

Long-term patterns of diameter and basal area growth of old-growth Douglas-fir trees in western Oregon

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Abstract: Diameter growth and age data collected from stumps of 505 recently cut old-growth Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) trees at 28 sample locations in western Oregon (U.S.A.) indicated that rapid early and sustained growth of old Douglas-fir trees were extremely important in terms of attaining large diameters at ages 100–300 years. The diameters of the trees at ages 100–300 years (D100–D300) were strongly, positively, and linearly related to their diameters and basal area growth rates at age 50 years. Average periodic basal area increments (PAI_{BA}) of all trees increased for the first 30–40 years and then plateaued, remaining relatively high and constant from age 50 to 300 years. Average PAI_{BA} of the largest trees at ages 100–300 years were significantly greater by age 20 years than were those of smaller trees at ages 100–300 years. The site factors province, site class, slope, aspect, elevation, and establishment year accounted for little of the variation observed in basal area growth at age 50 years and D100–D300. The mean age range for old-growth Douglas-fir at the sample locations was wide (174 years). The hypothesis that large-diameter old-growth Douglas-fir developed at low stand densities was supported by these observations.

Résumé : Des données d'âge et de croissance en diamètre collectées sur les souches de 505 vieux douglas de Menzies (*Pseudotsuga menziesii* (Mirb.) Franco) récemment abattus à 28 endroits dans l'Ouest de l'Oregon, aux États-Unis, montrent qu'une croissance juvénile rapide et soutenue est extrêmement importante pour atteindre de forts diamètres à 100–300 ans. Le diamètre des arbres à 100–300 ans (D100–D300) est fortement, positivement et directement relié au taux de croissance en diamètre et en surface terrière à 50 ans. L'accroissement périodique moyen en surface terrière (APM_{ST}) de tous les arbres a augmenté pendant les premiers 30–40 ans et a plafonné par la suite, demeurant relativement élevé et constant de l'âge de 50 à 300 ans. La valeur moyenne de APM_{ST} des plus gros arbres de 100–300 ans était significativement plus élevée à 20 ans que celle des plus petits arbres de 100–300 ans. Les facteurs de station de la province, la classe de station, la pente, l'exposition, l'altitude et l'année d'établissement contribuent peu à la variation observée dans la croissance en surface terrière à 50 ans et à D100–D300. L'écart entre l'âge moyen (174 ans) des vieux douglas dans les endroits échantillonnés est important. L'hypothèse voulant que les vieux douglas de fort diamètre se soient développés dans des peuplements de faible densité est supportée par ces observations.

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Introduction

Large-diameter overstory trees (e.g., Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) larger than 100 cm in diameter) are a structural element common to virtually all definitions of conifer-dominated old-growth forests in the Pacific Northwest region of North America (Franklin et al. 1981; Oliver 1981; Franklin and Spies 1991a, 1991b; Marcot et al. 1991; Oliver and Larson 1996). A great deal of

work in the Pacific Northwest has focused on describing current old-growth structure in terms of live and dead tree density (i.e., trees/ha) in relation to tree size, amount of dead wood on the forest floor, species, and age distribution (Juday 1977; Franklin and Waring 1980; Means 1982; Spies and Franklin 1991; Hershey 1995; Poage 1995; Bailey 1996; Goslin 1997; Bailey and Tappeiner 1998; Schrader 1998; Winter 2000). However, very little research has been done on how the individual components (e.g., large-diameter overstory trees) of old-growth forests actually developed over time (Tappeiner et al. 1997; Winter 2000; Poage 2001). Understanding how old-growth trees, particularly the large-diameter trees, grew is important for both the ecologist interested in forest development and the manager interested in accelerating the development of late-successional characteristics within young stands.

The first study to quantify the growth and development of individual old-growth Douglas-fir trees in western Oregon was published by Tappeiner et al. (1997). These authors found that the early diameter growth of many large old-growth Douglas-fir in the central Oregon Coast Range was rapid well beyond age 50 years and exceeded that in even-aged young-growth stands after about 40–60 years of age.

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The early diameter growth rates reported for the old stands were comparable to those from long-term growth studies of low-density young stands (100–120 trees/ha), leading these authors to suggest that initial stand densities in old-growth Douglas-fir forests in the central Oregon Coast Range were only one-fourth to one-fifth of those typically found in young-growth stands at present (where stand densities by age 20–50 years are typically over 500 trees/ha). The wide range of ages of old-growth Douglas-fir (95% confidence interval for mean = 77–223 years) observed in the stands investigated was interpreted as further evidence of low old-growth stand densities. Tappeiner et al. (1997) further suggested that unless stand densities were reduced (e.g., by thinning), trees growing in the higher-density, young-growth stands would require longer periods of time to develop the large diameters characteristic of old-growth forests than the old-growth trees did.

Several authors previously have speculated that large-diameter old-growth Douglas-fir trees developed at low densities (Franklin et al. 1981; Oliver and Larson 1996). The inverse relationship between stand density and the diameter, basal area, and volume growth and live crown ratios of individual trees in a stand is well documented (Assmann 1970; Drew and Flewelling 1979; Curtis and Marshall 1986; Oliver et al. 1986a, 1986b; Oliver and Larson 1996; Wilson 1998; Wilson and Oliver 2000). Less is known about the relationship between the early growth and size of a tree and its size and growth in the future. The results of the study by Tappeiner et al. (1997) suggest that the diameters of old-growth Douglas-fir at age 100 years were positively related to growth prior to age 50 years and that large-diameter old-growth Douglas-fir achieved the large diameters they did because low initial stand densities (i.e., 100–120 trees/ha) enabled them to grow rapidly when young. However, the relationship between diameter at age 100 years and the early growth of old-growth Douglas-fir trees was not quantified, growth beyond age 100 years was not measured, and all study sites were located in the central Oregon Coast Range.

The present study examines the growth (to age 100–300 years) of old-growth Douglas-fir in the Oregon Coast Range, Willamette Valley, and western Oregon Cascades. The first part investigates the relationships between size and growth at different ages and does so by focusing on the following questions: (i) how important were the early size and growth of old Douglas-fir in terms of attaining the diameters typical of large-diameter old-growth trees at ages 100–300 years, and (ii) did old-growth Douglas-fir that attained large diameters by some given reference age (e.g., DBH > 100 cm by age 200 years) exhibit long-term growth patterns that were different than those of trees that were smaller at that same reference age? The second section addresses the hypothesis that large-diameter old-growth Douglas-fir developed at low stand densities, which enabled them to grow rapidly when young and to sustain that growth for long periods (as opposed to growing on more productive sites or during more climatically favorable periods).

Study sites and fieldwork

This study was conducted at 28 recently cut old-growth forests in the Coast Range, Willamette Valley, and Cascades physiographic provinces of western Oregon (Pater et al.

1998). All sample locations fell within the area bounded by 43°20′–44°50′N and 121°50′–124°00′W. Douglas-fir accounted for over 75% of the total basal area at each sample location, on average, with varying amounts of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western redcedar (*Thuja plicata* Donn), incense-cedar (*Calocedrus decurrens* (Torr.) Florin.), grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.), red alder (*Alnus rubra* Bong.), and bigleaf maple (*Acer macrophyllum* Pursh) accounting for the majority of the remaining basal area (Poage 2001). Douglas-fir site classes did not vary greatly among the sample locations and generally reflected moderate levels of productivity: 2 of the 28 sample locations were site class 2, 24 were site class 3, and 2 were site class 4 (site class 1, highest productivity; site class 5, lowest productivity; Isaac 1949).

At each sample location, three to four circular 0.1-ha plots were systematically established at 50-m intervals along a randomly oriented transect. In each plot, diameter growth and age data, inside-bark diameter, bark thickness, stump height, slope, elevation, and aspect were collected from the stumps of all measurable old-growth Douglas-fir trees (age > 150 years). A total of 99 fixed-radius plots were sampled at the 28 sample locations (Table 1). Because we had a particular interest in the growth of the largest trees at each site, data from “big trees” also were collected opportunistically from stumps encountered outside the randomly located plots. The decision to sample the stump of a big tree was always made prior to observing tree growth or age. Data were collected over an elevation range of 210–1070 m (median = 495 m), slopes of 0–52° (median = 22°), and across all aspects.

When possible, radial-growth measurements were made on the uphill side of each stump. Radial increment was recorded by decade for the first 100 years; measurements were made in 2.5-decade increments for ages >100 years. Growth spanning 100, 150, 200, 250, and 300 years was measured on 505, 322, 281, 244, and 177 trees, respectively. Diameters as well as diameter and basal area growth at different ages were calculated from the radial-growth measurements. The age at time of cutting and establishment date of each tree were determined. All measurements were made on well-prepared stump surfaces in the field. Well-prepared surfaces were obtained in the field using a portable, rechargeable Dremel carving tool fitted with a router bit (Model 750, Dremel Co., Racine, Wis.). An estimated 30–60 min were required to prepare and measure each stump.

Although samples were not cross-dated (Stokes and Smiley 1968; Fritts 1976; Swetnam et al. 1985), we felt that errors arising as a result of not cross-dating the well-prepared samples would be more than offset by the increased speed and, consequently, geographic extent of sampling possible without cross-dating. Support for this approach comes from Weisberg and Swanson (2001), who reported that the estimates of year of tree origin differed by an average of only 1.5 years between cross-dated samples and otherwise well-prepared samples without cross-dating. Furthermore, cross-dating required over 20 times as much time as field counting (Weisberg and Swanson 2001).

Data analysis

The first set of analyses investigated the relationships between size and growth of old-growth Douglas-fir at different

Table 1. Number of sample locations, plots, and old-growth Douglas-fir trees sampled by physiographic province within the study area.

	Province			Total
	Coast Range	Willamette Valley	Oregon Cascades	
Sample locations	9	5	14	28
Plots	59	8	32	99
Plot trees ≥ 150 years	160	26	122	308
All trees ≥ 150 years	238	67	200	505
All trees ≥ 200 years	62	48	171	281
All trees ≥ 300 years	39	18	120	177

Note: "Plot trees" are the trees located within the randomly located, 0.10-ha fixed-radius plots. "All trees" includes both the plot trees and the big trees encountered outside the fixed-radius plots.

ages by focusing on (i) the relationships between diameter and basal area growth at age 50 years and diameters at ages 100–300 years, and (ii) the patterns of basal area increment growth over time. The second set of analyses addressed the hypothesis that large-diameter old-growth Douglas-fir developed at low stand densities (as opposed to growing on more productive sites or during more climatically favorable periods) by (i) comparing the relative effects of site factors and basal area growth at age 50 years on diameters at ages 100–300 years, and (ii) examining the age ranges of old-growth Douglas-fir within sample locations and plots. Support for the hypothesis would be strengthened by observations of (i) rapid early and sustained growth of large-diameter old-growth Douglas-fir, (ii) weak relationships between growth and site factors, and (iii) wide age ranges of old-growth Douglas-fir at different sample locations.

The diameters (cm) inside the bark at ages 50, 100, 150, 200, 250, and 300 years were designated by D50, D100, D150, D200, D250, and D300, respectively. Unless otherwise noted, tree growth was expressed in terms of periodic annual basal area increment (PAI_{BA} , $cm^2/year$) rather than diameter increment. Basal area increment is a more accurate measure of total tree growth (i.e., biomass accumulation) than is diameter increment. Even if basal area increment remains constant over time, diameter increment will decrease as tree diameter increases; thus when diameter increment alone is considered, it can lead to the erroneous conclusion that tree growth is slowing (Smith et al. 1997). The square-root transformation of PAI_{BA} , designated by BAI, was used in regression analyses involving basal area growth (the square-root transformation is often used to stabilize variances when the variance is proportional to the mean). For example, BAI50 refers to the square-root transformation of PAI_{BA} at age 40–50 years.

The question of whether to include the big trees in subsequent analyses was addressed by applying the strategy for dealing with potential outliers outlined by Ramsey and Schafer (1997). Preliminary comparison of linear regressions of D100–D300 on D50 and BAI50 indicated that coefficients and statistical conclusions of the resulting regression equations did not differ significantly between analyses of data sets with and without the big trees included. (For example, linear regression of D100 on D50 without the big trees resulted in 95% confidence intervals for the slope and inter-

cept coefficients of 1.20–1.32 and 7.67–12.10, respectively. With the big trees included, the 95% confidence intervals for the slope and intercept coefficients were 1.26–1.36 and 7.51–11.76, respectively.) Based on these preliminary results, we decided to include data from the big trees in all subsequent analyses.

Size and growth at different ages

Diameter and periodic annual basal area increment at age 50 years and diameters at ages 100–300 years

The nature and strength of the relationships between D50 and BAI50 and the diameters at ages 100, 150, 200, 250, and 300 years (D100–D300) were assessed by using simple and multiple linear regression. Separate simple linear regressions of D100–D300 on D50 as well as of D100–D300 on BAI50 were performed. Preliminary analyses also indicated that D50 and BAI50 were strongly, positively, and linearly correlated (Pearson's correlation coefficient, r , of 0.92). The relative strengths of D50 and BAI50 in explaining the variation observed in D100–D300 were assessed by including both D50 and BAI50 as explanatory variables in multiple linear regressions of D100–D300 on D50 and BAI50.

Patterns of basal area increment growth over time

The 99% confidence intervals (CI) for the average PAI_{BA} for all trees were plotted for the periods 0–100, 0–200, and 0–300 years to describe basal area growth patterns over time. The next approach was similar to the previous one except that the trees were divided in two groups based on their diameters at the end of the period in question, and separate plots of average PAI_{BA} were examined for the larger- and smaller-diameter groups. For each period in question, the larger-diameter group contained the largest 23–30% of the trees, based on the diameter at the end of the period (i.e., D100 for 0–100 years, D200 for 0–200 years, D300 for 0–300 years); the smaller-diameter groups contained the remaining 70–77% of the trees. For the 0–100 years plots, large-diameter trees had D100 >70 cm and smaller-diameter trees had D100 <70 cm; for the 0–200 years plots, large-diameter trees had D200 >100 cm and smaller-diameter trees had D200 <100 cm; for the 0–300 years plots, large-diameter trees had D300 >120 cm and smaller-diameter trees had D300 <120 cm.

The third approach to describing basal area increment growth patterns differed from the first two in that individual trees were examined separately and only the portion of growth from age 50 years on was analyzed. An individual linear regression of PAI_{BA} on age from age 50 to 100 years was done for each tree >150 years old (505 regression equations in total, i.e., one for each of 505 trees), and the regression slopes and coefficients of variation (CV) were examined. The rationale for this approach was the assumption that the closer the slope and CV were to zero, the more constant the PAI_{BA} from 50 to 100 years. Individual linear regressions of PAI_{BA} on age from age 50 to 200 years and from age 50 to 300 years also were done for each tree >200 years old ($n = 281$) and for each tree >300 years old ($n = 177$).

Evidence for low stand densities

Relative effects of site factors and periodic annual basal area increment at age 50 years on diameters at ages 100–300 years

Multiple linear regressions were used to assess the relative effects of site factors and BAI50 on D100–D300. Multiple linear regressions of (i) BAI50 on site factors, and (ii) D100–D300 on BAI50 and site factors were performed. Separate multiple linear regressions of D100–D300 on BAI50 and site factors were performed. BAI50 and site factors were included together in the regression models. The results from the multiple linear regressions of D100–D300 on BAI50 and site factors were compared with the results of the simple linear regressions of D100–D300 on BAI50 (above).

The following site factors were included in the multiple linear regression models: province (i.e., physiographic province), site class, slope, aspect, elevation, and establishment year. Province (Coast Range, Willamette Valley, and Oregon Cascades) was included to account for broad-scale differences among sample locations in terms of climate, geology, and soils. Site class reflected differences in productivity. Prior to analysis, slope and aspect were combined into “heat”, the estimated annual direct solar radiation at 45°N (Buffo et al. 1972) multiplied by the heat load index. In the northern hemisphere, heat load index equals $(1.5 - 0.5 \cos(\text{aspect}_{\text{deg}} - 45))$ and ranges from 1 on cooler northeast-facing slopes to 2 on hotter southwest-facing slopes (modified from Beers et al. 1966). Establishment year was included to account for changes in climate that may have occurred during the past 150–700 years (i.e., the range in ages of old-growth Douglas-fir sampled).

Age ranges of old-growth Douglas-fir at sample locations and within plots

The age ranges of old-growth Douglas-fir trees at each sample location and within its more fine-scale 0.10-ha sample plots were determined from the age data collected from the cut stumps.

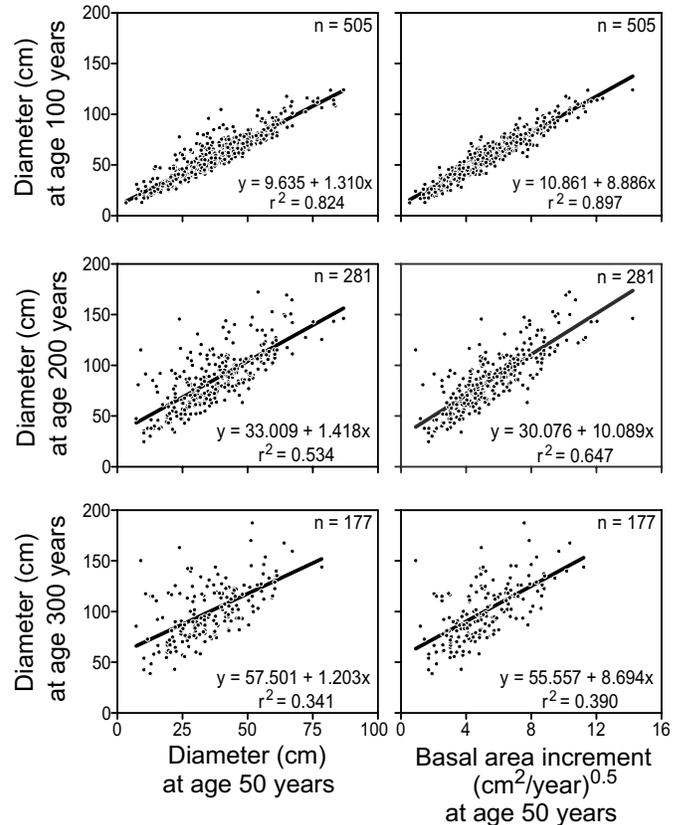
Results

Size and growth at different ages

Diameter and periodic annual basal area increment at age 50 years and diameters at ages 100–300 years

The diameters of the old-growth trees at ages 100, 150, 200, 250, and 300 years (D100–D300) were strongly, positively, and linearly related to their diameters and basal area growth rates as young, 50-year-old trees (D50 and BAI50, respectively; Fig. 1 and Tables 2 and 3). Large-diameter old-growth trees at ages 100, 150, 200, 250, and 300 years were generally large in diameter and (or) fast growing at age 50 years, with D50 and BAI50 being highly correlated ($r = 0.92$). Trees that were small at ages 100–300 years tended to be small and slow growing at age 50 years. For example, 86 of the 281 trees for which the diameters at ages 50 and 200 years were measured attained diameters of 100 cm or more by age 200 years. Over 50% of these large-diameter trees at age 200 years had diameters at age 50 years of over 50 cm. In contrast, small-diameter old-growth trees were generally small and slow growing when young; 95% of the

Fig. 1. Relationships between diameter or periodic annual basal area increment at age 50 years and diameters at ages 100, 200, and 300 years. Data are shown for all old-growth Douglas-fir (>150 years) sampled in western Oregon. Periodic annual basal area increment at age 50 years was square-root transformed prior to analysis.



old-growth trees with diameters smaller than 100 cm at age 200 years were smaller than 50 cm at age 50 years. Although a few trees that were large at ages 100–300 years were relatively small and (or) slow growing at age 50 years, 95% prediction intervals for the regression lines plotted in Fig. 1 indicated that less than 5% of the trees had D100–D300 above the upper limit of the 95% prediction interval.

The amount of variation (r^2) in D100–D300 explained by D50 and BAI50 was substantial, ranging from 82–90% at age 100 years to 34–39% at age 300 years (Fig. 1 and Tables 2 and 3). Over 50% of the variation observed in D250 was explained by BAI50, the basal area growth 200 years earlier (Table 3). Although BAI50 and D50 were highly correlated, the diameters at ages 100–300 years of the old-growth Douglas-fir investigated in this study were more strongly influenced by how well the trees were growing at age 50 years than by their diameter at age 50 years. For example, a 70-cm-diameter tree at age 50 years with average annual diameter growth of 0.60 cm/year during the previous decade (i.e., $\text{BAI50} = (64 \text{ cm}^2/\text{year})^{0.5}$) would be expected to have a D200 of 104 cm (Table 4). In contrast, a larger D200 of 137 cm would be expected for a smaller, 50-cm-diameter tree at age 50 years with a higher average annual diameter growth of 1.54 cm/year during the previous decade, i.e., $\text{BAI50} = (100 \text{ cm}^2/\text{year})^{0.5}$.

Table 2. Simple linear regression models of cumulative diameter at 100, 150, 200, 250, and 300 years (D100–D300, cm) on cumulative diameter at 50 years (D50, cm) for old-growth Douglas-fir 150 years and older sampled in the entire study area.

Dependent variable	Model					
	Intercept	D50	MSE	r^2	F	n
D100	9.6 (1.1)	1.3 (0.0)	74	0.82	2350*	505
D150	25.0 (2.5)	1.4 (0.1)	283	0.61	492*	322
D200	33.0 (3.2)	1.4 (0.1)	371	0.53	320*	281
D250	43.3 (3.9)	1.4 (0.1)	468	0.45	196*	244
D300	57.5 (4.7)	1.2 (0.1)	518	0.34	91*	177

Note: Values in parentheses are SEs.

*Significant at $p < 0.0001$.

Table 3. Simple linear regression models of cumulative diameter at 100, 150, 200, 250, and 300 years (D100–D300, cm) on square-root transformed basal area increment at 50 years (BAI50, $(\text{cm}^2/\text{year})^{0.5}$) for old-growth Douglas-fir 150 years and older sampled in the entire study area.

Dependent variable	Model					
	Intercept	BAI50	MSE	r^2	F	n
D100	10.9 (0.8)	8.9 (0.1)	43	0.90	4369*	505
D150	20.4 (2.0)	9.9 (0.3)	187	0.74	907*	322
D200	30.1 (2.7)	10.1 (0.5)	281	0.65	512*	281
D250	40.9 (3.4)	9.9 (0.6)	393	0.54	279*	244
D300	55.6 (4.5)	8.7 (0.8)	480	0.39	112*	177

Note: Values in parentheses are SEs.

*Significant at $p < 0.0001$.

In the simple linear regressions of D100–D300 on BAI50, the mean square errors (MSE) were consistently lower and the coefficients of determination (r^2 values) were consistently higher than those in the simple linear regressions of D100–D300 on D50 (Tables 2 and 3). The multiple regression equations of D100–D300 on both D50 and BAI50 (Table 4) indicate that after accounting for BAI50, D50 contributed relatively little as an explanatory variable, and its significance decreased with time (Table 4). The F statistics for BAI50 were 10–80 times larger than the F statistics for D50, indicating that BAI50 was a stronger explanatory variable than D50 (Table 4).

Independent confirmation of the strong, positive, and linear relationships observed between D100–D300 and D50 and BAI50 was found after analyzing radial-growth data collected independently by Tappeiner et al. (1997) from the stumps of 119 recently cut old-growth Douglas-fir (age > 150 years) in the Oregon Coast Range. Simple linear regressions using the data of Tappeiner et al. (1997) indicated that 86 and 91% of the variation (r^2) observed in D100 was explained by D50 and BAI50, respectively. These r^2 values were very similar to those reported in the present study for the simple linear regressions of D100 on D50 and BAI50 (Fig. 1 and Tables 2 and 3).

Patterns of basal area increment growth over time

Plotting the average PAI_{BA} of trees >150 years old for the first 100 years indicated that the average PAI_{BA} increased for

the first 30–40 years and then plateaued, remaining relatively high and constant from age 50 to 100 years (Fig. 2a). (The corresponding radial increments were also plotted in Fig. 2a, as well as in Figs. 2b and 2c, to illustrate that a decrease in radial growth does not necessarily correspond to a decrease in basal area growth.) Similar growth patterns were observed for trees >200 and >300 years old, with 150–250 years of relatively constant growth following an initial 30- to 40-year period during which growth accelerated (Figs. 2b and 2c, respectively). Approximate statistical tests between the average basal area growth at two or more ages in Figs. 2a–2c were made by determining whether the 99% CI of the average PAI_{BA} in question overlap. Such comparisons indicated that there was no difference between the average PAI_{BA} for ages 50–100, 50–200, and 50–300 years ($p < 0.01$).

Average PAI_{BA} remained constant after age 50 years for the groups of larger and smaller trees. Plotting the average PAI_{BA} of the larger (D100 > 70 cm) and smaller (D100 < 70 cm) trees at age 100 years revealed several interesting points (Fig. 3a). First, the average PAI_{BA} of the larger trees were significantly greater by age 20 years than those of smaller trees. Second, the smaller trees' average PAI_{BA} peaked at age 30 years while the average PAI_{BA} of the larger trees continued to increase for two more decades. Third, both groups of trees exhibited a pattern of an early acceleration of basal area growth followed by a period of relatively high and constant growth. Similar basal area growth patterns occurred for larger and smaller trees at age 200 years (D200 > 100 cm and D200 < 100 cm, respectively) and for larger and smaller trees at age 300 years (D300 > 120 cm and D300 < 120 cm, respectively) (Figs. 3b and 3c).

The analyses of the individual tree basal area growth patterns done separately for each tree further indicated that the PAI_{BA} of trees generally remained constant after age 50 years. The regression lines for PAI_{BA} on age from 50 to 100 years were relatively flat for trees >150 years old, with 50% of the trees having slopes from -0.13 to 0.27 and CVs from 0.15 to 0.29 ; 80% had slopes from -0.33 to 0.54 and CVs from 0.10 to 0.40 . The regression lines for PAI_{BA} on age from 50 to 200 years and on age from 50 to 300 years were similarly flat: 80% of the trees >200 years old had slopes from -0.25 to 0.23 and CVs from 0.17 to 0.49 ; 80% of the trees >300 years old had slopes from -0.13 to 0.16 and CVs from 0.19 to 0.64 .

Evidence for low stand densities

Relative effects of periodic annual basal area increment at age 50 years and site factors on diameters at ages 100–300 years

The relationship between basal area growth at age 50 years (BAI50) and province, site class, slope, aspect, elevation, and establishment year was weak (Table 5). Less than 8% of the variation observed in BAI50 was accounted for by these site factors. (Slope and aspect were combined prior to analysis and modeled as heat.) The site factors did not contribute substantially to the simple linear regressions of D100–D300 on BAI50 (Tables 3 and 6). With the site factors as additional explanatory variables in the linear regression of D100 on BAI50, MSE decreased by only 10% (from 43 to 39), and the r^2 values increased only slightly from 0.90

Table 4. Multiple linear regression models of cumulative diameter at 100, 150, 200, 250, and 300 years (D100–D300, cm) on cumulative diameter at 50 years (D50, cm) and square-root transformed basal area increment at 50 years (BAI50, (cm²/year)^{0.5}) for old-growth Douglas-fir 150 years and older sampled in the entire study area.

Dependent variable				F		Model			
	Intercept	D50	BAI50	D50	BAI50	MSE	r ²	F	n
D100	9.1 (0.8)	0.3 (0.1)	6.9 (0.3)	42****	427****	40	0.91	2385****	505
D150	21.5 (2.0)	-0.4 (0.1)	12.3 (0.9)	7**	175****	183	0.75	466****	322
D200	31.6 (2.8)	-0.4 (0.2)	12.5 (1.3)	4*	94****	278	0.65	261****	281
D250	42.1 (3.6)	-0.3 (0.3)	12.0 (1.7)	2	48****	392	0.54	141****	244
D300	56.0 (4.6)	-0.2 (0.4)	9.7 (2.6)	0	14***	482	0.39	56****	177

Note: Values in parentheses are SEs. *, $p \leq 0.05$; **, $p < 0.01$; ***, $p < 0.001$; ****, $p < 0.0001$.

to 0.91 (Tables 3 and 6). The maximum decrease in MSE observed, 25%, occurred at age 300 years. In all of the multiple linear regression models of D100–D300 on both BAI50 and the site factors, the F statistics for BAI50 were 2–3 orders of magnitude larger than the F statistics for any of the site factors, indicating that basal area growth at age 50 years was a much stronger explanatory variable than were province, site index, slope, aspect, elevation, and establishment year (Table 7).

After accounting for BAI50 and the other site factors, trees in the Coast Range and Oregon Cascades had slightly smaller D100–D300, on average, than trees in the Willamette Valley (Table 6). For example, the mean D100 of trees in the Oregon Cascades was 3.0 cm smaller than that of trees in the Willamette Valley. Slight decreases in mean D100–D300 occurred with increasing heat and elevation. If growth were consistently high where heat was low (i.e., on moister, northeast-facing slopes in Oregon), then a polar diagram of tree slope and aspect with symbols scaled by D100 would resemble the inverse of the plot in Fig. 4a (the polar diagram of tree slope and aspect with symbols scaled by heat). Scaling the symbols in Fig. 4a by D100 indicated that the relationship between heat and D100 was weak at best; large-diameter and small-diameter trees occurred on all slopes and aspects (Fig. 4b). The scatterplot of D100 by elevation illustrates the similarly weak relationship between growth and elevation (Fig. 5a). With the single exception of D250 and establishment year, D100–D300 did not vary significantly by site class or by establishment year (Table 6). (The nine trees shown in Fig. 5b establishing around the year 1300 were all from the same sample location and did not alter the conclusion that the relationship between D100 and establishment year was weak.) Although not shown, similar results were obtained for D200 and D300.

Age ranges of old-growth Douglas-fir at sample locations and within plots

The mean range in ages for old-growth Douglas-fir at the sample locations was 174 years (95% CI for mean = 134–214 years, $n = 27$). The mean range in ages in the 0.10-ha plots was 73 years (95% CI for mean = 56–91 years, $n = 69$). A quarter of the sample locations had age ranges of old-growth Douglas-fir that were greater than 264 years, with a maximum range of 430 years; 25% of the plots had a range in ages greater than 119 years, with a maximum age range of 381 years observed within a single 0.10-ha plot. Old-

growth Douglas-fir on 95% of the sites had age ranges of more than 48 years.

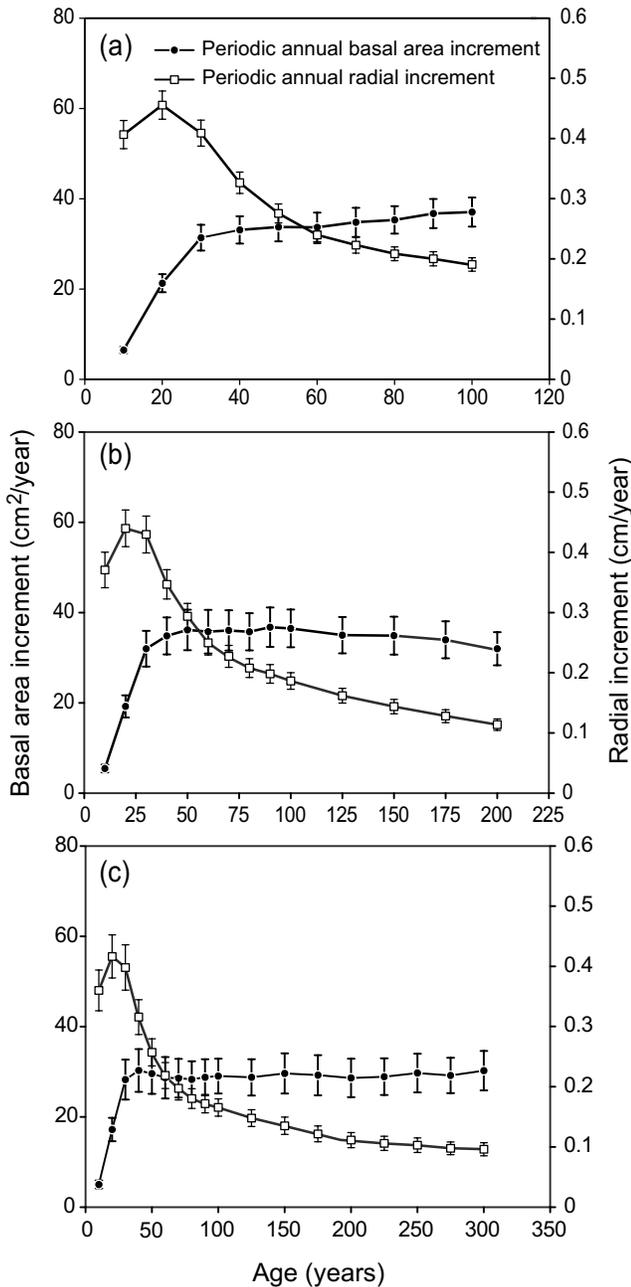
Discussion

Support for the hypothesis that large-diameter old-growth Douglas-fir developed at low stand densities comes from observations of (i) rapid early and sustained basal area growth of large-diameter old-growth Douglas-fir (Figs. 1–3 and Tables 2–4), (ii) weak relationships between growth and site factors (Tables 5–7), and (iii) wide age ranges of old-growth Douglas-fir at different sample locations. The early diameters and, more significantly, basal area growth of the old Douglas-fir in this study were extremely important in terms of attaining the large diameters typical of old-growth trees at ages 100–300 years. Our results suggest that trees attaining large diameters typical of old-growth at age 100–300 years generally did so because they were able to (i) accelerate basal area growth more rapidly and for a longer period of time during the first 50 years of life than did trees with smaller diameters at ages 100–300 years, and (ii) sustain high basal area growth rates after age 50 years. Because the diameters and basal area growth of individual trees are inversely correlated with stand density (Assmann 1970; Drew and Flewelling 1979; Marshall 1990; Oliver and Larson 1996; Smith et al. 1997), large diameters and rapid growth rates when trees are young strongly suggest that the large-diameter old-growth trees developed with relatively few neighbors.

Comparisons of the diameters at age 50 years of the old-growth trees investigated in the present study with those of 50-year-old young-growth trees growing in the lowest stand density treatment at the Hoskins level-of-growing-stock study in the Oregon Coast Range support this point (Marshall et al. 1992). The largest 25% of the old-growth trees had diameters at age 50 years equal to, or greater than, those of the 50-year-old young-growth trees growing at stand densities of 110–130 trees/ha (Poage 2001). Young-growth stands of Douglas-fir within the study area at present typically have stand densities by age 50 years of over 500 trees/ha (Tappeiner et al. 1997).

The wide range in establishment ages and weak relationships between growth and site factors (Tables 5–7) also support the hypothesis that large-diameter old-growth Douglas-fir developed at low stand densities, as opposed to growing on more productive sites or during more climatically favor-

Fig. 2. Average periodic annual basal area increments (PAI_{BA}) and average periodic radial increments (PAI_R) of all old-growth Douglas-fir (a) >150 years (n = 505), (b) >200 years (n = 281), and (c) >300 years (n = 177) sampled in western Oregon. Data are plotted for the following periods: (a) 0–100 years, (b) 0–200 years, and (c) 0–300 years. The error bars are the 99% confidence interval for the average value at that point. None of the data were transformed.



able periods. The mean range in ages reported here for sample locations (95% CI for mean = 134–214 years) was similar to that reported by Tappeiner et al. (1997) for old-growth Douglas-fir >150 years old (95% CI for mean = 77–223 years). The wide age ranges of old-growth Douglas-fir reported in the present study and by Tappeiner et al. (1997) are in contrast with the narrow age range of Douglas-fir ob-

Fig. 3. Average periodic annual basal area increments (PAI_{BA}) of all old-growth Douglas-fir (a) >150 years (n = 505), (b) >200 years (n = 281), and (c) >300 years (n = 177) sampled in western Oregon. (a) Large-diameter trees (>70 cm at age 100 years). Small-diameter trees (n = 373) had diameters <70 cm at age 100 years. Data are plotted for the period 0–100 years. (b) Large-diameter trees (n = 85) had diameters >100 cm at age 200 years. Small-diameter trees (n = 196) had diameters <100 cm at age 200 years. Data are plotted for the period 0–200 years. (c) Large-diameter trees (n = 40) had diameters >120 cm at age 300 years. Small-diameter trees (n = 137) had diameters at age 300 years <120 cm. Data are plotted for the period 0–300 years. The error bars are the 99% confidence interval for the average value at that point. None of the data were transformed.

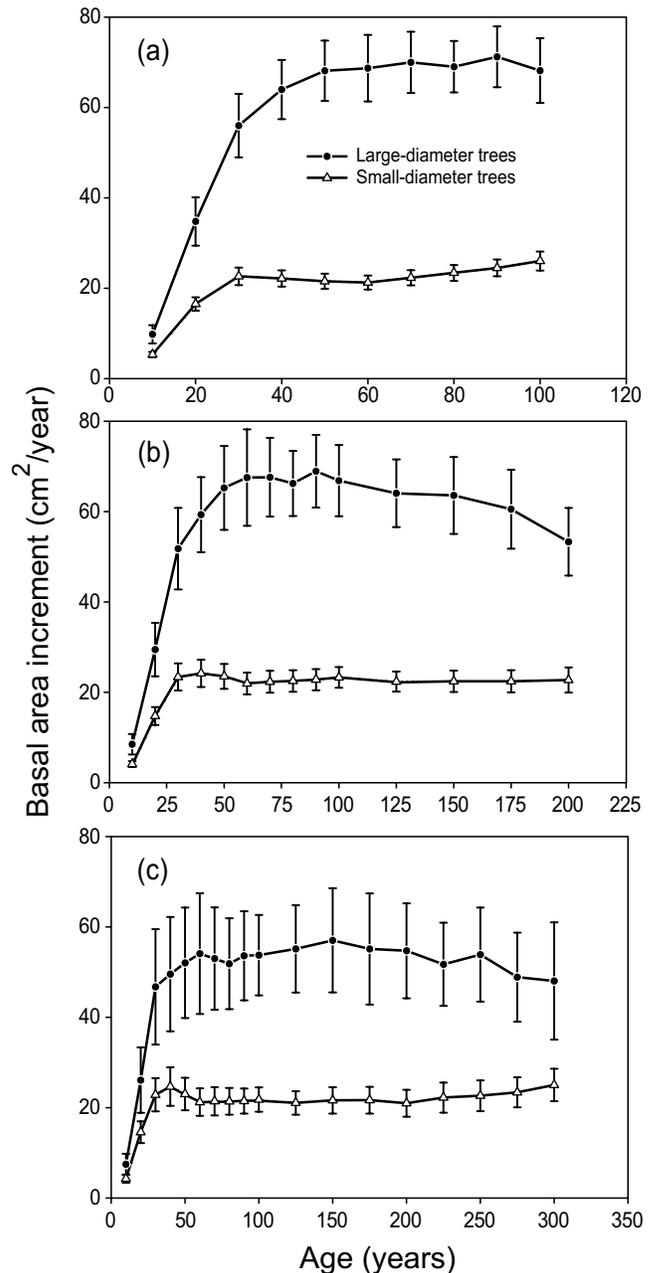


Table 5. Multiple linear regression of square-root transformed basal area increment at 50 years (BAI50, (cm²/year)^{0.5}) on site factors and establishment year.

Dependent variable	Province					Site class					Model				
	Intercept	CR	WV	OC	2	3	4	Heat	Elevation	Heat × elevation	Establishment year	MSE	r ²	F	n
BAI50	-1.1 (2.4)	-0.6* (0.3)	0.0	-0.6 (0.5)	0.2 (0.7)	1.3** (0.4)	0.0 (0.4)	-1.8×10 ⁻⁶ (2.6×10 ⁻⁶)	1.5×10 ⁻³ (1.5×10 ⁻³)	2.3×10 ⁻⁹ (4.5×10 ⁻⁹)	3.2×10 ^{-3**} (1.2×10 ⁻³)	5	0.07	5***	505

Note: Values in parentheses are SEs. *, p ≤ 0.05; **, p < 0.01; ***, p < 0.001; ****, p < 0.0001. CR, Coast Range; WV, Willamette Valley; OC, Oregon Cascades.

Table 6. Multiple linear regressions of cumulative diameter at 100, 150, 200, 250, and 300 years (D100–D300, cm) on square-root transformed basal area increment at 50 years (BAI50, (cm²/year)^{0.5}) and site factors.

Dependent variable	Province					Site class					Model					
	Intercept	BAI50	CR	WV	OC	2	3	4	Heat	Elevation	Heat × elevation	Establishment year	MSE	r ²	F	n
D100	14.6* (7.1)	8.9*** (0.1)	-0.5 (0.9)	0.0 (1.4)	-3.0* (1.4)	-0.3 (2.0)	-0.9 (1.3)	0.0 (1.3)	-2.2×10 ^{-5**} (7.6×10 ⁻⁶)	-1.3×10 ^{-2**} (4.3×10 ⁻³)	3.1×10 ^{-8*} (1.3×10 ⁻⁸)	4.2×10 ⁻³ (3.6×10 ⁻³)	39	0.91	549***	505
D150	26.1 (16.4)	9.7*** (0.3)	-8.2** (2.5)	0.0 (3.2)	-10.7*** (3.2)	2.9 (4.9)	-3.3 (3.5)	0.0 (3.5)	-5.3×10 ^{-5*} (2.1×10 ⁻⁵)	-2.4×10 ^{-2*} (1.0×10 ⁻²)	6.5×10 ^{-8*} (3.2×10 ⁻⁸)	1.5×10 ⁻² (0.8×10 ⁻²)	150	0.80	135***	322
D200	49.6* (22.7)	9.8*** (0.4)	-11.2*** (3.4)	0.0 (4.1)	-15.3*** (4.1)	-0.6 (6.2)	-5.8 (4.3)	0.0 (4.3)	-7.0×10 ^{-5*} (2.8×10 ⁻⁵)	-3.3×10 ^{-2*} (1.3×10 ⁻²)	8.7×10 ^{-8*} (4.1×10 ⁻⁸)	1.5×10 ⁻² (1.2×10 ⁻²)	223	0.73	81***	281
D250	44.7 (28.8)	10.2*** (0.6)	-8.7 (4.6)	0.0 (4.9)	-16.0** (4.9)	-0.3 (7.4)	-5.7 (5.1)	0.0 (5.1)	-8.8×10 ^{-5*} (3.6×10 ⁻⁵)	-4.3×10 ^{-2**} (1.6×10 ⁻²)	9.7×10 ⁻⁸ (5.2×10 ⁻⁸)	3.0×10 ^{-2*} (1.5×10 ⁻²)	298	0.66	50***	244
D300	87.9* (37.7)	10.1*** (0.8)	-11.2 (6.1)	0.0 (6.5)	-17.8** (6.5)	-0.5 (9.0)	-4.3 (5.8)	0.0 (5.8)	-8.9×10 ⁻⁵ (5.1×10 ⁻⁵)	-5.2×10 ^{-2*} (2.2×10 ⁻²)	7.0×10 ⁻⁸ (7.0×10 ⁻⁸)	1.7×10 ⁻² (2.1×10 ⁻²)	359	0.56	24***	177

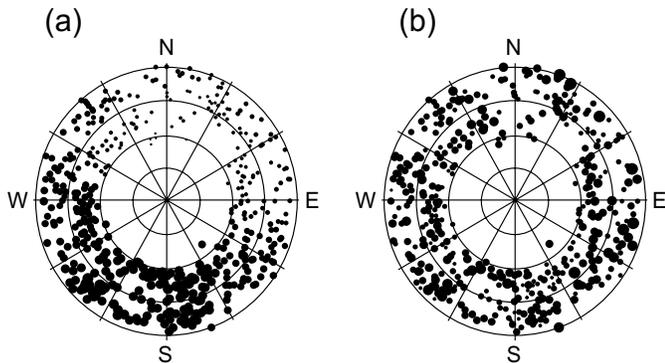
Note: Values in parentheses are SEs. *, p ≤ 0.05; **, p < 0.01; ***, p < 0.001; ****, p < 0.0001. CR, Coast Range; WV, Willamette Valley; OC, Oregon Cascades. F statistics for the model parameters are presented in Table 7.

Table 7. *F* statistics for the parameters of the multiple linear regression models presented in Table 6.

Dependent variable	BAI50	Province	Site class	Heat	Elevation	Heat × elevation	Establishment year
D100	4524****	4*	0	8**	8**	5*	1
D150	964****	7***	3*	6*	6*	4*	3
D200	520****	8***	2	6*	6*	5*	2*
D250	338****	5**	2	6*	7**	4	4*
D300	155****	4*	1	3	6*	1	1

Note: *, $p \leq 0.05$; **, $p < 0.01$; ***, $p < 0.001$; ****, $p < 0.0001$.

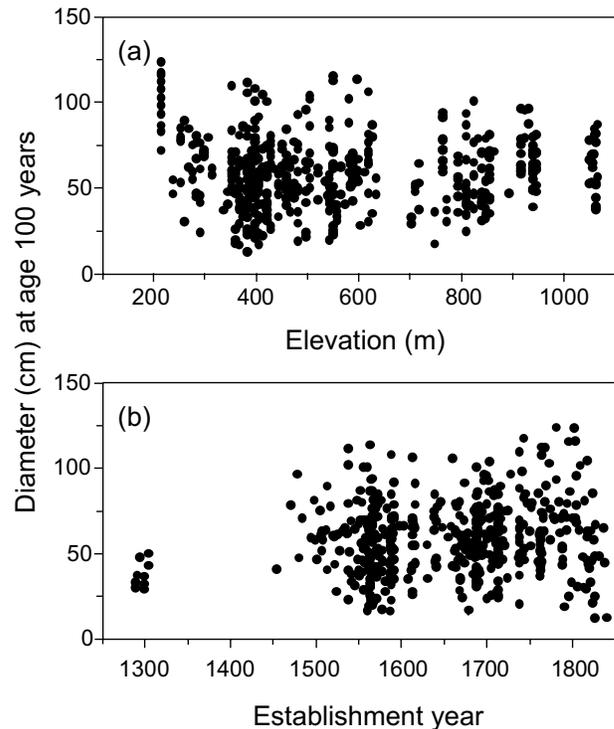
Fig. 4. Polar diagrams of topographic slope and aspect measured at each tree with symbols scaled proportionally to (a) heat at each tree and (b) diameter at age 100 years. Slope increases from 0° at the edge of each diagram to 90° at the center. Heat is the estimated annual direct solar radiation at 45°N (Buffo et al. 1972) multiplied by the heat load index. In the northern hemisphere, heat load index equals $(1.5 - 0.5 \cos(\text{aspect}_{\text{deg}} - 45))$ and ranges from 1 on cooler northeast-facing slopes to 2 on hotter southwest-facing slopes. Data are shown for all old-growth Douglas-fir (>150 years) sampled in western Oregon ($n = 505$).



served by Winter (2000) in a recent and thorough study of the structural development of a 500-year-old old-growth forest in the western Cascades of southern Washington. Winter (2000) reported that all Douglas-fir surviving to the present within a single 3.3-ha study area established within 21 years of each other (between 1500 and 1521) following a stand-replacing fire in the late 1400s. Less than 5% of the locations in the present study had age ranges for old-growth Douglas-fir as narrow as those reported by Winter (2000).

Stand densities at the locations in the present study must have been low initially and (or) were reduced periodically to low enough levels to permit the observed establishment and sustained growth of Douglas-fir over long periods of time. Low stand densities may occur in a number of ways. The number of individuals initially establishing following a disturbance may have been limited by lack of seed source, sporadic seed production, predation on seed, inadequate safe sites for seedling establishment, climatically unfavorable periods, early competition from herbaceous plants and shrubs, or herbivory of young seedlings. Minor disturbances like fire, wind, insects, and diseases may reduce the number of trees in stands that originally established at high densities or may create a limited number of microsites suitable for regeneration of new cohorts. For example, recent research indicates that repeated, low-intensity fires were more common

Fig. 5. Scatterplots of diameter at age 100 years and (a) elevation measured at each tree and (b) establishment year of each tree. Data are shown for all old-growth Douglas-fir (>150 years) sampled in western Oregon ($n = 505$).



within the present study area than previously believed (Impara 1998; Weisberg 1998). Even if initial stand densities had been high following a catastrophic, stand-replacing fire, subsequent low-intensity fires may have produced low-density stands by killing some of the trees. Climate-based models indicate that the probability of lightning ignitions increases from north to south in the Pacific Northwest (Agee 1991), suggesting that repeated, low-intensity fires may have played a more significant role in shaping old-growth forests in Oregon than in forests further north.

Site conditions such as available soil nutrients and water clearly can influence tree growth (Albrektson et al. 1977; Brix 1981; Waring 1985; Waring and Schlesinger 1985; Oliver and Larson 1996). All other factors being equal, large-diameter trees will develop more quickly on more productive sites. Although the relationships between growth and site factors observed in this study were weak, it is reasonable to assume that at least some of the trees that attained

large diameters grew on more productive sites. Site conditions also may have an indirect effect on stand density and, consequently, tree growth. For example, early competition from herbaceous vegetation and shrubs may increase with site productivity, leading to lower stand densities of trees on more productive sites. However, stand density and tree size and position are important determinants of diameter growth, regardless of site productivity. In a series of replicated experiments on a productive site, the mean tree diameter of young Douglas-fir stands thinned to low densities 20 years previously was 46 cm, while unthinned stands averaged 23 cm (Marshall et al. 1992). Heavily thinned and unthinned stands of similar ages and initial stand densities on a less productive site had mean diameters of 38 and 22 cm 20 years after treatment, respectively, (Curtis 1992). Stand density had a greater effect on tree diameter than did site productivity in these studies. Furthermore it appears that tree crown size and position in the stand are strongly related to the ability for Douglas-fir to maintain high rates of diameter growth at old ages or large sizes as trees in our study did. Trees whose crowns extend over about 60% of their height and who have low density of trees of similar sizes around them grew at rates similar to the trees in this study when they were over 100 cm in diameter (Hann and Larsen 1991).

Although low stand densities are more likely to produce large-diameter old-growth trees, a few large-diameter trees may develop at high mean stand densities if the local density of competing neighbors is low because of spatial and (or) temporal variations in establishment. For example, Winter (2000) found that 5 of 57 (9%) 500-year-old Douglas-fir surviving to the present attained inside-bark diameters at age 200 years of over 100 cm while growing at an estimated mean stand density at age 40 years of 800 trees/ha, presumably because these trees grew at relatively low local densities or because they established before their neighbors (the observed age range of Douglas-fir in Winter's study was 21 years). Similarly, low-density stands of Douglas-fir may result from mixed-species stands of Douglas-fir and red alder (a shorter-lived species with greater juvenile height growth on productive sites than Douglas-fir). If local spacings are wide enough between the Douglas-fir and red alder or if the Douglas-fir establish before the red alder, then a limited number of Douglas-fir may survive and eventually overtop the red alder to form a low-density stand of Douglas-fir (Newton et al. 1968; Poage 1995; Oliver and Larson 1996). Given that red alder is much shorter-lived than Douglas-fir and that shrub community densities are affected by overstory densities (Tappeiner et al. 1991), it would be difficult (albeit interesting) to determine if these were a common cause of low stand density of Douglas-fir in very old forests.

The results of this study have implications for young-growth stands where the acceleration of the development of late-successional forest characteristics is a management objective. Young-growth stands of Douglas-fir within the study area typically have stand densities by age 50 years of over 500 trees/ha and in young plantations tend to be spaced evenly and are far more uniform in age than even the 21-year age range of old-growth Douglas-fir noted by Winter (2000) above. Density-dependent mortality within dense young-growth stands typically leads to self-thinning during a recog-

nizable stem exclusion stage of stand development (Oliver and Larson 1996). It appears that thinning such dense young-growth stands will accelerate the development of old-growth structural characteristics. Heavy or repeated thinning of some stands or in some places in a stand may be desirable, because it would stimulate rapid diameter growth rates (similar to those measured in the larger old-growth trees in this study) and would lead to the development of trees with big stems, crowns, and branches. Thinning young stands to variable densities will likely improve habitat for a number of species (Carey et al. 1999). Thinning also has been shown to initiate the development of multiple tree layers and an understory of shrubs, both characteristics of old-growth forests (Bailey and Tappeiner 1998).

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