

Development of old-growth structure and timber volume growth trends in maturing Douglas-fir stands

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Abstract

Interest in the contributions to biological diversity of old-growth forests has increased in many regions of the world. In the Pacific Northwest of the United States, concern for the contributions has led to proposals to extend the rotation between timber harvests from the conventional 40–80 years to 150 years and longer. However, the implications of such a change for both development of old-growth structure and timber production are unknown. We examined long-term records (up to 82 years) from permanent plots established in 20 stands of *Pseudotsuga menziesii* (Mirb.) Franco in western Oregon and Washington that are approaching these proposed rotation ages. Similarity to old-growth structure was assessed by comparing the observed values of four structural variables to published mean values for young and old-growth forest. The assessment of similarity to old-growth structure was limited to characteristics of the live forest stand, due to the lack of measurements of snags and downed logs at initiation of the permanent plots. Timber production was assessed by examining trends in mean annual increment (MAI) of cubic volume. Development towards old-growth structure was rapid up to about age 80 years, and gradual thereafter. About half of the transition from young to old-growth forest structure occurred by age 100 years. Stands least similar to old-growth in early observations had relatively high tree densities and relatively small trees of uniform size. In later observations, stands most similar to old-growth structure were those with higher densities of large (> 100 cm DBH) *P. menziesii*. In general, MAI declined gradually, averaging about 0.3% per year. Thus, longer rotations may not result in large declines of timber growth while providing for forest structure similar to old-growth. Early control of tree density may serve to hasten development of old-growth structure. Our approach to understanding the development of old-growth forest structure could be applied to long-term plot data from forests in other regions, as long as there is adequate information on old-growth and other forest stages. © 1998 Elsevier Science B.V.

Keywords: Forest; Permanent plots; Pacific Northwest; Mean annual increment; Shade-tolerant species

1. Introduction

There is increasing interest in old-growth forests as important components of biological diversity in many regions of the world (Foster et al., 1996; Spies

and Franklin, 1996). Among the fundamental questions concerning the ecology of forests are how long old-growth structure takes to develop and whether some aspects of this structure develop more quickly than others. By understanding the processes underlying old-growth development in natural forests, it may be possible to devise practices that will hasten such development in managed forests (Vora, 1994; Cole,

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1996; Dunwiddie et al., 1996; Foster et al., 1996; Spies and Franklin, 1996).

Attempts to quantify the rate at which old-growth structure develops must be based on a clear definition of the old-growth state. Many definitions have been proposed and used (reviewed by Spies and Franklin, 1996), and these vary between ecological regions (Burgman, 1996) and with differences in the objectives and values of the people creating the definitions (Spies and Franklin, 1996). No single definition of old-growth structure is likely to encompass the myriad biological (and aesthetic) values associated with old-growth forests (Spies and Franklin, 1988). In addition, any precise definition of the old-growth state requires detailed information on the biological and ecological characteristics of old-growth and other successional stages of forests within a particular region (Spies and Franklin, 1996). While many regions lack such information (e.g., Burgman, 1996; Dunwiddie et al., 1996), scientific studies of old-growth forests are beginning to fill many of the information gaps (Foster et al., 1996; Spies and Franklin, 1996). Some of the earliest attempts to define old-growth were for *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir) forests in the Pacific Northwest of the United States (Burgman, 1996), and hence, the old-growth forests in this region may be the best known in the world (Spies and Franklin, 1996).

Once the old-growth state is defined for a particular region, a variety of approaches may be taken to document development of old-growth structure, including pollen analysis, stand reconstruction, computer modeling, chronosequences, and long-term permanent plots (Foster et al., 1996). Chronosequences have been used to quantify the structural differences between old-growth and other forest successional stages in the *P. menziesii* region of the Pacific Northwest (Spies and Franklin, 1991). The chronosequence method is also referred to as 'space-for-time' (SFT) substitution, because stands of different ages are compared to infer general changes over time (Pickett, 1989). The advantage of SFT is obvious for a phenomenon as potentially slow as development of old-growth forest structure. However, SFT does not shed much light on the processes underlying the general trends. Long-term observation of permanent plots is much better suited to providing such critical

details (Pickett, 1989), for example rates of growth of individual trees or stands, or rates of development of old-growth structural characteristics. Thus, direct observation of development of natural forest stands complements chronosequence and other studies, and provides reference points for evaluating new management methods.

Various practices have been proposed to hasten development of old-growth structure after timber harvest (Cole, 1996; Spies and Franklin, 1996). These include leaving large trees unharvested (either scattered or in groups), thinning dense regenerating stands, and lengthening the rotation between harvests (Vora, 1994; Spies and Franklin, 1996). In *P. menziesii* forests of the Pacific Northwest, for example, new plans for management of federal forests include lengthening the rotation from the conventional 40–80 years to 150 years and longer (Forest Ecosystem Management Assessment Team, 1993). However, without direct, long-term observations of the temporal patterns of development of old-growth structure, it is difficult to predict the effects of these changes in management.

In many cases, forests managed for development of old-growth structure will also be expected to produce timber (Vora, 1994; Cole, 1996). Thus, it is important to consider how management to promote old-growth structure might affect timber yield. In *P. menziesii* forests in the Pacific Northwest, the rate of timber volume accumulation peaks between 70 and 90 years, and then decreases monotonically (Curtis, 1992). However, direct field observations are lacking for stands > 100 years old; therefore, estimates of tree volume growth rates are speculative (Curtis and Marshall, 1993).

The purpose of this paper is to explore trends in development of old-growth characteristics and timber volume growth rates from long-term observations of permanent plots in maturing *P. menziesii* forests in western Oregon and Washington. When observations began, the stands were between 45 and 85 years old, representing young (40 to 80 years) or mature (80 to 195 years) forest (as defined by Spies and Franklin, 1991). The stands have been measured periodically for between four and eight decades; all were mature stands at the most recent observation. Thus, this set of long-term observations of forest dynamics is pertinent to evaluating changes in forest

management now being debated and, in some cases, implemented in the Pacific Northwest. Also, our method of quantifying the development of old-growth forest structure may be generally applicable to other regions.

Rather than focusing on a particular function of old-growth forest (e.g., enhancement of biological diversity, critical habitat for particular species, carbon sequestration), our objective is to document development of old-growth conditions. Our approach to quantifying old-growth conditions is based on a set of descriptors of the structure of the live forest stand (see below). Thus, to draw inferences from this study to particular structural, compositional, or functional aspects of old-growth forest would require critical examination of the relationship between our

general measure of old-growth structure and the particular old-growth attribute of interest.

2. Study areas

All 20 of the stands examined were originally established as permanent plots to provide reliable estimates of timber volume growth of natural, young, well-stocked stands of pure *P. menziesii* (Williamson, 1963). Researchers from the Pacific Northwest Forest and Range Experiment Station established the plots between 1910 and 1940 in what are now the Mt. Hood, Siuslaw, Willamette, Gifford Pinchot, and Olympic National Forests in Oregon and Washington

Table 1
Location, age, and productivity of study stands

Group	National forest, state/stand	Latitude	Longitude	Elevation (m)	Year established	Initial stand age (years)	Site index ^a
<i>Siuslaw, OR</i>							
CH1	CH14	45.04	123.92	135	1935	85	121
CH2	CH41	45.03	123.92	140	1940	67	114
	CH42	45.03	123.92	110	1940	67	119
<i>Gifford Pinchot, WA</i>							
GP1	GP01	46.46	121.86	475	1927	50	125
	GP03	46.46	121.86	465	1927	50	115
	GP05	46.45	121.85	410	1927	53	120
GP2	GP07	46.55	121.98	555	1927	52	118
	GP09	46.55	121.98	580	1927	58	91
<i>Mt. Hood, OR</i>							
MH	MH01	45.31	121.91	605	1930	45	86
	MH02	45.31	121.90	585	1930	45	92
	MH03	45.31	121.90	565	1930	45	96
<i>Olympic, WA</i>							
OL	OL01	47.80	122.92	160	1926	51	92
	OL02	47.79	122.92	150	1926	51	96
<i>Willamette, OR</i>							
WI	WI01	43.82	122.62	400	1910	54	106
	WI02	43.82	122.62	440	1910	54	120
	WI03	43.82	122.62	395	1910	54	111
<i>Gifford Pinchot, WA</i>							
WR1	WR04	45.83	121.87	315	1914	72	116
	WR05	45.84	121.87	365	1914	72	126
WR2	WR02	45.88	121.91	740	1914	72	103
	WR09	45.88	121.90	715	1924	83	90

^a50-year site index for *Pseudotsuga menziesii* by King (1966), in feet.

(Table 1). Plots that are in close proximity and have identical (or very similar) stand ages were placed in the same group for some analyses (Table 1). The plots are all 0.4 ha (1 horizontal acre), with the exceptions of plots WR04 (0.397 ha (0.98 acre)) and WR05 (0.38 ha (0.94 acre)). Trees were tagged at breast height (1.37 m (4.5 feet)); diameters at breast height (DBH) were measured at the tag. Only trees with DBH \geq 6.6 cm (2.6 in.) are included in this analysis. When the permanent plots were established, stand ages were determined by counting rings on increment cores taken from a sample of the trees. At first measurement, total tree basal area ranged from 40.8 to 80.3 m² ha⁻¹; *P. menziesii* accounted for 80% to 100% of basal area (Table 2). *Tsuga heterophylla* (Raf.) Sarg. (western hemlock) was present in half the stands at first observation and accounted for as much as 18% of tree basal area.

Stands were remeasured every five years until the mid-1950s, when interest in the study slackened.

Many of the stands were not measured again for 15 to 20 years. Two of the stands included in this analysis were harvested in the mid-1960s (WR02 and WR09; Sollins, 1982). Since the early 1980s, the remaining 18 stands have been remeasured every five years.

3. Data analysis

3.1. Assessment of old-growth characteristics

To evaluate the degree of old-growth character of each stand at each measurement, we used a multivariate comparison of 196 *P. menziesii* stands of known ages (ranging from 40 to 900 years) from Washington and Oregon (Spies and Franklin, 1991). Although old-growth forests differ from younger forests in a large number of attributes (Franklin et al., 1981), Spies and Franklin (1991) identified four

Table 2
Basal area of stands when study was initiated

Stand	Tree basal area (m ² ha ⁻¹)				
	Total	<i>Pseudotsuga menziesii</i>	<i>Tsuga heterophylla</i>	Other conifers ^a	Hardwoods ^b
CH14	80.3	64.1	14.3	1.1	0.8
CH41	68.2	64.0	1.4	0.1	2.7
CH42	62.4	54.6	5.7	0	2.1
GP01	59.7	59.7	0	0	0
GP03	56.4	56.4	0	0	0
GP05	55.1	53.0	0	0.3	1.8
GP07	51.5	48.8	0.7	0	2.1
GP09	52.1	52.0	0	0	0.1
MH01	40.8	38.7	0	1.3	0.8
MH02	53.1	50.4	0.2	1.0	1.5
MH03	49.4	44.2	0.7	0.9	3.6
OL01	44.9	42.2	1.2	0.5	1.0
OL02	40.9	38.7	1.8	0.1	0.3
WI01	43.8	41.7	0	0	2.0
WI02	49.7	49.3	0	0	0.4
WI03	49.4	48.2	0	0	1.2
WR04	49.5	48.4	0	1.2	0
WR05	56.1	55.9	0.1	0.1	0
WR02	50.8	50.3	0	0.5	0
WR09	53.6	51.7	0.4	1.1	0.4

^a*Abies amabilis*, *A. grandis*, *A. procera* Rehd. (noble fir), *Pinus monticola* Dougl. (western white pine), *Picea sitchensis* (Bong.) Carr. (Sitka spruce), *Thuja plicata*, *Tsuga mertensiana*.

^b*Acer macrophyllum* Pursh (big-leaf maple), *Alnus rubra* Bong. (red alder), *Arbutus menziesii* Pursh (Pacific madrone), *Castanopsis chrysophylla* (Dougl.) DC. (giant chinkapin), *Cornus nuttalli* Aud. (Pacific dogwood), *Populus trichocarpa* T. and G. (black cottonwood), *Prunus emarginata* (Dougl.) Walp. (bittercherry), *Prunus* sp., *Rhamnus purshiana* DC. (cascara).

structural variables that successfully discriminated among age classes of forest:

1. standard deviation (SD) of tree DBH;
2. density of large (> 100 cm DBH) *P. menziesii* trees (trees ha⁻¹);
3. mean tree DBH (cm); and
4. density of all trees > 5 cm DBH (trees ha⁻¹).

Mean values of each variable reported by Spies and Franklin (1991) for young and old-growth forests are listed in Table 3.

Spies and Franklin (1991) selected these four variables from a set of 22 descriptors of live forest structure, all of demonstrated or hypothesized importance for wildlife habitat, ecosystem function, and successional development. Increased variability in tree size (i.e., SD of tree DBH) is associated with increased diversity of microhabitats within forest stands (Spies and Franklin, 1988). Among other ecological roles, large *P. menziesii* trees provide habitat for a large number of species of epiphytes (including nitrogen-fixing lichens), arthropods, birds, and mammals, and are a source of large snags and downed logs (Franklin and Spies, 1991a). Mean tree DBH and density of trees are indicators of successional development that tend to have a reciprocal relationship (Oliver and Larson, 1990), with mean tree DBH increasing and density of trees decreasing over the first few centuries of development of *P. menziesii* stands (Spies and Franklin, 1991). However, it is important to note that in very old *P. menziesii* stands (e.g., 1000-year-old stand in Fig. 6

of Franklin et al., 1981), the density of trees may increase and cause mean tree DBH to decline.

These four structural variables were used as follows to compute an old-growth index (I_{og}) for the stands in this study:

$$I_{og} = 25 \sum_i \left| \frac{x_{i,obs} - x_{i,young}}{x_{i,old} - x_{i,young}} \right| \quad (1)$$

where $i = 1$ to 4, representing each of the four structural variables, $x_{i,obs}$ is the observed value of i th structural variable, $x_{i,young}$ is the mean value of i th structural variable for young stands (Table 3), $x_{i,old}$ is the mean value of i th structural variable for old-growth stands (Table 3).

If observed values of the structural variables are more extreme than the mean values for either young or old-growth forest, the values of I_{og} would be inappropriately large (e.g., observed values more extreme than the mean value for young stands would make a positive contribution to I_{og}). To avoid this possibility, $x_{i,obs}$ was constrained as follows:

$$x_{i,obs} = \begin{cases} x_{i,young}, & \text{if } x_{i,obs} < x_{i,young} \text{ for } i = 1 \text{ to } 3 \text{ and} \\ & \text{if } x_{i,obs} > x_{i,young} \text{ for } i = 4; \\ x_{i,old}, & \text{if } x_{i,obs} > x_{i,old} \text{ for } i = 1 \text{ to } 3 \text{ and} \\ & \text{if } x_{i,obs} < x_{i,old} \text{ for } i = 4 \end{cases}$$

Thus, I_{og} ranges from 0 (for a typical young stand structure) to 100 (for a typical old-growth structure).

I_{og} is a special case of the dissimilarity measure known as the Gower metric (Greig-Smith, 1983). I_{og} measures dissimilarity to young stand conditions and

Table 3
Summary of structural variables and old-growth index (I_{og}) values

Stand	SD of tree DBH ^a	Density of large ^b <i>Pseudotsuga menziesii</i> (trees ha ⁻¹)	Mean tree DBH (cm)	Density of all trees (trees ha ⁻¹)	I_{og}
Young forest ^c	12	0.5	21	935	0
Study stands ^d					
Minimum ^e	13	0	32	678	43
Mean	17	0.6	42	373	54
Maximum ^f	24	3	60	253	67
Old-growth forest ^c	32	19	31	448	100

^aSD = standard deviation; DBH = diameter at breast height.

^bLarge trees, > 100 cm DBH.

^cMean values from Spies and Franklin (1991).

^dFrom observations when stands were closest to age 100 years.

^eMaximum for density of all trees.

^fMinimum for density of all trees.

is constructed such that young and old-growth stands represent opposite ends of a one-dimensional continuum.

To assess net changes over different time intervals, the differences between ending and beginning values of I_{og} were computed for each stand. These values were divided by the interval length to compute average annual change. T -tests were used to test the null hypothesis of no increase in similarity to old-growth structure (measured as I_{og}) over time. To determine which components of old-growth structure included in I_{og} were most strongly related to differences in I_{og} between the stands, we computed correlation coefficients between I_{og} and each of the structural variables as well as among the structural variables. We computed the correlations at two different stand ages: in the 6th and 12th decades (i.e., 51 to 60 and 111 to 120 years old, respectively). Pairwise scatterplots of I_{og} and the structural variables augmented the correlation analysis; we summarized trends in the pairwise relationships with the robust, local smoothing procedure, ‘loess’ (Cleveland, 1979; Chambers et al., 1983).

Shade-tolerant coniferous trees are a significant component of the live structure of old-growth stands (Old-Growth Definition Task Group, 1986; Franklin and Spies, 1991b; J. Franklin, personal communication; T. Spies, personal communication), but are not included in I_{og} . To document the development of this component of old-growth structure, we computed the density of shade-tolerant individuals > 40 cm DBH (Franklin and Spies, 1991b) for each stand at each observation. Franklin and Spies (1991b) found that a density of ten shade-tolerant trees ha^{-1} of this size distinguished old-growth from younger stands. In decreasing order of abundance, shade-tolerant species in the data-set were *T. heterophylla*, *Thuja plicata* Donn. (western red cedar), *Abies grandis* (Dougl.) Forbes (grand fir), *Abies amabilis* (Dougl.) Forbes (Pacific silver fir), and *T. mertensiana* (Bong.) Carr. (mountain hemlock).

3.2. Volume and volume growth rate

To assess changes in productivity of timber volume during stand development, it was necessary to

estimate volume from measured DBHs and, in some cases, heights. Data availability differed; therefore, separate approaches were taken to estimate volume of (1) *P. menziesii* and (2) all other tree species.

P. menziesii was, by far, the most abundant species in the data set (83% of all observations), and it was the only species with numerous height measurements. Given that the relationship between DBH and height of this species (and hence DBH and volume) might vary between the different stands, we evaluated the relationship between DBH and volume separately for each stand.

We were concerned that standard volume equations in the literature for *P. menziesii* might underpredict volume for the older and larger trees in this study (i.e., up to 147 years old and 118 cm DBH). For example, Browne (1962) developed the following equation from whole-tree harvest data for total wood volume of coastal *P. menziesii* up to 140 years old:

$$\begin{aligned} \log_{10}(\text{volume}) = & -4.325605 \\ & + 1.739925 \log_{10}(\text{DBH}) \\ & + 1.133187 \log_{10}(\text{height}) \quad (2) \end{aligned}$$

where volume is in m^3 , DBH is in cm, and height is in m; 99% of Browne’s sample had $DBH \leq 71$ cm. To test the suitability of Eq. (2), we used regression analysis to compare observed volumes from a published data-set with volumes predicted by the equation. The observed volumes were measured with an optical dendrometer over a broad size-range of *P. menziesii* in the Pacific Northwest (data-set AND001 in Michener et al., 1990). We regressed the logarithm of observed volumes on the logarithm of predicted volumes and tested the hypotheses that the slope = 1 and the intercept = 0 (Mayer et al., 1994). The intercept was not significantly different than 0 ($p = 0.54$) and the slope was not significantly different than 1 ($p = 0.20$). Eq. (2) slightly underpredicted the observed dendrometer volumes of very large trees (e.g., predicted volume was 6.8% less than the observed volume of $100 m^3$, which corresponded to $DBH \approx 200$ cm in the observed dendrometer data-set).

To determine whether acceptable stand-level volume-DBH relationships could be developed, we regressed the predicted tree volume on DBH for each stand as follows:

$$\log_{10}(\text{volume}) = \beta_0 + \beta_1 \log_{10}(\text{DBH}) \quad (3)$$

Volume was predicted from Eq. (2) for each tree with a height measurement. For trees with multiple height measurements, only the observation with the largest diameter was used. All regressions were significant ($\alpha = 0.01$); sample sizes ranged from 51 to 144; R^2 values were between 0.97 and 1.00.

To determine whether stand age should be included in volume-estimation models, we fit the following regression model to data for each stand:

$$\log_{10}(\text{volume}) = \beta_0 + \beta_1 \log_{10}(\text{DBH}) + \beta_2 \log_{10}(\text{age}) \quad (4)$$

Although stand age was statistically significant for most stands, we wished to determine if it was bio-

Table 4

Sample sizes and goodness-of-fit statistics for nonlinear regression models to estimate volume (including top and stump) of *Pseudotsuga menziesii*

Stand	<i>n</i>	MSE ^a	R^2
CH14	59	0.2036	0.990
CH41	72	0.1940	0.988
CH42	51	0.2811	0.976
GP01	89	0.1827	0.965
GP03	106	0.0576	0.989
GP05	97	0.1648	0.983
GP07	97	0.0828	0.989
GP09	95	0.0131	0.995
MH01	76	0.0282	0.987
MH02	63	0.0198	0.993
MH03	67	0.0243	0.994
OL01	127	0.0389	0.983
OL02	144	0.0247	0.992
WI01	87	0.2641	0.974
WI02	96	0.1131	0.985
WI03	105	0.1380	0.981
WR02	71	0.0588	0.983
WR04	85	0.0701	0.989
WR05	75	0.1392	0.981
WR09	65	0.0206	0.988

^aMSE, mean square error. The regression model that predicted volume from DBH only (Eq. (5)) was used for all stands except GP09, MH01, and OL02, for which the regression model that predicted volume from DBH and stand age (Eq. (6)) was used.

Table 5

Volume equations from Means et al. (1994) used for tree species other than *Pseudotsuga menziesii*. For conifers, volume equations are derived from the biomass equations and species-specific wood densities in Means et al. (1994)

Species	Eq. no. in Means et al. (1994)
<i>Abies amabilis</i>	249
<i>Abies grandis</i> ^a	378
<i>Abies procera</i>	252
<i>Acer macrophyllum</i> ^b	655
<i>Alnus rubra</i>	423
<i>Arbutus menziesii</i> ^b	674
<i>Castanopsis chrysophylla</i> ^b	664
<i>Cornus nuttalli</i> ^c	423
<i>Picea sitchensis</i>	309
<i>Pinus monticola</i> ^d	390
<i>Populus trichocarpa</i> ^c	423
<i>Prunus emarginata</i> ^c	423
<i>Prunus sp.</i> ^c	423
<i>Rhamnus purshiana</i> ^c	423
<i>Thuja plicata</i>	399
<i>Tsuga heterophylla</i> ^c	312
<i>Tsuga heterophylla</i> ^f	258
<i>Tsuga mertensiana</i>	339

^aNo equation available; equation for *Abies concolor* (Gord. and Glend.) Lindl. (while fir) used.

^bVolume estimated from DBH and height; height estimated from DBH using species-specific equation from Garman et al. (1995).

^cNo equation available; equation for *Alnus rubra* used.

^dNo equation available; equation for *Pinus lambertiana* Dougl. (sugar pine) used.

^eUsed for stands CH14, CH41, CH42.

^fUsed for all other stands.

logically important. To do so, we established the following criterion to assess the precision of regression models: 95% of the volumes predicted by the regression model of interest must be within 10% of the corresponding volume predicted by Eq. (2). Chi-squared tests (Freese, 1960) that were performed to assess the regression model without stand age (Eq. (3)) indicated that the criterion was met in all but three stands. Further chi-squared tests to assess the regression model with stand age (Eq. (4)) for these three stands indicated that two stands met the criterion. The third stand had one unusual tree (a small tree that was relatively short and long-lived for its DBH). When this tree was dropped, the criterion was met. Therefore, we felt that it was reasonable to use Eq. (4). However, this tree was not excluded in computing the final model.

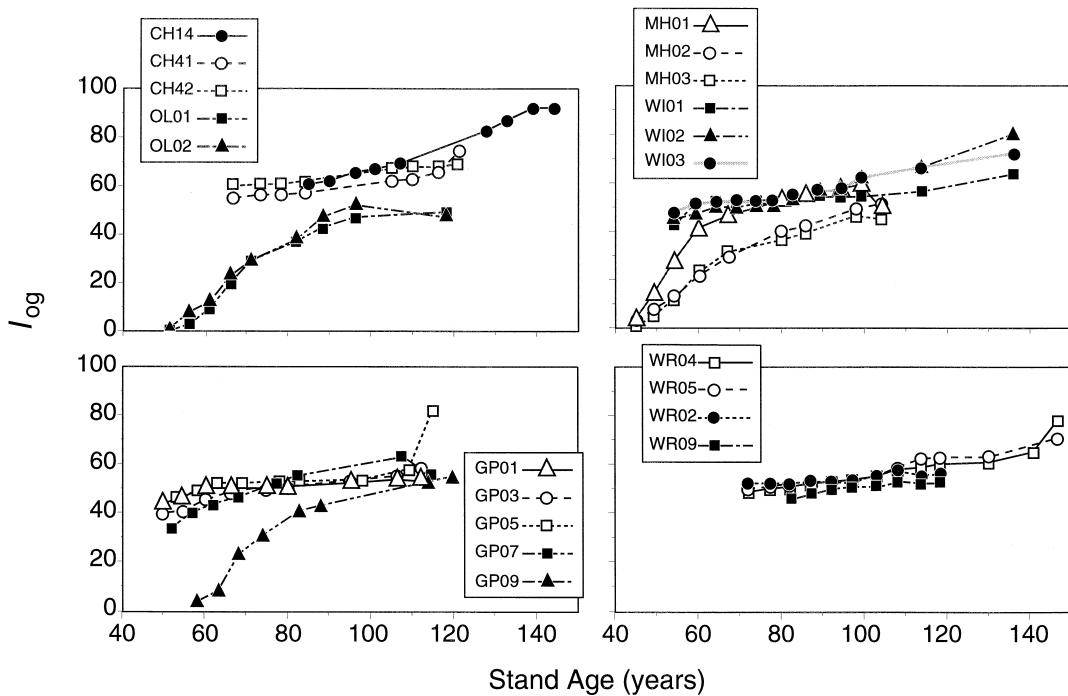


Fig. 1. Trends in old-growth index (I_{og}) versus stand age. Stands in the same panel and with the same symbol type (filled or open) belong to the same group (see Table 1).

Finally, the equations were computed separately for each stand using nonlinear regression of the form:

$$\text{volume} = \beta_0(\text{DBH}^{\beta_1}) \tag{5}$$

and

$$\text{volume} = \beta_0(\text{DBH}^{\beta_1})(\text{age}^{\beta_2}) \tag{6}$$

We chose nonlinear regression over back-transforming Eqs. (3) and (4) because back-transformation will estimate the median, not the mean response that is required for stand-level volume estimation. Sample sizes and goodness-of-fit statistics for the resulting models are listed in Table 4.

For tree species other than *P. menziesii*, we used regional, species-specific equations to estimate volume from DBH (Means et al., 1994). Table 5 lists the equations by species.

In order to compare timber volume growth and to assess the most appropriate interval between harvests, trends of timber volume over time are com-

monly expressed as mean annual increment (MAI) (Husch et al., 1982; Curtis and Marshall, 1993):

$$\text{MAI} = \frac{\text{live volume}}{\text{stand age}} \tag{7}$$

We computed MAI for each observation of each stand. To assess net changes over different time intervals, the annualized percent change in MAI

Table 6
T-tests of temporal trends in I_{og}

Interval (decades)	n	Annual change in I_{og}			p
		Mean	SE	Range	
$I_{og} \gg 0$ at first observation					
7th to 12th	9	0.24	0.15	0.06 to 0.58	0.00075
6th to 9th	7	0.34	0.17	0.2 to 0.7	0.0095
9th to 12th	14	0.28	0.22	0.03 to 0.91	0.00025
$I_{og} \approx 0$ at first observation					
7th to 12th	3	0.73	0.14	0.61 to 0.88	0.0058
6th to 9th	6	1.05	0.21	0.84 to 1.3	0.00001
9th to 12th	3	0.32	0.07	0.25 to 0.39	0.0077

Table 7

Correlations between I_{og} and the structural variables and correlations among the structural variables for stands in the 6th decade ($n = 13$). Values are Pearson's correlation coefficients; p -values are in parentheses

Variable	SD of tree DBH	Mean tree DBH (cm)	Density of all trees (trees ha ⁻¹)
Mean tree DBH (cm)	0.49 (0.0862)		
Density of all trees (trees ha ⁻¹)	-0.73 (0.0048)	-0.88 (0.0001)	
I_{og}	0.70 (0.008)	0.93 (0.0001)	-0.98 (0.0001)

No large (> 100 cm DBH) *Pseudotsuga menziesii* trees were present in any of the stands in the 6th decade.

(C_m) was computed for each stand as follows:

$$C_m = 100 \left[\frac{(MAI_2 - MAI_1) / (MAI_1)}{(age_2 - age_1)} \right] \quad (8)$$

where MAI_1 is the MAI at beginning of interval, MAI_2 is the MAI at end of interval, age_1 is the stand

age at beginning of interval, age_2 is the stand age at end of interval. T -tests were used to test the null hypothesis of no decrease in MAI over time.

We summarized time trends in MAI for each stand using linear regression. To remove the effect of differences in productivity between stands, MAI val-

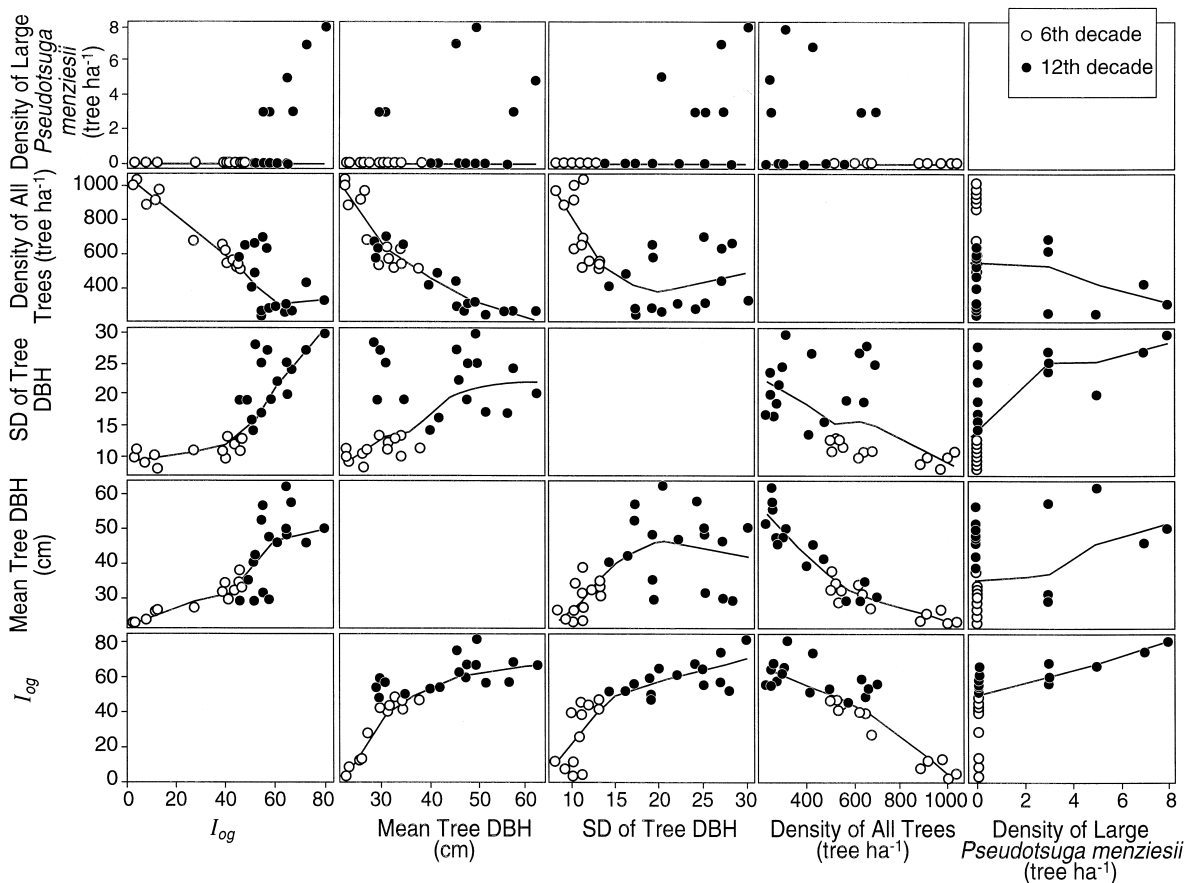


Fig. 2. Pairwise scatterplots of old-growth index (I_{og}) and structural variables in the 6th and 12th decades. Trends were fit to the data with the loess procedure (Cleveland, 1979; Chambers et al., 1983). Open circles are observations in the sixth decade (stand ages 51 to 60 years); filled circles are observations in the 12th decade (stand ages 111 to 120 years).

Table 8

Correlations between I_{og} and the structural variables and correlations among the structural variables for stands in the 12th decade ($n = 17$). Values are Pearson's correlation coefficients; p -values are in parentheses

Variable	SD of tree DBH	Density of large (> 100 cm DBH) <i>Pseudotsuga menziesii</i> (trees ha ⁻¹)	Mean tree DBH (cm)	Density of all trees (trees ha ⁻¹)
Density of large <i>P. menziesii</i> (trees ha ⁻¹)	0.58 (0.0143)			
Mean tree DBH (cm)	-0.16 (0.5479)	0.23 (0.3744)		
Density of all trees (trees ha ⁻¹)	0.20 (0.4306)	-0.06 (0.8262)	-0.92 (0.0001)	
I_{og}	0.63 (0.0066)	0.77 (0.0003)	0.56 (0.019)	-0.51 (0.0372)

ues were converted to percent difference relative to the initial value for each stand prior to regression:

$$D_t = 100 \left(\frac{MAI_t - MAI_1}{MAI_1} \right) \quad (9)$$

where D_t is the percent difference in MAI at time t relative to first observed value of MAI for the stand, MAI_t is the MAI value for stand at time t , MAI_1 is the MAI value for stand at first observation.

We performed a T -test to evaluate the null hypothesis that, on average, the regression slopes were greater than 0. We also performed a one-way analysis of variance (ANOVA) to test the null hypothesis of no difference in slope between the groups of stands. For pairwise comparisons between groups, we used pairwise T -tests when ANOVA detected significant differences (SAS Institute Inc., 1989).

For all statistical tests pertaining to old-growth characteristics and volume growth, the Type I error rate was 0.05.

4. Results

4.1. Development of old-growth characteristics

The overall trend among all the stands was rapid increase in I_{og} (i.e., rapid development of old-growth characteristics) up to about age 60 to 80, followed by a more gradual increase in I_{og} (i.e., slower development of old-growth characteristics) (Fig. 1). At the measurement closest to 100 years of age, observed I_{og} values ranged from 43 to 67 (Table 3). Thus, in terms of I_{og} , the stands completed roughly half the transition to old-growth structure in half the nominal

age of old-growth (i.e., 200 years, Franklin et al., 1981).

The stands exhibited two types of temporal trends over the period of observation. Fourteen of the 20 stands had already undergone considerable development toward old-growth structure by the first observation. During the study period, this set of stands displayed slow and steady (rather than rapid) devel-

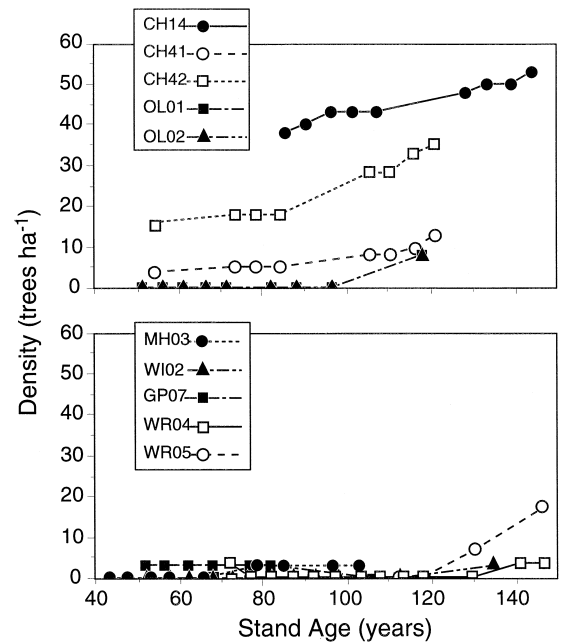


Fig. 3. Trends in density of shade-tolerant coniferous trees > 40 cm DBH versus stand age. Stands in the same panel, with the same symbol type (filled or open) and identified by the same letters belong to the same group (see Table 1). Species include *Tsuga heterophylla*, *Thuja plicata*, and *Abies grandis*. Stands without shade-tolerant species were excluded (stands MH01, MH02, WI01, WI03, GP01, GP03, GP05, GP09, WR02, WR09).

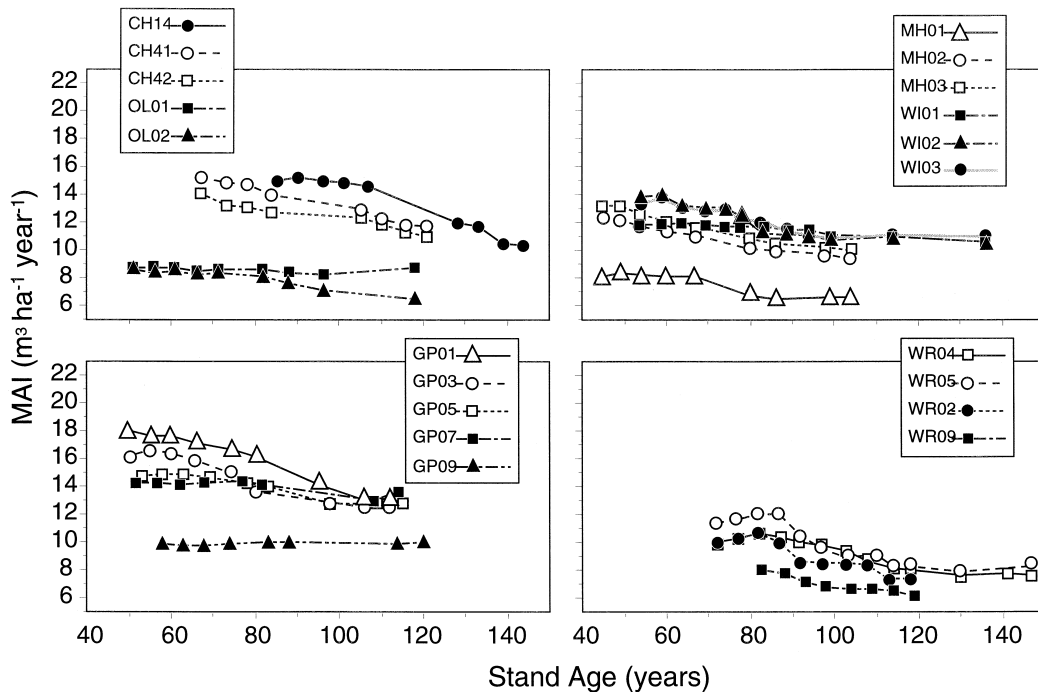


Fig. 4. Trends in mean annual increment (MAI) versus stand age. Stands in the same panel and with the same symbol type (filled or open) belong to the same group (see Table 1).

opment of old-growth characteristics. The other six stands were indistinguishable from typical young stands at the first observation (i.e., $I_{og} \approx 0$). This set of stands did display a period of rapid development of old-growth characteristics. For the most part, these stands continued to lag behind the other set in the degree of similarity to typical old-growth structure. In light of these two temporal trends, we tested changes in old-growth structure separately for the two sets of stands.

I_{og} increased for both sets of stands and for all intervals examined (Table 6). The annual changes in I_{og} were larger for the stands initially lacking old-growth characteristics and for the earlier rather than the later interval. The annual change in I_{og} ranged from 0.24 (stands with old-growth characteristics at first observation, 7th to 12th decade) to 1.05 (stands initially without old-growth characteristics, 6th to 9th decade). In all cases, the increase in I_{og} was significant (Table 6).

The structural variables that were most responsible for differences in I_{og} changed over time. For the

6th decade, I_{og} was significantly correlated with density of all trees, mean tree DBH, and SD of tree DBH (in decreasing order of absolute value of R) (Table 7, Fig. 2). None of the stands contained large *P. menziesii* at that time. The correlation with density of all trees was negative; correlations with the other structural variables were positive. There were also significant negative correlations between density of all trees and mean tree DBH, as well as between density of all trees and SD of tree DBH (Table 7, Fig. 2).

By the 12th decade, I_{og} was significantly correlated with density of large *P. menziesii*, SD of tree DBH, mean tree DBH, and density of all trees (in decreasing order of absolute value of R) (Table 8, Fig. 2). The correlation with density of all trees was negative; correlations with the other structural variables were positive. There were also significant correlations between density of all trees and mean tree DBH (negative) as well as between density of large *P. menziesii* and SD of tree DBH (positive) (Table 8, Fig. 2).

The four structural variables contributing to I_{og} had different patterns of temporal change. At the observation closest to 100 years of age, for example, all the stands had mean tree DBH equal to or greater than the old-growth value, and most of the stands had the same or lower density of all trees as did typical old-growth (Table 3). For most of the stands, however, SD of tree DBH was closer to the mean value for young forests than to the value for old-growth (Table 3). Only five of the stands contained any large *P. menziesii*.

Density of shade-tolerant conifers tended to increase with time, although not consistently across all stands (Fig. 3). Between the 7th and 12th decades, the density of shade-tolerant conifers > 40 cm DBH increased by 3.2 trees ha⁻¹ on average (SE = 1.7; $n = 12$; range -3.0 to 18.0; $p = 0.046$ for T -test of the null hypothesis of no increase in density of shade-tolerants). Ten of the 20 stands had no large shade-tolerant conifers throughout the study period. Two of the stands already had more than 10 large shade-tolerant trees ha⁻¹ at first observation. On only two of the other stands did the density of large shade-tolerants surpass 10 trees ha⁻¹ during the study period.

4.2. Trends in mean annual increment

Overall, there was a gradual decline in MAI over the study period (Fig. 4). The rate of decline was rather consistent for different decade intervals: $C_m \approx 0.3\%$ per year (Table 9). In all cases, the declines in MAI were statistically significant (Table 9).

Based on regression of D_i on stand age for the entire study period for all stands, the average slope was -0.36% per year (SE = 0.042; $n = 20$; range -0.71 to 0.03). In a T -test, the null hypothesis that

Table 9
 T -tests of temporal trends in C_m , annualized percent change in MAI^a

Interval (decades)	n	C_m (% year ⁻¹)			p
		Mean	SE	Range	
7th to 12th	12	-0.27	0.05	-0.48 to 0.02	0.00005
6th to 9th	13	-0.32	0.06	-0.67 to 0.07	0.00015
9th to 12th	17	-0.38	0.07	-0.86 to 0.06	0.00015

^aMAI, mean annual increment.

Table 10

Pairwise comparisons of slopes of percent change per year of mean annual increment for groups of stands defined in Table 1. Values followed by the same letter were not significantly different at $\alpha = 0.05$ (pairwise T -tests)

Group	Mean slope
GP2	-0.04 a
OL	-0.20 ab
WI	-0.26 ab
GP1 ^a	-0.40 bc
CH2 ^a	-0.39 bcd
WR1	-0.42 bcd
MH	-0.42 bcd
CH1	-0.60 cd
WR2	-0.66 d

^aGroups GP1 and CH2 are switched with respect to ordering by mean slope because of the comparison of these two groups with WR2. The larger sample size for GP1 resulted in a smaller standard error of mean slope than for CH2. Thus the difference between GP1 and WR2 is significant while difference between CH2 and WR2 is not.

the average slope was greater than or equal to 0 was rejected ($p = 0.00005$). One-way ANOVA of the slopes based on the groups of stands was significant ($F = 4.46$; $p = 0.0125$; $df = 8,11$; $MSE = 0.015$). There were several significant pairwise comparisons between groups. Most apparent was that group GP2 (stands GP07 and GP09) had a significantly slower rate of decline of MAI than did most other groups of stands (Table 10).

5. Discussion

5.1. Trends in old-growth development

Although all the stands were developing old-growth structure over the entire course of the study, two different patterns were apparent. Most of the stands already had considerable old-growth structure at the first observation and continued to develop slowly and steadily towards old-growth thereafter. A smaller number of stands had very little in common with old-growth at the first observation. These stands had an initial period of rapid change toward old-growth, followed by a period of slower development of old-growth features. Throughout the study, these

stands were less similar to old-growth than was the other subset.

Correlations between I_{og} and the structural variables as well as among the structural variables indicate which components of old-growth structure contribute most to these patterns. In the 6th decade, density of all trees was the component most strongly (negatively) correlated to I_{og} . This variable was also significantly (negatively) correlated with mean tree DBH and SD of tree DBH. The stands least similar to old-growth in the early observations had relatively high tree density and, correspondingly, relatively small and uniform trees. Thus it is possible that limiting tree density in the first several decades of the development of managed stands may speed development of old-growth structure. This approach to hastening development of old-growth structure has been suggested in several recent reviews (Spies et al., 1991; Cole, 1996; Spies and Franklin, 1996).

In the 12th decade, density of large *P. menziesii* was the structural variable most strongly correlated with I_{og} . Also, correlations between density of large *P. menziesii* and SD of tree DBH were significant and positive. This suggests that in mature stands, management activities that promote growth of large individuals and accentuate heterogeneity of tree sizes may be the most important steps for speeding development of old-growth structure.

For all the stands, some aspects of old-growth structure were slower to develop than others. Mean tree DBH and density of all trees approached old-growth values relatively quickly. This had largely occurred by 100 years. SD of tree DBH and density of large *P. menziesii* developed more slowly. Again, this suggests that later in stand development, management that promotes heterogeneity of tree sizes and enhances the growth of vigorous dominant trees could hasten development of old-growth structure. This concept has been demonstrated in a limited number of cases (Newton and Cole, 1987).

Although density of shade-tolerant conifers did not emerge as a discriminator between old-growth and other forest age classes in the analysis of Spies and Franklin (1991), they are a notable aspect of old-growth forest structure (Old-Growth Definition Task Group, 1986; Franklin and Spies, 1991b). On average, the density of shade-tolerant conifers > 40 cm DBH increased between the 7th and 12th decades.

However, half of the stands had no shade-tolerant conifers of this size throughout the study. Thus, if the presence of large shade-tolerant conifers is a management goal, it may be necessary in many cases to plant trees or promote growth of smaller individuals already present.

Old-growth forest differs from earlier stages of succession in a number of structural, compositional, and functional attributes (Franklin and Spies, 1991a). In addition to the components of live stand structure included in I_{og} , other workers have frequently suggested including in definitions of old-growth (1) measures of snags and downed logs; (2) density of trees of shade-tolerant species; and (3) the degree to which forest canopies are multilayered (Franklin et al., 1981; Old-Growth Definition Task Group, 1986; Spies and Franklin, 1988; Franklin and Spies, 1991a,b; Spies and Franklin, 1991; Burgman, 1996). These measures were not included in I_{og} either because measurements were not taken over the entire period of record of the permanent plots (e.g., snags, logs, number of canopy layers), and/or because the variables did not emerge in the analysis of Spies and Franklin (1991) as the best discriminators between forest age-classes (density of shade-tolerants). However, these attributes have considerable functional significance. For example, snags provide habitat for a variety of species, and logs both provide habitat and are a source of energy and nutrients for old-growth ecosystems (Franklin and Spies, 1991a). High values of I_{og} may in many cases be associated with high values of these other characteristics of old-growth structure (e.g., old-growth stands in the dataset of Spies and Franklin (1991). However, future efforts to monitor the development of old-growth structure should include measurements of as many important structure features as possible, rather than assuming that a selected subset of measures (e.g., the live stand variables included in I_{og}) adequately represent other aspects of stand structure (e.g., abundance of snags and logs). A more inclusive approach to quantifying old-growth structure may be especially critical in studies of managed stands. Whereas in the set of naturally regenerated stands studied by Spies and Franklin (1991), young and old-growth forest had similarly high volumes of snags and logs, plantation management in the Pacific Northwest typically has included removal of snags and logs (Spies

and Franklin, 1988). Thus, use of I_{og} to study development of old-growth structure in managed stands would run a great risk of overlooking essential aspects of old-growth structure. In general, whether applying the results of this study, or employing I_{og} in other studies, it must be borne in mind that I_{og} is based on a limited set of measures of live stand structure. Thus, in any particular case, high values of I_{og} may or may not correspond to the presence or absence of other aspects of old-growth structure, composition, or function.

5.2. Changes in volume growth

This study confirms that, on average, timber volume growth rate declines as *P. menziesii* stands exceed common rotation lengths (i.e., 40 to 80 years; Scott, 1980). However, for these stands, the decline was neither precipitous (averaging around 0.3% to 0.4% per year relative to values observed between ages 45 and 85 years) nor universal. For example, two of the 20 stands had no change or an increase in volume growth rate over the entire study period. Although a gradual decline in MAI for maturing stands has been inferred from stand simulation model studies, prior to this study direct observations to confirm or refute those inferences have been mostly lacking (Curtis and Marshall, 1993; Curtis, 1994).

The rate of change in volume growth (measured as change in MAI over time) varied significantly between groups of stands. Within groups, stands occupied very similar environments and experienced similar histories (e.g., density of tree establishment, extreme weather events, pathogens; Williamson, 1963). Thus, differences in volume growth rates between groups of stands could be due to differences in environment, stand history, or both. For example, in simulation studies, MAI peaks later and declines more slowly on less productive sites (Curtis, 1994). Simulation studies also suggest that, under some circumstances, thinning may delay the peak in MAI (Curtis, 1994). Thus, mortality episodes in natural stands may have an effect on the changes in MAI over time. Further investigation of these stands is warranted, as it may suggest details of stand management that could enhance timber yields under longer rotations or indicate the types of sites that are more or less suited to long rotations.

The stands included in this study regenerated naturally and for the most part have not been directly managed, whereas the vast majority of younger *P. menziesii* stands in the Pacific Northwest now are managed. However, with increasing emphasis on forest management for ecological objectives, managed stands may come to resemble natural stands more closely (Swanson and Franklin, 1992). For natural stands such as those in this study, it appears that the decline in timber volume growth rate over longer rotations is small and that, with interventions such as density control and underplanting, a reasonable facsimile to old-growth structure may be achievable within the longer intervals between harvest now under discussion (e.g., 150 to 180 years; Forest Ecosystem Management Assessment Team, 1993). Determining the degree to which these conclusions apply to managed stands depends on continuing experiments such as those described by Curtis and Marshall (1993).

5.3. Application to old-growth research in other regions

This study demonstrates again that direct, long-term observation of forest succession complements chronosequences and other methods (Pickett, 1989). Although characteristics of old-growth forests may be better understood in the Pacific Northwest of the United States than in many other regions (Burgman, 1996; Spies and Franklin, 1996), our approach may prove valuable for quantifying old-growth development elsewhere. Our approach requires (1) long-term records from forest plots, and (2) quantitative definitions of old-growth and other stages of forest development appropriate to the region.

Far from being limited to the Pacific Northwest, long-term plots are used to study forests throughout the world, and interest in them is growing, especially in relation to biological diversity (MacBryde, 1995). Quantitative information to distinguish old-growth from other forest stages may be a more serious limitation outside of the Pacific Northwest (Spies and Franklin, 1996). However, research to address this need is underway in many regions (e.g., Burgman, 1996; Foster et al., 1996; McCarthy and Bailey, 1996; Timoney and Robinson, 1996; Woodgate et al., 1996). Thus it is likely that our

approach of documenting old-growth development with long-term observations, and identifying which facets of old-growth structure develop most quickly, could be useful outside of the Pacific Northwest.

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