DETERMINATION OF THE FASCICLE SURFACE AREA FOR *PINUS RADIATA*

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ABSTRACT

The fascicle surface area, both for each cluster separately and for the tree by fascicle age class, was calculated for 12 **Pinus radiata** trees grown under widely different soil-moisture conditions. Four surface-area models and a control method were used. A model based on the square root of the product of volume (or, alternatively, weight divided by fascicle density) and length facilitated precise surface-area determinations, the predictions departing by less than 2% from the control method. The other three models tested incurred errors of 20-50% for individual cluster estimates and 14-25% for tree estimates.

Surface-area estimates were of the structural surface area, and after its definition functional surface area could be obtained as a later step.

INTRODUCTION

Pine foliage is composed of short shoots, or fascicles. In *Pinus radiata* D. Don. these consist mainly of three needles and a sheath which entirely covers the needles of the juvenile fascicle. As the latter develops, the needles extend beyond the sheath which remains as a partial cover over the basal portion of the needles. During its 3 or more years on the tree, the fascicle sheath (initially up to 3 cm in length) contracts, increasing the needle area in direct contact with the environment.

Surface area is widely held to be a characteristic that limits, or at least strongly influences, the physiological processes of the leaf, and is therefore widely used as a unit upon which to express these processes. The techniques for estimating fascicle surface area lack accuracy and precision. They are also very time-consuming.

Madgwick (1964) pointed out that not all the fascicle area is functional in terms of, for instance, photosynthesis and transpiration. A definition of functional area needs to take into consideration the portion of the needle area covered by the sheath and the distribution of stomata.

From a practical point of view, functional area may best be derived from the more easily defined and calculated structural area. A conversion factor determined for a process under investigation could then serve to convert the structural area estimate to the appropriate functional one.

An approach utilising geometric models offers the most promise for determining the structural area of fascicles. In such models surface area is related to the dimensions of the object by a constant appropriate to the shape.

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Surface Area of Individual Fascicles

The surface area s of a geometric shape ranging between a cone and a cylinder may be determined from the basal diameter d (d_1 in Fig. 1), the length l, and the shape constant k_1 by the formula

$$s = k_1 \, d \, l \qquad (1)$$

If s is defined as the lateral area (excluding the base) plus the area of six internal faces, then k_1 varies from $((\pi + 3)/2)$ for a cone to $(\pi + 3)$ for a cylinder.

Alternatively, if d is replaced by volume v, a third-order function of l, we may use

$$s = k_2 \, (v \, l)^{\frac{1}{2}} \qquad (2)$$

In this formula, k_2 varies from 6.00 for a cone to 6.93 for a cylinder.

In practice the value of k_i must be determined empirically for a pine fascicle. Since k_2 varies less than k_1 with shape, and since volume is more easily determined than diameter, Formula (2) is more useful than Formula (1).

Obtaining Total Fascicle Surface-area

Total fascicle surface-area S can be obtained by summing the values obtained from Formula (2) over all fascicles N, by the expression

$$S = \sum_{i=1}^{N} s_i = \sum_{i=1}^{N} k_{fas,i} \, (v_i \, l_i)^{\frac{1}{2}} \qquad (3)$$

where $k_{fas,i}$ is the shape constant for the *i*th fascicle with volume v_i and length l_i.

The determination of S would be easier if S could be expressed as a function of the mean shape coefficient, length, and volume.

Using the ratio of means estimator (Cochran, 1967), the total fascicle surface-area model fulfilling these requirements is given by the expression

$$R_I = \Sigma \, s_i / \Sigma \, (v_i l_i)^{\frac{1}{2}} = N \, s_{av} / N \, \overline{(vl)^{\frac{1}{2}}} \qquad (4)$$

where R_I is equal to the mean shape coefficient* for fascicles k_{fas}, since s_{av} is equal to $k_{fas} \, \overline{(v \, l)^{\frac{1}{2}}}$. Total fascicle surface-area would therefore be predicted using the model

$$S = k_{fas} \, [N \, \overline{(v \, l)^{\frac{1}{2}}}] \qquad (5)$$

which is referred to later as the control method.

In Formula (5), $\overline{(v \, l)^{\frac{1}{2}}}$ is very time-consuming to obtain since the volumes and lengths of fascicles need to be individually measured. However, from Taylor's series (M. Smith, pers. comm.)

$$\overline{(v \, l)^{\frac{1}{2}}} = (v_{av} \, l_{av})^{\frac{1}{2}}(1 - F) \qquad (6)$$

where F is a correction factor. Solving to the third-order terms

$$-F = -C^2{}_v/8 + rC_v \, C_l/4 - C^2{}_l/8 \qquad (7)$$

That is, the correction factor depends on the coefficients of variation of volume and length, C_v and C_l respectively, and on the simple correlation coefficient, r, between volume and length. Both the calculation and the properties of the correction factor are given in an unpublished supplement obtainable from the Editor on request.

Making this substitution Formula (5) becomes

$$S = k_{fas} \, [N(v_{av} \, l_{av})^{\frac{1}{2}}(1 - F)] \qquad (8)$$

* For typographical reasons, means are indicated by the subscript **av** in the case of single symbols and by a superior bar for compound expressions.

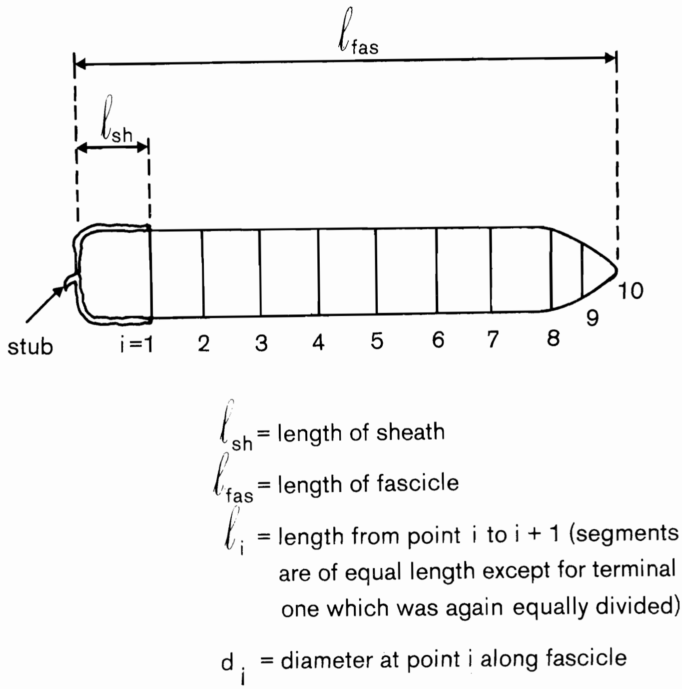

FIG. 1—Measurements for calculating surface area of a fascicle.

In the determining of fascicle surface area, if the correction factor is omitted, a positive bias results. This bias was shown to never exceed 3%, usually being less than 1% (Beets, 1974). The high positive correlation occurring between volume and length when C_v and C_l are high and, alternatively, the low C_v and C_l when r is small accounts for this. The geometric and arithmetic means are therefore approximately equal:

$$(v_{av}\ l_{av})^{\frac{1}{2}} \cong \overline{(v\ l)^{\frac{1}{2}}} \qquad (9)$$

and Formula (8) reduces to model I (uncorrected)

$$S \cong k_{fas}\ N(v_{av}\ l_{av})^{\frac{1}{2}} \qquad (10)$$

Thus, the sum of the individual fascicle suface-area estimates is approximately equal to the total surface-area obtained directly from the total of the correlative variables.

Special Cases of the Total Fascicle Surface-area Model

The total fascicle surface-area models used by previous investigators are special cases of model I. Using the ratio of means estimator, three models occurring in the literature (Harms, 1971; Cable, 1958; McLaughlin and Madgwick, 1968; Madgwick (1964) gives references to previous investigators) are given by the expressions

$$R_{II} = \Sigma\ s_i / \Sigma\ l_i = N\ s_{av}/N\ l_{av} \qquad (11)$$

$$R_{III} = \Sigma s_i / \Sigma\ v_i = N\ s_{av}/N\ v_{av} \qquad (12)$$

$$R_{IV} = \Sigma\ s_i / \Sigma\ v_i^{2/3} = N\ s_{av}/N\ \overline{(v^{2/3})} \qquad (13)$$

Correcting for the arithmetic-geometric mean differences using the approximation given by Formula (9), substitute $k_{fas}\ (v_{av}\ l_{av})^{\frac{1}{2}}$ for s_{av} in models II to IV, and $(v_{av})^{2/3}$ for $\overline{(v^{2/3})}$ in model IV (that $(v_{av})^{2/3} \cong \overline{(v^{2/3})}$ is given without proof). The expressions obtained, written also in terms of basal diameter only for illustrative purposes, are given in Table 1.

The ratios R_{II} to R_{IV} are, according to Table 1, the product of k_{fas} and the remaining terms, of which v_{av} (or alternatively d_{av}) and l_{av} are variables. Models II and III are therefore dependent upon the mean basal diameter, and model IV, which is independent of fascicle volume since surface area varies linearly as volume raised to the two-thirds power, is dependent upon the ratio between mean length and mean basal diameter.

Hence the need previously apparent (Harms, 1971) to recalculate the coefficients of models II to IV wherever average fascicle morphology changes.

TABLE 1—Ratios of means for Models II to IV

Ratio	Volume-based model	Basal-diameter-based model*
R_{II}	$k_{fas}\ (v_{av}/l_{av})^{1/2}$	$k_{fas}\ k_1\ d_{av}$
R_{III}	$k_{fas}\ (l_{av}/v_{av})^{1/2}$	$k_{fas}\ k_2/d_{av}$
R_{IV}	$k_{fas}\ (l_{av}/(v_{av})^{1/3}\ )^{1/2}$	$k_{fas}\ k_3\ (l_{av}/d_{av}\ )^{1/3}$

* For cones $k_{cone} = 6.00$, $k_1 = (\pi/12)^{1/2}$, $k_2 = (12/\pi)^{1/2}$ and $k_3 = (12/\pi)^{1/6}$

Role of Fascicle Density

In practice, total fascicle weight W is easier to measure than total fascicle volume and, as weight is the product of density β and volume, a more easily applied model than that given by Formula (10) would be

$$S \cong k_{fas}\ N(\beta)^{-\frac{1}{2}}\ (w_{av}\ l_{av})^{\frac{1}{2}} \qquad (14)$$

Study Objectives

The objectives of this study were to:

(1) Calculate the mean shape coefficient for fascicles k_{fas} and estimate its precision, as well as the coefficients of models II to IV;

(2) Examine the variation in fascicle density β;

(3) Compare the total fascicle surface-area estimates of models I to IV with those of the control method;

(4) Examine the influence of the surface-area definition on the total surface-area predictions.

MATERIALS AND METHODS

Thirteen trees were selected from a stand established during the winter of 1967 at the Forest Research Institute, Rotorua. One tree (Clone 450) which was 10.3 m in height at sampling date (April 1973) was used for calculating the coefficients of models I to IV. The remaining 12 trees (three clones, four treatments, height range 7-10 m at sampling date) had been growing in lysimeters under almost open-grown conditions. The soil-moisture-deficit treatments to which these trees had been subjected over the previous 4 years, markedly affected the dimensions of the fascicles. These trees were therefore expected to test the general applicability of the total fascicle surface-area models.

Sampling Method

Eighty-four entire fascicles were systematically selected from the Clone 450 tree, each labelled by fascicle age and position in crown. The surface area, displacement volume, and length of these fascicles were individually measured.

For each of the other 12 trees the total fascicle dry-weight was obtained by crown categories (that is, by branch cluster for each fascicle age class separately) using a standard crown-dry-matter sampling procedure. From each category 30 fascicles were selected randomly and their individual displacement volume, length, and oven-dry weight determined.

Measurement of Fascicle Length and Diameter

The fresh length (excluding stub) both of the fascicle and of the sheath were recorded separately to the nearest 0.5 mm (Fig. 1). Fascicle diameters were measured to the nearest 0.1 mm with a microscope and micrometer eyepiece at nine points along the fascicle (two diameters measured at right angles to each other and averaged), the needles first being secured together with a fine thread (Fig. 1).

Calculation of Fascicle Surface Area

Surface area S was defined as the smooth area of the lateral face, assumed to be circular in outline (Wood, 1971), plus the internal faces, assumed to be radii of the solid fascicle (Wood, 1971), including the area covered by the sheath. This structural area can be adjusted as necessary for sheath size and corrugations in a later step.

Using the symbols given in Fig. 1, S (calculated using, for example, the trapezoidal rule) is given by the expression

$$S = (n + \pi)\, l_{sh}\, d_1 + \sum_{i=1}^{9} (n + \pi)\, l_i\, ((d_i + d_{i+1})/2)$$

where n is the number of needles in the fascicle (three in this example).

Displacement Volume of Fascicles

The volume of an object (cm^3) is given by the weight (g) of water that it displaces. Using this principle, a fascicle supported by a pin attached to the sheath was entirely immersed in a container of 6% detergent, standing on a balance. The weight increase registered by the balance was recorded to the nearest 0.001 g. Consistent results were obtained by presoaking the fascicle in 6% detergent for approximately 1 minute and then blotting it before determining its displacement volume. Care was taken to avoid dehydration of any fascicles.

Fascicle displacement volumes were adjusted for the miniscus effect between the pin and the solution (calculated to be 0.01446 g, the intercept coefficient of the displacement-volume/dry-weight regression equation for all trees and fascicle ages combined).

Data analysis

The ratio estimator, although appropriate for the theory presented earlier, was replaced by linear least squares when processing these data. This was found necessary since the relationship between the dependent and independent variables had an intercept coefficient.

Total fascicle surface-area S was calculated for the control method and for models I to IV using the expressions

Control estimator	$S = N[a_I + k_{fas}\ (\beta)^{-\frac{1}{2}}\ \overline{(wl)^{\frac{1}{2}}}]$	(15)
Model I (corrected)	$S = N[a_I + k_{fas}\ (\beta)^{-\frac{1}{2}}\ (w_{av}l_{av})^{\frac{1}{2}}\ (1\text{-}F)]$	(16)
Model I (uncorrected)	$S = N[a_I + k_{fas}\ (\beta)^{-\frac{1}{2}}\ (w_{av}l_{av})^{\frac{1}{2}}]$	(17)
Model II	$S = N[a_{II} + R_{II}\ (l_{av})]$	(18)
Model III	$S = N[a_{III} + R_{III}\ (\beta)^{-1}\ (w_{av})]$	(19)
Model IV	$S = N[a_{IV} + R_{IV}\ (\beta)^{-2/3}\ (w_{av})^{2/3}]$	(20)

Estimates of S were obtained by category and by tree totals of the correlative variables for each fascicle age class separately, where w_{av} and l_{av} were the appropriate means of the dry-weight (dried to constant weight at 65°C) and length, respectively, based on the 30 fascicles measured per category; N was the appropriate total fascicle dry-weight divided by w_{av}. Density β was obtained for each tree by fascicle age class (see "Fascicle density" in the following section).

In practice the coefficients in models II to IV should be recalculated after a change in the mean dimensions of the fascicle, as indicated in the theory presented earlier. To show the general applicability of the models the coefficients a_i to R_i ($R_I = k_{fas}$) were evaluated in the following analyses only once for the 84 Clone 450 fascicles.

For the 12 sample trees the area estimates obtained using Formulas (16) to (20) were expressed as percentage departures from the control estimator (15), the most accurate of the estimators since arithmetic and geometric means are not equated.

RESULTS AND DISCUSSION

Evaluating the Coefficients of Models I to IV

The 84 fascicles of Clone 450 varied widely both in size and in their relative dimensions (Table 2).

TABLE 2—Variation in the dimensions of the 84 Clone 450 fascicles

Variable		Mean	Minimum	Maximum
diameter	d (cm)	0.18	0.10	0.34
length	l_{fas} (cm)	12.4	4.8	18.2
	d/l_{fas}	0.015	0.011	0.035
volume	v (cm^3)	0.327	0.075	0.987

An estimate of the mean shape coefficient and its precision is given in Table 3 (see model I). Though fascicle shape is not constant, the variation in shape is small. Since the fascicles used for evaluating k_{fas} varied widely in their dimensions, it seems reasonable to suppose that the mean shape coefficient for the Clone 450 tree will be representative of a broad range of conditions.

Estimates of the coefficients and their precision for models II to IV are given in Table 3. Model IV depends on the ratio of l_{av} and $(v_{av})^{1/3}$ (Table 1), so is not as precise as model I, but is more precise than models II and III. These depend not only on the ratio of the mean dimensions of the fascicles, but on fascicle volume as well. All the models are dependent upon fascicle shape, but this is nearly constant.

TABLE 3—Regression analysis of models to IV, based on the 84 Clone 450 fascicles

Model	Intercept	Slope coefficient	RMS	SE (slope)	Coeff. deter. (r^2)
I	0.200	6.955	0.060	0.027	0.993
II	—4.596	1.448	7.562	0.300	0.746
III	5.288	26.824	2.521	0.173	0.915
IV	0.609	29.491	1.510	0.134	0.949

Fascicle Density

From the displacement volume and dry weight of the 30 fascicles measured per category, the influence of fascicle size, cluster position, age, and between-tree position on fascicle density could be examined.

Plots of displacement volume against dry weight indicated that fascicle size and cluster position did not influence density (Beets, 1974). Regressions of fascicle volume on dry weight could therefore be calculated by individual trees for each age class separately. The constant terms were ascribed to the miniscus effects (Beets, 1974).

A comparison of the regression equation slopes ($1/\beta$) indicated that 2-year-old fascicles were denser than 1-year-old fascicles (i.e., smaller slope coefficients) in eight trees at the 99% probability level, one at the 95% level, and the remaining three at less than the 95% level. Differences between ages ranged from 0.7 to 11.6% with a mean difference of 4%.

Between-tree differences in fascicle density attained 19%. As the 12 trees from Rotorua were sampled over a period of 4 months, between-tree comparisons of density were not considered to be valid, using these data. Additional data collected from 25 trees from Canterbury indicated that, within a fascicle age class, between-tree fascicle density could vary by up to 22% (Beets, 1974).

The 24 slope coefficients (Table 4) were used in Formulas (15), (16), (17), (19), and (20) as the estimates of $(1/\beta)$.

TABLE 4—Regressions of volume on weight for the 12 Rotorua trees by foliage age class

Tree no.	Age 1 year Intercept	Slope coeff.	Coeff. det. (r^2)	Age 2 years Intercept	Slope coeff.	Coeff. det. (r^2)
1	—0.019	3.22	0.987	—0.023	3.10	0.988
2	—0.010	3.07	0.993	—0.012	2.95	0.988
3	—0.005	3.02	0.969	—0.015	2.93	0.981
4	0.000	3.01	0.972	—0.000	2.87	0.978
6	—0.008	2.80	0.987	—0.008	2.72	0.997
7	—0.011	2.97	0.995	0.000	2.71	0.981
8	—0.009	2.82	0.988	—0.011	2.72	0.989
10	—0.014	2.86	0.977	—0.014	2.76	0.983
18	—0.021	2.84	0.988	0.000	2.51	0.960
20	—0.019	2.80	0.991	—0.012	2.72	0.989
21	—0.012	2.72	0.984	—0.020	2.70	0.987
22	—0.011	2.72	0.992	—0.011	2.61	0.987
	—0.014	2.94	0.977	—0.017	2.85	0.975

Comparison of the Performance of Models I to IV

The 12 trees from Rotorua varied widely in their mean dimensions. The mean length and weight of the fascicles at the top and bottom of the crown (Table 5) usually also represent the range in mean dimensions for the trees (Beets, 1974).

(1) *Area estimates by cluster totals of the correlative variables*

The range and mean departure of models I to IV from the control are presented in Table 6. The relationship of the departures to cluster position is given in Fig. 2.

For model I the bias of the uncorrected model is small, and inclusion of the correction factor is considered unnecessary. Solved to the third-order terms, the correction factor was only partially effective for individual clusters. However the mean departure of all clusters combined was adequately corrected for.

The cluster areas for model II were underestimated at the top of the crown and overestimated at the base (Fig. 2). From the dependencies of this model (Table 2) the pattern evident in Fig. 2 is to be expected.

TABLE 5—Fascicle length (cm) and weight (g) for the 12 Rotorua trees. First and second lines for each numbered tree give values (mean and coefficient of variation) at the bottom and top of the crown respectively

Tree no.	Age 1 year Length	c.v.	Weight	c.v.	Age 2 years Length	c.v.	Weight	c.v.
1	8.7	13	0.03	24	9.6	17	0.05	37
	14.8	22	0.21	29	15.4	14	9.18	18
2	7.8	16	0.02	34	8.7	15	0.04	25
	14.6	3	0.18	7	15.1	3	0.19	11
3	8.5	13	0.03	21	8.2	17	0.04	38
	11.4	7	0.15	10	11.6	18	0.16	30
4	9.0	12	0.03	21	8.0	19	0.03	40
	10.2	12	0.11	22	10.7	13	0.12	21
6	9.3	21	0.05	36	10.0	24	0.06	42
	13.1	9	0.13	16	14.9	4	0.20	13
7	6.8	24	0.02	34	10.7	21	0.05	48
	15.7	9	0.17	15	11.9	10	0.09	19
8	11.1	12	0.05	42	8.8	17	0.04	23
	15.5	10	0.16	24	13.4	11	0.13	18
10	8.2	25	0.03	46	8.6	24	0.04	40
	10.6	6	0.09	9	12.5	7	0.11	13
18	9.4	15	0.05	29	8.3	26	0.04	44
	12.4	13	0.15	27	12.0	10	0.14	14
20	9.6	19	0.05	38	8.3	14	0.04	37
	12.6	7	0.18	17	10.9	19	0.12	37
21	7.7	26	0.04	44	8.8	16	0.05	29
	9.2	12	0.07	19	10.5	13	0.11	29
22	7.6	21	0.03	33	7.9	35	0.04	61
	12.6	7	0.16	15	8.7	21	0.06	43

For model III areas were overestimated, particularly at the base of the crown, a pattern not explained by the dependencies of the model alone.

The tendency of model IV to overestimate area at the top of the crown more than at the bottom is to be expected. The large departures occurring in model III are not evident in model IV.

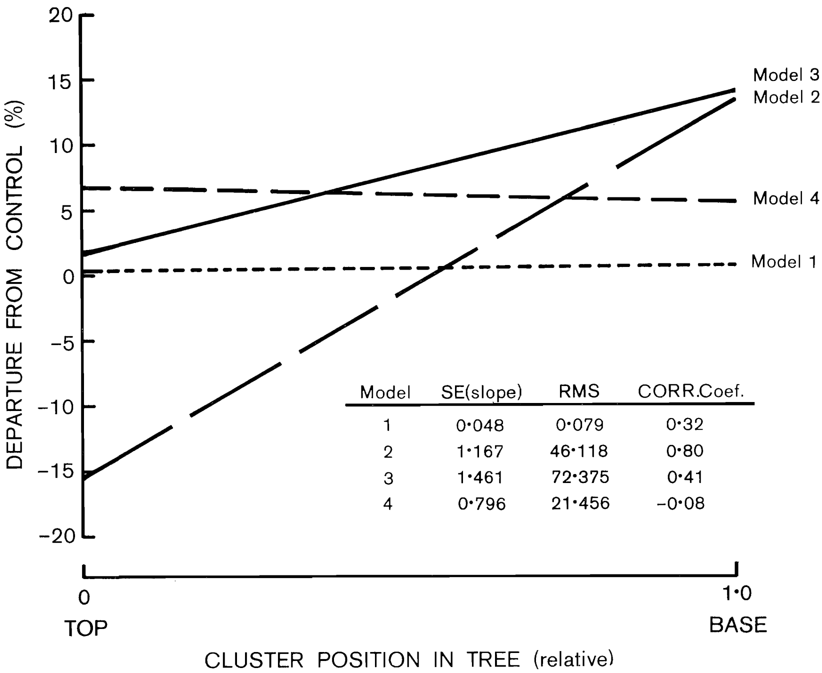

Fig. 2—Performance of the models in the estimating of surface area by cluster, based on the 12 Rotorua trees.

(2) *Area estimates by tree totals of the correlative variables (by fascicle age class)*

The range and mean departure of models I to IV from the control are presented in Table 6. The relative precision of the models is explicable in terms of the theory presented earlier. Model I yields precise area estimates when dealing with these trees, which possessed a wide range in mean fascicle dimensions. A change in the mean dimensions of the fascicles results in large errors for the other total fascicle area models.

TABLE 6—Departure (%) of the surface-area estimates of models I to IV from those of the control method, for the 12 Rotorua trees

Model	Cluster totals (by age class) of the correlative variable(s)			Tree totals (by age class) of the correlative variable(s)		
	Minimum	Maximum	Mean	Minimum	Maximum	Mean
I (corrected)	— 1.6	0.7	—0.04			
I (uncorrected)	0.0	1.6	0.45	0.6	1.7	1.1
II	—25	33	—1.10	—3.1	15.0	3.5
III	— 9	50	7.83	—3.0	24.5	8.2
IV	— 5	20	6.12	1.3	13.5	6.8

Effect of the Surface Area Definition

Two alternative surface-area definitions were developed and the percentage departures from the structural-area estimate calculated (all the estimates were obtained using model I uncorrected).

Subtracting from the structural area the internal and lateral face area covered by the sheath, which leaves the photosynthetically active exposed area, resulted in area reductions ranging from 7.7 to 10.4% with a mean reduction of 9.1% for the 1-year-old fascicles. For the 2-year-old fascicles reductions ranged from 6.4 to 8.2%, averaging 7.3%.

Subtracting the internal face area covered by the sheath, which leaves the area in direct contact with the environment, resulted in area reductions ranging from 4.0 to 5.4%, averaging 4.8% for the 1-year-old fascicles. For 2-year-old fascicles area reductions ranged from 3.4 to 4.2%, averaging 3.9%.

Errors due to biological assumptions or requirements, averaging 4 to 9%, are comparable in magnitude to those due to geometric assumptions, averaging 1 to 8%.

CONCLUSIONS

Precise fascicle surface-area predictions are possible using a model based on fascicle weight, length, and density. These are related in the expression

$$S = N[a_I + k_{fas} (\beta)^{-\frac{1}{2}} (w_{av}\ l_{av})^{\frac{1}{2}}]$$

where k_{fas} is the mean shape coefficient for fascicles.

This model applies both to individual fascicles and to many fascicles combined because of the close approximation between the geometric and arithmetic means $\overline{(v\ l)^{\frac{1}{2}}}$ and $(v_{av}\ l_{av})^{\frac{1}{2}}$, respectively.

The variation in fascicle density indicated that density needed to be determined for each tree by fascicle age class. Samples containing 20-30 fascicles each would suffice for calculating density.

The other total fascicle surface-area models examined were special cases of this new model but they require in addition a fascicle stratification procedure to ensure that the constraints of the models are met.

Despite the possibility of precise fascicle surface-area predictions with this new model, the accuracy of the estimate awaits the definition of functional area. Adjusting the easily defined and calculated structural-area estimate by means of appropriate conversion factors would provide a practical solution for obtaining the functional area of fascicles.

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