Distribution and increment of biomass in adjacent young Douglas-fir stands with different early growth rates[1]

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Total biomass increments were determined for three adjacent 22-year-old Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) plantations in the Oregon Coast Range that had widely different early growth rates. Estimated total aboveground biomass of the stands, designated slow, intermediate, and fast, was 98.7, 148.7, and 203.7 $Mg \cdot ha^{-1}$, respectively; estimated mean biomass increment in the 5 years previous to sampling was 8.9, 12.6, and 12.3 $Mg \cdot ha^{-1} \cdot year^{-1}$. The slow stand had a greater proportion of aboveground biomass in branches and a smaller proportion in stem wood than the intermediate and fast stands. Differences in biomass increment were primarily due to stem rather than crown growth. Total belowground biomass was highest in the fast stand, the difference being due to roots >5 mm in diameter; weight of roots <5 mm was greater in the slow and intermediate stands. Roots >5 mm comprised about 77% of the total root system in those stands and 90% in the fast stand. Increment of roots >5 mm was 2.2, 2.5, and 3.0 $Mg \cdot ha^{-1} \cdot year^{-1}$ in the slow, intermediate, and fast stands. The ratio of productivity to total leaf nitrogen suggests that nitrogen is a principal limiting resource in the intermediate stand. The fast stand, with a leaf area index 50% greater than the others, is probably limited by light. The slow stand has anaerobic soils during at least part of the year, which may restrict rooting depth and thereby induce water stress during summer drought.

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La biomasse totale et les accroissements en biomasse ont été déterminés dans trois plantations adjacentes de 22 ans de sapin de Douglas (*Pseudotsuga menziesii* (Mirb.) Franco) de la chaîne côtière de l'Orégon ayant des taux de croissance initiale très différents. Les biomasses aériennes totales estimées des peuplements ont été désignées lente, intermédiaire et rapide et étaient de 98,7, 148,7 et 203,7 $Mg \cdot ha^{-1}$ respectivement; les estimés de l'accroissement de la biomasse pour les 5 années antérieures étaient de 8,9, 12,6 et 12,3 $Mg \cdot ha^{-1} \cdot an^{-1}$ respectivement. Le peuplement à croissance lente avait une plus forte proportion de sa biomasse aérienne dans ses branches et une plus faible proportion dans la tige comparé aux peuplements à croissance intermédiaire et rapide. Les différences d'accroissement en biomasse étaient dues principalement à la croissance de la tige plutôt qu'à la croissance de la cime. La biomasse totale souterraine était la plus élevée dans le peuplement à croissance rapide, la différence étant due aux racines >5 mm de diamètre; la masse des racines <5 mm était plus élevée dans les peuplements à croissance lente et intermédiaire. Les racines >5 mm compaient pour environ 77% de la biomasse racinaire totale pour les peuplements à croissance lente et intermédiaire alors qu'elles comptaient pour 90% dans les peuplements à croissance rapide. Les accroissements des racines >5 mm étaient de 2,2, 2,5 et 3,0 $Mg \cdot ha^{-1} \cdot an^{-1}$ dans les peuplements à croissance lente, intermédiaire et rapide respectivement. Le ratio de productivité sur l'azote foliaire total suggère que l'azote est la principale ressource limitante dans le peuplement à croissance intermédiaire. Le peuplement à croissance rapide, avec un indice de surface foliaire de 50% plus élevé que les autres peuplements, est probablement limité par la lumière. Le sol du peuplement à croissance lente présente des problèmes d'anaérobiose durant une certaine partie de l'année, pnénomène qui peut restreindre la profondeur d'enracinement et de cette façon, peut induire des stress hydriques durant le sécheresse d'été.

[Traduit par la revue]

Introduction

In this study, we compare leaf area, biomass distribution and increment, and growth efficiency among three adjacent 22-year-old Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) plantations with widely differing early growth rates. While such comparisons have often been made among stands of different ages or among stands occupying different environments (e.g., Turner and Long 1975; Keyes and Grier 1981; Binkley 1983), detailed studies of local variability among stands of the same age are rare. Knowledge of local patterns in productivity and, where possible, their environmental correlates, is essential to accurate forestwide yield estimates and planning.

Stand and site characteristics

The three plantations occupy an area of about 51 ha on the properties of the Weyerhaeuser Company, 3.2 km southwest of Bellfountain, Benton County, Oregon (44°20′N, 123°21′W). The area, a former agricultural site, was planted with Douglas-fir seedlings in 1960 (2-m spacing) for Christmas tree and timber production. The stand designations used throughout this paper, slow, intermediate, and fast, refer to early differences in site productivity suggested by basal area and stand heights rather than to current growth rates. Basal areas, average height and dbh, and number of trees per hectare in 1981 are given in Table 1. At that time, the fast stand had 20% and 50% greater basal area than the intermediate and slow stands, respectively.

Despite large differences in stocking density and average tree size among stands, relative density, an integrated measure of tree size and stocking density that is correlated to intertree competition (Drew and Flewelling 1979; Perry 1985), was similar: 0.38, 0.42, and 0.44, respectively, for the slow, intermediate, and fast stands. According to Drew and Flewelling (1979), crown closure in Douglas-fir stands occurs at a relative density of about 0.15, and competition-related mortality begins at some point after 0.55. Relative densities in the range found in this study indicate moderate competition for space, but probably not enough to warrant thinning (Espinosa Bancalari 1985).

No reliable stand histories are available, but it appears that the fast and slow stands were thinned and pruned during 1968–1970, that the intermediate stand was selectively thinned in 1970, and that all sites

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were prepared by light scarification or burn and initial spraying (one or two times) for grass control.

The stands are adjacent at 250- and 300-m elevation and have similar topography. Slopes range from 5 to 30% in the slow stand, from 5 to 15% in the intermediate stand, and from 4 to 12% in the fast stand. The slow stand lies immediately upslope from the fast stand, and the intermediate stand, about 200 m east, spans roughly the same elevation range as the other two. The climate is wet and mild, mean annual temperature averaging 8 to 9°C, and precipitation not exceeding 1500–1600 mm annually, most of it in rainfall during winter months (Knezevich 1975). Neither the fast nor slow stand contained understory vegetation, and the intermediate stand had only scattered patches of grasses and forbs in light gaps. Data on soil nitrogen (N) and phosphorus (P) (Espinosa Bancalari 1985) indicate differences in soil fertility among the stands (Table 1). The intermediate stand has the highest soil N and P concentrations, the slow stand the lowest. When adjusted for bulk density, which was highest in the slow stand and lowest in the intermediate stand, these rankings still held, but differences were narrowed (Table 1). Nevertheless, the intermediate stand has about 25% more N and 40% more P in the top 15 cm of mineral soil than the slow stand.

In a preliminary investigation, Dr. Joel A. Norgren described the soils as follows (personal communication).

The fast stand

Five of six plots in this stand contain soils close to Jory silty clay loam: well-drained, red, clayey soils, approximately 1.5 m deep to very soft, weathered, micaceous sandstone. These intergrade to Honeygrove silty clay loam, a similar red, clayey soil that receives 1500 mm or more average annual rainfall. Honeygrove soils are mapped approximately 0.8 km west of this stand. A southwest corner plot contains soil approximating Bohannon gravelly loam, 0.5 m deep to soft,weathered, micaceous sandstone. This plot is near a soil boundary and is not representative of the stand. The USDA Soil Survey of the Benton County Area, Oregon, shows the stand as Bellpine silty clay loam, a red clayey soil less than 100 cm deep to soft weathered sandstone.

The intermediate stand

All plots examined in this stand have soil similar to the Jory silty clay loam of the fast stand, but depth to weathered sandstone is somewhat greater, and the soils are somewhat more uniform.

The slow stand

Soils of this stand are the most variable. Five of seven plots are waterlogged for part of the wet season (mottled at 45- to 60-cm depth). Effective rooting depth is therefore less than in the other stands. In areas adjacent to the slow stand, trees are dead or dying as a result of very wet soil. One plot in the slow stand has moderately deep (50–100 cm), well-drained, red, clayey soils (Bellpine silty clay loam) on which effective rooting is limited by soil depth rather than poor drainage. Only one plot in this stand contains Jory silty clay loam similar to that in the other stands. The wet soils that predominate come closest to Dupee silt loam and Hazelair silt loam, neither of which has a woodland suitability rating.

Methods

During September 1981, dbh was measured on every tree in each of 55 0.01-ha plots located systematically within the three stands. Either four of five diameter classes (6- to 7-cm intervals) were designated on the basis of diameter distribution in each stand. Forty sample trees were selected by stratified random sampling from these size classes, 16 in each of the slow and intermediate stands, and 8 in the fast stand, which was shown by cruise plot data to have more uniform size distribution. Sampling intensity in a given diameter class was proportional to its frequency in the stand. Sampling was stratified by tree size because random sampling may include too few large trees that in terms of biomass are more important than small trees (Cunia 1979).

Aboveground biomass sampling

In August 1982, before felling, trees were marked and diameters

TABLE 1. Stand descriptors and soil characteristics of three adjacent 22-year-old Douglas-fir stands with different early growth rates in the Oregon Coast Range

Stand	Stand descriptors*					Soil characteristics†				
	Density (trees/ha)	dbh (cm)	Basal area (m^2/ha)	Height (m)	Volume (m^3/ha)	Bulk density (g/cm^3)	Nitrogen (%)	Phosphorus (%)	Nitrogen (kg/ha)	Phosphorus (kg/ha)
Slow	1030 (110) *b*	18.7 (0.7) *c*	29.9 (2.1) *c*	15.9 (0.9) *b*	188	1.27 (0.02) *b*	0.093 (0.006) *b*	0.052 (0.005) *b*	1772	800
Intermediate	770 (41) *a*	24.0 (0.4) *b*	36.3 (0.8) *b*	17.4 (0.3) *a*	242	1.13 (0.04) *a*	0.131 (0.005) *a*	0.067 (0.001) *a*	2220	1136
Fast	690 (39) *a*	28.4 (0.5) *a*	44.1 (1.4) *a*	18.5 (0.5) *a*	310	1.22 (0.03) *ab*	0.113 (0.004) *c*	0.057 (0.003) *c*	2068	1043

NOTE: Standard error of the mean is in parentheses. In each column, values with the same letter do not differ significantly ($p < 0.05$, Tukey's test).
*Based on data collected in 1981 by Weyerhaeuser, 1 year before this study. Dbh is arithmetic mean.
†Means of 10 samples per stand of the mineral content of the <2-mm fraction in the top 15 cm of the soil profile (from Espinosa Bancalari 1985).

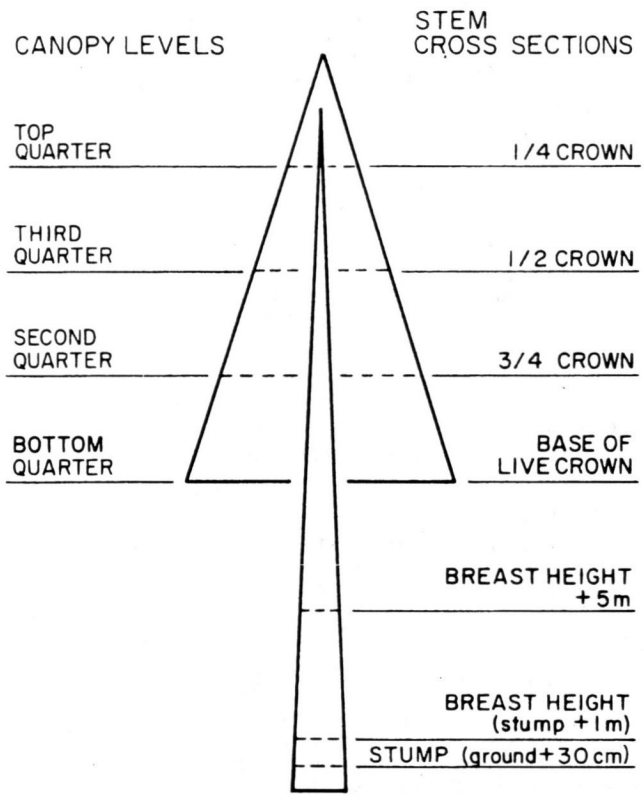

FIG. 1. Schematic diagram of sampling points in the tree crown and stem.

were measured at 30 cm and 1.30 m above the soil surface. After felling, the base of the live crown was determined, and total tree height (including stump height) and canopy length were recorded. A 2 to 4 cm thick disk was cut at stump, breast height, and thereafter at 5-m intervals to the base of the live crown. The crown was divided into quarters along the main stem, and cross sections were cut at the lower end of each (Fig. 1). Stem cross sections were weighed in the field and used for determining green weight : dry weight ratios, bark weight, bark thickness, specific gravity of wood, volume, age, sapwood thickness, and radial increment for each of the previous 5 years.

All branches were removed and weighed fresh in the field. A subsample of five branches within each crown quarter was randomly selected for determining dry-weight conversions.

The 20 branches from each tree were stored in a cold room at 3°C before processing. All twigs were clipped from branches and weighed with the needles. Subsamples of twigs were taken at random from each quarter for computing dry weight : fresh weight ratios of twigs and of needles. Needles were removed from all twigs, and twigs and needles weighed separately before being dried at 70°C for 48 h. After drying, needles and twigs were weighed again. A subsample of fresh needles was kept for surface area determination with a Li-Cor Li-300 area meter. The ratios computed for estimations of dry weight of needles and twigs were (*i*) fresh weight of needles + twigs to fresh weight of total branch (wood, bark, twigs, needles), (*ii*) fresh weight of needles to fresh weight of twigs + needles, (*iii*) dry weight of needles or twigs to fresh weight of needles or twigs. The product of these ratios and the total weight of each quarter of each tree canopy gave foliage and twig dry weight for each crown quarter, and the sum of the four quarters gave the total weight of foliage and twigs per tree. The projected leaf surface area of each crown section was computed by multiplying foliar dry weight by specific leaf area (fresh leaf area/needle dry weight). Total projected leaf area of the whole tree was obtained by summing section estimates.

Branch weight was determined in the same way as weight of twigs and needles; however, dry weight : fresh weight ratio of the stem cross section at the top of the crown was used because no dry weight : fresh weight ratio was estimated for branches. Since no significant differences were found among stands, a single value of 0.428 was applied to all.

TABLE 2. Biomass equations derived from pooled site data from three adjacent 22-year-old Douglas-fir stands with different early growth rates

Y	*a*	*b*	R^2	SEE	*E*
Foliage	−6.0934	2.7229	0.93	0.24	1.27
Twigs	−6.8020	2.7361	0.93	0.23	1.26
Branches	−5.7108	2.6788	0.92	0.24	1.27
Total crown	−5.0145	2.7060	0.93	0.23	1.26
Stem wood	−4.7470	2.9674	0.89	0.32	1.38
Stem bark	−5.6097	2.7009	0.85	0.34	1.40
Total stem	−4.4346	2.9216	0.89	0.32	1.38
Total aboveground	−3.9371	2.8427	0.93	0.23	1.26

NOTE: Equations are of the form $\ln W = a + b \ln \text{dbh}$ for the different dependent variables (W, in kg) on breast height diameter (dbh, in cm), where a and b are regression coefficients, R^2 is the coefficient of determination, SEE is the standard error of the estimate, and E is the relative error. Corrections for logarithmic bias (Baskerville 1972) were applied to all regressions.

Wood density of stem cross sections was determined in the laboratory by immersing fresh sections in water to obtain volume, then oven-drying and weighing them (Hush *et al.* 1972). Stem wood and total stem volume were computed from field measurements of stem dimension according to the geometric form of the tree stem portion (Hush *et al.* 1972): stump volume as a cylinder, the breast height section as a frustum of a neiloid, the sections between breast height and the third quarter of the crown as frustums of a paraboloid (Smalian's formula), and the top section of the crown as a paraboloid. The product of stem section volume and specific gravity gave the dry weight of stem wood. The difference between the total dry weight and the wood weight + total volume + wood volume of a stem cross section provided an estimate of bark dry weight and volume. Dry weight of breast height and crown sections was calculated from field weights and fresh weight : dry weight ratios of stem cross sections.

Foliage was analyzed for N content by the micro-Kjeldahl technique and for P content by the molybdophosphoric method.

Belowground biomass sampling

In September 1983, total root biomass was estimated from values derived from excavation and soil coring. Four stumps of previously felled trees in each stand were randomly selected for determinations of coarse root biomass. Stumps with attached roots were extracted by backhoe, cleaned with hand tools, and cut at ground level for weighing on a 200-kg scale. Lateral roots were removed and separated into five size classes: <2, 2–5, 5–20, >50 mm. Roots broken off during excavation were hand extracted and stored with the others for dry weight determination. Two 5 cm thick disks were removed along the taproot, weighed green, and oven-dried at 75°C to constant weight before moisture content determination. Fresh weight of roots greater than 50 mm in diameter was measured in the field.

Biomass of roots <5 mm in diameter was determined from small and fine roots sorted from soil cores taken in late September 1983 during the summer drought. Cores were sampled with a steel tube (4 cm inside diameter at the mouth) hammered 45 cm into the soil and extracted with a jack. Sampling sites were located close to trees sampled for aboveground biomass. Ten soil samples each were taken in the slow and intermediate stands and 6 in the fast stand, each sample a composite of four soil cores taken equidistant from the center of a rectangle formed by four trees. Samples were then returned to the laboratory in paper bags for sorting.

In the laboratory, each soil sample was separated through a set of screens (pore size >4.00, 1.651, 0.833, and 0.495 mm) into homogeneous particle fractions. After root material was hand sorted from each sieve, material passing the 0.495 mm screen was floated in water and picked with tweezers. Roots extracted from the soil cores were separated with vernier calipers into fine roots (<2 mm) and small

TABLE 3. Estimated aboveground and belowground biomass in three adjacent 22-year-old Douglas-fir stands with different early growth rates

Biomass component	Slow stand		Intermediate stand		Fast stand	
	$Mg \cdot ha^{-1}$	% of total	$Mg \cdot ha^{-1}$	% of total	$Mg \cdot ha^{-1}$	% of total
Aboveground						
Foliage	8.9 (1) *b*	6.7	10.7 (1) *b*	5.6	14.5 (1) *a*	5.7
Twigs	4.4 (0.5) *b*	3.3	6.0 (0.3) *ab*	3.1	6.9 (0.4) *a*	2.7
Branches	11.3 (1) *a*	8.5	14.6 (0.7) *a*	7.7	16.0 (0.9) *a*	6.2
Total crown	24.6 (3) *b*	18.5	31.3 (2) *ab*	16.4	37.4 (2) *a*	14.6
Stem wood	62.4 (8) *c*	46.9	100.5 (5) *b*	52.7	140.7 (7) *a*	54.9
Stem bark	11.7 (1) *c*	8.8	16.9 (1) *b*	8.9	25.6 (1) *a*	10.0
Total stem	74.1 (9) *c*	55.7	117.4 (6) *b*	61.6	166.3 (8) *a*	64.9
Total aboveground	98.7 (12) *c*	74.2	148.7 (8) *b*	78.0	203 (11) *a*	79.5
Belowground						
Fine roots (<2 mm)	5.9 (0.7) *a*	4.4	7.7 (1) *a*	4.0	4.2 (0.6) *b*	1.6
Small roots (2–5 mm)	2.2 (0.2) *a*	1.7	1.9 (0.2) *ab*	1.0	1.1 (0.2) *b*	0.4
Large roots (>5 mm)	26.3 (4) *b*	19.8	32.4.(2) *b*	17.0	47.2 (3) *a*	18.4
Total belowground	34.4 (4) *b*	25.9	42.0 (2) *b*	22.0	52.5 (3) *a*	20.5
Total tree	133.1 (17) *c*		190.7 (10) *b*		256.2 (13) *a*	
Sapwood basal area ($m^2 \cdot ha^{-1}$)	15.7 (1.6) *a*		18.8 (0.9) *a*		19.5 (0.9) *a*	
Leaf area index*	6.0 *b*		7.5 *b*		10.1 *a*	

NOTE: Standard error of the mean is in parentheses. In each row, means with the same letter do not differ significantly ($P < 0.05$, Tukey's test).
*Allometric equations used to derive leaf area index are given in Espinosa Bancalari *et al.* (1987) and Espinosa Bancalari (1985).

roots (2 to 5 mm). Those larger than 5 mm were discarded. After washing, all fine and small roots were oven-dried at 75°C and then weighed to the nearest milligram. No correction was made for adhering soil particles. Fine root and small root biomass was determined from soil cores and expanded to a per hectare basis by dividing the weight of the roots by the area of the soil core. The resulting values, divided by the number of trees per hectare, yielded the average fine root and small root biomass per tree.

Fine roots were analyzed for N content by the micro-Kjeldahl technique and for P content by the blue molybdophosphoric method.

Data analysis

Weight per tree was expressed in the linear form of the allometric equation: $\ln W = a + b \ln D$, where W is the dry weight of the tree component (in kg), a and b the regression coefficients, and D the dbh (in cm). Regressions were corrected for logarithmic bias (Baskerville 1972), giving the following corrected weight estimator: $W = \exp(S^2/2) \exp(a + b \ln D)$, where S^2 is the mean square error. The relative closeness of the regression was estimated by the relative error E, the antilog of the standard error of estimate (Whittaker and Woodwell 1971). An antilog value of 1.14, for example, would indicate an expected error range from $W/1.14$ to $1.14W$, or from −12% to +14% of the predicted value of W.

Data from the sample trees in each stand were used to derive allometric equations relating the weight of various tree components to dbh. The giant-size regression model (Cunia 1973) was used to discern possible differences among equations for the three stands. None appeared at the $p < 0.05$ level; therefore, equations derived from sample trees in all three stands (Table 2) were applied to Weyerhaeuser cruise plot data in order to derive estimates of biomass and biomass components for the three stands. LAI was estimated similarly (equations in Espinosa 1985; Espinosa Bancalari *et al.* 1987).

Biomass increment during the 5 years before sampling was estimated for each component by predicting dbh (outside bark) in 1977 as a function of dbh (inside bark) in 1977, calculating 1977 biomass as a function of dbh (outside bark) in 1977, and then calculating the difference in biomass between 1977 and 1982. These increments were divided by five to obtain the average annual increment per tree. Regression of increment values against the current dbh yielded equations that were applied to trees in the previously established cruise plots within each stand. Stand weights for each biomass component were then derived as the sum of individual trees within cruise plots (divided by plot area to obtain per hectare values).

Data were subjected to analysis of variance, and stand means were compared by the Tukey–Kramer method for multiple comparisons at $P < 0.05$. Analyses in this study were performed by means of the Statistical Analysis System (SAS Institute Inc. 1982).

Results

Biomass distribution and increment

Total biomass was 133.1, 190.7, and 256.2 $Mg \cdot ha^{-1}$ in the slow, intermediate, and fast stands, respectively (Table 3). The proportion in crowns (14 to 19%) and roots (20 to 26%) correlated negatively with total biomass; however, the fast stand supported about 40% more leaf weight per unit weight of branches and small and fine roots (0.51 $Mg \cdot Mg^{-1}$) than the slow and intermediate stands (0.37 and 0.35 $Mg \cdot Mg^{-1}$, respectively). This was due to a lower proportion of branch weight and lower absolute weight of small and fine roots in the fast stand.

Sapwood basal area does not differ significantly among the stands (Table 3), although, because of height differences, sapwood volumes probably do. Nevertheless, even with the probable differences in sapwood volume, it seems likely that the fast stand carries significantly greater photosynthesizing biomass per unit of respiring biomass than the other stands.

Average yearly biomass increment between 1977 and 1982 (without fine and small roots because past values could not be estimated) was 11.1, 15.0, and 15.3 $Mg \cdot ha^{-1} \cdot year^{-1}$ for the slow, intermediate, and fast stands, respectively (the latter two not significantly different). Differences were primarily due to stem growth; crown and coarse-root increment did not differ significantly (Table 4). The ratio of aboveground biomass increment to leaf area during this period averaged 184, 211, and 147 $g \cdot m^{-2} \cdot year^{-1}$ for the slow, intermediate, and fast stands,

TABLE 4. Estimated mean annual biomass increment* between ages 17 and 22 years and its distribution in three adjacent 22-year-old Douglas-fir stands with different early growth rates

Biomass component	Slow stand		Intermediate stand		Fast stand	
	$Mg \cdot ha^{-1}$	% of total	$Mg \cdot ha^{-1}$	% of total	$Mg \cdot ha^{-1}$	% of total
Foliage	0.7 (0.09) *a*	6.3	0.9 (0.04) *a*	6.0	1.0 (0.06) *a*	6.5
Twigs	0.4 (0.05) *a*	3.6	0.5 (0.02) *a*	3.3	0.5 (0.03) *a*	3.3
Branches	1.0 (0.12) *a*	9.0	1.2 (0.06) *a*	8.0	1.1 (0.06) *a*	7.2
Total crown	2.1 (0.26) *a*	18.9	2.6 (0.13) *a*	17.3	2.6 (0.15) *a*	17.0
Stem wood	5.9 (0.73) *b*	53.2	8.5 (0.41) *a*	56.7	8.4 (0.47) *a*	54.9
Stem bark	0.9 (0.10) *b*	8.1	1.4 (0.07) *a*	9.3	1.3 (0.07) *a*	8.5
Total stem	6.8 (0.83) *b*	61.3	9.9 (0.48) *a*	66.0	9.7 (0.54) *a*	63.4
Total aboveground	8.9 (1.1) *b*	80.2	12.5 (0.60) *a*	83.3	12.3 (30.67) *a*	80.4
Roots (>5 mm)	2.2 (454) *a*	19.8	2.5 (0.12) *a*	16.7	3.0 (0.17) *a*	19.6
Total tree	1.1 (1.5) *b*		15.0 (0.72) *a*		15.3 (0.85) *a*	

*Growth period 1977–1982. There was no indication that mortality occurred in this period. In each row, means with the same letter do not differ significantly ($P < 0.05$, Tukey's test).

respectively. (Past leaf areas were estimated by applying 1982 specific leaf area values to estimated leaf biomass.)

Foliar and fine root nutrients

Foliage N concentration tended to increase with increasing height in the crown (Table 5). It differed only in the base crown quarter, where concentrations were lower in the slow than in the fast stand. N concentration in the crown as a whole was similar for all stands, averaging about 1.3%. Although the difference was not significant for any single crown level, P concentrations were consistently lower in the fast than in the other stands; and for the whole crown, the difference between the fast and intermediate stands became statistically demonstrable. The ratio of N:P in foliage varied from 7.5 in the intermediate stand to 8.9 in the fast stand. This ratio is a better indicator of N deficiency in loblolly pine than is foliage N concentration (Comerford and Fisher 1984). P content of fine roots did not differ among the stands. N content of fine roots was similar for the slow and intermediate stands, but significantly higher for the fast stand.

If we assume 1982 N concentrations, the ratio of average yearly biomass increment to total foliage N, a measure of efficiency of N use (Ågren 1983), was 102, 118, and 81 $Mg \cdot Mg^{-1}$ for the slow, intermediate, and fast stands, respectively. The lower value for the fast stand probably reflects light limitation due to the higher leaf area. Because the slow and intermediate stands had the same leaf area, the lower value of the former must reflect another limiting resource or condition, perhaps related to anaerobic soils.

Discussion

Estimates of total biomass of the three stands and biomass distribution among tree components (Table 3) are within the range of values reported for other northwest Douglas-fir stands of comparable age, basal area, and site index (Tables 6 and 7). Percentages of bole biomass, 79%, 82%, and 85% of total aerial biomass in the slow, intermediate, and fast stands, respectively, are close to those reported for other Douglas-fir stands. The proportion of biomass maintained in stem appears to increase with stand age, density, and site quality. Turner and Long (1975), working in a series of stands growing on low-quality sites, found that foliar and total crown biomass increased until crown closure, and then reached a steady state between 40 and 50 years, depending upon stand density. From that point, boles formed an increasing proportion of aboveground biomass. In a 450-year-old stand on the H. J. Andrews Experimental Forest in the central Cascade Mountains, crowns constituted only 10.8% of aboveground biomass (Grier *et al.* 1974). Binkley (1983) found that a much greater proportion of total Douglas-fir biomass was allocated to stem on a fertile site than on an infertile site. Lack of difference among our stands in the allometric relation between dbh and foliage biomass probably reflects the fact that, despite different tree sizes and stocking densities, relative densities (Drew and Flewelling 1979) were similar.

In contrast to what is usually found in studies of tree allometry, foliage biomass in our stands was predicted more accurately from dbh than was stem biomass. We cannot say why this is so. Perhaps the method for estimating stem biomass (different geometric formulas for different stem sections) was less precise than the method for estimating crown components, thereby introducing an artifact. Perhaps environmental differences between stands, or the greater structural heterogeneity of the slow and intermediate stands relative to the fast, affected form class to a greater extent than crown components.

Like estimates of total biomass, estimates of fine root and small root biomass in this study were similar to those obtained in other Douglas-fir stands in the Pacific Northwest (Table 7). Mean values (Keyes and Grier 1981) of 2.2 and 1.8 $Mg \cdot ha^{-1}$ for small roots on low site and high site stands, respectively, are almost identical to the values we found in the slow and intermediate stands (2.2 and 1.9 $Mg \cdot ha^{-1}$). The fast stand had only 1.1 $Mg \cdot ha^{-1}$ in that size class. Fine root biomass in the slow stand (5.9 $Mg \cdot ha^{-1}$) is less than the 8.3 $Mg \cdot ha^{-1}$ reported by Keyes and Grier for a poor site, but their value is close to that for the intermediate stand (7.7 $Mg \cdot ha^{-1}$). If small root and fine root biomass are combined, the 5.3 $Mg \cdot ha^{-1}$ for the fast stand is similar to the values found on a better site by Keyes and Grier, in a 70-year-old Douglas-fir stand by Santantonio (1982), and in a younger stand by Fogel and Hunt (1983). The 8.1 $Mg \cdot ha^{-1}$ of the slow stand is close to that reported for two older stands (Santantonio 1982), and values for the intermediate stand compare well with those for an old growth Douglas-fir stand (Santantonio *et al.* 1977). Fine root biomass and fine root N content of our stands are also similar to the values Nadelhoffer *et al.* (1985) reported for deciduous and coniferous stands in

Wisconsin. The proportion of tree biomass in roots previously reported for forest ecosystems ranges between 15 and 25% (Assmann 1970; Harris *et al.* 1980), which compares favorably with the 21 to 27% range of this study.

Considering the formidable sampling problems and consequent large error associated with root studies, the values summarized in Table 7 are remarkably similar. Roots less than 5 mm constituted 6.1%, 5.0%, and 2.1% of the total tree biomass in the slow, intermediate, and fast stands, respectively, a higher proportion than that found by Keyes and Grier (1981) and Fogel and Hunt (1983) in older stands. This suggests that, like foliage, fine root biomass may peak early in stand life and thereafter remain relatively constant, forming a decreasing proportion of total biomass as stands age.

Although our finding of fewer fine roots on more productive sites is consistent with those of Keyes and Grier (1981), it does not necessarily follow that productive stands allocate less carbohydrate to fine roots. Nadelhoffer *et al.* (1985) have, in fact, argued the opposite: that lower standing crops on good sites are due to faster turnover rather than to lower allocation. Comparisons between the slow stand and the other two of this study must be made cautiously, because in the deeper, better aerated soils of the latter, a higher proportion of total root biomass may be below the sample depth (45 cm).

Values for annual biomass increment in this study compare well with those for other young Douglas-fir stands in the Pacific Northwest (Table 6). The ratios for aboveground increment: aboveground tree biomass (AI:AB) were greater in the three stands than in older stands studied by Keyes and Grier (1981), Fogel and Hunt (1983), and Turner and Long (1975), but comparable to those of Binkley (1983) and Turner and Long (1975) in stands of the same age. AI:AB in the three stands are among the highest reported by O'Neill and DeAngelis (1981) for the International Biological Program (IBP) Woodlands Data Set, comparable to those of other managed evergreen and beech plantations.

Stands in this study allocated more net aboveground growth to stem than to crown, and more to branches than to foliage than other stands shown in Table 6. Wood increment (branch plus bole) per unit of leaf biomass was two to three times greater than in any of the needle-leaved stands of the Woodlands Data Set (O'Neill and DeAngelis 1981). Net foliage increment was lower than in other Douglas-fir studies (Table 6), both in absolute terms and in percentage of tree foliage biomass. It is impossible to say whether the difference is real or a result of differing sampling and estimation procedures. One source of error in this study is the assumption of constant allometry over a 5-year period. As trees are likely to maintain proportionally more in crowns and less in stems at the beginning than at the end of the period, crown increment is probably overestimated and bole increment underestimated, which would increase the discrepancy between this study and others. The ratio of stem production to foliage production in the Douglas-fir stands shown in Table 6 ranged from 1.39 to 1.22 $Mg \cdot Mg^{-1}$, with a tendency to decline with age and increase with site quality. Total aboveground biomass increment per unit of foliage biomass ranges from 0.70 to 1.74 $Mg \cdot Mg^{-1}$, with our stands in the middle of the range.

Although aboveground and belowground compartments of the slow stand of this study have almost half the biomass of the fast, net biomass increments of the two differs by only 27%. If fine root increment were included, the difference would probably be smaller; fine root production in the low and high

TABLE 5. Mean percent dry weights of nitrogen and phosphorus in foliage and fine roots of three adjacent 22-year-old Douglas-fir stands with slow, intermediate, and fast early growth rates

Component	Nitrogen						Phosphorus					
	Slow stand	*n*	Intermediate stand	*n*	Fast stand	*n*	Slow stand	*n*	Intermediate stand	*n*	Fast stand	*n*
Foliage												
Base crown quarter	1.104 (0.12) *b*	9	1.114 (0.05) *ab*	3	1.399 (0.18) *a*	2	0.163 (0.010) *a*	9	0.182 (0.007) *a*	3	0.155 (0.015) *a*	2
Second crown quarter	1.178 (0.05) *a*	8	1.279 (0.04) *b*	16	1.099 (0.07) *ab*	5	0.152 (0.005) *a*	8	0.160 (0.006) *a*	16	0.147 (0.009) *a*	5
Third crown quarter	1.433 (0.08) *a*	10	1.332 (0.05) *a*	4	1.207 (0.06) *a*	8	0.147 (0.016) *a*	10	0.153 (0.010) *a*	4	0.148 (0.009) *a*	8
Top crown quarter	1.429 (0.10) *a*	3	1.600 (0.27) *a*	8	1.539 (0.18) *a*	2	0.177 (0.018) *a*	3	0.213 (0.010) *a*	8	0.140 (0.015) *a*	2
Mean, all crown levels	1.286 (0.08) *a*	30	1.331 (0.10) *a*	31	1.311 (0.07) *a*	17	0.160 (0.007) *ab*	30	0.177 (0.010) *a*	31	0.147 (0.003) *b*	17
Fine roots (<2 mm diameter)	0.786 (0.02) *b*	10	0.780 (0.02) *b*	10	0.887 (0.002) *a*	6	0.138 (0.003) *a*	10	0.136 (0.006) *a*	10	0.148 (0.010) *a*	6

NOTE: Standard error of the mean is in parentheses. In each row, percentages of nutrient content with the same letter do not differ significantly ($P < 0.05$, Tukey's test).

TABLE 6. Biomass accumulation and increment in several young stands of Douglas-fir in the Pacific Northwest

	Washington							Oregon			
									This study*		
	Binkley 1983		Turner and Long 1975			Keyes and Grier 1981		Fogel and Hunt 1983	Slow stand	Intermediate stand	Fast stand
Stand descriptors											
Age (years)	23	23	22	30	42	40	40	35–50	22	22	22
Stand density ($Mg \cdot ha^{-1}$)	650	1860	2756	1800	1289	—	—	1626	1030	770	690
Site index (m)†	24.0	45.0	25.6	25.6	25.6	24.4	39.6	26.8	31.4	35.4	38.1
Basal area ($m^2 \cdot ha^{-1}$)	10.5	54.1	42.4	34.4	44.5	—	—	52.1	30.4	36.9	45.0
Aboveground biomass ($Mg \cdot ha^{-1}$)											
Foliage	9.6	15.5	5.0	6.5	9.4	10.0	16.0	14.7	8.9	10.7	14.5
Branches	13.3	24.6	8.2	10.2	13.7	17.1	27.7	22.8	11.3	14.6	16.0
Stem	35.0	218.2	113.3	145.9	206.2	221.5	424.0	263.3	74.1	117.4	166.3
Total	57.9	258.3	126.5	162.6	229.3	248.6	467.7	300.8	94.3	142.7	196.8
Belowground biomass ($Mg \cdot ha^{-1}$)											
Fine roots (<5 mm)						10.5	4.5	5.9	8.1	9.6	5.3
Large roots (>5 mm)						47.1	83.6	61.5	26.3	32.4	47.2
Total						57.6	88.1	67.4	34.4	42.0	52.5
Total biomass ($Mg \cdot ha^{-1}$)						306.2	555.8	368.2	128.7	184.7	249.3
Aboveground biomass increment ($Mg \cdot ha^{-1} \cdot year^{-1}$)											
Foliage	1.9	3.1	2.1	2.1	2.4	2.0	3.2	2.7	0.8	0.9	1.0
Branches	0.9	1.8	0.5	0.5	0.5	0.2	0.6	1.0	1.0	1.2	1.1
Stem	4.1	18.3	6.1	5.0	3.7	5.1	9.9	7.0	6.8	9.9	9.7
Total	6.9	23.2	8.7	7.6	6.6	7.3	13.7	10.7	8.6	12.0	11.8
Belowground biomass increment ($Mg \cdot ha^{-1} \cdot year^{-1}$)											
Fine roots (<5 mm)						7.0	2.5	5.7	—	—	—
Large roots (>5 mm)						1.1	1.6	—	2.2	2.5	3.0
Total						8.1	4.1	5.7	2.2	2.5	3.0
Total biomass increment ($Mg \cdot ha^{-1} \cdot year^{-1}$)						15.4	17.8	16.4	10.8	14.5	14.8
Component ratios											
Foliage biomass/fine root biomass	—	—	—	—	—	0.95	3.6	2.5	1.1	1.1	2.7
Stem biomass/aboveground biomass	0.60	0.84	0.90	0.90	0.90	0.89	0.91	0.88	0.79	0.82	0.85
Belowground biomass/total biomass	—	—	—	—	—	0.19	0.16	0.18	0.27	0.23	0.21
Wood (stem and branch) increment/foliage biomass	0.52	1.30	1.32	0.85	0.45	0.53	0.66	0.54	1.09	1.31	0.90
Aboveground increment/foliage biomass	0.72	1.50	1.74	1.17	0.70	0.73	0.86	0.73	1.05	1.30	0.86
Total biomass increment/foliage biomass	—	—	—	—	—	1.54	1.11	1.12	1.31	1.56	1.07

*Increment efficiencies of the three stands are based on average biomass and biomass increments during the 5 years previous to sampling.
†50-year base (King 1966).

TABLE 7. Douglas-fir fine root and small root biomass in Pacific Northwest stands

Location	Stand age (years)	50-year site index* (m)	Sample depth (cm)	Root biomass ($Mg \cdot ha^{-1}$)				Biomass of <5 mm roots as % of total	Source
				Total	<2 mm	2–5 mm	<5 mm		
Oregon	450	—	100	822.8	—	—	9.7	1.2	Santantonio *et al.* 1977
	170	—	60	532.0	—	—	7.7	1.4	Santantonio 1982
	120	—	60	531.0	—	—	7.4	1.4	Santantonio 1982
	70	—	60	422.0	—	—	5.8	1.4	Santantonio 1982
	35–50	26.8	—	375.9	—	—	5.9	1.6	Fogel and Hunt 1983
Washington	40	39.6	45	555.8	2.7	1.8	4.5	0.8	Keyes and Grier 1981
	40	24.4	45	306.2	8.3	2.2	10.5	3.2	Keyes and Grier 1981
Oregon	22	38.1	45	256.2	4.2	1.1	5.3	2.1	This study, fast stand
	22	35.4	45	190.7	7.7	1.9	9.6	5.0	This study, intermediate stand
	22	31.4	45	133.1	5.9	2.2	8.1	6.1	This study, slow stand

*50-year base (King 1966).

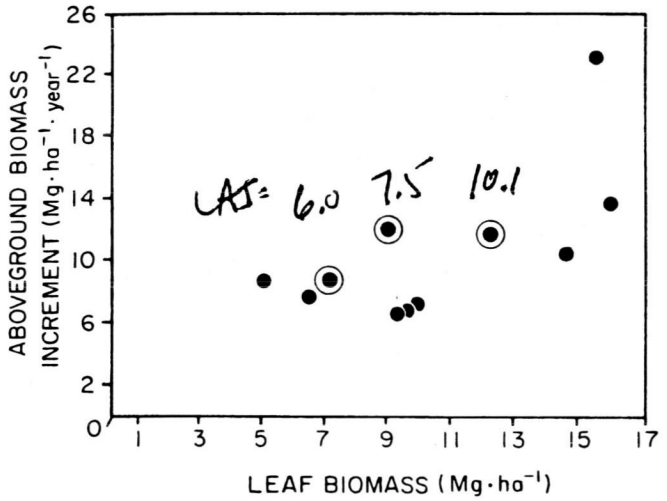

FIG. 2. Relation of aboveground biomass increment to leaf biomass of young Douglas-fir in the Pacific Northwest. Circled values are from this study, Table 6. Foliar biomass is adjusted to reflect the average during the 5 years previous to sampling in which the increment was calculated.

productivity sites of Keyes and Grier (1981) differed by only 13%. The intermediate and fast stands have nearly equal growth rates primarily because the smaller leaf biomass in the former is used more efficiently.

The 14.5 $Mg \cdot ha^{-1}$ of foliage in the fast stand is close to the upper range of leaf biomass reported by Parde (1980, after Tadaki 1966) for evergreen coniferous forest. The total biomass is almost twice that of the slow stand and the ratio between foliage and biomass of roots <5 mm is 2.5 times greater (Table 6). The projected leaf area index (LAI) of 10.1 $m^2 \cdot m^{-2}$ is less than that found in other studies of Douglas-fir in the Pacific Northwest (e.g., Gholz *et al.* 1976; Grier and Running 1977; Waring *et al.* 1978; Gholz 1982). However, Marshall and Waring (1986) believe that equations based on dbh overestimate LAI and that a maximum of 12 $m^2 \cdot m^{-2}$ for this species is realistic. As a stand approaches maximum leaf area, its growth efficiency declines. Waring and Schlesinger (1985) reported decreasing growth efficiency with increasing LAI in a thinning experiment in Douglas-fir stands on a good quality site. C. D. Tamm, Swedish Agricultural University, Uppsala, Sweden (cited by Waring and Schlesinger 1985) found a decrease in growth efficiency as LAI exceeded 8.0 in Swedish *Picea* and *Pinus* forests. Waring and Schlesinger (1985) estimate that aboveground biomass increment and wood production peak or reach a plateau at LAI 5 or 6 because of a corresponding peak in growth efficiency. Comparison of the intermediate and fast stands of this study suggests that a plateau indeed exists but it is unlikely to be the same throughout the Douglas-fir region. Figure 2 shows the relation between values for aboveground biomass increment and leaf biomass of the Douglas-fir stands compared in Table 6. The values do not include leaf-branch mortality or death of individuals (not a factor in this study), and therefore underestimate productivity. Excluding one high value for a high site stand (Binkley 1983), there appear to be two overlapping plateaus: one, including the slow stand, ranging from 5 to 10 $Mg \cdot ha^{-1}$ leaf biomass (LAI about 3.5 to 7.0) and a second, higher plateau, including the intermediate and fast stands, that ranges from 9 to 15 $Mg \cdot ha^{-1}$ (LAI about 4.5 to 10.5). Our intermediate stand uses foliage almost two times more efficiently than the other stands with similar foliage biomass.

All Douglas-fir stands shown in Table 6 produce more wood (bole plus branch) per unit of leaf biomass than the needle-leaved stands reported by O'Neill and DeAngelis (1981) for the IBP Woodlands Data Set. Wood production efficiency of the latter does not much exceed 0.45 $Mg \cdot Mg^{-1} \cdot year^{-1}$, whereas values for all but one of the Douglas-fir stands were higher, and four (including the intermediate and slow stands) had values equal to or greater than 1.0 $Mg \cdot Mg^{-1} \cdot year^{-1}$. These production values probably reflect site as well as species differences. Many of the IBP stands were boreal or montane spruce and fir forests. Wood production (bole plus branch) in our intermediate and fast stands is very close to the average reported by Jordan (1983) for tropical plantations.

In loblolly pine, a foliar N:P ratio of 14 to 15 is the critical point below which stands respond to N fertilization (Comferford and Fisher 1984). The "critical" N:P ratio is likely to vary with both species and site, however. In the Oregon Cascade Mountains, stands of the same age as those in this study are unresponsive to fertilization at N:P ratios as low as 5; however, the low N:P ratios are due to high foliar P rather than low foliar N (D. A. Perry, submitted for publication). For Douglas-fir in the Netherlands, 1.7% N and 0.15% to 0.20% P in current upper-crown foliage is considered a "critical" level below which growth is reduced by at least 10% (Mohren *et al.* 1986). Considering that all age classes of needles were sampled in our

study, the N and P concentrations in the foliage do not indicate serious deficiency in any of the stands. N production efficiencies suggest that, of the three, N is most limiting in the intermediate stand. Because of high LAI and low N production efficiency, it seems likely that light is the primary limiting factor in the fast stand. Its rapid early growth may have been due to shallower clayey surface soils, which would allow trees to reach available water in the underlying decomposed sandstone more quickly than trees in the intermediate stand.

Despite lower soil N in the slow stand, its relatively low N production efficiency indicates that some other factor is limiting growth. The anaerobic soils probably limit rooting depth, which, paradoxically, may prevent trees from reaching water in lower soil layers during the summer drought common to the area. Greater bulk density of soils in the slow stand would probably exacerbate this effect.

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