percentage occurrence. The results indicate that the significant species are not strongly restricted to one age-class but differ in their development in the age-classes.

Discussion

Species Diversity

Various patterns of plant species diversity during succession have been hypothesized (Odum 1969, Pielou 1966, Whittaker 1965) including increases and decreases, and multiple peaks in diversity. Because this study did not examine the earliest stages of forest succession, the entire pattern of changes in diversity in Douglas-fir forests cannot be examined with these data. Other studies (Halpern 1987, 1989; Schoonmaker and McKee 1988), however, show that after stand-replacing disturbance in old-growth Douglas-fir stands, plant species diversity (both N_0 and N_2) increases to a peak early in succession as shade-intolerant herbs and shrubs invade the surviving community of shade-tolerant forest species. These studies indicate that as a forest canopy develops and closes, between 20 and 40 years, diversity declines to a low point when the dense tree canopy shades-out all but the most shade tolerant of the understory species.

The results of this study indicate that after canopy closure, the trend in understory diversity was to increase slightly from young to old growth. The increase may, in fact, be stronger than indicated by this study. The wide age range of the old-growth age-class may mask a steeper increase, followed by a decline in diversity as the stand becomes entirely composed of shade-tolerant tree species such as western hemlock. In the Coast Range, where old growth was almost 100 years younger than the Cascade old growth and had a lower basal area of hemlock, understory richness and diversity showed the strongest increase with age-class. Habeck (1968) found that forests dominated by western hemlock in Montana had lower species richness than earlier stages containing a mix of early- and late-successional species. This finding suggests that within the old-growth age-class, diversity may be high in the early stages of old growth (from 200 to 400 years) and low in the later stages (after 400 years), when western hemlock reaches dominance in the stand (Spies and others, unpubl. manuscript).

The overstory component of diversity appears to follow the general pattern described above, with peaks early and late in succession. The tendency for overstory diversity to be higher in young stands than in mature stands in the Oregon Cascades and Coast Range suggests that early successional species, such as red alder, bitter cherry, and madrone persist in young stands and drop out during the mature stage. During the old-growth stage, shade-tolerant species reach the canopy, contributing to an increase in canopy tree diversity during this period. A decline in overstory diversity probably occurs as Douglas-fir drops out of the stands.

Species Occurrence

The list of species associated with succession should be viewed as a first approximation, requiring further verification and more controlled study. Given that 398 individual nonparametrical statistical tests were conducted, about 40, or 10 percent of the tests, might be expected to yield significant results at $P < 0.1$ by chance. Consequently, the statistical tests should be viewed with caution. The results do suggest, however, that many species were different among the age-classes because about 20 percent of the tests in both analyses were significant"and many of those were significant at $P < 0.01$. The results should also be viewed with caution because some species that increase or decrease in abundance with stand age may have occurred too infrequently to show statistical significance. The influence of site and historical factors in this geographically broad chronosequence study can never be fully evaluated; however, the similarities in average site and vegetation characteristics (see Methods) do not indicate that these factors played a strong role in the community and species patterns among the age-classes.

Several of the species most common in old growth have been associated with late-successional coniferous forests in other studies. *Tiarella unifoliata* was most common in late-successional forests in Montana (Habeck 1968) and Washington (Moir and others 1979). Pacific yew reached highest abundance in late-successional cedar forests in Montana (Habeck 1968, McCune and Allen 1985). Alaback (1982) found that C. *canadensis* and *Vaccinium alaskaense* had highest biomass in old growth in a chronosequence of Sitka spruce/western hemlock stands in southeastern Alaska.

Some species had different successional relationships than were reported in other studies. Habeck (1968) found that *Vaccinium membranaceum,* a species associated with old growth in this study, was most frequent in early-successional stands in Montana, and *Adenocaulon bicolor,* which was most abundant in mature stands in this study, was most frequent in late-successional stands in Montana (Habeck 1968). Alaback (1982) found that V. parvifolium, which had highest percentage cover in old growth in the Washington Cascades, had high biomass in mature stands and low biomass in old growth in southeastern Alaska. Many factors, such as climate, genetics, competition, and disturbance regime, could lead to geographically different successional distributions for a single species.

Even within this study, some species did not show consistent successional patterns. For example, bigleaf maple had lowest basal area in old growth in the Cascade provinces but highest basal area in old growth in the Coast Range. This pattern may be because bigleaf maple has not yet dropped out of Coast Range old-growth stands, which are younger than the stands in the Cascade provinces. In addition, the lower basal area of western hemlock, a competitor for light, in old growth in the Coast Range may allow bigleaf maple to persist longer than it does in the Cascade stands.

Factors Contributing to Successional Change

Assuming that many of the patterns of vegetation and stand age are a consequence of forest succession, four related mechanisms of change in understory communities and plant species abundance are hypothesized.

The first mechanism is change in resources, particularly light, and competitive abilities to capture those resources. Old-growth forests develop many areas of dense hemlock canopies in addition to the relatively open Douglas-fir canopies and canopy gaps. Small, very shade-tolerant herbs and shrubs such as *Clintonia, Syntheris, Tiarella,* and *Cornus* are favored in the deep-shade areas. In mature and young forests"with more uniform, open canopies"aggressive, less shade-tolerant shrubs such as Gautheriu shallon often form large, dense patches that may exclude smaller, less-competitive herb and shrub species (Long and Turner 1974). The increase of shade-tolerant herbs and shrubs in coniferous forest development has been observed by Alaback (1982) and Stewart (1988). Some shade-tolerant understory herbaceous plants and tree species such as Pacific yew and westem hemlock may also be favored in old growth by cool, moist microclimates during the dry, warm season. Although the relative microclimates of the age-classes have not been quantified, old-growth understories are likely to be relatively cool and humid during the dry season because they are protected from radiation and drying winds by deep, multiple canopy layers. In addition, soil moisture may be higher as a consequence of the large accumulations of litter on the forest floor (Spies and Franklin, this volume) and pieces of decomposed wood that store moisture in the soil.

A second mechanism of understory change may be an increase in the horizontal spatial heterogeneity of resources and environments. As Douglas-fir stands develop, they become a mosaic of canopy gaps, and dense hemlock canopies overlying a forest floor with accumulations of woody debris, tip-up mounds, and shrub patches. This structural heterogeneity may create a shifting mosaic of resources and environments that favors species that can both tolerate low light and spread laterally to take advantage of increased light. In addition, if canopy gaps also represent areas of low root occupancy, then soil moisture and nutrients may be relatively more available. Species that can take advantage of resource heterogeneity include *Linnaea* borealis, *Rubus lasiococcus* and Clintonia unifrora, which spread rapidly by stolons or rhizomes (Antos and Zobel 1984) to occupy gaps that form above or near the plant. These species can apparently persist with low abundance in shaded areas but may require canopy gaps to survive for long periods in some stands.

A third mechanism in plant community change is the increase in vertical environmental diversity, specifically the increase in the height and number of canopy layers. The canopies of old-growth trees provide moist, cool environments that favor the growth of foliose lichens such as *Lobaria oregana* (Pike and others 1975). Because the canopy flora was not sampled directly, other epiphytic plant species may also be associated with tall, structurally and environmentally diverse canopies.

A fourth mechanism may be sensitivity to fire and slow rates of reestablishment and growth after fire. Fire-sensitive species such as western hemlock and Pacific yew are typically killed by moderate to high-severity fires and can take relatively long periods to reach maturity, growing slowly in the understory for many years. They are often present as scattered seedlings and saplings in young and mature stands but do not reach maximum size and density until the old-growth stage, one hundred to several hundred years later. This distribution does not mean that old-growth stands where these species occur have been free of fire during their entire development. Many old-growth stands have had a history of patchy low-intensity fires (Morrison and Swanson 1990), which miss individuals of these species or only injure them. Best development of these species appears where a stand has not been subjected to low-intensity fire for several centuries, however.

Conclusions and Management Implications

The majority of species did not show any differences in their frequency or abundance within the age-classes. At least 20 percent of the species did differ among the age-classes, and many of those were more frequent and abundant in old growth. Most species associated with old growth, however, were not restricted to old-growth forests and could be found with moderate frequencies and abundances in at least one younger age-class. Of all the species showing an age-class effect, only Pacific yew and *Lobaria* spp. showed strong preference for old-growth in all three provinces, suggesting that these species would suffer the greatest decline in regional populations if most of the current old growth is clearcut and converted to short-rotation plantations. Many of the ecological conditions that favor old-growth-associated plant species can be found in lesser amounts in younger unmanaged forests. Gaps, deeply shaded and cool understories, and accumulations of woody debris on the forest floor can be found in at least small areas in many unmanaged young and mature stands. Conditions such as long periods since catastrophic disturbance, development of massive tree crowns, and buffered canopy microclimates, which favor Pacific yew and *Lobaria* are not typically found in unmanaged young or mature stands that regenerated after stand-replacing fire, however.

The suggestion that the composition of the forest understory community changes with overstory succession has important implications for using vegetation to assess site conditions and for maintaining biological diversity in managed landscapes. The abundance (cover) of many understory species is used to classify forests into plant associations used for management. If the influence of succession on understory plant communities is not taken into account, then understory plant communities may incorrectly estimate site conditions and potential (Spies and Barnes 1985). Stewart (1988) has found that many understory species in Douglas-fir forests are influenced by tree canopies and warns that understory communities may reflect canopy-disturbance history more than site quality. Species such as *Tiarella*, which may be affected by changes in light intensity and understory microclimate, will have limited value in identifying plant associations and indicating physical site conditions. A better understanding of the autecologies of many understory shrubs and herbs, will help resolve uncertainty of the indicator value of some understory species.

The effect of forest management on understory and overstory species composition is not well known. This lack is partly a consequence of the limited research studies but is also a result of the varied nature of “managed” stands. Managed forests range from young stands that originated from railroad logging in the early 1900’s to second- and third-rotation stands on non-Federal lands that have been burned, sprayed with herbicides, planted, fertilized, or thinned. Speculating on how old-growth-associated plant species might be affected by some specific management practices may be useful, however. Management effects can be divided into effects on the initial plant population in an old-growth stand from activities such as clearcutting and site preparation, and effects on recovering plant populations from activities such as stand-density control and short rotations. Initial old-growth populations of many species will suffer at least temporary declines as a consequence of clearcutting and site preparation, especially broadcast burning. The current practice of clearcutting removes all the overstory trees, leaving no habitat for canopy epiphytes such as Lobaria. In landscapes where no large canopy trees occur and no plans are made to grow them, Lobaria and other canopy plant species will probably decline to very low populations. Where site preparation includes broadcast burning, fire-sensitive species such as Pacific yew, Chimaphila, and Linnaea will show strong declines (Halpern 1987) without return to old-growth populations for at least 20 years. If stands are planted to high densities and not thinned, then recovery of understories may be delayed if very dense canopies develop and shade-out the understory. On the other hand, if canopy density is controlled by planting density, precommercial thinning, or both, then forest understories may recover more quickly. If species composition is strongly controlled during this process to favor one species such as Douglas-fir, however, then both canopy and understory diversity will be reduced. The practice of short rotations may reduce populations of understory and overstory species associated with old growth before their populations can recover from the effects of clearcutting and burning. In the long term, the combination of clearcutting, site preparation, and short rotations could greatly reduce populations of some old-growth-associated plant species.

By creating and managing microsites, however, managers have many opportunities to maintain populations of plant species associated with old growth in managed stands and landscapes. Leaving some live canopy trees in cutting units can maintain canopy species that might recolonize the young forest canopy more rapidly than if no refuge trees were present. Leaving large Pacific yew trees in cutting units may provide for this species, but no studies have evaluated how well such trees survive broadcast burning, hotter drier microclimate, and increased herbivory from ungulates. Using cooler, more patchy site-preparation fires, or not using fire on some sites, could help maintain fire-sensitive species. Creating more diverse canopies by planting a mix of conifers, allowing hardwoods to regenerate, thinning dense stands, and cutting canopy openings could help create a more heterogenous understory environment and allow plant species populations to recover more rapidly. Finally, growing some stands on long rotations would help maintain species such as Pacific yew that require long recovery after catastrophic disturbance. Possibilities for maintaining populations of old-growth-associated species in managed stands and landscapes appear to be good, but additional information is needed about the autecologies of many understory species and the effects of management practices on those species to develop more specific management recommendations.

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