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Leaf area – sapwood area relationships in adjacent young Douglas-fir stands with different early growth rates[1]

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The relationship between foliage area and sapwood basal area was studied in three adjacent 22-year-old Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands that differed in early growth rates. Sapwood width was fairly constant for most of the stem above the stump, but the number of annual rings in the sapwood decreased gradually with height. Sapwood area also decreased with increasing height in the tree, the stands differing significantly only at breast height. The proportion of heartwood from stump to near the base of the crown was significantly higher for the stand of fastest early growth. Ratios of leaf area to sapwood area were significantly higher for that stand and varied in every stem section, the ratio lower at breast height than at the base of the live crown. At the base of the crown, the ratio of leaf area to sapwood area was 1.33 and 1.57 times greater in the fast-growing stand than in the intermediate- and slow-growing stands, respectively. Leaf area was as closely related to dbh as to sapwood area at breast height. Sapwood area at the crown base was more accurate than sapwood area at breast height for predicting leaf area in the fast stand and was equally accurate in the other two stands. Ratios of leaf area to sapwood area correlated positively with sapwood ring width. However, because sapwood ring width also correlated closely with sapwood area, it did not improve predictive equations. The results suggest that the "pipe model" theory must be modified to account for the internal structure of the "pipe" and that caution should be exercised when using published leaf area to sapwood area ratios.

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La relation entre la surface foliaire et la surface terriere d'aubier fut étudiée dans trois peuplements adjacents de douglas (*Pseudotsuga menziesii* (Mirb.) Franco) agés de 22 ans, mais différant par leurs taux initial de croissance. La largeur de l'aubier en haut de la souche était passablement constante pour la plupart des tiges, mais le nombre de cernes annuels dans l'aubier diminuait graduellement avec la hauteur. La surface de l'aubier allait aussi en décroissant avec l'augmentation de la hauteur dans l'arbre, les peuplements montrant des différences significatives seulement à hauteur de poitrine. La proportion de bois de coeur depuis la souche jusqu'aux environs de la base de la cime était significativement plus grande chez le peuplement ayant la plus grande croissance initiale. Pour ce peuplement, les ratios surface foliaire : surface d'aubier étaient significativement plus élevés et variaient dans chaque section de la tige, le ratio étant plus faible à hauteur de poitrine qu'à la base de la cime verte. A la base de la cime, le ratio était 1,33 fois et 1,57 fois plus élevé que ceux des peuplements à croissance intermédiaire et à croissance lente, respectivement. La surface foliaire était reliée aussi étroitement au dhp qu'à la surface d'aubier à hauteur de poitrine. Pour prédire la surface foliaire dans le peuplement à croissance rapide, la surface de l'aubier à la base de la cime était plus précise que la surface de l'aubier à hauteur de poitrine; elle était aussi exacte dans les deux autres peuplements. Les ratios surface foliaire : surface d'aubier était corrélés positivement avec la largeur des cernes d'aubier. Cependant, comme la largeur des cernes d'aubier était aussi en étroite corrélation avec la surface d'aubier, elle n'a pas amélioré les équations de prédiction. Les présents résultats suggèrent que la théorie du «pipe model» doit être modifiée pour tenir compte de la structure interne du «pipe» et qu'on doit être prudent dans l'emploi des ratios publiés surface foliaire : surface d'aubier.

[Traduit par la revue]

Introduction

Leaf area, and its spatial distribution, is a structural feature critically important to studies of terrestrial ecosystem productivity (Jarvis and Leverenz 1983). However, accurate determination of leaf area by direct sampling is time consuming and expensive. An indirect approach is to estimate it from sapwood basal area (Long *et al.* 1981; Waring *et al.* 1982). Because sapwood conducts water and nutrients to the foliage, and also because it stores water (e.g., Waring and Running 1978), it is functionally related to leaf area in a way that external measurements such as basal area or diameter at breast height are not.

Although good relationships between foliage area or biomass and sapwood basal area have been reported for coniferous and hardwood trees (Grier and Waring 1974; Snell and Brown 1978; Whitehead 1978; Rogers and Hinckley 1979; Kaufmann and Troendle 1981; Waring *et al.* 1982; Albrektson 1984), sapwood measurements taken from a few cores or from small-diameter trees may yield no better estimates of leaf area than basal area or diameter alone (Snell and Brown 1978; Newman 1979; Ford 1982; Brix and Mitchell 1983; Schonenberger 1984). In such cases, better estimates may be gained by measuring tree circumference and deriving cross-sectional area (R. H. Waring, personal communication). Slope of the relationships between leaf area and sapwood area may differ with site (Whitehead 1978; Binkley 1984; J. W. Leverenz, unpublished), species (Kaufmann and Troendle 1981; Waring *et al.* 1982; Whitehead *et al.* 1984), and growing conditions (Granier 1981; Brix and Mitchell 1983). Albrektson (1984) added annual ring width at breast height to sapwood area as an independent variable to

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account for differences in the ability of the sapwood to conduct water.

Some studies have found a nearly constant ratio of cumulative foliar area or mass to sapwood basal area from the base of the crown upward (e.g., Kaufmann and Troendle 1981; Long *et al.* 1981; Waring *et al.* 1982). However, others have shown, such as Brix and Mitchell (1983) for a young stand of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), Whitehead *et al.* (1984) for mature Sitka spruce (*Picea sitchensis* (Bong,) Carr.) and lodgepole pine (*Pinus contorta* Doug. ex Loud.), and J. W. Leverenz (unpublished) for young lodgepole pine, that the ratio changes with increasing depth in the crown, attributing the changes to differences in wood permeability.

The objectives of this study were as follows: (*i*) to compare the relationship between leaf area and sapwood basal area in three adjacent 22-year-old Douglas-fir stands that differed in early growth rates; (*ii*) to ascertain whether sapwood to leaf-area coefficients alter in response to mean annual ring width in the sapwood; and (*iii*) to compare sapwood area at the crown base with sapwood area at breast height as a predictor of leaf area.

Methods

Forty 22-year-old trees from three adjacent stands near Bellfountain in the Oregon Coast Range (latitude 44°20′ N, longitude 123°21′ W) were randomly selected for destructive sampling in August 1982. The stands, on a plantation currently owned by Weyerhaeuser Company, have similar histories, aspect, and topography. Tree, stand, and soil characteristics are given in Espinosa Bancalari (1985) and Espinosa Bancalari and Perry (1987). Stem volumes distinguish the stands as having had "slow," "intermediate," and "fast" early growth rates, and the designations used here refer to those early rates rather than to current growth. Growth differences are probably related to soil depth, fertility, and aeration (Espinosa Bancalari and Perry 1987).

Sixteen trees each were selected from the "slow" and "intermediate" stands and eight were selected from the "fast" stand, which was previously determined to have more uniform size distribution. Trees were felled and partitioned into foliage, twigs, live branches, stem-bark, and stemwood. Areas of sapwood and heartwood were estimated from seven 2 to 4 cm thick disks cut from the main stem of each tree at stump height, breast height, 5 m above breast height, the base of the live crown, and from the bottom of the second, third, and top quarters within the crown (Fig. 1).

Sapwood and heartwood were differentiated by color after immersion in water. On each disk, the width of the sapwood was calculated as the average of two to four measurements taken at right angles; mean annual ring width in the sapwood of each was calculated as sapwood width divided by the number of annual sapwood rings. Diameter and sapwood thickness of each disk were recorded to the nearest 0.5 mm. Sapwood cross-sectional area was determined by subtracting heartwood area from the total cross-sectional area.

The total fresh weight of foliage and branches of each crown section (base, second, third, and top quarters) was measured in the field. Five representative branches from each section were returned to the laboratory where all twigs were clipped from each branch and weighed fresh with the needles. All age-classes of needles, removed from twig subsamples taken at random from each section, were then weighed separately. The twigs were dried at 70°C for 48 h and then weighed again with the needles. A subsample of fresh needles was kept for determination of surface area with a Li-Cor LI-3300 area meter. Area was determined on fresh foliage because foliage may shrink as much as 25% in drying (Waring *et al.* 1982).

The foliage dry weight of each crown quarter section was computed by multiplying the fresh weight of each quarter of each tree canopy by the following ratios: (*i*) fresh weight of twigs with needles to fresh weight of total branch, (*ii*) fresh weight of needles to fresh weight of twigs with needles, and (*iii*) dry weight of needles to fresh weight of needles. The projected leaf surface area (one sided) of each section was then computed by multiplying foliar dry weight by specific leaf area (fresh leaf area per needle dry weight). Leaf area of the whole tree was calculated by summing section estimates.

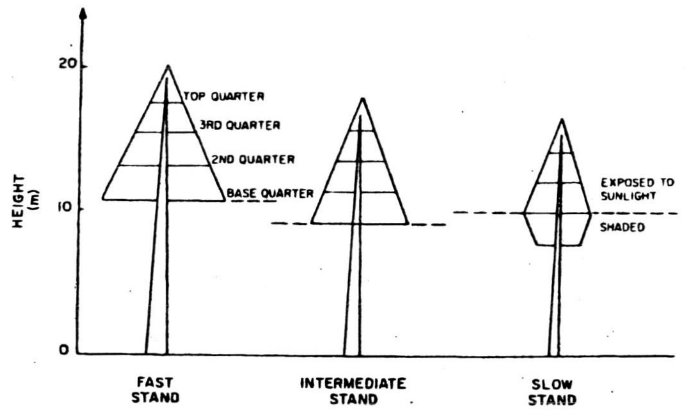

FIG. 1. Distribution of leaf area in quarter sections of the canopy of three adjacent 22-year-old Douglas-fir stands growing at different rates in the Oregon Coast Range. The width of the crown (assumed to be symmetrical) is in proportion to the leaf area of each stand.

Values from each stand for sapwood radius, sapwood area, projected leaf area, and leaf area per unit of sapwood area were subjected to analysis of variance, the significant differences among means tested by the Tukey–Kramer method of multiple comparisons at $p < 0.05$ (SAS Institute Inc. 1982). Regression equations of leaf area and the several independent variables were linearized by log transformation. Bias of the intercept estimates of the original dependent variable (the model passed through the geometric rather than true mean) was corrected by Baskerville's (1972) procedure. Relative closeness of the regression was estimated by the relative error, the antilog of the standard error of estimate (Whittaker and Woodwell 1971). The "giant" regression model approach of Cunia (1973) was used to discern differences among regression equations for the three stands. All statistical analyses were performed by means of the Statistical Analysis System (SAS Institute Inc. 1982).

Results

Sapwood distribution

All stands showed a consistent pattern of sapwood distribution, narrowest at the top and widest at the base of the tree (Table 1). In the fast and intermediate stands, sapwood rings were widest at the base of the crown; in the slow stand, they were widest in the lower half of the crown. Above the stump, sapwood width was fairly constant to the top crown section, where it decreased sharply. The fast stand had less sapwood width than others in almost every section but differences were not significant. The slow stand had the most annual rings in the sapwood of each section and the fast stand the least. The number of rings decreased gradually from stump to top of the tree in all stands, a pattern also reported by Brix and Mitchell (1983). Sapwood cross-sectional area decreased gradually and consistently with increasing height, differing significantly among stands only at breast height. The proportion of sapwood in each stem section was similar in the slow and intermediate stands but significantly lower in the fast stand from stump to the base of the crown. The proportion did not differ within crown sections. Regression equations for the fast stand of sapwood area on basal area at breast height and on basal area at the crown base were also significantly different (Table 2).

Vertical distribution of leaf area

The projected average leaf area of each crown quarter (Table 3) was used for describing the form of the canopy of an average

TABLE 1. Mean values for sapwood in three adjacent 22-year-old Douglas-fir stands with different early growth rates

	Sapwood radial width (cm)			No. of sapwood rings			Sapwood area (cm^2)			Sapwood area /total area under bark		
Tree section	Slow stand	Intermediate stand	Fast stand	Slow stand	Intermediate stand	Fast stand	Slow stand	Intermediate stand	Fast stand	Slow stand	Inter-mediate stand	Fast stand
Stump	4.8(0.3)*a*	5.3(0.3)*a*	4.4(0.2)*a*	9.8(0.4)*a*	9.6(0.2)*a*	9.5(0.6)*a*	294.9(27)*a*	385.4(38)*a*	385.5(43)*a*	0.63*b*	0.62*b*	0.49*a*
Breast height	4.1(0.2)*a*	4.6(0.3)*a*	4.2(0.2)*a*	9.3(0.3)*a*	8.8(0.2)*a*	8.9(0.5)*a*	211.6(19)*b*	293.8(29)*a*	299.6(29)*a*	0.65*b*	0.63*b*	0.53*a*
Breast height + 5 m	4.7(0.2)*a*	4.4(0.2)*a*	4.1(0.3)*a*	7.6(0.2)*a*	7.2(0.3)*a*	7.0(0.3)*a*	194.4(15)*a*	228.2(22)*a*	234.3(29)*a*	0.77*b*	0.70*b*	0.60*a*
Base crown quarter	4.4(0.2)*a*	4.7(0.2)*a*	4.3(0.3)*a*	7.0(0.2)*a*	5.7(0.1)*b*	5.6(0.3)*b*	140.6(13)*a*	161.1(15)*a*	169.3(23)*a*	0.84*a*	0.86*a*	0.76*a*
Second crown quarter	4.0(0.2)*a*	4.1(0.2)*a*	4.0(0.3)*a*	6.2(0.2)*a*	5.3(0.1)*b*	5.3(0.3)*b*	85.6(7)*a*	95.7(9)*a*	105.2(16)*a*	0.94*a*	0.93*a*	0.88*a*
Third crown quarter	3.3(0.2)*a*	3.4(0.2)*a*	3.4(0.3)*a*	5.8(0.2)*a*	5.0(0.3)*a*	4.9(0.4)*a*	40.1(4)*a*	44.4(5)*a*	52.6(8)*a*	0.99*a*	0.99*a*	0.96*a*
Top crown quarter	1.7(0.1)*a*	1.7(0.1)*a*	1.7(0.2)*a*	4.1(0.1)*a*	3.6(0.1)*ab*	3.4(0.3)*b*	10.2(2)*a*	10.8(1)*a*	10.2(2)*a*	1.00*a*	1.00*a*	0.99*a*

NOTE: For slow and intermediate stands n = 16 and for the fast stand n = 8. Standard errors of the means are in parentheses. In each row, mean values with the same letter do not differ significantly ($p < 0.05$, Tukey's test).

TABLE 2. Regression equations for sapwood area on basal area under bark taken at breast height and at the base of the crown in three adjacent 22-year-old Douglas-fir stands with different early growth rates

Independent variable	Early growth rate	b	SEE	R^2
Basal area at breast height	Slow	0.6443	18.3	0.95
	Intermediate	0.6106	32.4	0.92
	Fast	0.4994	47.1	0.82
Basal area at crown base	Slow	0.8261	15.7	0.91
	Intermediate	0.8344	12.7	0.96
	Fast	0.6621	39.9	0.77

NOTE: All equations follow the form $Y = a + bX$, where a and b are regression coefficients, R^2 is the coefficient of determination, and SEE is the standard error of the estimate. Equations for the fast stand are significantly different ($p < 0.05$). R^2 values through the origin are inflated artificially; values shown are for the full model. Intercept coefficients are not reported because they were not significant.

tree in each stand (Fig. 1). Leaf area per crown quarter increased from the top to the base of the crown in both the fast and intermediate stands but in the slow stand it reached maximum in the second crown quarter. Although leaf area per tree differed among the stands (Table 3), the fast stand having highest values in every crown quarter, differences were significant only at the base (the slow stand significantly lower) and third quarter (the fast stand significantly higher). Mean crown length and live-crown ratio were surprisingly similar among stands: 8.9, 8.9, 9.4 m and 0.53, 0.47, 0.46, respectively, for the slow, intermediate, and fast stands.

Leaf area – sapwood area relationship

The average ratio of foliar area above a stem section to sapwood area of that section shows a clear pattern: an increase with height to the base of the crown in the fast-growing and intermediate stands and through the base crown quarter in the slow-growing stand, then a decrease from those points to the top of the crown (Fig. 2). The fast stand had significantly higher ratios of leaf area to sapwood area in almost every tree section, while intermediate and slow stands did not differ. A unit area of sapwood at the base of the crown supported 1.35 and 1.60 times more leaf area in the fast stand than in the intermediate and slow stands, respectively. The leaf area to sapwood area ratio at the crown base was 1.8 times greater than at breast height in the fast and intermediate stands, 1.5 times greater in the slow stand.

Regressions of total leaf area against the independent variables sapwood area at breast height, sapwood area at the crown base, sapwood area at breast height × sapwood ring width at breast height, and stem diameter at the crown base were highly significant (Table 4). Scatter plots indicated the need for a curvilinear model, so regression functions were linearized by logarithmic transformation (base e). The log transformation fit the data better than other commonly used transformations such as reciprocal, square, or cross products (Neter and Wasserman 1974). Regression slopes for the fast stand were higher than those for the intermediate and slow stands with all variables but stem diameter at the crown base and sapwood area at the crown base. Sapwood area at the crown base was more accurate than sapwood area at breast height for predicting leaf area in the fast stand and equally accurate in the intermediate and slow stands. Diameter at breast height (dbh) predicted leaf area almost as well as sapwood area at breast height. Sapwood area at the crown base was clearly a better predictor of leaf area than diameter at the crown base in slow and intermediate stands. In general, total leaf area of trees in the fast stand showed higher

TABLE 3. Projected mean leaf area per tree in three adjacent 22-year-old Douglas-fir stands with different early growth rates

	Slow stand		Intermediate stand		Fast stand	
Crown section	m^2	% of total	m^2	% of total	m^2	% of total
Top quarter	2.8(0.5)*a*	3.3	2.8(0.5)*a*	2.4	3.3(0.9)*a*	2.0
3rd quarter	15.9(2.3)*b*	18.6	16.9(2.4)*b*	14.6	33.4(7.5)*a*	20.6
2nd quarter	36.4(4.3)*a*	42.9	47.0(5.7)*a*	40.6	60.4(14.9)*a*	37.2
Base quarter	30.4(4.3)*b*	35.5	49.1(5.2)*a*	42.4	65.2(10.0)*a*	40.2
Total crown	85.5(10.6)*b*		115.8(12.4)*ab*		162.3(28.1)*a*	

NOTE: Standard errors of the means are in parentheses. In each row, mean values with the same letter do not differ significantly ($p < 0.05$, Tukey's test).

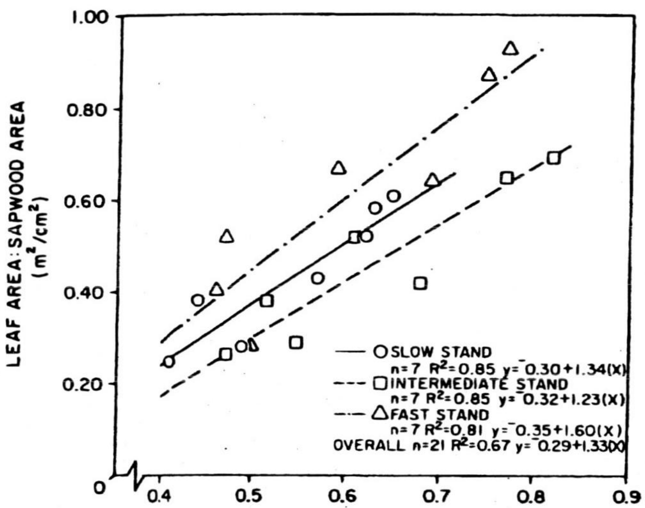

FIG. 2. Slope coefficients of the linear regression between leaf area and sapwood area of cross sections cut from the base of different stem sections: S, stump; B, breast height; B+, breast height + 5 m; CB, crown base; C2, crown second quarter; C3, crown third quarter; and CT, crown top quarter. At any one stem section, points with the same letter do not differ at the 0.05 level.

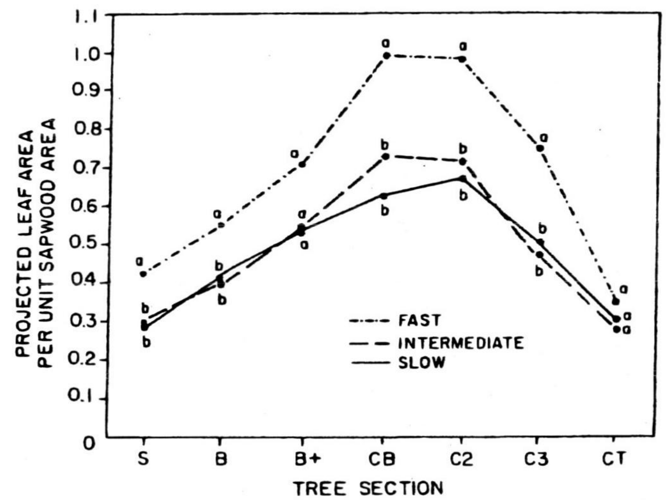

FIG. 3. Relationship of the leaf area to sapwood area ratio and sapwood ring width for seven stem sections of the average tree in each stand.

correlation and lower relative error with measurements taken at the crown base rather than at breast height, while leaf area of slow and intermediate stands showed the opposite trend.

The addition of ring width to sapwood area at breast height did not improve the precision of estimates, nor did leaf area estimated as ring width × the ratio leaf area to sapwood area, as noted by Albrektson (1984) for Scots pine. However, the leaf area to sapwood area ratio for each of the seven stem sections correlated positively with sapwood ring width of that section (Fig. 3), r^2 values ranging from 0.81 to 0.85 ($p < 0.01$) for the average tree in each of the three stands. Although ring widths at the crown base (the point of widest rings) were similar in the fast and intermediate stands, the leaf area to sapwood area ratio was about 30% greater in the former.

Discussion

According to the pipe model theory (Shinozaki *et al.* 1964; Waring 1983), the rate of transpiration of foliage is proportional to leaf area and the rate of water supply to the canopy is proportional to the cross-sectional area of sapwood. Because of these interactions, it follows that a measure of sapwood area can predict leaf area of standing trees. Close linear relationships between leaf area and sapwood area at breast height have been found in numerous studies, all of which have used a wide range of tree sizes (Grier and Waring 1974; Waring *et al.* 1977; Whitehead 1978; Rogers and Hinckley 1979; Kaufmann and Troendle 1981; Long *et al.* 1981; Waring *et al.* 1982; Whitehead *et al.* 1984). The assumption is that sapwood area increases proportionally below the live crown and hence leaf area can be conveniently estimated from measurements at breast height. From the crown base upwards, sapwood area is generally believed to decrease in direct proportion to the reduction in leaf area. The ratio between sapwood area and leaf area should therefore be the same for different portions of the crown. Fairly constant ratios for different crown sections have been found for four Douglas-fir trees (Long *et al.* 1981), several western coniferous species (Waring *et al.* 1982), and four subalpine tree species (Kaufmann and Troendle 1981). However, when Brix and Mitchell (1983) calculated the sapwood area to leaf area ratio in a thinning and fertilizer experiment with Douglas-fir, they found different relationships in different portions of the crown in all treatments. They also observed that the ratio at the crown base varied considerably from that at breast height.

Leaf area to sapwood area relationships also vary among

TABLE 4. Equations predicting estimated leaf area with different independent variables in three adjacent 22-year-old Douglas-fir stands with different early growth rates

Independent variable	Stand growth rate	a	b	R^2	SEE	E
dbh	Slow	−4.3388	2.8045	0.94	0.21	1.23
	Intermediate	−4.3969	2.7683	0.94	0.22	1.25
	Fast	−4.9752	2.9530	0.85	0.25	1.28
Sapwood area at breast height	Slow	−2.4649	1.2858	0.95	0.20	1.22
	Intermediate	−3.6062	1.4682	0.95	0.21	1.23
	Fast	−5.3794	1.8296	0.85	0.25	1.28
Diameter at crown base	Slow	−2.3819	2.4654	0.91	0.27	1.31
	Intermediate	−2.7678	2.6690	0.94	0.23	1.26
	Fast	−0.5444	1.9161	0.94	0.16	1.17
Sapwood area at crown base	Slow	−2.2037	1.3402	0.94	0.21	1.23
	Intermediate	−2.4050	1.4046	0.94	0.22	1.25
	Fast	−1.5759	1.2962	0.89	0.21	1.23
Sapwood area at breast height × mean annual sapwood ring width	Slow	0.2274	0.9252	0.92	0.25	1.28
	Intermediate	−0.5036	1.0371	0.93	0.24	1.27
	Fast	−0.2879	1.0729	0.84	0.26	1.30

NOTE: Equations are of the form $\ln Y = a + b \ln X$, 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. Equations for the fast stand are significantly different for all variables except dbh.

species and between trees of the same species growing under different conditions. Binkley (1984) found a significantly higher ratio in a Douglas-fir stand growing without *Alnus rubra* and *Alnus sinuata* than he found in a stand containing these species. Different ratios of leaf area to sapwood area were also reported for Sitka spruce and lodgepole pine (Whitehead *et al.* 1984) and for lodgepole pine trees growing on five different sites (J. W. Leverenz, unpublished). In stands of this study, sapwood area to leaf area ratios varied for every stem section and were significantly greater in the fast stand. The ratio increased from stump to base of the crown because leaf area remained constant while sapwood area decreased. In contrast to the findings of Long *et al.* (1981), sapwood area in this study was not constant below the live crown but decreased consistently with increasing stem height, a pattern also observed by Brix and Mitchell (1983) in Douglas-fir. The ratio changed from the crown base upwards because leaf area decreased proportionally more than sapwood area, particularly from the middle to the top of the crown (Table 1); therefore, contrary to the basic assumption of the pipe model theory, the relationship between leaf area and sapwood area in these stands was not constant.

The leaf area to sapwood area ratio has been used to assess tree vigor (Waring *et al.* 1980) with the implicit assumption that the ratio was constant for a given species. Binkley (1984) found significant effects of red alder on growth per unit of leaf area of Douglas-fir only when he used measured rather than estimated ratios of leaf area to sapwood area. Use of a constant sapwood area to leaf area ratio may yield underestimates of leaf area in productive stands and therefore yield overestimates of growth efficiency (Binkley and Reid 1984), or the reverse. For comparison, we calculated leaf area from sapwood area taken at breast height and at the base of the crown with coefficients estimated by Waring *et al.* (1982). With breast height area, leaf area was overestimated 18 and 19% in the slow and intermediate stands and underestimated 13% in the fast stand. With crown base area, leaf area was underestimated by 11, 25, and 44% in the slow, intermediate, and fast stands, respectively. Clearly, leaf area to sapwood area coefficients should differ between these two points because of sapwood taper (Granier 1981; Waring *et al.* 1982) or, as Brix and Mitchell (1983) suggest, because of differences in sapwood conductivity. Considerable error may also be incurred when leaf area is estimated with generalized regression equations, as has been shown with *Pinus contorta* (J. W. Leverenz, unpublished).

In spite of the functional relationship between leaf area and sapwood area, several studies have shown that dbh and basal area predict leaf area as well as or better than sapwood area at breast height (Snell and Brown 1978; Newman 1979; Ford 1982; Brix and Mitchell 1983; Schonenberger 1984). Brix and Mitchell (1983) found the relationship of leaf area to basal area of Douglas-fir better than the relationship of leaf area to sapwood area. Ford (1982) did not improve the prediction of leaf mass of young Sitka spruce trees, in which no clear heartwood–sapwood boundary was found, by using sapwood area rather than dbh. Because of sapwood irregularity, an easy, nondestructive evaluation of leaf area by cores was not possible in four stands of *Nothofagus solandri* (Hook. f.) Oerst. var. *cliffortioides* (Hook. f.) Poole in New Zealand (Schonenberger 1984). Newman (1979) suggests that irregularity in stem form and sapwood formation in partially open-grown Douglas-fir trees may alter the sapwood area to leaf area relationship.

Marshall and Waring (1986) suggest that sapwood area may be a better predictor of leaf area than dbh in less uniform stands or in stands with a high proportion of heartwood. Comparing dbh with sapwood area in an old-growth Douglas-fir stand, they found that the former predicted twice as much leaf area as the latter. In uniform stands with a clear and identifiable heartwood–sapwood boundary, either variable may predict leaf area effectively, probably because the variables correlate highly. In this study, leaf area was as closely related to dbh as to sapwood area at breast height, which was more strongly correlated with dbh in the slow and intermediate stands than in the fast stand.

Of the other independent variables tested for predicting leaf area, diameter at the crown base was better than dbh only for the fast stand; sapwood area at the crown base was as good as sapwood area at breast height for the two other stands. Mean annual ring width in breast height sapwood did not improve the relationship of leaf area to sapwood area. Ring width in trees of this study, unlike that found by Albrektson (1984) but like that of Brix and Mitchell (1983), was fairly constant throughout the stem, while sapwood area gradually decreased (Table 1). Although ring width did not improve the predictive equations, the positive correlation between sapwood ring width and leaf area to sapwood area (Fig. 3) might indicate a causal relationship, perhaps related to earlywood area. On the other hand, despite similar ring widths, the fast stand has a significantly greater leaf area to sapwood area ratio at the crown base than does the intermediate stand, confirming that the differing ratios among the stands cannot be fully explained by differences in ring widths.

As in this study, Brix and Mitchell (1983) and Binkley (1984) found a positive correlation for Douglas-fir between site quality and the leaf area supported per unit of sapwood area. Climate, age, time, and method of sampling cannot account for the differences among the adjacent stands of this study, which are the same age and which were destructively sampled within a 3-week period. Moreover, a very regular sapwood–heartwood boundary was easily identifiable in all sample trees.

Why does the fast stand have significantly more foliage per unit of sapwood than the other stands? Genetic differences are unlikely because the trees were artificially regenerated, probably from a common seed source. The higher total leaf area of the fast stand may result in lower vapor-pressure deficits (because of reduced wind speed and temperature) and therefore in lower transpiration per unit leaf area. Differences in soil water availability may also play a role. The fast and intermediate stands are growing on similar soils, except that the depth to weathered sandstone, with its higher moisture availability, is greater in the latter stand (Espinosa Bancalari and Perry 1987). Soils on the slow stand are waterlogged for part of the wet season; therefore, rooting depth is probably limited and as a consequence moisture uptake during drought may also be restricted.

Some authors suggest that differences in the leaf area to sapwood area relationship are due to differences in sapwood conductivity or permeability. J. W. Leverenz (unpublished) explains the large variation among lodgepole pine trees by differences in sapwood permeability and Whitehead *et al.* (1984) also suggest that the relationship in Sitka spruce and lodgepole pine depends on sapwood permeability. Differences in the ratios at breast height and at the base of the live crown may be related to differences in sapwood conductivity at these points of measurement (Brix and Mitchell 1983). Booker and Kininmonth (1978) found that the average permeability of the sapwood of Monterey pine (*Pinus radiata* D. Don) measured near the crown base was 1.89 times that measured near ground level. This may be a function of ring width. In lodgepole pine, sapwood permeability correlated positively with growth rate (Edwards and Jarvis 1982).

Since most water moves through earlywood rather than latewood cells (Zahner *et al.* 1964; Booker and Kininmonth 1978; Kramer and Kozlowski 1979), the proportion of earlywood in the sapwood may be decisive in the leaf area to sapwood area relationship. We did not measure earlywood to latewood ratios; however, fast growth is often associated with a relatively high proportion of earlywood (Panshin and deZeeuw 1970).

Even after one has accounted for differences in proportions of earlywood in the sapwood, some variability may remain owing to differences in permeability of the earlywood (Booker and Kininmonth 1978). Permeability increases with tracheid diameter (Nobel 1974; Ewers and Zimmermann 1984) and length (Krahmer 1961). The inability of ring width alone to account for differences in leaf area to sapwood area ratios may be due to variation in earlywood to latewood ratios and earlywood permeability that is independent of ring width.

Sapwood area is likely to remain the method of choice for leaf area estimation under some conditions (Marshall and Waring 1986). Where site-specific allometric equations can be developed, as in this study, dbh is likely to serve as a better independent variable for estimating leaf area because it can be measured more easily and accurately than sapwood area. However, for instances in which site-specific equations cannot be developed, sapwood area will probably provide a better estimate.

Correlation between sapwood ring width and sapwood area in our trees was sufficiently high to negate the value of using ring width as well as sapwood area as a predictive variable. However, there is little question that permeability is associated with ring width in the sapwood, and inclusion of ring width may improve predictability in some cases. Until these matters are resolved, caution is advised in the use of published leaf area to sapwood area ratios

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