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Family Differences in Equations for Predicting Biomass and Leaf Area in Douglas-Fir (*Pseudotsuga menziesii* var. *menziesii*)

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ABSTRACT. Logarithmic regression equations were developed to predict component biomass and leaf area for an 18-yr-old genetic test of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco var. *menziesii*) based on stem diameter or cross-sectional sapwood area. Equations did not differ among open-pollinated families in slope, but intercepts assuming equal slopes did differ for equations predicting leaf, branch, or bark biomass, or leaf area. These results may be explained by family differences in partitioning between stemwood and bark and between stem and crown. Predictions of biomass and leaf area based on equations developed in this study differed from predictions based on equations from other studies by as much as a factor of two, suggesting that discretion is needed when applying equations to other sites at other stages of stand development and with other ranges of tree sizes. FOR. SCI. 39(4): 743–755.

ADDITIONAL KEY WORDS. Plant biomass, leaf area, partitioning, allometric equations, genetic variation.

ESTIMATES OF COMPONENT BIOMASS AND LEAF AREA are important input parameters for process-based models of tree growth (West 1987, McMurtie et al. 1989, Bassow et al. 1990, Korol et al. 1991) and are essential for studies of forest production, forest health, nutrient cycling, hydrology, wildlife habitat, and fire behavior (Waring 1985, Long and Smith 1988). Direct measurement of biomass and leaf area by destructive harvest and sampling, however, is time consuming and expensive, and forest biologists have commonly relied on indirect, nondestructive measurements. Frequently, allometric equations or ratios are used in which biomass or leaf area is related to easily measured stem traits; in particular, stem diameter or cross-sectional area of sapwood. Sapwood area is assumed to be the best predictor of leaf biomass or leaf area based on the idea that these are functionally related through the role of sapwood in conducting water and nutrients to the foliage (Waring et al. 1982). Good linear relationships between sapwood area and leaf biomass or leaf area have been reported (Grier and Waring 1974, Waring et al. 1977, Snell and Brown 1978, Whitehead 1978, Kaufmann and Troendle 1981, Espinosa Bancalari et al. 1987), but estimates based on sapwood area are sometimes no better than estimates based on basal area or diameter (Snell and Brown 1978, Brix and Mitchell 1983, Espinosa Bancalari et al. 1987). Researchers have also questioned the appropriateness of a linear model for stands that include a large range of crown classes (Dean and Long

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1986, Thompson 1989). Furthermore, the relation between sapwood area and leaf area or biomass may differ with growing conditions, including site (Whitehead 1978, Albrektson 1984, Espinosa Bancalari et al. 1987), stand density (Pearson et al. 1984, Brix and Mitchell 1983), associated species (Binkley 1984), and soil fertility (Brix and Mitchell 1983, Grier et al. 1984). The appropriateness of predicting biomass of stems and branches by equations developed from stands of different ages and sites has been similarly questioned (Helgerson et al. 1988).

Although relations may differ between stands, a single relation is generally assumed to be usable for estimating biomass and leaf area of trees within a stand. In this study, biomass and leaf area equations are developed for a single stand, a young Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco var. *menziesii*) genetic test, and equations are compared among families within the stand. In addition, equations developed in this study are compared with those of previous studies to evaluate the appropriateness of using equations developed at different sites.

MATERIALS AND METHODS

The study site was an 18-yr-old genetic test located in the Coast Range near Newport, OR (44°31'N, 123°52'W), at an elevation of 100 m. The test was established in February 1974 with 1-yr-old seedlings. Trees chosen for sampling for biomass components and leaf area were a random sample of 20 open-pollinated families from a systematic thinning of half the trees in the test. The parents originated from a narrow geographic and elevational range (an area of 8.5 km × 4.5 km and elevations of 225 m to 300 m with the exception of a single family which came from approximately 30 km further south and an elevation of 75 m). The range of seed source environments sampled by parents in this study is well within the range of sources within a typical plantation.

The experimental design was a randomized block design with multiple-tree noncontiguous plots. Study trees came from 6 blocks with 2 trees sampled per family per block for a total of 240 trees. Trees that were forked, had large ramicorn branches, or showed signs of past damage were not chosen for study. Mortality was low in the genetic test, and all study trees were surrounded by competitors. Spacing between trees was 2.4 m × 3.0 m for an effective stand density of 1,346 trees/ha. Site productivity was high (Site Class I, McArdle et al. 1961), with an average stem volume of 218 m^3/ha at the time of thinning. Trees had been in competition for several years before measurement; relative density was 0.40, well above the value at crown closure (0.15) but not yet at the point of commencement of self-thinning (0.55) (Drew and Flewelling 1979). Trees ranged in diameter from 9 to 26 cm with an average of 18 cm.

This study is part of a larger study looking at genetic variation and covariation in biomass partitioning, crown structure, and tree size. Only measurements concerned with biomass and leaf area are described here. Before harvest, breast height (1.3 m) was marked and stem diameter at that point (dbh) measured with a diameter tape. Trees were cut 10 cm above the ground. The base of the live crown was determined after felling, and the live crown was divided into thirds for sampling branches and foliage. All live branches from each crown third were removed and weighed fresh in the field. A random sample of two branches with foliage was then chosen from each crown third and weighed fresh, and a random

sample of needles was collected from each crown third and sealed in a plastic bag. The entire stem was weighed fresh in two parts (above and below the base of the live crown), 8-cm-thick disks were cut at 1.3 m and at the internode below the base of the live crown, and the disks were sealed in plastic bags.

Foliage and stem-disk samples were stored in a cold room at 1°C until processing. A subsample of foliage from each crown third was weighed fresh, dried to a constant weight (about 24 hr), and weighed again to estimate the ratio of dry to fresh weight. The drying temperature for all samples in the study was 80°C. The crown samples from each crown third were dried to a constant weight (about 3 days). Needles were then separated from branches and weighed separately to obtain both foliage and branch dry weights. Foliage fresh weight of each sample was estimated by dividing the foliage dry weight by the dry to fresh weight ratio. Branch fresh weight of each sample was estimated by subtracting the estimated foliage fresh weight from the crown fresh weight of the sample. Total foliage dry weight for each crown third was calculated by multiplying the total crown fresh weight for each crown third by the ratio of foliage to crown fresh weight by the ratio of foliage dry weight to fresh weight. Branch dry weight was similarly calculated. Total foliage or branch dry weight for each tree was estimated by summation over the three crown sections.

Single-sided, projected leaf area was measured on a fresh subsample of 60 needles per crown section per tree using an electronic area meter. Oven-dried weight of the subsample was measured, and specific leaf area determined as the ratio of projected leaf area per needle to dry weight per needle. The leaf area of each crown section was determined by multiplying specific leaf area by the total foliage dry weight. Total projected leaf area per tree was estimated by summation over the three crown sections.

The sapwood-heartwood boundary was delineated by staining stem disks with alizarine red (Kutscha and Sachs 1962). After the boundary was marked, each disk was photocopied, and the total cross-sectional area and heartwood area of the photocopy of each disk were measured with the electronic area meter. Sapwood area was determined by subtracting heartwood area from the total cross-sectional area. The bark was peeled from each of the two disks per tree, and bark and stemwood were weighed fresh and after drying to a constant weight (about 3 days) to estimate ratios of dry to fresh weight and of bark or stemwood to total stem fresh weights. Bark and stemwood dry weights of each stem section (above or below the base of the live crown) were estimated by multiplying total stem fresh weight by the ratio of bark or stemwood to total stem fresh weight by the ratio of dry to fresh weight for bark or stemwood. This procedure assumed that the disk taken at 1.3 m was representative of the lower stem section and that the disk taken at the base of the live crown was representative of the upper stem section. Total bark or stemwood dry weight was estimated by summation over the two stem sections.

Regression equations for predicting biomass or leaf area were of the form of the allometric equation $\ln Y = \ln a + b \ln X$, where Y is component biomass (kg) or leaf area (m^2), X is dbh (cm) or sapwood cross-sectional area (cm^2), and ln is the logarithm to the base e. Residual analyses indicated that a linear model was appropriate, and errors were normally distributed with homogeneous variance. All regression equations were corrected for logarithmic bias (Baskerville 1972). Analysis of covariance was used to test differences in regression equations among

families (Steel and Torrie 1980, Freund et al. 1986). Comparison of intercepts assumed equal slopes among families. Regression equations for predicting component biomass were compared between studies by converting equations of other studies to the form of the allometric equation, if necessary, and correcting for logarithmic bias. Plots of the relations could then be compared. In addition, biomass estimates were compared for trees of 9 and 26 cm using equations from different studies. These tree sizes represent the range of diameters found in the present study. Leaf area estimates were also compared for the same range of tree sizes using equations from different studies, but plots and coefficients of regression equations could not be directly compared because different models for predicting leaf area were used in different studies.

RESULTS AND DISCUSSION

Regression equations predicting biomass components did not differ significantly among families in slope (Table 1); intercepts assuming equal slopes did differ significantly among families for equations predicting crown and stem bark components, but not for stemwood, total stem, and total aboveground components. The slopes of equations predicting leaf area based on diameter, sapwood area at breast height, or sapwood area at the base of the live crown also did not differ significantly among families, but intercepts did. Thus, at the same diameter or sapwood area, some families have more bark biomass, crown biomass, or leaf area than other families. Diameter may be used to compare families for differ-

TABLE 1.

Equations predicting aboveground biomass components and leaf area in an 18-year-old Douglas-fir genetic test and probability of family differences in regression coefficients.

						P-value for families	
Y	*X*	*a*	*b*	R^2	MSE	*a*	*b*
Total aboveground	dbh	−2.1253	2.2985	0.93	0.0110	0.10	0.92
Total stem	dbh	−2.3290	2.2621	0.93	0.0105	0.35	0.81
stemwood	dbh	−2.4750	2.2691	0.92	0.0114	0.27	0.79
stem bark	dbh	−4.3209	2.2124	0.87	0.0201	0.01	0.87
Total crown	dbh	−3.7604	2.4059	0.78	0.0421	0.00	0.47
branches	dbh	−4.4215	2.4394	0.74	0.0539	0.00	0.32
foliage	dbh	−4.4698	2.3603	0.76	0.0475	0.00	0.54
Leaf area	dbh	−2.1578	2.1827	0.73	0.0456	0.00	0.81
Leaf area	sapwood-bh	−1.3887	1.1160	0.69	0.0523	0.00	0.84
Leaf area	sapwood-lc	−0.8654	1.0685	0.71	0.0502	0.01	0.17

Note: Equations are of the form $\ln Y = a + b \ln X$ for the different dependent variables Y (biomass components in kg, leaf area in m^2) and independent variables X (diameter at breast height [dbh] in cm, sapwood area at breast height [bh] or base of live crown [lc] in cm^2), where a and b are regression coefficients, R^2 is the coefficient of determination, MSE is the mean square error, and the P-values for a and b are the probabilities that families do not differ in intercepts or slopes, respectively. Corrections for logarithmic bias (Baskerville 1972) were applied to all regressions.

ences in total aboveground, stem, and stemwood biomass, but may lead to erroneous conclusions with respect to bark or crown biomass. Similarly, diameter or sapwood area may not be used for reliable family estimates of leaf area. Nevertheless, single equations may still be used to provide reliable stand estimates of leaf area and leaf, branch, and bark biomass components.

Family differences in intercepts for equations predicting leaf area and leaf, branch, and bark biomass suggest that families differ in partitioning of biomass between stem and crown and between stemwood and bark. Analyses of variance indicated that families did, indeed, differ significantly in the proportion of crown to total biomass ($P > 0.001$) and in the proportion of bark to total stem biomass ($P = 0.002$). Furthermore, trees with large stems had a greater proportion of crown than trees with small stems, as evidenced by the steeper slopes and more negative intercepts of equations predicting crown biomass components relative to those predicting stem biomass components (Table 1). Competitive interactions may have magnified family differences in size and partitioning (St.Clair and Adams 1991). Nevertheless, large family differences have been found in partitioning in other genetic studies in which trees were not competing to any great degree (Matthews et al. 1975, Van Buijtenen 1978, Velling and Tigerstedt 1984).

Sapwood area at breast height and at the base of live crown was a somewhat less reliable predictor of leaf area than diameter at breast height, as indicated by lower coefficients of determination (Table 1). Brix and Mitchell (1983) and Espinosa Bancalari et al. (1987) found similar results. Their studies, as well as this one, were done in young, uniform stands. Marshall and Waring (1986) suggest that sapwood area may be a better predictor of leaf area than diameter in less uniform stands or in older stands with a higher proportion of heartwood. They found that in an old-growth Douglas-fir forest, the estimate of leaf area based on diameter was twice as high as the estimates based on sapwood area, litterfall, or light interception. The discrepancy, however, may be attributed to differences in deriving the equations for predicting leaf area; the equation for predicting leaf area based on sapwood area was from data collected by Waring et al. (1982) on five small trees at a single location, whereas the equation based on diameter was from consolidation of data from several stands of widely different tree sizes from throughout western Oregon and Washington (Gholz et al. 1979). Nevertheless, heartwood represents wood that was grown in the past, and is, in a sense, already invested with no necessary relation to present conditions including present leaf areas, particularly in older trees. However, a high correlation between diameter and sapwood may be expected in young trees with a high proportion of sapwood (proportion of sapwood at breast height was 0.68 in this study).

Several alternative independent variables were tried to see if prediction equations could be improved. The prediction of component biomass was not improved by including height in the regression, either as an additional variable or incorporated into a volume equation; equations predicting total aboveground dry weight or stem components were improved slightly (coefficients of determination increased by 0.03 or less), but prediction of crown components was less reliable (lower coefficients of determination). The prediction of leaf area was not improved by including wood density, crown length, or distance to crown center as independent variables. These variables were thought to be related to sapwood permeability, and would therefore be useful in removing some of the unexplained

variation in the relation between sapwood area and leaf area (Whitehead et al. 1984, Espinosa Bancalari et al. 1987). Prediction equations, however, were less reliable as indicated by lower coefficients of determination.

Equations predicting stem biomass components had higher coefficients of determination and lower mean square errors than equations predicting crown biomass components or leaf area (Table 1). The greater uncertainty in predicting crown biomass and leaf area might be expected, given that diameter is more directly associated with stem biomass because they both measure stem size. Genetic variation in partitioning to the crown may have also contributed to the greater variability in crown biomass. Coefficients of determination for crown biomass were lower in this study than in previous studies (Table 2). The greater variability in this study might be explained by a smaller range in the independent variable, or by larger differences in partitioning among stem and crown because of strong competition.

Although equations from this study may be used for reliable stand estimates of leaf area and biomass components, inference to stands at other sites and other stages of stand development may not be appropriate. Biomass predicted from the allometric equations developed in this study differed substantially from that predicted by equations from other studies of Douglas-fir (Table 3 and Figure 1), and suggest that discretion is needed when applying equations to other sites at other stages of stand development and with other ranges of tree sizes. Equations developed by Helgerson et al. (1988) and Espinosa Bancalari and Perry (1987) are most directly comparable to those developed in this study. Their stands are of similar ages (10 and 22 years, respectively), and are located in the same general area (in the Oregon Coast Range at latitudes 44°20'N to 44°30'N). Compared to the biomass estimates of my study, the equations from Helgerson et al. (1988) led to underestimates of stem biomass at all diameters, and overestimates of crown biomass at all diameters, except foliage dry weight at larger diameters. The equations from Espinosa Bancalari and Perry (1987), on the other hand, led to underestimates of stem biomass only at the lower stem diameters, but underestimates of all crown biomass components at nearly all diameters.

The differences in estimates of biomass components among these three studies is most likely related to differences in stand development. Trees partition more biomass to the stem and less to the crown with increasing stand age and increasing influence of competition (Pulkkinen et al. 1989). The three stands studied by Espinosa Bancalari and Perry (1987) were older (22 yr) and probably more developed than the other two studies, and, consequently, partitioned more biomass to the stem and less to the crown (partitioned 75% to 82% of the aboveground biomass to the stem as compared to 73% in the present study). The stand studied by Helgerson et al. (1988), on the other hand, was younger (10 yr) and probably less developed; it appeared to partition less to the stem and more to the crown. Interestingly, equations developed by Grier et al. (1984) led to estimates of biomass components that were most similar to those of my study, especially with respect to crown components, despite their study area being a long distance (the Puget Sound region of western Washington) from mine. Their study may have been most like this study in terms of stand development, because it was of a similar range of tree sizes (9 to 30 vs. 9 to 26 cm diameter in this study). Equations developed by Gower et al. (1987) led to estimates of biomass components that were least similar to those of my study; stem biomass was estimated

TABLE 2.

Biomass equations for aboveground components developed from data of several stands of Douglas-fir in the Pacific Northwest.

Y	a	b	R^2
Helgerson et al. 1988[1]:			
Total aboveground	−1.9236	2.1858	0.97
Total stem	−2.2688	2.1197	0.97
stemwood	—	—	—
stem bark	—	—	—
Total crown	—	—	—
branches	−4.0521	2.5033	0.94
foliage	−3.5791	2.0310	0.94
Espinosa Bancalari & Perry 1987[2]:			
Total aboveground	−3.9371	2.8427	0.93
Total stem	−4.4346	2.9216	0.89
stemwood	−4.7470	2.9674	0.89
stem bark	−5.6097	2.7009	0.85
Total crown	−5.0145	2.7060	0.93
branches	−5.7108	2.6788	0.92
foliage	−6.0934	2.7229	0.93
twigs	−6.8020	2.7361	0.93
Grier et al. 1984[3]:			
Total aboveground	—	—	—
Total stem	—	—	—
stemwood	−2.603	2.367	0.97
stem bark	−4.906	2.530	0.94
Total crown	—	—	—
branches	−4.456	2.469	0.86
foliage	−4.791	2.502	0.92
Gower et al. 1987[4]:			
Total aboveground	—	—	—
Total stem	—	—	—
stemwood	−3.528	2.798	0.99
stem bark	−4.073	2.414	0.97
Total crown	—	—	—
branches	−3.997	2.033	0.90
foliage	−3.173	1.754	0.92
Gholz et al. 1979[5]:			
Total aboveground	—	—	—
Total stem	—	—	—
stemwood	−3.0396	2.5951	0.99
stem bark	−4.3103	2.4300	0.99
Total crown	—	—	—
branches	−3.6941	2.1382	0.92
foliage	−2.8462	1.7009	0.86

Note: Equations are of the form $\ln Y = a + b \ln \text{dbh}$ for the different dependent biomass variables (Y, in kg) and the independent variable diameter at breast height (dbh, in cm), where a and b are regression coefficients, and R^2 is the coefficient of determination. Corrections for logarithmic bias (Baskerville 1972) were applied to all regressions.

[1] Based on a sample of 18 trees, 10 yr old, ranging in diameter from 1 to 13 cm. Study site was in the Oregon Coast Range (44°27′N, 123°55′W) at an elevation of 240 m.

[2] Based on a sample of 40 trees, 22 yr old, from three adjacent stands of various growth rates (range of tree sizes unknown). Study site was in the Oregon Coast Range at an elevation of 250–300 m (44°20′N, 123°21′W).

[3] Based on a sample of 26 trees, 23 yr old, ranging in diameter from 9 to 30 cm. Study site was in the Puget Sound region of western Washington.

[4] Based on a sample of 5 trees, 65–70 yr old, ranging in diameters from 6 to 20 cm. The study site was in an evenaged, mixed conifer stand on the eastern slopes of the Washington Cascades (47°39′N, 120°30′W) at an elevation of 1500 m.

[5] Based on a sample of 99 to 123 trees ranging in age from young growth to old growth and ranging in diameters from 2 to 162 cm. Data were compiled from several sources with study sites at several locations in western Oregon and Washington.

TABLE 3.

Biomass (kg) predicted from regression equations developed for Douglas-fir stands in the Pacific Northwest and percentage difference from predicted for trees of 9 cm and 26 cm diameter in this study[1].

	Total aboveground		Total stem		Stemwood		Stem bark		Total crown		Branches		Foliage	
	9 cm	26 cm	9 cm	26 cm	9 cm	26 cm	9 cm	26 cm	9 cm	26 cm	9 cm	26 cm	9 cm	26 cm
This study:														
Biomass	18.6	213.5	14.0	154.6	12.3	136.7	1.7	17.9	4.6	59.0	2.6	34.0	2.0	25.0
Helgerson et al. 1988[2]:														
Biomass	17.8	180.9	10.9	103.6	—	—	—	—	6.6	80.9	4.2	60.0	2.4	20.9
% Difference	96	85	78	67	—	—	—	—	143	137	161	176	120	84
Espinosa Bancalari & Perry 1987[3]:														
Biomass	10.1	205.3	7.3	161.5	5.9	137.2	1.4	24.3	2.5	44.8	1.6	28.7	0.9	16.1
% Difference	54	96	52	104	48	100	82	136	54	76	62	84	45	64
Grier et al. 1984[4]:														
Biomass	19.9	258.6	15.3	193.6	13.4	165.5	1.9	28.1	4.6	65.0	2.6	36.2	2.0	28.8
% Difference	107	121	109	125	109	121	113	157	100	110	100	106	100	115
Gower et al. 1987[4]:														
Biomass	20.7	337.9	17.1	311.4	13.7	267.2	3.4	44.3	3.6	26.5	1.6	16.8	2.0	12.7
% Difference	111	158	122	201	111	168	200	247	78	45	62	41	100	51
Gholz et al. 1979[4]:														
Biomass	22.2	303.0	17.1	261.8	14.3	224.9	2.8	36.9	5.1	41.2	2.7	26.4	2.4	14.8
% Difference	119	142	122	169	116	165	164	206	111	67	104	78	120	59

[1] See footnotes of Table 2 for details of each study.
[2] Estimates for total crown biomass are summation of branch and foliage components.
[3] Estimates for branch biomass are summation of branch and twig components.
[4] Estimates for total aboveground, total stem, and total crown biomass are summation of stemwood, stem bark, branch, and foliage biomass components.

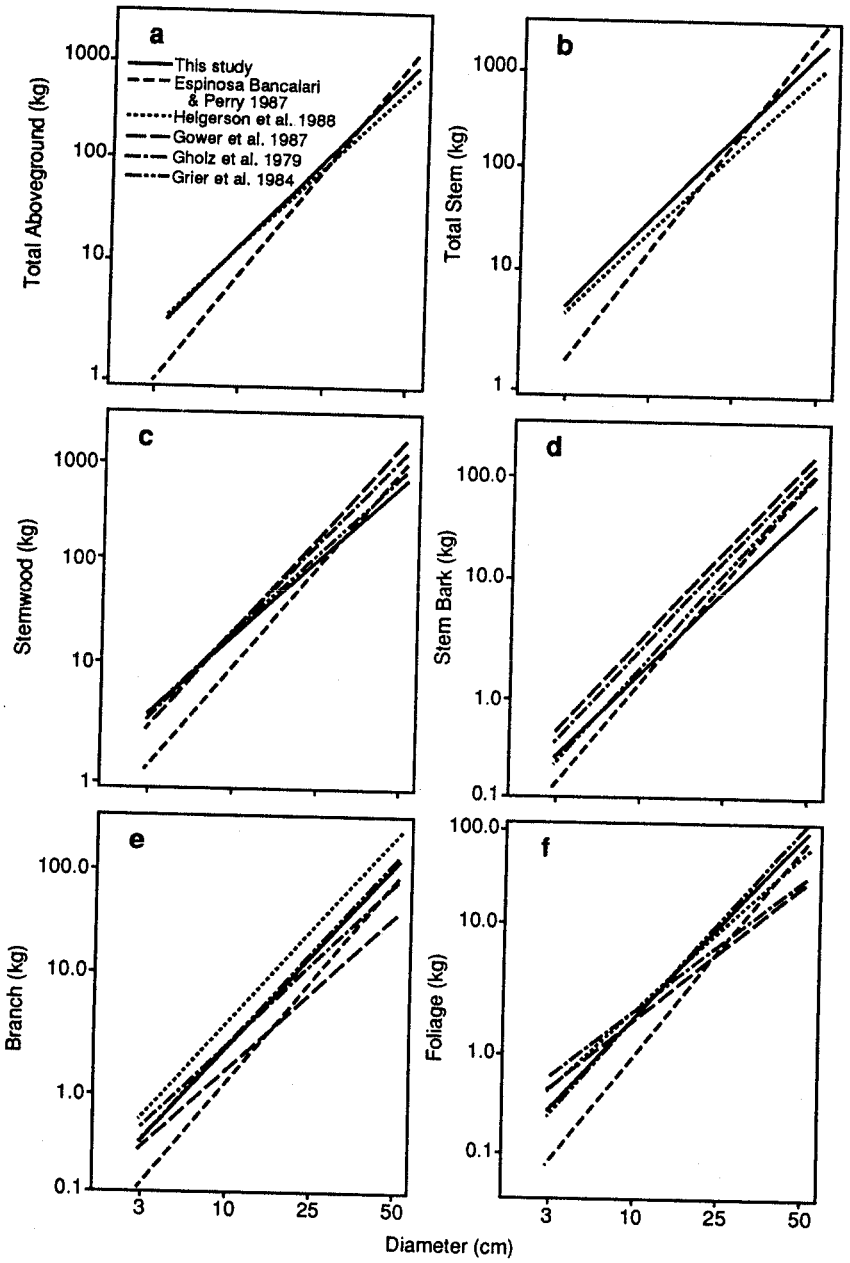

FIGURE 1. Relations of component biomass to diameter at breast height from data of several stands of Douglas-fir in the Pacific Northwest. Biomass components include (a) total aboveground dry weight, (b) total stem dry weight, (c) stemwood dry weight, (d) stem bark dry weight, (e) branch dry weight, and (f) foliage dry weight.

to be double that of this study, and crown biomass was estimated to be less than half. The stand chosen for their study was very different from mine; it was much older (65–70 yr), on the drier eastside of the Washington Cascades and at a higher elevation (1,500 m). Adaptation to an arid, fire-prone environment may be expected to lead to thicker bark and less leaf area per unit stem.

Gholz et al. (1979) developed regional biomass equations by using data from stands at various locations in western Oregon and Washington and at different stages of stand development. These regional equations predicted values for total aboveground, total stem, and stemwood biomass at 9 cm diameter of about the same magnitude as those predicted by equations developed in this study, but at 26 cm diameter, their equations led to stemwood biomass estimates that were over one and half times as large. Bark biomass was overestimated at all diameters (by twice as much at 26 cm diameter). Crown components, on the other hand, were overestimated at the lower diameters and substantially underestimated at higher diameters; for example, foliage biomass was underestimated by nearly half at 26 cm diameter. The differences in predicted values between my study and theirs calls into question the utility of combining data from disparate sources for purposes of accurately estimating biomass components at a specific site.

Leaf area predicted based on ratios or equations from different studies also differed from this study (Table 4). Leaf area equations from Espinosa Bancalari et al. (1987) led to underestimates of leaf area at nearly the entire range of diameters of the present study. Equations developed for fertilized treatments in the study of Brix and Mitchell (1983) led to underestimates at the lower diameters, but estimates at the higher diameters for fertilized stands, and at all diameters for unfertilized stands, were close to those of this study. The results of Espinosa Bancalari et al. (1987) and Brix and Mitchell (1983) also indicate that differences in leaf area equations can be found between stands growing under different conditions but in the same area. Equations developed by Gower et al. (1987) for the older stands of the eastside Cascades of Washington led to underestimates at all diameters.

Other researchers have used ratios of leaf area to sapwood area to estimate leaf area (Waring et al. 1981, Waring et al. 1982, Binkley 1984). Ratios assume a zero intercept and a linear relationship between dependent and independent variables, two assumptions that are frequently not addressed. Nevertheless, ratios of 0.44 (Waring et al. 1981) or 0.47 (Waring et al. 1982) led to estimates of leaf area at the upper end of diameters that were close to those of this study. A ratio of 0.63, as determined by Binkley (1984), greatly overestimated leaf area in this study. As with biomass equations, considerable differences can be found between leaf areas predicted from equations or ratios from different studies, and discretion is advised when using equations developed at different sites and under different growing conditions.

CONCLUSIONS

Genetic variation in partitioning resulted in family differences in the intercept of regression equations predicting bark biomass, crown biomass, and leaf area, although families did not differ in slopes. Thus, a single regression equation could not be used to explore genetic variation in bark biomass, crown biomass, or leaf area without first accounting for family differences in partitioning. Comparisons of equations from this study to those of other studies indicated that large differences may result in predicting biomass and leaf area for the range of tree sizes considered in this study. These results suggest that discretion is needed when applying equations developed at one site to estimating biomass or leaf area at another.

TABLE 4.

Leaf area (m^2) predicted from regression equations or ratios developed for Douglas-fir stands in the Pacific Northwest and percentage difference from predicted for trees of 9 cm and 26 cm dbh in this study.

Study/treatments	9 cm		26 cm	
	Leaf area	% Difference	Leaf area	% Difference
This study	15.9		133.7	
Espinosa Bancalari et al. 1987[1]				
Slow	10.2	64	118.5	89
Intermediate	6.5	41	105.7	79
Fast	4.2	26	137.4	103
Brix and Mitchell 1983[2]				
Unthinned, unfertilized	15.6	98	105.8	79
Thinned, unfertilized	16.3	102	127.9	96
Unthinned, fertilized	7.5	47	145.2	109
Thinned, fertilized	10.7	67	157.9	118
Gower et al. 1987[3]	14.1	88	70.8	53
Waring et al. 1981[4]	19.5	122	131.1	98
Waring et al. 1982[5]	18.3	114	122.7	92
Binkley 1984[6]	26.2	164	176.3	132

Note: All predictions of leaf area are based on equations that used sapwood area at breast height as the dependent variable. A tree of 9 cm dbh was determined to have 41.5 cm^2 sapwood area and a tree of 26 cm dbh was determined to have 278.9 cm^2 sapwood based on a prediction equation of ln (sapwood area at bh) = $-0.2205 + 1.7959$ ln (dbh) as determined from this study.

[1] Based on logarithmic regression equations for samples of 16, 16, and 8 trees of 22 yr in adjacent stands of slow, intermediate, and fast growth rates, respectively. Study site was in the Oregon Coast Range at an elevation of 250–300 m (44°20′N, 123°21′W).

[2] Based on regression equations of untransformed data for samples of 24 trees of 33–34 yr of age in each of four treatments, as indicated. Study site was on southern Vancouver Island, British Columbia.

[3] Based on a logarithmic regression equation for a sample of 5 trees, 65–70 yr old, ranging in diameters from 6 to 20 cm. The study site was in an even-aged, mixed conifer stand on the eastern slopes of the Washington Cascades (47°39′N, 120°30′W) at an elevation of 1500 m.

[4] Based on a sapwood to leaf area ratio of 0.44, as determined from previous estimates of sapwood to leaf biomass relationships (Grier and Waring 1974) and specific leaf area.

[5] Based on sapwood to leaf area ratio of 0.47, as determined from a sample of 5 trees of 5 to 25 cm dbh from a single site in western Oregon (42°20′N, 123°00′W).

[6] Based on a sapwood to leaf area ratio of 0.632, as determined from a sample of 5 trees, 23 yr old. Study site was near Nanaimo, Vancouver Island, British Columbia.

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