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Density, ages, and growth rates in old-growth and young-growth forests in coastal Oregon[1]

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Abstract: We studied the ages and diameter growth rates of trees in former Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) old-growth stands on 10 sites and compared them with young-growth stands (50–70 years old, regenerated after timber harvest) in the Coast Range of western Oregon. The diameters and diameter growth rates for the first 100 years of trees in the old-gowth stands were significantly greater than those in the young-growth stands. Growth rates in the old stands were comparable with those from long-term studies of young stands in which density is about 100–120 trees/ha; often young-growth stand density is well over 500 trees/ha. Ages of large trees in the old stands ranged from 100 to 420 years; ages in young stands varied by only about 5 to 10 years. Apparently, regeneration of old-growth stands on these sites occurred over a prolonged period, and trees grew at low density with little self-thinning; in contrast, after timber harvest, young stands may develop with high density of trees with similar ages and considerable self-thinning. The results suggest that thinning may be needed in dense young stands where the management objective is to speed development of old-growth characteristics.

Résumé : Les auteurs ont étudié sur 10 stations les âges et les taux de croissance en diamètre dans des forêts anciennes de sapin de Douglas (*Pseudotsuga menziesii* (Mirb.) Franco) et les ont comparés à ceux observés dans de jeunes peuplements (50–70 ans, régénérés après coupe) de la chaîne côtière de l'Ouest de l'Orégon. Les diamètres et les taux de croissance en diamètre étaient significativement supérieurs au cours des 100 premières années dans les forêts anciennes par rapport aux plus jeunes. Les taux de croissance dans les forêts anciennes se comparaient à ceux mesurés dans le cadre d'études à long terme de peuplements de seconde venue dans lesquels la densité se situait autour de 100 à 120 arbres à l'hectare. La densité des jeunes peuplements était souvent nettement supérieure à 500 tiges à l'hectare. L'âge des arbres de forte dimension dans les forêts anciennes variait de 100 à 420 ans; dans les peuplements de seconde venue il ne variait que de 5 à 10 ans. Apparemment, la régénération des forêts anciennes sur ces stations est survenue au cours d'une période prolongée, et les arbres ont crû sous de faibles densités avec peu d'éclaircie naturelle; par opposition, après la coupe, les jeunes peuplements peuvent se développer avec des densités élevées d'âge semblable et beaucoup d'éclaircie naturelle. Les résultats suggèrent que l'éclaircie pourrait s'avérer nécessaire dans les peuplements jeunes de forte densité lorsque l'objectif d'aménagement est d'accélérer le développement de caractéristiques de la forêt ancienne.
[Traduit par la Rédaction]

Introduction

The structure of old-growth forests in the Pacific Northwest plays an important role in the habitat for many species (Forest Ecosystem Management Assessment Team (FEMAT) 1993), including the northern spotted owl (*Strix occidentalis caurina*). The typical structure consists of large trees in the overstory, smaller trees of varying sizes and species in the lower and middle story, large standing and fallen dead trees, and patchy shrub and herb communities (Spies and Franklin 1991). Despite their ecological significance and importance in policy issues, little is known about how these old-growth forests developed or how the growth and development of young managed stands compares with them. Without this information, it will be difficult to know if young stands will develop old-growth structures, and if so, at what rate and what silviculture treatments could be applied in young stands so they do develop such structures.

Disturbance has played a major role in the development of old-growth forest structures. Wildfire occurred at frequencies of 80 to over 400 years in these forests prior to widespread European settlement, especially in the mid-19th century (Morris 1934; Juday 1976; Morrison and Swanson 1990; Agee 1991, 1993). Disturbance from wind may be locally chronic, and severe windstorms occasionally break and uproot trees throughout these forests (Spies and Cline 1988). Fire and wind as well as root diseases, insect outbreaks, floods, and ice storms have caused a complex pattern of disturbance through time. These disturbances made forest canopy openings ranging from several meters across to thousands of hectares (Spies and Franklin 1989).

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Studies of old-growth Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests in the Oregon Coast Range have focused on density, sizes, and ages of trees. They suggest that densities (trees/ha) of large trees are low but highly variable. For example, Spies and Franklin (1991) reported average density of Douglas-fir trees >100 cm diameter at breast height (DBH) ranging from 18 to 29 trees/ha with a 95% confidence interval of 2 to 57 trees/ha. Density of trees (54 cm in diameter averaged 39 trees/ha and ranged from 6 to 90 trees/ha in a survey of 30 spotted owl nest stands (Hershey 1995). Density of trees >90 cm DBH averaged 30 trees/ha with a 95% confidence interval of 19 to 41 trees/ha for 11 stands in the Coast Range (Bailey 1996).

Tree ages are also variable in old-growth Douglas-fir forests in the western Cascades (Franklin and Waring 1980; Means 1982). For example, Means (1982) found two dry-site Douglas-fir stands with trees ranging in age from 80 to 460 years. He concluded that the broad range of ages was the result of periodic fires that killed only some of the older, larger trees and enabled the prolonged establishment of Douglas-fir and incense-cedar (*Calocedrus decurrens* (Torr.) Florin.) among the large remnant trees. Spies et al. (1988) found that trees in old-growth Coast Range forests are on average 90 years younger than those in the Cascades; however, ranges of tree ages in coastal old-growth have not been reported.

The density of old-growth stands appears to be much less than that of young-growth Douglas-fir stands that are regenerated after logging. Curtis and Marshall (1986) reported ≥1000 trees/ha in 30- to 50-year-old stands that regenerated naturally following logging. Six stands ranging from age 50 to 60 years had an average of 363 trees/ha >20 cm DBH with a 95% confidence interval of 275–452 trees/ha (Bailey 1996). Plantations typically have over 600 trees/ha. Also, the range of ages in these young stands is apt to be quite narrow (Oliver and Larson 1990).

Relatively long-term studies in these young stands suggest that their natural development would follow the scenario of stand development outlined by Oliver (1981), including self-thinning and reinitiation of trees and other plants in the understory. After 30 years of stand growth, intertree competition and self-thinning have reduced density an average of 53%; individual tree growth is greatest in stands of low density (Curtis and Marshall 1986; Marshall 1991; Marshall et al. 1992). After many years and periodic disturbance from wind, fire, and other factors, these young stands may develop structures similar to old-growth stands (Agee 1991; Franklin and Spies 1991).

Understanding how these forests develop is basic to generating silvicultural prescriptions for multiresource management or restoring old-growth characteristics (McComb et al. 1993, 1994). Comparisons of the early development of young stands, regenerated after logging and fire, with that of old stands are lacking, yet they could be the basis for managing young stands to achieve old-growth characteristics (Spies et al. 1991). Data on density, growth rates, and ages in old stands could be used to develop guidelines for the intensity and timing of density management and regeneration treatments for young-growth stands so their early development resembles that of old-growth stands.

Diameter growth rates can be used to evaluate stand density and development. Numerous, detailed studies throughout temperate forests have documented the effects of tree density and intertree competition on diameter growth rates (Assmann 1970; Daniel et al. 1979; Drew and Flewelling 1979; Curtis and Marshall 1986; Smith 1986; Marshall et al. 1992). These studies consistently show a negative relationship between diameter growth rates and density. For stands starting at low density, diameter growth would remain high for a long period because there is little intertree competition. Rapid and consistent decrease in diameter growth would suggest intertree competition. A rapid, sustained increase could indicate that competition was reduced after a thinning or after fire, wind, or insects killed adjacent trees.

The purpose of this study was to determine if the early development of old-growth forests in the Oregon Coast Range was similar to that of young-growth stands. We wanted to know if the low density of large trees reported for old stands means that they developed with significantly lower densities than did young stands regenerated after timber harvest and fire. Other studies in old-growth forests measured tree age, diameter, and density (Franklin and Waring 1980; Means 1982; Spies and Franklin 1991). We measured these variables as well as diameter growth rates of individual trees. With this information, we inferred density during stand development and compared development of old-growth with that of adjacent young-growth forests.

Methods

We compared growth of main canopy trees in young-growth and former old-growth stands in several ways: (1) We compared the first 50–100 years of diameter growth in these two stand types on 9 of the 10 sites. (2) We compared our measurements of diameter growth in old-growth stands with data from long-term studies of young stands in which diameter growth had been monitored for 30 to 40 years. (3) We used a stand growth model to simulate 100 years of growth for a stand with high density and uniform tree sizes and one with low density and variable tree sizes; we compared the model estimates of density and tree sizes with our measurements from old-growth stands.

Study sites

This study was conducted on 10 sites with old-growth forests that had been clear-cut 5 to 10 years earlier. All sites were in the Oregon Coast Range; nine were in the western hemlock zone, and one (site 4) was in the Douglas-fir – grand fir zone (Franklin and Dyrness 1973). Locations ranged from Valsetz in the north to near Lorane in the south (45°45′–43°45′N), and from near Corvallis in the east to Drift Creek in the west (123°15′–124°00′W) (north–south and east–west ranges covered approximately 110 and 50 km, respectively.) Precipitation on the study sites ranged from 150 to over 200 cm, and summer and winter temperatures ranged from 17 to 5°C, respectively (NOAA 1987). Soils were loams or clay loams derived mainly from basalts; some were derived from sandstone. Douglas-fir was the principal tree species on these sites, with minor amounts of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.), red alder (*Alnus rubra* Bong.), and bigleaf maple (*Acer macrophyllum* Pursh). Shrubs included vine maple (*Acer circinatum* Pursh), salal (*Gaultheria shallon* Pursh), salmonberry (*Rubus spectabilis* Pursh), and California hazel (*Corylus cornuta* var. *californica* (DC.) Sharp).

Site selection criteria included the following: (1) former old-growth stands (10–30 ha) had not been partially cut or had no apparent human disturbance prior to clear-cutting; (2) older trees (≥150 years) were present before logging; (3) annual rings on tree stumps were measurable and had not been damaged by logging, burning for site preparation, or other activity; and (4) young-growth stands with 50- to 70-year-old trees regenerated naturally after logging were present on nearby, similar sites (except site 10). Unlogged parts of the old stands had many old-growth characteristics, such as snags, fallen logs on the forest floor, and multiple tree layers (Franklin et al. 1981; Franklin and Spies 1991). Hereafter in this paper, the former old-growth stands and the young-growth stands are referred to as old stands and young stands, respectively.

Measurements

Tree ages and diameters were measured on all stumps, and diameter growth rates of the previous overstory trees were estimated for young and old stands at each site except site 10. In each old stand, we randomly established four to six circular 0.1-ha plots, 50 to 100 m apart. In each plot, we tallied the number of stumps (≥10 cm diameter) of each species. For each stump, we estimated tree age by counting annual rings and also measured the diameter (outside bark; ±1 cm). For trees that had formed the main canopy (>50 cm DBH), we estimated growth rates (inside bark) by measuring annual rings in 10-year increments (±0.25 cm), starting at the pith, up to 100 years (or over all rings for trees <100 years old). Growth of Douglas-fir was estimated on an average radius where annual rings could be easily measured. We avoided variations in annual ring width that appeared to be reaction wood, resulting from mechanical stress.

Young stands at each site were at similar elevations and were within 1 km of the old stands (except site 6, at which the young stand was 5 km from the old stand and 200 m lower in elevation, and site 10, at which there were no young stands ≥50 years old). At all sites, except site 10, we established plots in young, unthinned stands; trees were 50–79 years old and had regenerated from natural seeding after logging. If available, we also established plots in young stands that had been thinned ≥10 years earlier. We included thinned stands to have a range of young stand densities to compare with the old stands, not to study the effects of thinning on stand development. We established three or four 0.025-ha circular plots in the thinned and unthinned young stands and used the same methods as described above to estimate ages, diameters, and diameter growth rates of all trees. If trees had not been cut, we took increment cores to the pith to determine ages and growth rates.

Long-term stand growth studies

Two long-term studies of stand density and growth, hereafter referred to as studies A and B, are being conducted within our study area. In study A (Curtis and Marshall 1986; Marshall et al. 1992), tree and stand growth had been monitored for 30 years (stand age 20–50 years) over a range of replicated density treatments. In study B (Curtis and Marshall 1993), growth of unreplicated treatments had been monitored for 40 years (stand age 40–80 years). Tree diameters from low density (123–135 trees/ha) and high density (407–531 trees/ha) treatments in studies A and B were compared with diameters of trees from old stands in this study that were on sites of similar productivity (sites 1, 3, 8, and 10; Table 1).

Measurements of diameter growth in studies A and B are made at breast height (137 cm). However, stump height in the old stands in this study ranged from 55 to 150 cm. To determine if estimates of diameter growth were affected by the height at which measurements were made, we took two increment cores from each of 20 trees near studies A and B, one at a height of 55 cm and the other directly above at breast height. The maximum difference in ring widths in the two cores for the same 10-year period was 0.2 cm (average 0.05 cm). Furthermore, the measurements at 55 cm were not consistently larger or smaller than those at breast height. Thus, the diameters and diameter growth rates of trees in studies A and B can be compared with those in the old stands, and they should not be affected by differences in the height of measurement.

Data analysis

We calculated basal area and relative density (Curtis 1982) for each plot in the young and old stands. We measured the diameter of uncut old trees adjacent to sites 4, 5, and 7 at DBH and at 75 cm (average stump height). We used the ratio of the diameter at stump height to DBH to estimate DBH for all cut trees, and we used the estimated DBH to calculate basal area and relative density for the old stands. For each tree, we converted the annual ring measurements to diameter and annual diameter growth rate (inside bark), for each decade from 10 to 100 years. The few hemlock and the younger, smaller Douglas-fir (<100 years and ≤50 cm diameter) that were clearly established in the understory of older trees (about 5% of the trees on the plots) were not included in the evaluation of growth. We used five trees from each of three sites and Morrison and Swanson's (1990) method to estimate total age of old trees from ring counts at stump height. Since this correction was ≤3 years for these rapidly growing trees, we did not correct for tree ages on any site.

Data were analyzed separately for each site. We used t-tests or analysis of variance and least significance multiple range tests on untransformed data to test the hypothesis that there was no difference in diameter and diameter growth at age 50 years (the oldest common age for all stands) among trees in old stands and in young thinned and unthinned stands.

The old stands may have been denser when stands were initiated, and many of the smaller trees could have been killed from fire, self-thinning, or other factors as the stands developed; that is, the old trees may be remnants of what once were dense stands. To test this hypothesis, we used analysis of variance and least significance multiple range tests or t-tests to determine if the average diameter and diameter growth rate at age 50 years were significantly different between the largest trees (equivalent of 60 trees/ha) in the young stands and the trees in the old stands; we assumed that differences in diameter growth would indicate different densities.

For trees ≥50 cm in each old stand, we used linear regression of tree diameter at 100 years on final tree age to determine if the older trees may have affected the rate of growth of the younger trees that became established among them. We also regressed tree diameter at age 100 years on diameter at age 20 years to further determine if intertree competition or release from it might have influenced the first 100 years of diameter growth.

We used Student's t-tests to test the hypothesis that there was no difference ($P \leq 0.05$) in average tree diameter at age 30 and 50 years from study A and average diameters at the same ages in the old stands. Since treatments were not replicated for study B, we determined if average diameters at age 50 and 80 years were within the standard errors of the diameters in the old stands.

Stand simulations

We tested the hypothesis that the old stands developed with low density by simulating two scenarios of stand development on three sites using organon (Hester et al. 1989): scenario 1, low-density stands with numbers of trees per hectare that we estimated from field measurements in this study (77–114 trees/ha); and scenario 2, high-density stands with 250 trees/ha at age 20 years and with no subsequent removal of trees to simulate disturbance. Stand growth was simulated for 120 years. For scenario 1, we used our field data to estimate tree diameter 120 years earlier and began the simulation with these diameters.

Results

Density

As in the studies cited above (Spies and Franklin 1991; Hershey 1995; Bailey 1996), density of old stands was generally low and variable. Average density of large trees (>50 cm diameter) that formed the previous main canopy ranged from 47 to 126 trees/ha (Table 1). Density of canopy trees was much

Table 1. Description of old and young stands on the 10 study sites.

Site	Density (trees/ha)* <50 cm	Density (trees/ha)* >50 cm	Age (years)	Diameter (cm)	Height (m)†	Basal area (m^2/ha)	Relative density‡
			Old stands				
1	18	62	71–137	26–207		73	51
2	18	59	63–145	33–193		66	45
3	10	59	90–226	35–173		68	52
4	15	69	70–300	60–220		91	55
5	72	54	63–250	20–150		46	67
6	72	104	80–412	20–190		53	43
7	17	47	50–414	20–225		73	49
8	16	98	68–144	30–170		84	60
9	25	49	60–300	35–170		46	29
10	67	126	40–250	24–130		58	49
			Young unthinned stands, all size classes				
1	600		48–65	15–60	41–43	73	75
2	531		38–52	20–62	42–46	46	59
3	455		69–79	17–55	41–45	74	55
4	364		48–53	30–40	38–40	51	55
5	365		41–60	25–59	35–37	63	67
6	291		52–70	28–85	45–47	71	55
7	272		55–60	26–47	37–39	61	63
8	223		50–56	30–91	38–39	69	70
9	321		46–52	30–53	37–39	44	50
			Young, thinned stands§				
1	260		58–70	45–80	42–45	70	57
2	148		50–60	40–67	43–46	46	60
3	208		40–66	23–61	40–44	51	53
5	194		45–73	35–76	37–38	46	42
6	173		60–72	35–72	42–45	55	53
8	209		50–56	46–69	37–38	47	51

*Young stands were not divided into size classes.

†Dominant and codominant trees.

‡Curtis (1982).

§No thinned stands were present at sites 4, 7, 9, and 10.

higher in the young unthinned stands and ranged from 223 to 600 trees/ha. In young thinned stands, density varied with the thinning prescription and ranged from 148 to 260 trees/ha, greater than in the old stands (Table 1).

At age 50 to 70 years, the relative density of the young unthinned stands (50–75) was generally greater than in the old stands (29–67) (Table 1). In most old stands (except at sites 5 and 8), average relative density was ≤55, the value at which self-thinning is likely to occur (Drew and Flewelling 1979). Neither natural nor commercial thinning in young stands had permanently reduced their relative density below that of the old stands. The basal area in young unthinned stands (44–74 m^2/ha) was similar to that in the old stands (46–84 m^2/ha), except at site 4 where it averaged 91 m^2/ha in the old stand (Table 1).

Ages

Tree ages in all 10 old stands were quite variable (Figs. 1 and 2). Site 7 had the maximum age range (364 years). Over 90% of the trees in this stand ranged from 100 to 280 years; however, there were a few trees (mostly Douglas-fir, with some hemlock) less than 100 years old, and there were four trees just over 400 years old. Site 1 had the smallest age range (66 years), with 60% of the trees over 100 years old. Ages in the young stands were much less variable, with a maximum range of 28 years and a minimum of 5 years (Table 1). Trees in these young stands were generally within 5–10 years of the same age.

Within-stand variation

Within each old stand, there was considerable spatial variation in number of trees, age, and diameter (Fig. 2). For example, on plot 4 of site 5, density was 152 trees/ha, and tree ages ranged from 65 to >200 years; however, on plot 2, density was 78 trees/ha, 50% of the trees were age 130–155 years, and tree ages ranged from 120 to 180 years. On site 7, plot 4, tree ages ranged from 110 to >400 years, with 50% of them from 140 to 390 years; tree ages on the other plots on this site ranged from 50 to 250 years. There was similar variation on other sites; for example, density on site 8 ranged from 25 to 198 trees/ha, and basal area ranged from 33 to 117 m^2/ha. Tree ages and sizes in the young stands were much less variable (Fig. 2).

Fig. 1. Diameter and age of trees in 10 old-growth stands in the Oregon Coast Range.

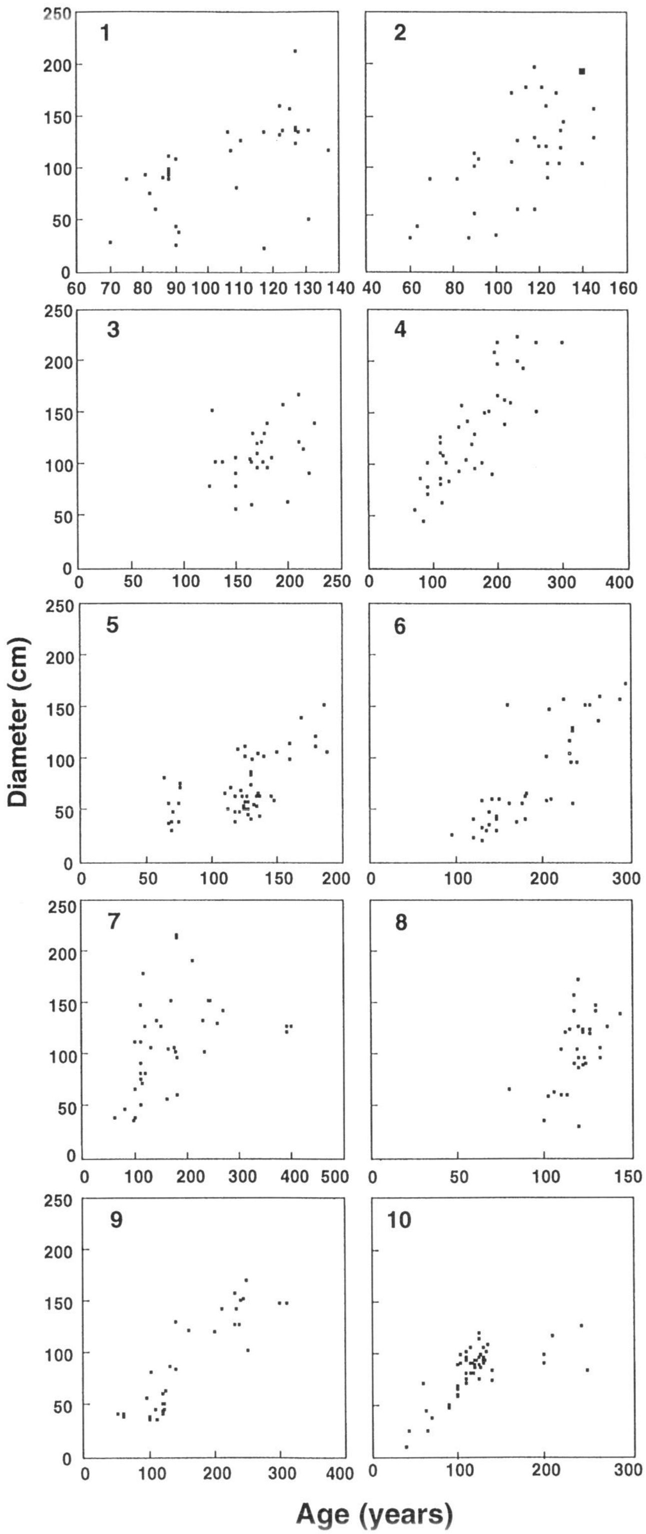
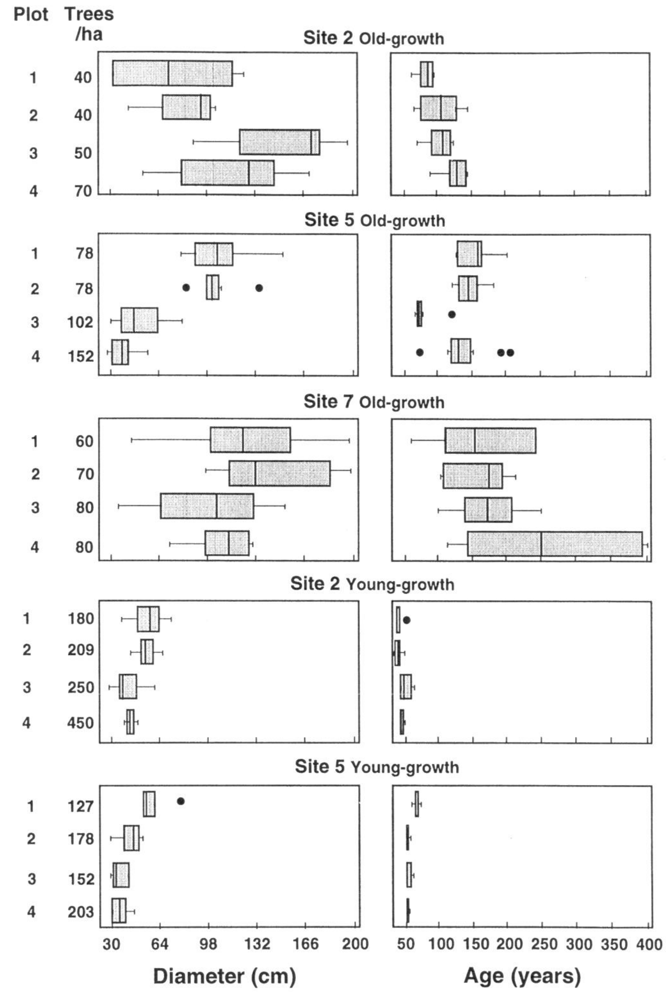


Fig. 2. Variation of tree diameter and age on four plots (0.1 ha) in each of three old-growth stands and two young-growth stands. Boxes represent the interquartile range (middle 50% of observations); vertical line is the median; horizontal lines include values 1.5 times the upper or lower quartile; circles represent values outside these ranges.



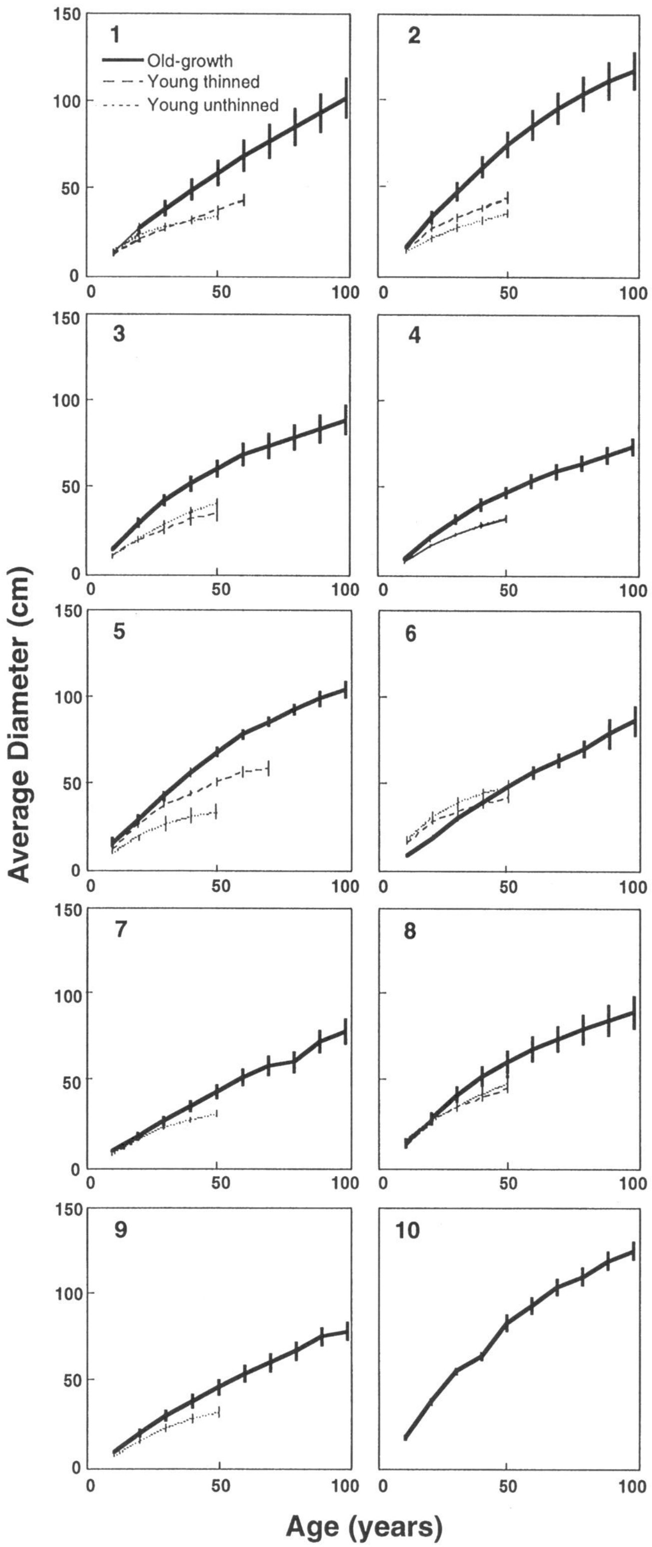
Diameter growth

Average diameter and diameter growth rates up to 100 years are presented in Figs. 3 and 4, respectively. For the old stands, these values represent the average size and growth rates for individual trees (>50 cm) within this age range. For young stands, these values also represent average diameter and diameter growth for the entire stand, because all trees are nearly the same age.

The large trees in old stands grew more rapidly than young trees during their first 100 years. For example, at age 50 years, diameters of trees at sites 2 and 5 averaged 68 and 69 cm, respectively (Fig. 3), and diameter growth rates averaged 1.35 and 1.19 cm/year, respectively (Fig. 4) (about 1.5 annual rings/cm). Average annual diameter growth at age 100 years in all old stands, except site 3, was ≥0.5 cm/year (Fig. 4) (about 4 annual rings/cm).

On all sites, except site 6, average diameters of trees at age 50 years were significantly greater in the old stands than in the young stands (thinned and unthinned) (Fig. 3) ($P \leq 0.001$ for all stands), and they were also significantly greater in the old stands than among the largest 60 trees/ha in the young stands (thinned and unthinned) (Table 2). In site 6, where the young stands occurred on more productive locations than did the old stands, there was no significant difference in diameter at age

Fig. 3. Average diameter of main canopy of trees from 10 to 100 years in old- and young-growth stands in the Oregon Coast Range. Error bars are SEs.



50 years among old and young stands when all trees were considered (Fig. 3); however, the largest trees in the young thinned stands were significantly larger ($P \leq 0.01$) than those

Table 2. Diameter and diameter growth rate at age 50 years (±SE) for old stands and for the largest 60 trees/ha in young (thinned and unthinned) stands at each site.

Site	Stand type	Diameter (cm)	Diameter growth rate (cm/year)
1	Old-growth	65.0±6.0*a*	1.12±0.14*a*
	Young thinned	39.4±2.6*b*	0.63±0.10*b*
	Young unthinned	38.6±2.4*b*	0.35±0.05*c*
2	Old-growth	69.1±7.1*a*	1.36±0.05*a*
	Young thinned	44.5±2.0*b*	0.56±0.05*b*
	Young unthinned	38.7±2.3*b*	0.42±0.04*b*
3	Old-growth	61.0±20.3*a*	0.72±0.05*a*
	Young thinned	45.2±5.6*b*	0.66±0.07*a*
	Young unthinned	39.1±2.5*b*	0.44±0.08*b*
4	Old-growth	55.1±2.8*a*	0.80±0.08*a*
	Young unthinned	40.4±3.2*b*	0.58±0.09*b*
5	Old-growth	68.1±2.0*a*	1.18±0.09*a*
	Young thinned	50.8±2.4*b*	0.22±0.08*b*
	Young unthinned	34.8±2.2*c*	0.11±0.04*c*
6	Old-growth	40.4±2.2*a*	0.88±0.08*a*
	Young thinned	49.8±2.6*b*	0.50±0.07*b*
	Young unthinned	41.9±1.5*a*	0.36±0.04*c*
7	Old-growth	43.2±4.5*a*	1.06±0.06*a*
	Young unthinned	29.7±0.6*b*	0.44±0.24*b*
8	Old-growth	62.5±5.6*a*	0.86±0.10*a*
	Young thinned	45.2±2.3*b*	0.56±0.20*b*
	Young unthinned	47.5±4.1*b*	0.60±0.10*b*
9	Old-growth	48.3±3.6*a*	0.90±0.14*a*
	Young unthinned	36.1±3.1*b*	0.60±0.13*b*

Note: Within columns for each site, means followed by different letters are significantly different ($P < 0.05$).

in the old and young unthinned stands, which were not significantly different ($P \leq 0.20$) (Table 2).

On all sites, except site 3, diameter growth rates of trees at age 50 years were significantly greater in the old stands than in the young stands (thinned and unthinned) (Fig. 4). Also, except in site 3, rates were significantly greater in old stands than among the largest trees in young stands (Table 2) ($P \leq 0.001$). At site 3, there was no difference in diameter growth rates between old and young thinned stands at tree age 50 years, but at age 60 years, rates were significantly greater in old stands than in young thinned stands ($P \leq 0.001$). On nearly all sites, diameter growth was greater for trees at age 100 years in the old stands than for trees at age 50 years in the young stands (Fig. 4).

Diameter growth rates of trees in the old stands peaked at age 10 to 30 years and then followed a constant decline to age 100 years on all sites (Fig. 4). We found no abrupt and sustained changes in rates after age 30 years that would indicate an abrupt change in density. In the young stands, growth rates were consistently higher following thinning at sites 1, 2, 3, and 5 (Fig. 4). In old stands, large, young trees at age 20 years tended to be the large trees at age 100 years. Linear regressions of diameter at age 100 years on diameter at age 20 years were significant at all sites ($P \leq 0.04$) and explained 53–92% of the variation in diameter at age 100 years.

In the old stands, trees became established among older, larger trees and grew well. For example, on site 3, Douglas-fir trees of age 120–130 years and with 80–137 cm diameter at

Fig. 4. Average annual diameter growth and age of trees in old- and young-growth stands in the Oregon Coast Range. Error bars are SEs.

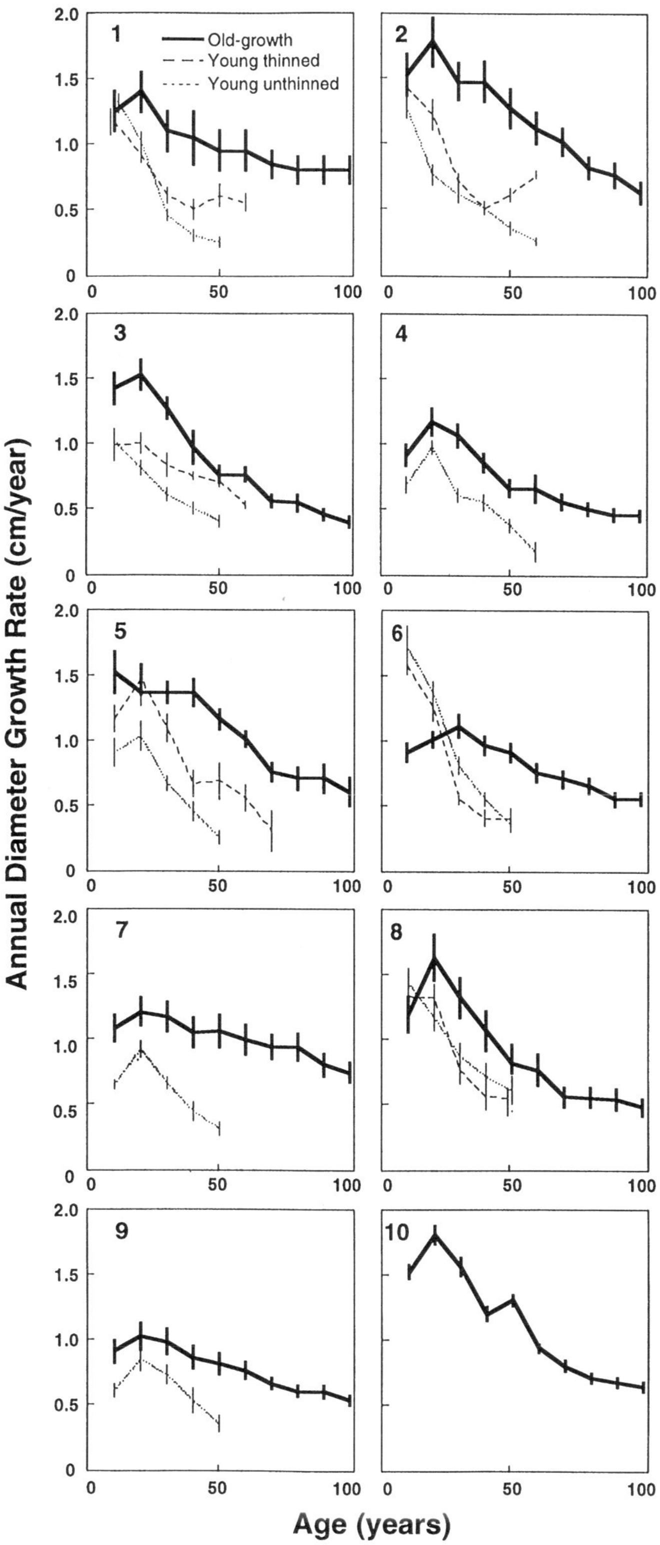
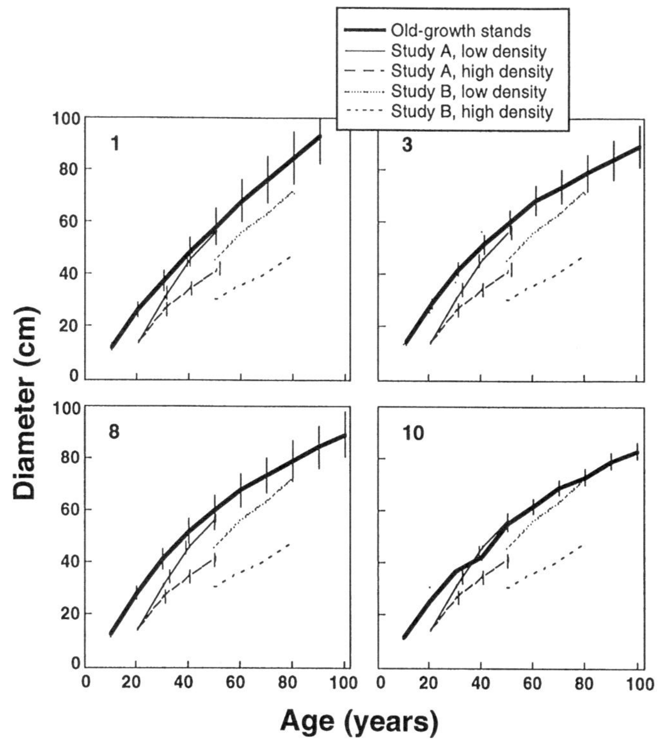


Fig. 5. Average diameter and age in four old-growth stands compared with four treatments in study A (Curtis and Marshall 1986; Marshall et al. 1992) and study B (Curtis and Marshall 1993). All sites were productivity class I or II (King 1966). Low stocking, 123–135 trees/ha; high stocking, 407–531 trees/ha. Error bars are SEs. Study B was not replicated; therefore, no standard errors are reported.



100 years were growing among trees of age 220–240 years. For trees ≥50 cm diameter, there was no significant relationship between final tree age and diameter at age 100 years ($P \leq 0.60$), indicating no detectable effect of intertree competition on the first 100 years of diameter growth. Also, on sites 4, 6, 7, and 9, which had a broad range of tree ages, we found no difference in diameter at age 100 years between trees older and those younger than 150 years. However, on all sites, we found small, apparently suppressed trees (20–50 cm diameter at age 90–120 years) located near older, larger trees. In site 7, there was an exception to the pattern of rapid growth rates of the larger, older trees; three trees of age 390–414 years on the same plot grew slowly throughout their lives and were only 135–140 cm in diameter.

Comparison with long-term growth studies

Diameters from age 20 to 80 years were similar for trees in the old stands and trees in the low-density treatments in both studies A and B (Fig. 5). For example, there was no significant difference in average diameter at age 50 years between the old stand at site 8 (60.2 cm) and the low density treatments of study A (55.9 cm). In study B, the average diameter of trees at age 80 years (72.3 cm) was also very similar to that of trees in the old stand at site 8 (78.0 cm). In contrast, average diameter at age 50 years at site 8 (60.2 cm) was significantly greater ($P \leq 0.01$) than that of the high density treatment in both study A (40.5 cm) and study B (30.5 cm). These patterns are very similar for sites 1, 3, and 10 (Fig. 5) and also for sites 2 and 5 (data not shown).

Table 3. Observed and predicted density (trees/ha) by diameter class.

Stand	Diameter class (cm) <50	50–75	75–100	100–125	>125	Total
Observed, site 1	18	6	6	38	12	80
Scenario 1	6	10	18	32	6	72
Scenario 2	0	101	76	0	0	177
Observed, site 2	18	6	19	12	22	77
Scenario 1	8	17	12	18	12	67
Scenario 2	0	101	76	0	0	177
Observed, site 8	16	8	24	57	8	114
Scenario 1	7	23	22	32	8	92
Scenario 2	0	101	76	0	0	177

Note: Observed values were measured in former old-growth stands. Predicted values were simulated under two scenarios: (1) actual tree numbers and sizes, and (2) 250 trees/ha.

Stand simulations

Simulations of stand development that began with low density (77–114 trees/ha; scenario 1) were best at approximating the observed density in each diameter class, and predictions of total density were within 8–22 trees/ha of the observed total (Table 3). In contrast, simulations of stand development that began with high density (250 trees/ha; scenario 2) predicted no trees in the largest diameter classes and overpredicted the observed total by 63–100 trees/ha.

Discussion

The results support the hypothesis that, on these sites in the Oregon Coast Range, today's young-growth stands that regenerated after logging are developing at much higher densities than during development of old-growth Douglas-fir stands. Further, tree establishment in the old stands typically occurred over long periods of time, unlike in the young stands. Five major findings support this hypothesis.

(1) For trees on all sites, except site 6, average diameter at age 50 years was significantly greater in old stands than in young stands with high density (Fig. 3). Diameter growth rate is highly related to stand density (Assmann 1970; Daniel et al. 1979; Curtis and Marshall 1986), and in the old stands in our study, growth rates continued to be rapid well beyond age 50 years, whereas they decreased dramatically in young, dense stands at about age 30 years (Fig. 4).

(2) The average diameter and diameter growth rate of trees up to age 50 years in the old stands were generally greater than those of the largest trees in the young stands (representing 60 trees/ha) (Table 2). These results are consistent with those of Reukema (1970) and Marshall et al. (1992), who reported that diameter growth in the largest trees decreased with increasing stand density.

(3) Tree growth from ages 20 to 80 years in the old stands was similar to that in the least dense stands in studies A and B (Fig. 5). The slower diameter growth in dense, young stands suggests substantial intertree competition and is consistent with the results of these studies (Curtis and Marshall 1986; Marshall 1991; Marshall et al. 1992), as well as those of Drew and Flewelling (1979) on other sites.

(4) Stand development simulations that began with low density at age 20 years (77–114 trees/ha; scenario 1) gave better estimates of the observed total density and the observed density in the larger diameter classes (>100 cm) than did simulations that began with high density (250 trees/ha; scenario 2; similar to the lower density in the young stands) (Table 3). The simulations under scenario 1 suggest that tree density and diameter growth in the young stands will be reduced substantially; these results are consistent with those from long-term studies (Marshall et al. 1992; Curtis and Marshall 1993). Our simulations probably underestimate total mortality, because the growth models account for mortality only from intertree competition and not from other causes, such as root disease or wind. However, our results suggest that very little intertree competition and self-thinning occurred in the old stands.

(5) All old stands had a broad range of tree ages and sizes (Fig. 1) and considerable within-stand heterogeneity (Fig. 2). The young stands had much more uniform tree ages and sizes.

Thus it appears that the old stands developed with low density, regenerated over time, and had little intertree competition. The young stands, however, are developing from a single cohort and with uniform, high density. The low density in these Coast Range old stands may help explain why Spies et al. (1988) consistently found low amounts of coarse woody debris in old-growth forests in the Coast Range.

It is not likely that the old stands once had high densities (as in the young stands) and that density was greatly reduced by a disturbance such as fire or wind, leaving only the larger trees. Tree diameters at age 50 years were smaller among the largest trees in the young stands than in the old stands. Also, if disturbance had greatly reduced density, we would expect to find a rapid increase in diameter growth afterwards, as we did in the young stands after thinning. We found no such increase. However, patchy mortality of single trees and self-thinning in some parts of the stand could have occurred early in development of the old stands (Bradshaw and Spies 1992).

Furthermore, some of the younger trees in the old stands grew rapidly and were 100–150 cm in diameter in 100–120 years, even though they became established among older, larger trees. Such rapid growth of Douglas-fir after seedling establishment would not occur in dense stands (Del Rio and Berg 1979; Bailey 1996).

The wide range of tree ages and low density of the old stands in our study sites suggest that periodic, low intensity fire killed some trees, temporarily reduced shrub cover, and likely enabled some seedling establishment. It is likely that a low supply of seed and a dense cover of shrubs and herbs may have limited conifer establishment after intense fires (Isaac 1938, 1940).

Young stands were regenerated differently. Soil disturbance during logging, followed by fire, probably delayed shrub and hardwood reinvasion and favored natural conifer regeneration. Exposure of mineral soil from logging is known to favor natural Douglas-fir regeneration (Isaac 1940; Hermann and Chilcote 1965; Tappeiner and Helms 1971; Williamson 1973).

Observations on our study sites and nearby stands suggest that disturbance sufficient to promote Douglas-fir regeneration had occurred in the old stands. For example, on site 5, a group of 70-year-old Douglas-fir was growing among 130- to 140-year-old trees (Fig. 2). On site 2, several 1- to 2-ha areas within the old stand supported several large (60 to >80 cm diameter) red alder and an understory of salmonberry and elderberry (*Sambucus* sp.), all early successional species (Harrington 1990; Tappeiner et al. 1991; Haeussler et al. 1995). The regeneration of alder and Douglas-fir among older Douglas-fir has been previously reported (Poage 1995). The variability of final tree ages and sizes (Fig. 2) suggests that trees became established at irregular intervals throughout the stands. Oliver and Larson (1990) and Means (1982) suggested that prolonged stand establishment is associated with exposed, less productive sites, on which natural seedling establishment may be slow. Our results suggest that long periods of Douglas-fir regeneration may lead to multiage forests on productive sites as well.

The lower diameter growth rates that we measured in the young stands are likely a result of stand densities rather than other factors, such as climate or reduced soil productivity after logging. The effects of stand density on diameter growth have been documented in many studies throughout temperate forests (Assmann 1970), including studies A and B near our sites (Curtis and Marshall 1986, 1993; Marshall et al. 1992). Also, the relative densities of the young stands were >55, the density at which reduced diameter growth and self-thinning is likely (Drew and Flewelling 1979). Heights of dominant and codominant trees in the young stands ranged from 35 to 47 m (Table 1), an indication of very productive sites (King 1966). Moreover, the standing net volume in the young unthinned stands at sites 3 and 6 ranged from 688 to 795 m^3/ha (Bailey 1996). Thus, at age 60–70 years, these stands have produced 62–81% of the standing volume in nearby old-growth stands. Also, the volume in long-term study A is quite high (433–679 m^3/ha in 50-year-old stands) and does not suggest reduced conifer growth potential (Marshall et al. 1992).

We suggest three reasons why change in climate was not likely to have a major effect on the growth of the trees in this study. First, the most compelling reason that stand density was the major cause of the differences in diameter growth that we observed comes from the long-term studies A and B, where trees are growing in the same climate and on the same sites. The differences in diameter attributed to density were 24.4 cm at 80 years in study B and 15.4 cm at 50 years in study A (Fig. 5), nearly the same as the differences between the old and young trees on our study sites (Table 2). Similar differences were reported for other long-term studies (Curtis and Marshall 1986). Second, the old trees grew in both dry and wet periods. Tree ring analysis suggests that there were frequent drought years in the 1790s, in the 1840s, from 1865 to 1895, and from 1920 to 1940, with a wet period from 1900 to 1919 (Brubaker 1980; Graumlich 1987). Thus, the old trees would have experienced both wet and dry periods during their first 100 years. For example, 175-year-old trees on sites 4 and 7 would have had two periods of drought during their first 70 years followed by a wet period. Trees of other ages would have experienced different dry and wet periods. However, the pattern of rapid early growth and then a gradual decline (Fig. 4) was similar on all sites. The young trees that grew the slowest were mostly established after the drought from 1920 to 1940. Finally, the trees that we studied were not likely to be strongly affected by climatic fluctuations. Trees that best reflect differences in climate in their annual rings are older (≥100 years) and are growing slowly on well-drained sites (Fritts 1976; Brubaker 1980), while in this study we measured growth on productive sites on clay loam soils when trees were young and growing rapidly.

The results of this study suggest new ways of interpreting old-growth forest development in the Oregon Coast Range. Multiage forests with variable structures might occur without the processes of self-thinning and reinitiating an understory that were suggested by Oliver (1981), Agee (1991), and Spies and Franklin (1991). Our results suggest that self-thinning did not generally occur during the development of the old stands we studied, although it is likely to have occurred in dense parts of some stands. Thus, canopy gaps in these forests are the result of low rates and irregular density of conifer establishment as well as the death of individual large trees (Stewart 1986, 1989; Spies and Franklin 1989).

Although some stands were probably very open, most old-growth forests formed closed canopy stands, even though they had low densities when they were young. Canopy closure occurs at densities below the density of self-thinning (Drew and Flewelling 1979). We have observed many naturally established, closed-canopy stands, 60–150 years old, that currently have densities that are similar to those of the current old-growth stands. Mortality in these stands appears to be a result of density-independent factors such as disease and insects.

In contrast with the old stands, dense young-growth stands that we studied will undergo self-thinning and reinitiation of the understory (Oliver 1981), but will they reach old-growth structure? If so, how long will it take? Additional work is needed to determine whether old-growth stands in the western Cascades and on other sites throughout the Pacific Northwest also developed with low densities, as in the Coast Range stands we studied.

Management implications

The results of this study have strong implications for management of forests in the Pacific Northwest. The area occupied by old-growth forests in Washington, Oregon, and California has declined by more than 50% since 1930 (Bolsinger and Waddell 1993). Old-growth forests have typically been replaced by dense, young conifer forests intended for timber production.

When the objective of forest management is to grow stands with old-growth characteristics, it appears that density management (e.g., one or more thinnings to low densities) will be required. Density of young-growth stands in this study was greater than that of old stands (Table 1), and diameter growth rates of individual trees were much less, even in the thinned stands. Our stand simulations also indicated that young stands with even as few as 250 trees/ha will develop along a different pathway than the old stands. Consequently, several thinnings might be prescribed to decrease density and increase tree growth (Newton and Cole 1987). Also thinning promotes natural conifer regeneration in the understory (Bailey 1996), and thus would help provide the multiple size and age characteristics of the old-growth stands (Spies and Franklin 1991).

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