Equations for estimating loblolly pine branch and foliage weight and surface area distributions

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Abstract: Equations to predict foliage weight and surface area, and their vertical and horizontal distributions, within the crowns of unthinned loblolly pine (*Pinus taeda* L.) trees are presented. A right-truncated Weibull function was used for describing vertical foliage distributions. This function ensures that all of the foliage located between the tree tip and the foliage base is included. Foliage distribution prediction is based on actual two-dimensional foliage location. It is shown that the average time of full foliage, and hence average foliage weight or surface area prediction, is highly variable for loblolly pine and subject to considerable error. To help account for the old and new foliage differences during the approximate time of "full leaf," the prediction equations for new and old foliage weight and surface area include a day-of-year term. New equations to predict branch weight, surface area, and the vertical distributions of branch biomass and surface area were also developed. The vertical distributions of branch biomass and surface area are described with logarithmic equations constrained to equal zero when relative crown depth is equal to zero, and to equal one when relative crown depth is one.

Résumé : Les auteurs présentent des equations qui servent à predire le poids et la surface du feuillage ainsi que sa distribution verticale et horizontale dans la cime de pins à encens (*Pinus taeda* L.) non Cclaircis. Une fonction de Weibull tronquée à droite a été utilisée pour dtcrire la distribution verticale du feuillage. Cette fonction assure que tout le feuillage situé entre l'extrémité et la base de la cime soit inclus. La prediction de la distribution du feuillage est basée sur sa localisation actuelle selon deux dimensions. 11 est démontré, qu'en moyenne, le moment où le feuillage est completest très variable et que, par consequent, la prediction du poids ou de la surface du feuillage dans le cas du pin a encens est sujette à d'importantes erreurs. Afin d'aider à tenir compte des differences entre le vieux et le nouveau feuillages pendant la ptriode approximative oh le feuillage est complet, les equations de prédiction pour le poids et la surface du jeune et du vieux feuillages cornportent un terme pour le jour de l'année. De nouvelles equations capables de predire le poids des branches, la surface et la distribution verticale de la surface et de la biomasse des branches, ont Cgalement été développées. La distribution verticale de la surface et de la biomasse des branches est décrite par des equations logarithmiques dont la valeur est Cgale à zéro lorsque la profondeur relative de la cime est tgale à zéro et à un lorsque la profondeur relative de la cime est Cgale à un.

[Traduit par la Redaction]

Introduction

The quantity and distribution of a tree's foliage, and the shape of its crown, are important factors for determining a tree's potential to utilize solar energy and assimilate carbon through photosynthesis (Grace et al. 1987; Russell et al. 1989). Hence most physiological process models require a mathematical description of foliage distribution.. For example, MAESTRO (Wang and Jarvis 1990) requires a mathematically defined three-dimensional crown shape, and functions that describe both vertical and horizontal distribution of leaf area, for each tree in a stand in order to solve for the intersections of beams of both diffuse and direct radiation within the tree crown. These intersections are necessary to model light interception and transmittance. The authors of this report, seeking to improve upon the present crown characteristics prediction equations used in the loblolly pine version of MAESTRO (Jarvis et al. 199 1), and in a new linked model system (Baldwin et al. 1993), have utilized new models to predict vertical and horizontal leaf area and weight distributions, branch and leaf area and weight, and crown shape of mature, unthinned loblolly pine. The work involving crown shape is reported elsewhere (Baldwin et al. 1995; Baldwin and Peterson 1997). The foliage and branch surface area and weight distribution equations are presented in this paper.

MAESTRO originally used the beta function fitted to leaf area data pooled from all sample trees to independently describe the vertical and horizontal distributions of leaf area (Wang and Jarvis 1990). Thus, the same fitted vertical or horizontal distribution was assumed for each tree no matter what its size or position in the canopy. Pooling the data for all sample trees, or sample trees within a particular treatment, has been the common practice in other studies of leaf area distribution (e.g., Kinerson et al. 1974; Vose 1988). It does not appear that sufficient data were collected in previous studies to do otherwise. In a recent study, to quantify individual tree size and silvicultural treatment effects on foliage quantity and its vertical distribution in 9- to 14-year-old loblolly pine, Gillespie et al.

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Table 1. Distribution of the sample trees by age and basal area per hectare.

Age (years)	Basal area (m^2/ha)				
	15-20	21-25	26-30	31-35	36–40
9-15	3 (5)*	4 (8)	1 (2)	3 (1)	1
16-20		1 (5)	1 (2)	1 (1)	(2)
21-28	1	1 (1)	(2)	(1)	(2)
29-34		2	3 (2)	2	
>34	1	2	2	1	

*Number of Virginia – North Carolina trees is in parentheses. All others are Louisiana trees.

Table 2. Distribution of the sample trees by age and diameter at breast height.

Age (years)	Diameter at breast height (cm)				
	<15	15-20	21-25	26-30	>30
9-15	5 (5)*	6 (10)	1 (1)		
16-20	(3)	2 (4)	(3)	1	
21-28		1 (5)	1 (1)		
29-34			4 (2)	2	1
>34				3	3

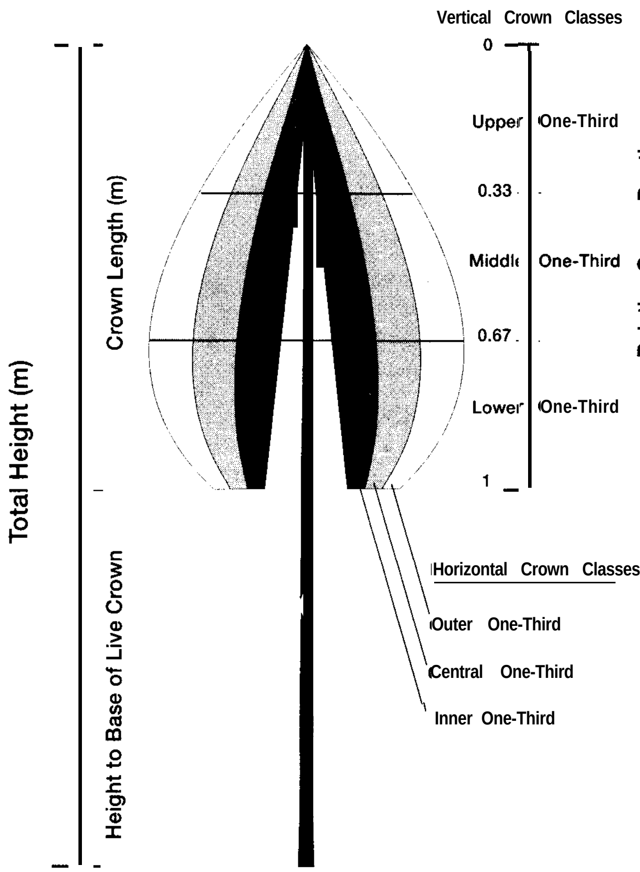
*Number of Virginia – North Carolina trees is in parentheses. All others are Louisiana trees.

Table 3. Distribution of the sample trees by age and total height.

Age (years)	Total height(m)					
	9-12	13-15	16-18	19–21	22–24	25-27
9-15	5 (8)*	7 (7)	(1)			
16-20	(1)	1 (7)	2 (2)			
21-28		2 (2)	(3)			(1)
29-34			(1)	(1)	5	2
>34					2	4

*Number of Virginia – North Carolina trees is in parentheses. All others are Louisiana trees.

Fig. 1. Schematic diagram of the crown of a typical mature loblolly pine tree showing the upper, mid, and lower crown one-thirds, and the outer, central, and inner envelopes used to define regions of application of the horizontal foliage weight and surface area distributions.

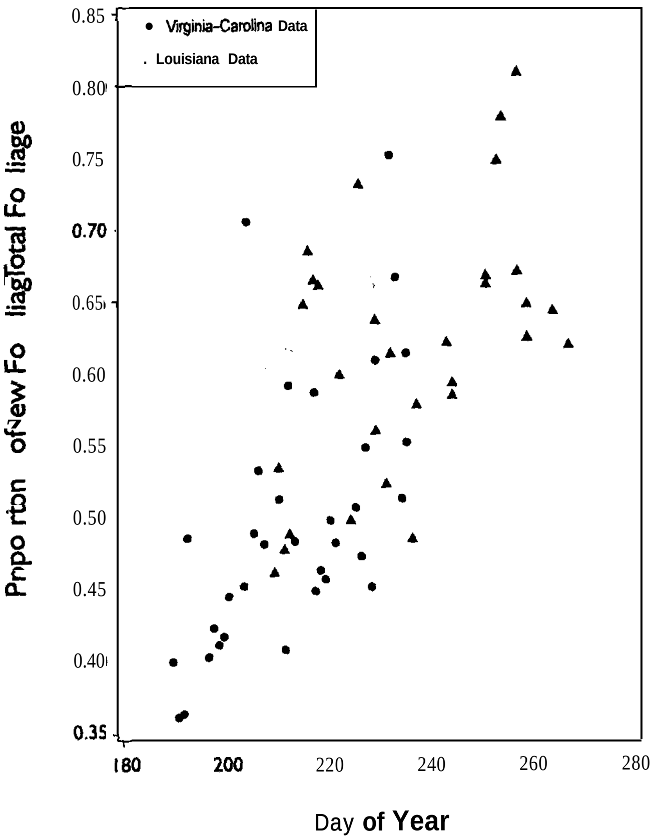


(1994) found no relationship between tree size, nor between thinning or fertilization treatment, and the vertical distribution of the foliage biomass. We hypothesized that for samples taken from a wide range of tree ages, sizes, stand densities, and crown positions, the leaf weight and surface area distributions would be significantly different. Thus, the first objective of this study was to fit vertical and horizontal distribution functions to each tree covering a range of tree ages, sizes, and crown classes. The next step was to determine whether the parameters of these functions could be predicted from functions of easily measured tree characteristics. Individually fitted distribution functions were then tested for equality.

Another problem in some earlier leaf weight or area distribution studies (e.g., Kinerson et al. 1974; Schreuder and Swank 1974; Vose 1988; Baldwin et al. 1993) was that the determination of leaf weight or surface area on the sample branches, sometimes at various distances from the bole, was referenced at the height that the branch was attached to the tree bole. Thus locational reference to that foliage within the distribution, whether normalized or not, was to the point of branch attachment to the bole. This is valid only if the branches extend out horizontally from the bole. This is not true with loblolly pine. The outer foliage on any given branch is usually located higher or lower (generally higher) than the height of branch attachment. Therefore, the second objective in this study was to provide vertical and horizontal distribution predictions that more accurately reflect the true foliage distributions on each tree.

The third objective was to develop equations to predict needle and branch weight and surface area for an individual branch or an entire tree. Separate needle weight and surface area equations would be developed for old and new needles. Although some equations providing loblolly pine needle weight and surface area have been developed (Shelton and Switzer 1984), equations more specific for the foliage's vertical location within the crown are required in MAESTRO. To our knowledge, equations to predict branch surface area of loblolly pine have not been developed; however, bole surface area equations were published several decades ago (Grosenbaugh 1954). Surface-area estimates were needed to provide respiration predictions in an alternative respiration predicton routine used in the current loblolly pine version of MAESTRO.

Fig. 2. Plot of the proportion of new foliage to total foliage weight over the day of the year for Virginia – North Carolina trees sampled in 199 1 and Louisiana trees sampled in 1992.



Data and analysis

Weight and surface area data were obtained from 64 dominant or codominant loblolly pine trees sampled from unthinned plantations located in Louisiana, Virginia, and North Carolina. The Virginia -North Carolina (VC) trees were sampled during the period July 6 through August 23, 1991, and the Louisiana (LA-l) trees were sampled between July 28 and September 23, 1992. The sampling procedures used in each region were nearly identical, although there were differences that required separate analyses. Also, in some cases the LA-l and VC data sets were analyzed separately and separate equations developed because of apparent regional differences. The different sampling dates turned out to be very important to the analysis, as will be discussed later. Overall, the stands varied in age from 9 to 41 years, and in site index (base age 25) from 14 to 22 m. Basal area per hectare ranged from 15 to 40 m^2 (Table 1). Trees were randomly selected for destructive sampling; however, if a chosen tree was noticeably deformed (forked, broken top, twisted, leaning, etc.), it was discarded and another sample was selected. The sample trees ranged from 10.2 to 35.9 cm in diameter at 1.37 m above groundline (DBH) (Table 2) and 8.9 to 26.2 m in total height (HT) (Table 3).

DBH was measured for each tree before felling. Trees were felled as carefully as possible to minimize damage to the crowns. On the ground, height to the base of the full live crown (HBLC) and HT were measured. Then, from each one-third of the vertical crown (Fig. 1), two sample branches were randomly selected and flagged for more detailed measurements. The basal diameter (about 2 cm from the bole) and height above groundline of each branch on the tree were then measured. The six sample branches, including about 0.5 m of the bole to which each branch was attached, were removed from the tree, transported to field headquarters, and immediately placed in cold storage until further detailed measurements could be accomplished, usually the next day.

At field headquarters each sample branch was placed in its "natural" position by securing the bole portion vertically on a spike welded to a heavy flat sheet of steel that was placed on a plywood platform. Heavier branches often required support with lines suspended from overhead in order to secure the branch in its "natural" position, assuming the tree stood vertical before felling. Branch length, length to first foliage, and horizontal and vertical lengths to the point of maximum branch curvature and to the branch tip were measured to provide data for fitting vertical and horizontal distribution functions. Measurements were obtained of outside-bark diameters at each branch internode and internode lengths for all orders of branches.

Finally, the foliage on the sample branches was divided into horizontal one-thirds, and the old and new foliage was placed separately in labeled plastic bags. Each of these components was then placed in a cooler. Green weights were obtained in the laboratory. The samples were then oven-dried and reweighed.

Linear regression models proved to be adequate for all data fitting. A model of the following form (Schumacher and Hall 1933), or slight variation thereof, was used to model branch or tree component quantities:

$$[1] \quad \ln f(x) = b_0 + b_1 \ln(x_1) + b_2 \ln(x_2) + \ldots + b_n \ln(x_n)$$

where $f(x)$ is branch or tree component weight or surface area.

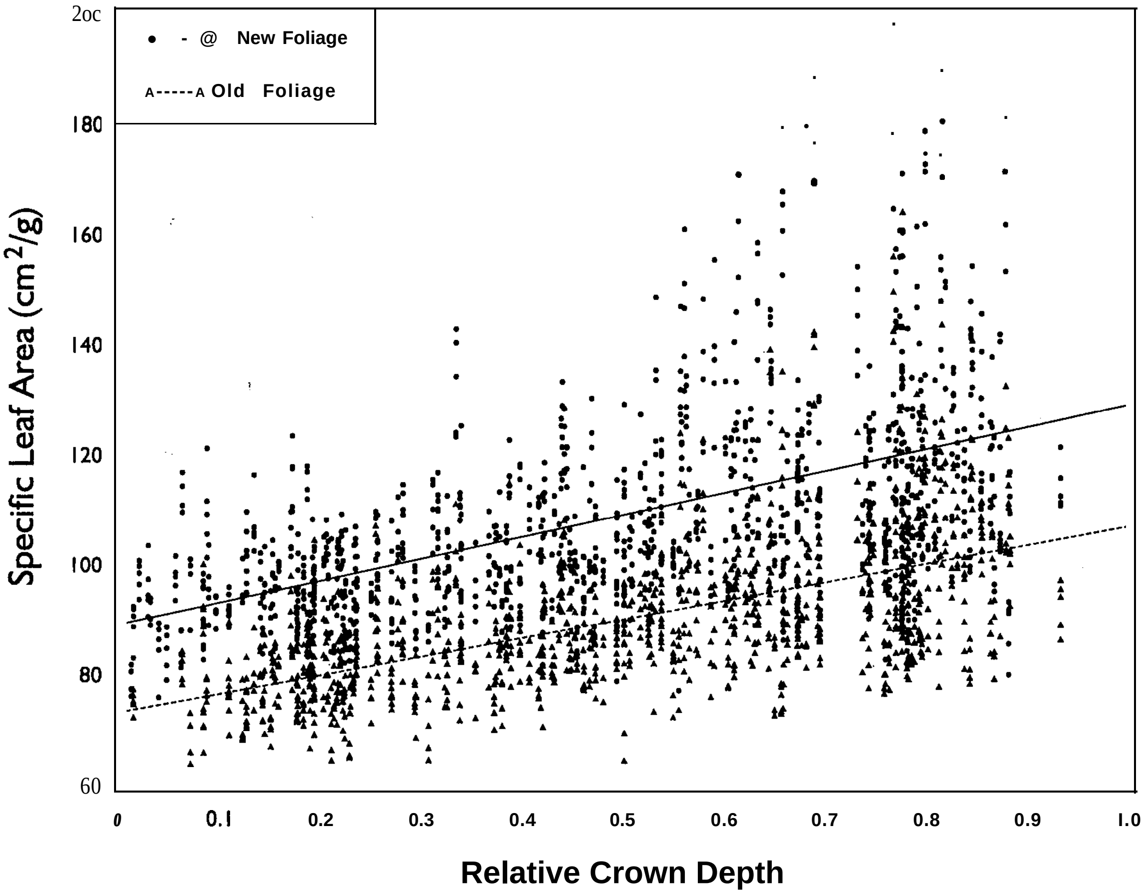
This model was chosen because the relationships are allometric in nature, it fits these kinds of data well, and reduces the effects of variance heteroscedasticity (Ruark et al. 1987). Transformation bias was corrected by Snowdon's procedure (Snowdon 1991).

Equation goodness of fit statistics, developed and reported in the original (untransformed) units, are the standard error of the mean and R^2 (Kvalseth 1985). Additionally, plots of residuals were prepared for all prediction equations and checked for any unusual patterns.

Equations were developed from VC and LA-l data individually and combined and then tested for significant parameter differences using the covariance analysis procedure given in Freese (1964). In some cases there were significant differences (at the 5% level), suggesting that regional equations might be better than one combined equation. However, it was surmised that the relatively small sample sizes for each region, and age and time of sampling differences between the two data sets, were probable confounding factors that weakened the validity of the test results. For example, some predictor variables found to be significant in combined equations were not significant in each regional equation. Hence, only equations from the combined data set are presented in this report.

Branch and foliage weights for the entire tree were estimated by developing equations to predict individual branch wood and bark or foliage weight as a function of branch basal diameter and crown depth. Given this information, the measured

Fig. 3. Linear relationships between specific leaf area and relative crown depth for new and old loblolly pine needles sampled from Louisiana trees in 1995.



and estimated individual branch weights for each component were summed to give total branch or foliage weights for each tree. Then equations were fitted to predict the total tree's branch and foliage weights (new and old foliage separately) as functions of DBH, HT, and either crown length (CL) or crown ratio (CRAT). However, when analyzing the new and old foliage weight data an anomaly was discovered that required a modification in the analysis procedure.

A study goal was to provide foliage equations to predict weight and surface area at the time of full leaf, i.e., at the time before old needle senesence had begun and new needle growth was essentially complete. It was assummed that this would be for several weeks in late summer when the proportion of new to total foliage would not change significantly. However, as shown in Fig. 2, the proportion of new to total foliage weight (sum of new foliage weight/sum of total foliage weight for the six sample branches on each tree) changed 128% over the period that the trees were sampled. A variable "day of year" (DAY) was added into the individual new and old foliage weight and surface area equations to account for this daily variation. This variable works well for users who need to predict changes in the proportions and the amounts of old and new foliage between days 190 and 270. Foliage weight, foliage surface area, and their respective vertical distribution equations are presented with and without the DAY variable. The equations without the DAY variable assume the maximum foliage or full-leaf condition, and can be used with a user-supplied phenology curve to proportion new and old foliage quantities.

Development of branch surface area estimates was the same as for branch and foliage weights. However, adequate needle surface area measurements were not taken with the VC and LA-l data sets to develop foliage surface area equations. An equation describing the relationship between foliage depth within the crown and specific leaf area (e.g., Kinerson et al. 1974; Shelton and Switzer 1984; Vose 1988) was needed to convert foliage weights to foliage surface area. The data required to model this relationship were collected in August 1995 from unthinned loblolly pine stands and are designated LA-2.

The LA-2 trees had about the same diameter distribution as the LA- 1 trees and were obtained from the same stands as those that supplied the LA-l data. New and old foliage samples (five fascicles each) were obtained from eight sample branches randomly selected within four equidistant vertical crown layers from 32 trees. For each of the 80 fascicles from each tree, the length of the photosynthetically active portion of the fascicle was first measured (tip to start of bundle sheath). Then each fascicle was examined under a microscope with a retical eyepiece in order to obtain needle widths. The widest width (not the fascicle radius) was measured on any two of the three needles within each fascicle and the values were averaged. The fascicle radius was then computed by geometry. The fascicle tip was assumed to be a cone of 0.5 cm length. Given

Table 4. Regression coefficients for branch weight and surface area components.

Dependent variable*	Parameter estimates				Statistics†		
	b_0	b_1	b_2	b_3	R^2	$S_{\bar{y}}$	N
BrchWt	2.6418	2.6174	0.4068		0.76	15.7	363
BrchSa	5.2122	1.9741	0.4281		0.81	62.2	380
NFolWtDay	-5.3141	2.3134	-0.6808	1.5911	0.71	3.8	377
NFolWtNod	3.2613	2.472 1	-0.7586		0.67	4.1	377
OFolWtDay	12.1206	2.0136	-0.1342	-1.7427	0.58	3.3	343
OFolWtNod	2.7413	1.8312	-0.0359	—	0.58	3.3	343

Note: The model is $\ln(\hat{y}) = b_0 + b_1 \ln(\text{Brdiam}) + b_2 \ln(\text{Crndepth}) + b_3 \ln(\text{Day})$, where $\hat{y}$ is predicted weight or surface area (in grams or cm*), Brdiam is diameter outside bark (cm) of branch 2.0 cm from bole intersection, Cmdepth is crown depth (m) from tip of tree to branch-bole intersection, Day is day of year, and b_0, b_1, b_2, b_3 are coefficients estimated from the data.

*BrchWt, branch dry weight (g) of wood and bark; BrchSa, branch surface area (cm^2) outside bark; NFolWtDay, branch dry weight (g) of new foliage using day of year; NFolWtNod, branch dry weight (g) of new foliage without day of year; OFolWtDay, branch dry weight (g) of old foliage using day of year; and OFolWtNod, branch dry weight (g) of old foliage without day of year.

†R^2 and $S_{\bar{y}}$ are the R-squared and standard error of the mean statistics in untransformed units.

this information, the exposed needle surface area of an open fascicle was calculated. Then the fascicles were individually weighed both green and dry, and specific leaf area calculated from the surface area and dry weight measurements. Figure 3 illustrates the linear relationships of new and old foliage specific leaf area with relative crown depth for the LA-2 data.

The Weibull distribution (Weibull 195 1) was selected to model the vertical distributions of foliage weight and surface area. The two-parameter form of this distribution has been used by others to represent foliage distributions (Schreuder and Swank 1974; Vose 1988, Baldwin et al. 1993; Gillespie et al. 1994). However, if one end of the vertical distribution is not truncated at the crown base (if considering crown depth) or at the tip (if considering crown height) the model cannot accurately describe the foliage distribution because the right tail is infinite. Therefore, we elected to use the right-truncated form of the two-parameter distribution. Maximum likelihood estimates for the parameters of the right-truncated distribution have been derived by A. Clifford Cohen[2] and an estimation procedure programmed by Ray A. Souter.[3]

The probability density function form of the right-truncated two-parameter Weibull distribution (in terms of our application) is

$$[2] \quad f(\text{RCD}) = (\gamma/\beta)\,(\text{RCD}/\beta)^{\gamma-1}\left(\frac{\exp[-(\text{RCD}/\beta)^{\gamma}]}{1-\exp[-(\text{CL}/\beta)^{\gamma}]}\right)$$

where

RCD is relative crown depth (depth within the crown/crown length)

CL is crown length (m)

$f(\text{RCD})$ is the probability of foliage occurring at RCD

β and y are parameters to be estimated

The truncated Weibull distribution could not be used to model the horizontal distribution of foliage because there were too few data points at each crown depth. Foliage weight samples were taken only along the inner, central, and outer one-third length of each sample branch. Because of different branch angles and lengths, each sample did not necessarily fall within the corresponding crown horizontal one-third (Fig. 1). Therefore, these locations of foliage were placed within each tree's specific three-dimensional shape that was developed for the same study (Baldwin and Peterson 1997). After this adjustment, there were sufficient samples within the nine radial volumetric regions defined (Fig. 1) to develop discrete foliage distributions for each tree. Equations were developed to predict the proportions of foliage weight within each of those regions.

Results

Branch foliage weight and individual branch weight and surface area

The combined VC and LA- l data for both old and new foliage weights were modeled in two ways: (I) by using the diameter of the branch about 2 cm from the bole (BRNDIA), and the distance from the tree tip to the branch at its attachment to the bole (CRNDEP), with and without the DAY as predictor variables, or (2) by using BRNDIA, with and without DAY, in separate equations for each vertical crown one-third. Procedure 1 proved to be the better alternative. Therefore, equations to predict the dry weight of new or old foliage on a branch of a given size and location on planted loblolly pines, with and without DAY, are given in Table 4. Equations to predict the dry weight or surface area of individual live branches (wood and bark without foliage) are given in the same table.

Foliage surface area prediction

As mentioned earlier, foliage surface area was estimated from its relationship with foliage mass at a given vertical location within a tree crown. First, it was necessary to develop equations to predict specific leaf area (needle surface area/needle weight)(SLA) from the LA-2 data. The equation for new foliage is

$$[3] \quad \ln(\text{SLA}) = 4.8852 + 0.3732(\text{RELDEP}) - 0.1175\ln(\text{AGE})$$

$$S_{\bar{y}} = 0.44\ \text{cm}^2/\text{g},\ R^2 = 0.37,\ n = 1279$$

[2] A. Clifford Cohen. The Truncated Weibull Distribution. Unpublished manuscript on file with the Department of Statistics, University of Georgia, Athens.

[3] Ray A. Souter. A computer program to provide maximum likelihood estimates for the right-truncated Weibull distribution. Unpublished computer program written for analysis in Statistical Analysis System (SAS) code.

Table 5. Regression coefficients for tree weight and surface area components.

Dependent variable*	Parameter estimates					Statistics†		
	b_0	b_1	b_2	b_3	b_4	R^2	$S_{\bar{y}}$	N
BrchWt	1.6365	2.93 14		0.8965		0.93	484.7	64
BrchSa	5.3848	2.2997		0.9352	—	0.93	1987.9	64
NFolWtDay	-8.4841	2.2315	–0.4908	0.8607	2.1833	0.90	123.6	64
NFolWtNod	2.8282	2.5557	-0.7117	0.8732		0.88	124.4	64
OFolWtDay	8.4943	1.7600		0.5634	–0.9622	0.88	67.5	64
OFolWtNod	3.4926	1.6673		0.5016		0.88	65.8	64
NFolSaDay	i12.7744	2.2176	-0.6136	1.0080	2.2241	0.90	1.3	64
NFolSaNod	-1.2446	2.5444	-0.8365	1.0204		0.88	1.3	64
OFolSaDay	3.7786	1.6704		0.6218	-0.892 1	0.86	0.6	64
OFolSaNod	-0.8601	1.5834		0.5603		0.86	0.6	64

Note: The model is $\ln(\hat{y}) = b_0 + b_1 \ln(\text{DBH}) + b_2 \ln(\text{Crnlen}) + b_3 \ln(\text{Crnrat}) + b_4 \ln(\text{Day})$, where $\hat{y}$ is predicted weight or surface area (in grams or m^2), DBH is bole dianieter outside bark (cm) at 1.37 m, Crnlen is distance from tree tip to lowest live branch (m), **Crnrat** is Crnlen divided by total height of tree, Day is day of year, and b_0, b_1, b_2, b_3, b_4 are coefficients estimated from the data.

*BrchWt, tree dry weight (g) of branch wood and bark; **BrchSa,** tree surface area (cm^2) of branches; NFolWtDay. tree dry weight (g) of new foliage using day of year; **NFolWtNod,** tree dry weight (g) of new foliage without day of year; OFolWtDay, tree dry weight (g) of old foliage using day of year; OFolWtNod, tree dry weight (g) of old foliage without day of year; NFolSaDay, tree surface area (m^2) of new foliage using day of year; NFolSaNod, tree surface area (m^2) of new foliage without day of year; OFolSaDay, tree surface area (m^2) of old foliage using day of year; and OFolSaNod, tree surface area (m^2) of old foliage without day of year.

†R^2 and $S_{\bar{y}}$ are the R-squared and standard error of the mean statistics in untransformed units.

Table 6. Regression coefficients for weight and surface area Weibull distribution β parameters.

Dependent variable*	Parameter estimates						Statistics†		
	b_0	b_1	b_2	b_3	b_4	b_5	R^2	$S_{\bar{y}}$	N
TFolWtDay		0.3418	-0.0023	0.0068		0.0093	0.68	0.044	64
TFolWtNod	2.1485	0.3251	-0.002 1	0.0065			0.71	0.041	64
TFolSaDay		0.3391	-0.0023	0.0065		0.0102	0.60	0.050	64
TFolSaNod	2.3979	0.3153	-0.0020	0.0063			0.64	0.047	64
NFolWtDay		0.3413		0.0068	-0.000 19	0.0067	0.75	0.039	64
NFolWtNod	1.5080	0.3160		0.0087	-0.000 22	—	0.75	0.038	64
NFolSaDay		0.3295		0.0078	-0.000 22	0.0075	0.72	0.042	64
NFolSaNod	1.7305	0.2938	—	0.0102	–0.000 25	—	0.71	0.042	64
OFolWtDay		0.4024	–0.0009			0.0105	0.57	0.051	64
OFolWtNod	2.3490	0.398 1	-0.0008				0.63	0.048	64
OFolSaDay		0.3861	-0.0010			0.0120	0.44	0.062	64
OFolSaNod	2.8010	0.3674	-0.0009				0.48	0.061	64

Note: The model is $\hat{y} = b_0 + b_1\text{Crnlen} + b_2\text{DBH} \times \text{Age} + b_3\text{Crnlen} \times \text{Age} + b_4\text{Crnlen} \times \text{Age}^2 + b_5\text{Day}$, where $\hat{y}$ is predicted β parameter for Weibull distribution, Cmlen is distance from tree tip to lowest live branch (m), DBH is bole diameter outside bark (cm) at 1.37 m, Age is age from planting, Day is day of year, and b_0, b_1, b_2, b_3, b_4, b_5 are coefficients estimated from the data.

*..Fol...Day, β parameter for total, new, or old foliage weight or surface area vertical distribution using day of year; .Fol...Nod, β parameter for total, new, or old foliage weight or surface area vertical distribution without day of year.

†R^2 and $S_{\bar{y}}$ are the R-squared and standard error of the mean statistics in untransformed units.

For old foliage the equation is

$$[4] \quad \ln(\text{SLA}) = 4.6052 + 0.3721\ (\text{RELDEP}) - 0.0910 \ln(\text{AGE})$$

$$S_{\bar{y}} = 0.30\ \text{cm}^2/\text{g}, R^2 = 0.42, n = 1224$$

where

SLA is specific leaf area in cm^2/g

RELDEP is depth within the crown/crown length

AGE is age of the tree in years

$S_{\bar{y}}$ is the standard error of the sample mean, $\{[\Sigma(y - \hat{y})^2/(n - p)]/n\}^{1/2}$, where n is the number of observations, p is the number of coefficients estimated in the model, $\bar{y}$ is the sample mean of SLA, and $\hat{y}$ is the predicted value of SLA

$$R^2 = 1 - [\Sigma(y - \hat{y})^2/\Sigma(y - \bar{y})^2]$$

These two equations were used to convert all new and old foliage weight samples to surface area. Then the process of fitting the surface area data to the Weibull function for the vertical distribution of leaf area was identical with that used to derive the weight distribution. Since it was assumed that specific leaf area does not change horizontally from the bole, the discrete horizontal solution presented below represents both weight and surface area.

Table 7. Regression coefficients for weight and surface area Weibull distribution γ parameters.

Dependent variable*	Parameter estimates								Statistics+		
	b_0	b_1	b_2	b_3	b_4	b_5	b_6	b_7	R^2	$S_{\bar{y}}$	N
TFolWtDay	3.8504	-0.0766	4.3384	0.0097	0.0182	-0.000 42			0.30	0.032	64
TFolWtNod	3.7748	-0.0704	4.3349	0.0100	0.0174	–0.000 42		—	0.29	0.032	64
TFolSaDay	3.9209	-0.0782	–0.3635	0.0107	0.0192	–0.000 45		—	0.29	0.034	64
TFolSaNod	3.8112	-0.0710	-0.3562	0.0110	0.0184	–0.000 46	—		0.29	0.034	64
NFolWtDay	2.7267	XI.0170	-0.1202			—	1.1764	-0.8353	0.59	0.022	64
NFolWtNod	2.8525	-0.0237					0.8303	-0.7027	0.45	0.026	64
NFolSaDay	2.7407	4.0168	-0.1167				1.0146	-0.7004	0.51	0.026	64
NFolSaNod	2.8276	-0.0223		—	—		0.6309	a.5197	0.37	0.030	64
OFolWtDay	3.3099	-0.0219	–0.1591	—	—		1.5256	-1.1178	0.64	0.026	64
OFolWtNod	3.5370	-0.0322			—		1.0997	-0.9823	0.58	0.027	64
OFolSaDay	3.3660	-0.022 1	-0.1604			—	1.3289	-0.9512	0.58	0.030	64
OFolSaNod	3.5670	-0.03 14	—		—		0.8386	-0.7497	0.51	0.03 1	64

Note: The model is $\hat{y} = b_0 + b_1\text{DBH} + b_2\text{Crnlen} + b_3\text{Crnlen} \times \text{Age} + b_4\text{DBH} \times \text{Cmlen} + b_5\text{DBH} \times \text{Cmlen} \times \text{Age} + b_6\beta\text{NewFol} + b_7\beta\text{OldFol}$, where; is the predicted γ parameter for Weibull distribution, DBH is bole diameter outside bark (cm) at 1.37 m, Cmlen is distance from tree tip to lowest live branch (m), Age is age from planting, βNewFol is the corresponding β parameter for new foliage, βOldFol is the corresponding β parameter for old foliage, and b_0, $b_,$, b_2, b_3, b_4, b_5, b_6, b_7 are coefficients estimated from the data.

*...Fol...Day, γ parameter for total, new, or old foliage weight or surface area vertical distribution using day of year; .Fol .Nod, y parameter for total, new, or old foliage weight or surface area vertical distribution without day of year.

†R^2 and $S_{\bar{y}}$ are the R-squared and standard error of the mean statistics in untransformed units.

Table 8. Proportions of foliage weight or surface area along a horizontal line at a proportionate height within the upper, middle, or lower stratum and within the inner, central, or outer envelope of the crown of an unthinned, planted loblolly pine tree.

	Stratum								
	Upper			Middle			Lower		
Foliage age-class	Inner	Central	Outer	Inner	Central	Outer	Inner	Central	Outer
New foliage	0.147	0.379	0.474	0.197	0.400	0.403	0.136	0.240	0.624
Old foliage	0.240	0.423	0.337	0.260	0.404	0.336	0.142	0.262	0.596
Total foliage	0.178	0.395	0.427	0.224	0.403	0.373	0.138	0.251	0.611

Tree branch weight and surface area, and tree foliage weight and surface area

Equations to predict the total weight and surface area of loblolly pine branches, and the total weight and surface area of new and old foliage on a loblolly pine tree are presented in Table 5. As explained earlier, for foliage weight and surface area, four equations are given for each characteristic-two contain the variable DAY, and two do not.

Foliage weight and surface area distributions

Vertical weight distribution

The Weibull function was fitted to each tree's vertical foliage distribution, and values for the parameters were estimated by the maximum likelihood procedure. The parameter values were then graphed and regressed against several easily measured tree and stand variables. Significant relationships were found to exist, thus indicating a measurable and predictable relationship between a tree's size and its foliage distribution. Numerous regressions, utilizing different variable combinations, were computed, and the best prediction equations were selected. Linear regression models proved adequate and no variable transformations were necessary. There were strong relationships between the right-truncated Weibull distribution scale parameter and several tree and stand variables, but these variables had little correlation with the shape parameter. The results were similar to those found by Baldwin et al. (1993). However, in this study it was found that the predicted scale parameter values for new and old foliage, used as predictor variables along with some interaction variables, improved the prediction of the shape parameter for new and old foliage by an average of 37% compared with the earlier R^2 value. Appropriate equations with and without the DAY variable are used to predict the truncated Weibull distribution parameters in order to model the vertical distribution of total, new, and old foliage weight (Tables 6 and 7).

Horizontal weight and surface area distribution

As mentioned earlier, the horizontal distributions for new, old, and total foliage weight were developed by fitting a discrete distribution of foliage proportions for each vertical crown one-third of total crown depth (Table 8). Equations to predict the proportions of old and new needle weight within the outer and central envelopes for each vertical strata were solved simultaneously. Values of the fit index ranged from 0.20 to 0.52, and the standard error of the estimate ranged from 3.95 g to 16.7 g. Proportions for the inner envelope for each stratum were obtained by subtraction.

Thus for any predicted foliage amount for a specified crown depth category, the horizontal weight distribution of that foliage

Fig. 4. A visual comparison, using probability density form functions (PDF), of the difference between the predicted vertical foliage weight and surface area distributions for a typical loblolly pine tree.

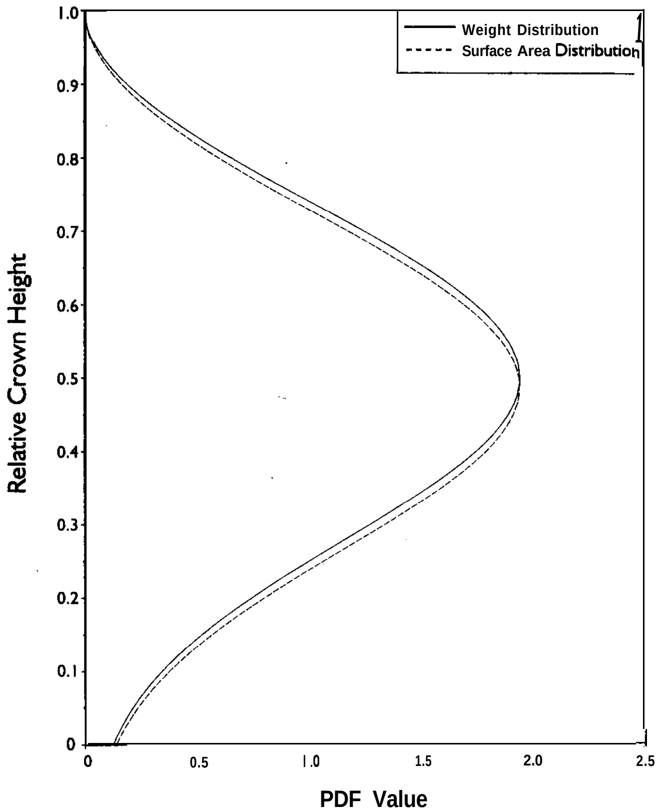
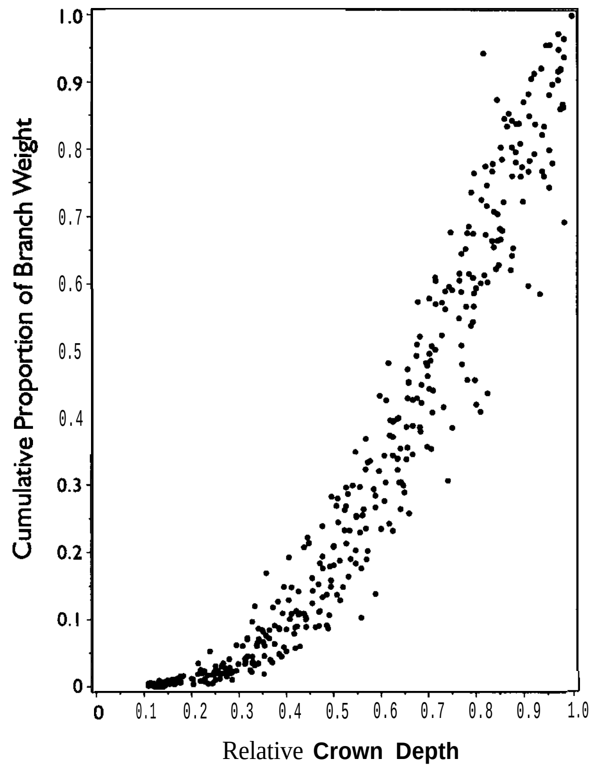


Fig. 5. Scattergram showing the cumulative proportion of loblolly pine branch weight as related to depth within the crown.



would be in the proportions specified in the table. Since it was assumed that specific leaf area within a crown does not vary horizontally at a given depth, the proportions in Table 8 are also the horizontal distribution values for leaf area. Although the model utilized here is the same as that used in Baldwin et al. (1993), the proportions are different because (1) in this study they represent crown horizontal one-thirds rather than branch horizontal one-thirds and (2) in this study the inner foliage boundary was the cone-shaped region defined in Baldwin and Peterson (1997) (see Fig. 1), whereas in the earlier study the inner boundary was the tree bole.

Vertical surface area distribution

Relationships were similar to those described above for the weight distribution. The simultaneous solution fitting process (Borders 1989) yielded Weibull distribution parameter estimates for the equations in Tables 6 and 7 for modeling the vertical distribution of total, new, and old foliage surface area for a specified tree.

Figure 4 illustrates the difference between the foliage vertical weight and surface area distributions for the same tree. For surface area, the distribution is shifted slightly towards the crown base. This occurs because specific leaf area increases with crown depth (Fig. 3).

Branch weight and surface area distributions

The individual tree relationships between crown depth and branch weight increased linearly with crown depth and were highly variable. However, with all branch data combined and normalized, the exponential relationship shown in Fig. 5 was evident. A transformed (logarithmic) model, constrained to equal zero when RELDEP is zero, and equal one when RELDEP is one, was fitted to the combined data. Because of the model's design characteristics, the equations can serve as branch weight or surface area cumulative distribution functions. Therefore, given the total branch weight or surface area predicted with the first or second equation in Table 5, respectively, the following equations portion the total branch weight or surface area (wood and bark only) within the tree crown:

Total branch weight distribution:

$$[5] \quad \ln(\text{CUMPRTBRWT}) = 2.3818 \ln(\text{RELDEP}) - 0.2460 \ln(\text{RELDEP})^2$$

$$S_{\bar{y}} = 0.067,\ R^2 = 0.96,\ n = 441$$

Total branch surface area distribution:

$$[6] \quad \ln(\text{CUMPRTBSA}) = 2.1162 \ln(\text{RELDEP}) - 0.2070 \ln(\text{RELDEP})^2$$

$$S_{\bar{y}} = 0.059,\ R^2 = 0.97,\ n = 440$$

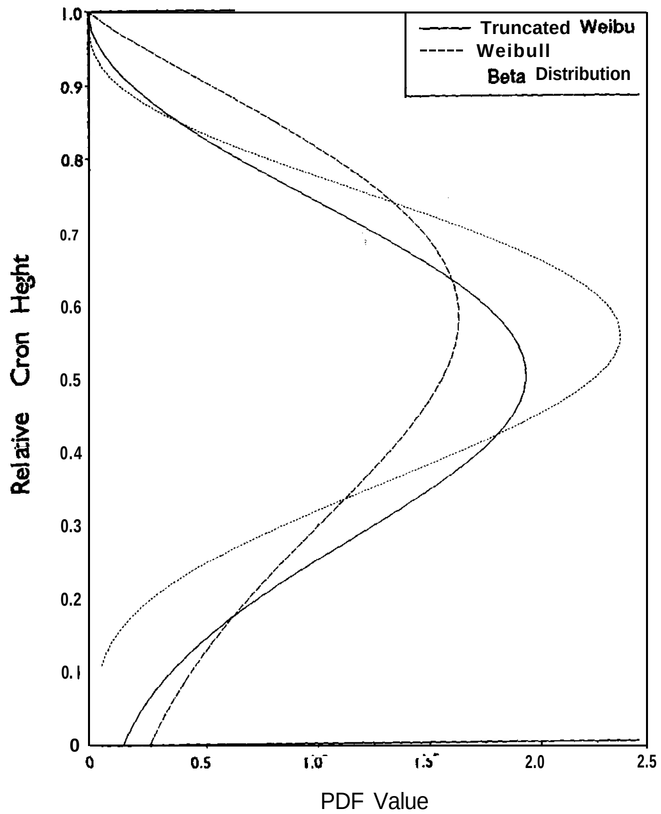
where

CUMPRTBRWT is cumulative proportion of the total branch weight

CUMPRTBSA is cumulative proportion of the total branch surface area

RELDEP is relative crown depth

Fig. 6. Predicted probability density form functions (PDF) in term of relative height within the crown of a 30-year-old unthinned loblolly pine for beta, Weibull, and right-truncated Weibull distributions.



These total branch weight and surface area distribution functions were developed from all data combined. We did not attempt to fit the distributions to the branch data for each tree and find relationships between the distribution parameters and other tree or stand characteristics. These equations, and the earlier equations to predict individual branch or tree woody surface area, are apparently the first developed for loblolly pine.

Discussion and conclusions

Predictions from the new foliage and branch weight equations based on the sample trees for the combined LA- 1 and VC data set were compared with predictions for the same trees using Baldwin (1987) equations for prediction of foliage and branch weight of loblolly pine in unthinned stands. The latter equations came from data collected in similar stands from the same geographical area as the LA-I data, although the sampling procedures were different. The new foliage weight equations (sum of old and new foliage, without DAY) predict the foliage weight, on average, 12% lower than the earlier Baldwin (1987) equation.

This result is similar to that found by Valentine et al. (1995). They compared a foliage weight equation (using bole cross-sectional area at the base of the live crown as the predictor), developed from data from the same LA-1 sample trees, with other published equations using the same predictor variable. That comparison included an equation developed by Baldwin (1989) from a subset of the Baldwin (1987) sample trees from both thinned and unthinned stands. The Valentine et al. equation predicted lower foliage weights for the same trees than the Baldwin equation. Possible reasons for that result, such as seasonal patterns of stem growth versus the seasonal growth of foliage, and weather influences, are discussed by Valentine et al. (1995).

However, the opposite relationship was found with branch weight prediction. That is, the current equation predicts branch weight on average 11% higher than the older Baldwin (1987) equation. Therefore, although the exercise did show that the predictions of both foliage and branch weight were relatively close to those obtained using other published equations, we concluded, as did Valentine et al. (1993, that additional work is needed in this area.

In the prediction of old and new foliage weight, surface area, and their respective vertical distributions, the DAY variable was used to help account for the changes in proportions of old and new foliage observed in two samplings taken in different years, between days 190 and 270. Although new data are needed to better define the relationships, these results clearly show the importance of foliage phenology in accurately describing how much foliage a tree has and how it is distributed within the crown during the year. Foliage phenology is especially critical during the growing season. Thus far, researchers have addressed this problem in loblolly pine by presenting foliage weight or surface area equations either for the dormant season (Kinerson et al. 1974; Amateis et al. 1992) or at approximate time of full leaf (e.g., Baldwin 1987; Valentine et al. 1995). Phenology curves have also been utilized to proportion the new and old foliage for a given time of year.

Phenology curves have been shown to be strongly affected by yearly climate conditions (Hennessey et al. 1992; Dougherty et al. 1995). For this reason, until further research is accomplished in this area, average full-leaf equations, and those containing DAY, are presented here to give the user a choice in how to best handle this situation. If various predictions are needed from days 190 through 270, the equations with DAY can be used. Equations without DAY are used if full-leaf prediction is needed or if one desires to use a phenology curve along with the equations to proportion the old and new foliage.

A goal in this project was to apply a vertical distribution function to individual tree foliage weight and surface area data that would describe the data well. It was hypothesized that the vertical distribution could be predicted based on common tree or stand characteristics. The right truncated Weibull distribution appears appropriate and its parameters can be predicted from simple tree measurements. MAESTRO previously used a beta distribution. As noted earlier, the Weibull distribution has been shown to work well for this purpose. The right-truncated Weibull, when fitted by the maximum likelihood procedure, has the further advantage of having the full distribution bounded by the crown tip and foliar crown base. In previous applications of the Weibull or the beta distributions, the functions were fitted by least squares regression procedures. This insured a "best tit" over the range of the data from the crown tip to the crown base, but did not insure that the total distribution of weight or surface area was predicted between those limits.

Figure 6 shows the foliage weight distribution for a typical 30-year-old loblolly pine using the beta, Weibull, and right-truncated Weibull distribution predicted according to the procedures in Jarvis et al. (1991), Baldwin et al. (1993), and this paper. In this example, the right-truncated Weibull distribution shows a greater proportion of foliage weight lower in the crown than the other two, with the distribution mode occurring at about midcrown. The other two forms predict the mode closer to 0.6 relative crown height. With respect to MAESTRO applications, this change, among others, had a noticeable affect on predictions of carbon gain under current environmental conditions (Baldwin et al. 1997; Cropper et al. 1997).

In conclusion, the equations presented in this paper were specifically developed to improve upon various initial equations in the loblolly pine version of MAESTRO (Jarvis et al. 1991). The foliage weight and surface area prediction equations provide estimates for old and new needles between days 170 and 290 without the need of a foliage phenology curve. Other equations are provided to make predictions at other times when used with a foliage phenology curve. The vertical distributions of foliage weight and surface area for old and new needles can now be predicted for individual trees based on commonly measured tree variables. When the vertical and horizontal distributions are combined, the complete foliage weight or surface area distribution can be predicted. Equations are also presented to predict the surface area and vertical distribution of branches so that branch respiration may be estimated as a function of surface area. It is hoped that these equations may also be useful in other applications as we seek to understand and quantify tree and stand growth processes.

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