Describing Leaf Area Distribution in Loblolly Pine Trees with Johnson's S_B Function

Mauricio Jerez, Thomas J. Dean, Quang V. Cao, and Scott D. Roberts

ABSTRACT. The objective of this study is to evaluate the fit of Johnson's S_B distribution function to vertical foliage distributions of variously aged and treated loblolly pine trees when the function is fit with two percentiles of the observed distributions. Foliage distributions are linked to various stand properties, and straightforward means of quantifying foliage distribution may lead to a convenient method of characterizing forest stands using remote sensing technology such as LiDAR. Regression analyses indicate that the 15th and 50th percentiles of the distributions were best correlated with variables of crown structure and tree age. Skewness and kurtosis of the distributions calculated with the function's parameters also varied with crown structure and age. Cumulative fractions of leaf area calculated with fitted S_B functions matched measured values well; cumulative values of absolute leaf area showed less correspondence with measured values, but residuals of both centered around zero. Incompatibilities between the continuous S_B function and the irregular and discrete nature of foliage distribution of single trees occasionally produced large prediction errors. Based on these results, the S_B function fitted with the two-percentile method suitably describes the vertical distribution of leaf area of a wide variety of loblolly pine trees. FOR. SCI. 51(2):93–101.

Key Words: Probability density functions, two-percentile method, crown structure, LiDAR.

MODELS THAT SIMULATE GROWTH and yield of forest stands often require a quantitative description of vertical leaf area distribution because the distribution of foliage and its supporting structures determine the pattern of light attenuation and the distribution of photosynthesis, transpiration, and nutrient cycling within the crown (Massman 1982). The vertical distribution of leaf area has also been related to stem taper and size (Larson 1963, Dean and Long 1986a, West et al. 1989, Dean et al. 2002). Because silvicultural practices influence foliage distribution, quantitative descriptions of the vertical distribution of leaf area provide an avenue for calculating the response of canopy gas exchange and stem radial increment to cultural treatments (e.g., West et al. 1989).

Probability density functions are common devices for describing leaf area distribution, and the normal distribution was the first probability function used to describe leaf area distribution (Stephens 1969, Kinnerson and Fritschen 1971). The normal distribution has fixed symmetry, which rarely matches actual foliage distributions, and infinite endpoints, requiring arbitrary cutoff points at both ends of the function to account for the top and the bottom of the live crown. The Weibull distribution has been used widely to describe vertical foliage distributions because it is not restricted to symmetric distributions (e.g., Gillespie et al. 1994, Baldwin et al. 1997, Maguire and Bennett 1996, Xu and Harrington 1998), but while it starts at a fixed value (usually the top of the live crown), the other end of the Weibull function extends to infinity. Johnson's S_B function has several advantages over the normal and the Weibull functions for describing leaf area distributions. The Johnson S_B function (Johnson 1949) has fixed endpoints that naturally correspond to the top and the bottom of the live crown, and it can describe the largest range of shapes of all of the distribution functions commonly used in forestry applications (Parresol 2003). Furthermore, the parameters of the Johnson's S_B function can be calculated directly with the relative crown locations of two percentiles of the foliage distribution (Knoebel and Burkhart 1991). Although this procedure may not produce the best parameter estimates (Kamziah et al. 1999), it may have utility in developing quantitative descriptions of leaf area distribution from remotely sensed data such as LiDAR, an airborne-based, scanning laser technology. Magnussen and Boudewyn (1998) have shown that the vertical distribution of laser pulses reflected from the canopy match the upper portion of

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the vertical distribution of leaf area in Douglas-fir canopies. Since leaf area distribution is affected by properties such as stand density and age (Mori and Hagihara 1991, Maguire and Bennett 1996, Xu and Harrington 1998), the ability to easily calculate the parameters of the Johnson S_B distribution may provide a convenient means of characterizing stands across forested landscapes.

While pursuing various studies in the western Gulf region of the United States, we destructively measured the vertical distribution of leaf area of loblolly pine trees growing across a wide range of stand ages, stand structures, and soil nutrition. The vertical distributions of leaf area measured in these studies encompass the range of distributions expected within commercial stands of loblolly pine. The objective of this study is to evaluate the effectiveness of Johnson's S_B distribution to describe these vertical foliage distributions using the two-percentile method for calculating the function's parameters.

Materials and Methods

Data

A sample of 172 trees was used to evaluate the S_B function for describing vertical foliage distribution of loblolly pine trees. Data came from five studies established on planted and naturally regenerated stands growing in the western Gulf region of the United States. Studies differed in age, stand density, and soil nutrition. Trees were destructively sampled with a common protocol. The youngest trees at 4 years old were sampled from a planted study near Fred, Texas, investigating the long-term effects of harvest disturbance, bedding, and fertilization on loblolly pine growth (Carter et al. 2002). Ten-year-old trees were sampled from a recently thinned plantation near Newton, Mississippi, and subjected to applications of chicken litter at equivalent nitrogen additions of 0, 200, and 800 kg/ha (Roberts et al. 2004). Trees from a 12-year-old spacing trial near Pine, Louisiana, were measured during Dec.: the only trees in this analysis that were measured during the winter (Dean et al. 2002). Fifteen-year-old trees were sampled from a common garden near Starkville, Mississippi, consisting of seven half-sib, loblolly pine families (Roberts et al. 2003). Also sampled near Pine, Louisiana, were 36-year-old trees growing in a naturally regenerated stand that had been thinned at age 28 years. All stands were even-aged.

The procedures for the destructive harvests follow Dean and Long (1986b) with some modifications. The goal of the sampling was to quantify the vertical distribution of leaf area at relatively small intervals in the crown. Live crowns were typically segmented into 1-m intervals, with the exception of the 4-year-old trees, where the crowns were segmented into 0.5-m intervals. Total leaf area per interval is the sum of the leaf area produced during the current year and leaf area produced in previous years. For the 12-year-old trees sampled in Dec., the current year's leaf area comprised an overwhelming majority of the total leaf area per section. With the exception of the 12-year-old and 36-year-old trees, leaf area was based on a 100% sample of the fresh foliage in the interval. For the 12-year-old and 36-year-old trees, leaf area was based on one branch per segment selected with probability proportional to branch leaf area using the product of branch diameter squared and branch length as a surrogate for leaf area. Leaf area of the branch was expanded to leaf area per segment by dividing the leaf area by the selection probability for the particular branch. Dean et al. (2002) report this procedure in greater detail. Fresh foliage mass was converted to projected leaf area with moisture contents and specific leaf areas of subsamples taken from each combination of crown segment and foliage age.

Based on treatment and genotype effects on allometric relationships, data were grouped according to age and fertilization treatment. The primary intent of collecting these data was to develop prediction equations for calculating leaf area of loblolly pine trees growing in managed stands; therefore, data collected from trees with disfigured stems or crowns were discarded from the data set. The 10-year-old trees receiving applications of chicken litter, regardless of rate, were grouped separately from the trees receiving no chicken litter based on the analyses of Roberts et al. (2004). According to Roberts et al. (2003), only two of the seven half-sib families included in this study had significantly different relationships between individual-tree leaf area and stem diameter. A preliminary analysis of the distributions in terms of mean, symmetry, and kurtosis did not show appreciable differences among families. Consequently, the data for the seven families were not separated for this analysis. Mean heights and diameters of the various groupings ranged from 3.2 to 25.0 m and from 3.4 to 35.3 cm, respectively (Table 1). Leaf areas ranged from 5.8 to 124.1 m^2.

Model Development

The S_B Probability Distribution and Parameter Prediction

The Johnson S_B distribution (Johnson, 1949) belongs to a family of distributions based on transformations of a random variable, x, to the standard normal variable, z, as

$$z_x = \gamma + \delta \ln\left(\frac{x - \lambda_1}{\lambda_2 - x}\right), \tag{1}$$

where λ_1 and λ_2 are lower and upper limits of the range of x, respectively, and γ and δ are parameters controlling the shape of the distribution. The cumulative distribution function (cdf) of the S_B can be expressed as

$$F(x; \lambda_1, \lambda_2, \gamma, \delta) = \Phi(z_x), \tag{2}$$

where Φ is the cdf of the standard normal variable. In this study, x is defined as relative crown depth ($0 < x < 1$, with 0 set at the top of the crown). This sets λ_1 and λ_2 to 0 and 1, respectively, reducing the cdf to

$$F(x; \gamma, \delta) = \Phi\left[\gamma + \delta \ln\left(\frac{x}{1 - x}\right)\right]. \tag{3}$$

Table 1. Mean and standard deviation (SD) values of stem diameter, total height, crown length, and total leaf area for destructively harvested loblolly pine trees

		Stem diameter††		Total height		Crown length		Total leaf area	
Group*	n†	Mean	SD	Mean	SD	Mean	SD	Mean	SD
		...........(cm)		..............................(m)		....		.............(m^2).............	
1	18	3.44	1.83	3.23	0.75	2.54	0.63	5.76	5.30
2	25	4.62	2.27	3.55	0.96	2.93	0.96	7.95	7.18
3	9	8.23	2.83	8.48	1.29	5.37	1.23	10.03	6.92
4	18	9.16	2.33	8.67	1.07	5.44	1.00	12.27	5.99
5	24	11.38	2.71	11.70	1.09	5.04	1.35	8.39	5.46
6	60	18.82	3.38	16.58	1.49	6.32	1.52	27.24	13.80
7	18	35.32	7.70	25.03	1.93	10.64	2.13	124.14	66.20

* Groups: (1) unfertilized 4-year-old trees, (2) fertilized 4-year-old trees, (3) unfertilized 10-year-old trees, (4) fertilized 10-year-old trees, (5) 12-year-old trees sampled during winter, (6) 15-year-old trees, (7) 36-year-old trees.
† Number of sample trees
†† Root collar diameter for groups 1 and 2; otherwise, dbh.

Equation 3 can be used to calculate the cumulative fraction of leaf area at any relative crown depth.

The two-percentile method for calculating the shape parameters γ and δ has been described by Knoebel and Burkhart (1991). This method uses the 50th percentile and another convenient quantile of the distribution to calculate the value of δ with the equation

$$\delta = \frac{z_{xp}}{\ln(x_p/(1-x_p)) - \ln(x_{50}/(1-x_{50}))}, \tag{4}$$

where z_{xp} is the value of the standard normal variable z corresponding to the x_p cumulative percentile, and x_{50} and x_p are the respective relative crown depths associated with the 50th and pth percentiles of cumulative leaf area. The value of γ is calculated using the following equation using x_{50} and the value of δ from Equation 4:

$$\gamma = -\delta \ln\left(\frac{x_{50}}{1-x_{50}}\right). \tag{5}$$

The value of the pth percentile to determine x_p was selected by comparing the accuracy and precision with which a particular value of x_p could be predicted from easily measured tree dimensions. Both linear and nonlinear models were explored. Predictor variables included stem diameter (D) at breast height or at the root collar, depending on tree size and vertical crown dimensions. Vertical crown dimensions included total height (H_T), height to base of the live crown (H_B), crown length ($C_L = H_T - H_B$), crown ratio ($C_R = C_L/H_T$), height to crown midpoint ($H_{MC} = \{H_T + H_B\}/2$), and relative height (H_{REL}). Relative height is an indicator of the competitive status of a tree within the stand and was defined as total tree height divided by the average height of dominants and codominants in the stand (Maguire and Bennett 1996). Crown ratio and height to the crown midpoint are related to tree size and crown position within the stand. Combinations of D and vertical crown dimensions such as D^2H_T and D/H_T were also analyzed. This procedure is typical for predicting function parameters (Parresol 2003). The statistical quality of candidate models was assessed with the adjusted coefficient of determination (adj-R^2) and the square root of the mean square error. Residuals were checked for normality, homogenous variance, autocorrelation, and multicollinearity. A value of $\alpha = 0.05$ was set to test the hypothesis that regression coefficients did not differ from zero.

Prediction of Total Leaf Area

The model chosen to predict total leaf area (A_T, m^2) was the following nonlinear equation adapted from the model developed by Dean and Long (1986b) for lodgepole pine:

$$A_T = \left(\frac{1}{H_{MC}}\right)\left(\frac{D}{a}\right)^b + \varepsilon \tag{6}$$

where D is stem diameter (dbh or root collar diameter, in millimeters), H_{MC} is height to the center of the crown, a and b are parameters to be estimated, and ε is the error term. This model showed the lowest bias across ages and stand conditions among a variety of available models derived from tree dimensions. The statistics of the fitted model for each group are shown in Table 2.

Model Evaluation

In this study, all data were used in model construction to obtain the best possible estimates of the prediction error. Given the small sample size for each group, splitting the data into fit and validation data sets would result in little gain in reliability (Roecker 1991). The ability of the models to predict leaf area distribution was evaluated by comparing the observed cumulative distribution against the predicted cumulative distribution for each tree using residual-based statistics. These statistics include the mean deviations (MD) for detecting bias, its complementary measure, the mean of absolute deviations (MAD), and the fit index (FI) for measuring model precision. The MD is computed as

$$\mathrm{MD} = \frac{1}{n}\sum_{i=1}^{n}(y_i - \hat{y}_i), \tag{7}$$

where y_i and $\hat{y}_i$ are the observed and predicted value of

Table 2. Statistics from the regression model, $A_T = (1/H_{MC})(D/a)^b + \varepsilon$, to predict total leaf area for the various categories of destructively sampled loblolly pine trees. In the equation A_T is total leaf area, D is stem diameter (dbh or root collar diameter, in mm), and H_{MC} is height to the crown midpoint

			Coefficients††			
Group*	Age (yr)	n†	A	B	$Sy.x$§ (m^2)	Adjusted R^2
1	4	18	14.2857	2.3592	2.12	0.84
2	4	25	19.6582	2.5838	4.04	0.63
3	10	9	14.3488	2.1800	1.48	0.96
4	10	18	11.2061	1.9475	2.48	0.84
5	12	24	27.4115	2.8771	1.95	0.88
6	15	60	14.6389	2.2586	7.63	0.70
7	36	18	8.0585	2.0287	25.92	0.86

*Groups: (1) unfertilized 4-year-old trees, (2) fertilized 4-year-old trees, (3) unfertilized 10-year-old trees, (4) fertilized 10-year-old trees, (5) 12-year-old trees sampled during winter, (6) 15-year-old trees, (7) 36-year-old trees.
†Sample size.
††All coefficients significant with $P < 0.05$.
§Standard error of the estimate.

cumulative leaf area at relative crown depth *i,* respectively, and n is the number of values calculated for each tree. Models with low bias will have values of MD close to zero, and the sign of MD indicates whether the bias is positive or negative. The value of MD can be misleading when large positive and negative deviations sum to zero. The value of MAD measures the average magnitude of bias—the value of MAD is computed as

$$\text{MAD} = \frac{1}{n}\sum_{i=1}^{n} |y_i - \hat{y}_i|. \quad (8)$$

The fit index (FI) measures the precision of the model being analogous to the R^2 value (Kvälseth 1985), but it varies between $-\infty$ and 1, with 1 indicating a perfect fit. The value of FI is computed as

$$\text{FI} = 1 - \frac{\sum_{i=1}^{n} (y_i - \hat{y}_i)^2}{\sum_{i=1}^{n} (y_i - \bar{y}_i)^2}, \quad (9)$$

where $\bar{y}$ is the mean of the observed leaf area for each tree. Mayer and Butler (1993) discuss the interpretation of these statistics in detail. The bias and precision of the models were analyzed in detail for each group by comparing differences between the observed and predicted fractions of leaf area and absolute amounts of leaf area at measurement points. However, to be able to compare predictions among groups at similar levels of crown depth, and to plot residuals, predicted and observed values were calculated at 10% fractions of crown depth. In this case, the values at 10% intervals of crown depth for the observed cumulative distribution were determined using lineal interpolation.

Results and Discussion

Prediction of Percentiles from Tree Dimensions

Based on the regression analyses, the 15th percentile was the most highly predictable using the candidate tree characteristics and model forms. Nonlinear models with variables related to crown structure such as live-crown ratio and height to the crown midpoint were the best predictors of x_{15} and x_{50}. Including age (A) as a variable in the models produced considerable improvement in the fitted equations. The final set of equations for predicting x_{15} and x_{50} were

$$x_{15} = \exp(-2.81548 + 2.41914 \cdot C_R - 0.20063 \cdot H_T + 0.335959 \cdot H_{MC} - 0.03129 \cdot A) \quad (10)$$

(Adjusted $R^2 = 0.42$, $Sy.x = 0.069$, $n = 172$)

and

$$x_{50} = \exp(-1.38954 + 1.251551 \cdot C_R - 0.13616 \cdot H_T + 0.212386 \cdot H_{MC} - 0.01849 \cdot A) \quad (11)$$

(Adjusted $R^2 = 0.35$, $Sy.x = 0.083$, $n = 172$)

Because the residuals of the individual fitted equations were correlated, the final set of equations was fit with seemingly unrelated regression following the recommendations of Borders (1989).

The relationship between the location of the leaf percentiles and variables describing crown structure suggest that the specific properties of leaf area distribution are indicative of stand density in a manner consistent with previous studies. Dean and Baldwin (1996) found that live-crown ratio in loblolly pine plantations in southwest Louisiana decreased with increasing stand density as measured by Reineke's stand density index. Smith and Long (1987) found similar results for lodgepole pine in southeastern Wyoming and northern Utah. According to Equations 10 and 11, as live-crown ratio decreases with increasing stand density, the location of the 15th and 50th percentiles moves toward the top of the tree. Dean and Baldwin (1996) also found that the relationship between live-crown ratio and stand density was age-dependent in that the mean value of live-crown ratio decreased with increasing age, which agrees with Equations 10 and 11 in that the relative height of these percentiles and live-crown ratio are also age-dependent, moving toward the top of the tree as it ages.

Model Evaluation

The residual statistics indicate that the cumulative form of the S_B function has sufficient flexibility to describe the various shapes of the cumulative distribution of relative leaf area within these trees. The mean values of MD of the predicted relative leaf area accumulated from the top of the crown to any lower crown segment were all close to zero for any group of trees (Table 3). In several groups, the mean difference in the accumulated value of relative leaf area predicted with the S_B function and the corresponding measured value to any lower crown segment was less than 0.01 for the average tree. Averaged across all groups, the mean per-tree value of MD was also less than 0.01. All of the values of MD were greater than zero, indicating that predicted values of cumulative relative leaf area were less than the measured cumulative values of relative leaf area to a particular crown segment. The close correspondence between predicted and measured values of relative leaf area accumulated to a given crown segment is also evident in the values of mean absolute deviation (MAD) and the fit indices (FI). Averaged across the trees within a group, the absolute value of the difference between predicted and measured cumulative leaf area varied between 0.03 and 0.08. The FI values for relative cumulative leaf area were all greater than 85%.

Predicting the cumulative value of absolute leaf area with the S_B function was less precise than predicting the cumulative value of relative leaf area. Whereas the FI for cumulative values of relative leaf area averaged 0.93, the FI for absolute values of leaf area averaged 0.85 across all groups (Table 3). Although it is logical to assume that prediction errors in the values of total leaf area per tree are the cause of the lower precision in predicting cumulative leaf area with the S_B function, this does not seem to be the dominant cause. For example, for group 3 (the unfertilized 10-year-old trees), the S_B model explained 95% of the variation in cumulative values of relative leaf area, and Equation 6 explains 96% of the variation in total leaf area per tree; however, the S_B value explains only 71% of the variation in cumulative values of absolute leaf area in this group. The close correspondence between the predicted and measured values of relative leaf area between the top of the crown and a given crown segment for trees of various ages, stages of development, and soil nutrition demonstrates the flexibility of the S_B in representing a wide range of shapes. However, the function cannot adequately describe curves that do not monotonically rise and fall around a single peak. Where the S_B function explains greater than 85% of the variation in cumulative leaf area, leaf area per crown segment increases steadily to a peak then declines steadily to the base of the crown (e.g., Figure 1d–g). Where the S_B function explains less than 75% of the variation in the cumulative leaf area, leaf area per crown segment increases or decreases too quickly with relative crown depth to be adequately described with a single S_B function (Figure 1a–c). These deviations have a large effect when cumulative leaf area is expressed in absolute terms resulting in values of FI that are lower than the corresponding FI values for cumulative leaf area expressed on a relative basis.

Other methods of fitting S_B functions were used to explore the possibility of improving the precision of the fitted distributions. However, for these data the precision obtained with the two-percentile method was superior to other fitting procedures (e.g., linear regression and the nonlinear regression methods that use five or more percentiles as described by Zhou and McTague (1996) and Kamziah et al. (1999)) or distribution functions (e.g., the beta function fitted with the moments method and maximum likelihood). The use of distribution mixtures as applied by Cao and Burkhart (1984) or free distribution methods produce nearly perfect fits of distribution functions to data (even multimodal distributions). The ability to describe a distribution, however, does not necessarily produce a method for predicting a distribution (Uusitalo and Veli-Pekka 1998).

The values of MD for total cumulative leaf area were smaller in absolute value than 1.0 m^2, and with the exception of the unfertilized 4-year-old trees, they were all negative (Table 3). This indicates that on average the S_B closely predicts the leaf area from the top of the crown to a given crown segment, but it generally overestimates the value. Both MD and MAD values for cumulative leaf area are not

Table 3. Average values of mean deviations (MD), mean absolute deviations (MAD), and fit index (FI) for various groups of loblolly pine relative and absolute cumulative leaf areas

Group*	$n^{\dagger}$	Relative cumulative leaf area			Absolute cumulative leaf area		
		MD	MAD	FI	MD	MAD	FI
					(m^2)		
1	18	0.02	0.08	0.85	−0.06	0.62	0.49
2	25	<0.01	0.07	0.91	0.37	1.31	0.73
3	9	0.07	0.04	0.95	−0.25	0.91	0.71
4	18	0.01	0.06	0.94	−0.03	1.38	0.92
5	24	<0.01	0.07	0.91	−0.23	0.94	0.88
6	60	0.01	0.04	0.95	−0.55	3.55	0.95
7	18	<0.01	0.03	0.97	−1.98	14.08	0.97
Mean	172	<0.01	0.06	0.93	−0.40	3.29	0.85

*Groups: (1) unfertilized 4-year-old trees, (2) fertilized 4-year-old trees, (3) unfertilized 10-year-old trees, (4) fertilized 10-year-old trees, (5) 12-year-old trees sampled during winter, (6) 15-year-old trees, (7) 36-year-old trees.
†Number of sampled trees.

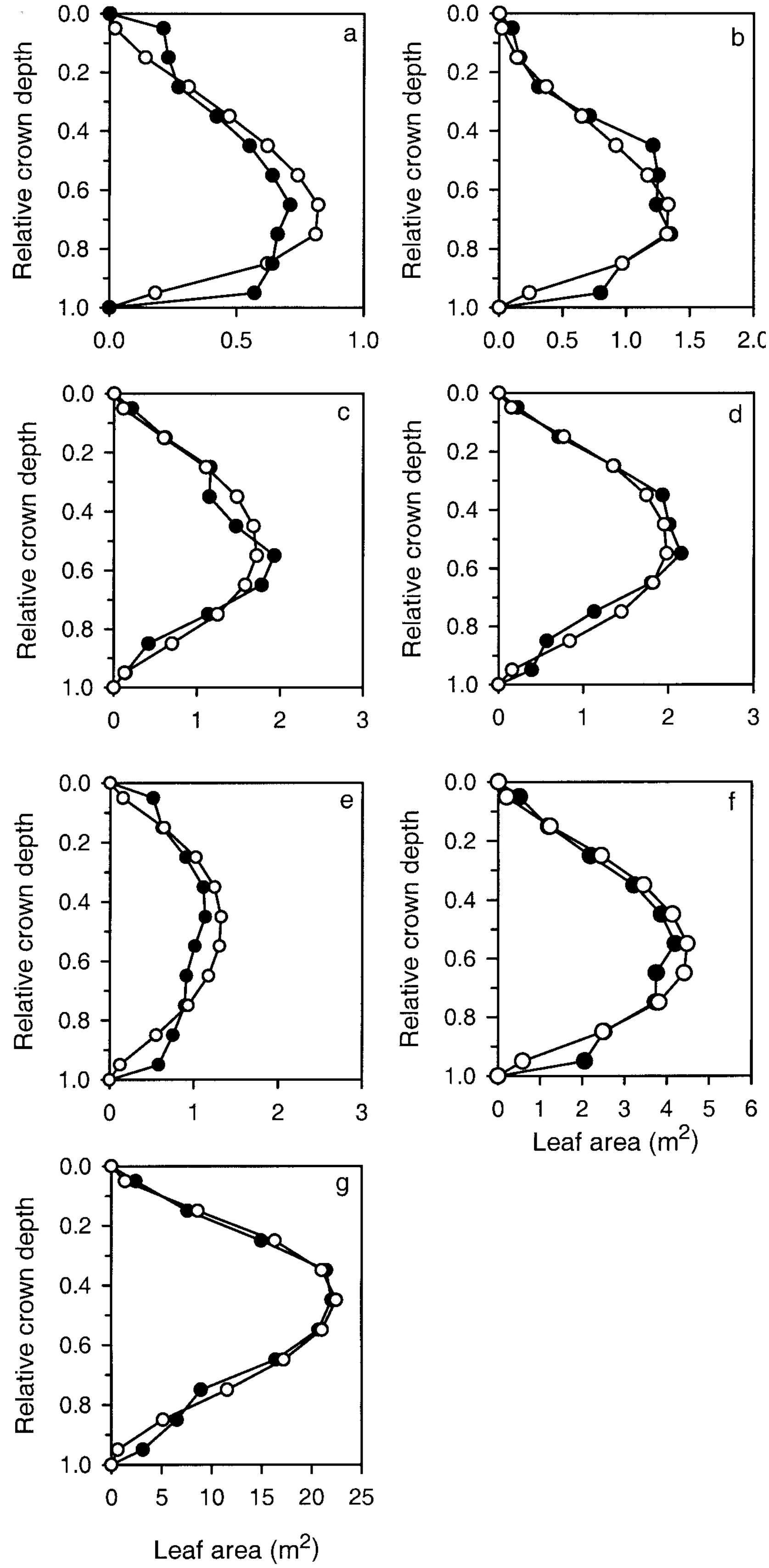

Figure 1. Observed (●) and predicted (○) average leaf area (m^2) as a function of relative crown depth for loblolly pine. Predicted leaf area was obtained from the S_B fitted with predicted percentiles from crown dimensions. Data for loblolly pine trees that are (a) unfertilized 4-year-old trees, (b) fertilized 4-year-old trees, (c) unfertilized 10-year-old trees, (d) fertilized 10-year-old trees, (e) 12-year-old trees sampled during the winter, (f) 15-year-old trees, and (g) 36-year-old trees.

comparable between groups because the values are related to the average leaf area per tree within a group.

Residuals between cumulative leaf area predicted with the S_B functions and the measured cumulative leaf area for 10% intervals of crown depth illustrate the residual statistics for the cumulative leaf area in absolute terms. In most cases, the residuals center nearly on zero (Figure 2), with the exception of group 2 (fertilized 4-year-old trees), which shows a positive bias toward the bottom of the crown. Absolute cumulative residuals increased toward the center of the crown, and then generally remained relatively constant toward the bottom of the crown. Figure 3 shows the boxplots of the residuals for the cumulative, absolute values of leaf area expressed as a percentage of the actual cumulative leaf area at 0.1 intervals of canopy depth. It is apparent that for most groups the percentage error is greater toward the top of the crown, where average percentage error is between 25 and 50% with positive bias. However, with the exception of group 2, the percentages and biases tend to decrease with canopy depth. At the bottom of the crown, the average percentage residuals were 7, 17, −18, −22, −3, −12, and −4% for groups 1 through 7, respectively.

Parameter Interpretation

The values of γ and δ describe the properties of the various leaf area distributions because the parameter γ is associated with the skewness (degree of asymmetry) and δ is associated with the kurtosis (degree of peakedness) of the underlying distribution (Siekierski 1992). Since the values of γ and δ are systematic functions of x_{15} and x_{50}, skewness and kurtosis should also be related to stand density and age. The parameter γ takes a value of zero when the distribution is symmetric, is positive when the distribution is skewed positively (leaf area concentrated upward), and negative when the distribution is negatively skewed (leaf area concentrated downward). The larger the value of δ, the larger the kurtosis of the distribution. The average value of γ for the various groups of trees ranged from −0.50 to 0.13, and the average value of δ ranged from 0.90 to 1.20 (Table 4). The negative values of γ for the 4-year-old and 15-year-old age groups indicate leaf area is concentrated toward the bottom of the crown. Positive values of γ as observed in the 10, 12, and 36-year-old age groups indicate that leaf area is concentrated around or slightly above the center of the crown. Within the 4- and 10-year-old age groups, the value of γ for the fertilized trees was greater than the value for the unfertilized trees. With the exception of the trees measured near Starkville, MS, the value of γ increased with age, indicating a shift in foliage distribution from the lower portions of the crown to the upper canopy positions. This is consistent with Equations 10 and 11. No statistically detectable effects of age or soil nutrition on the value of γ were

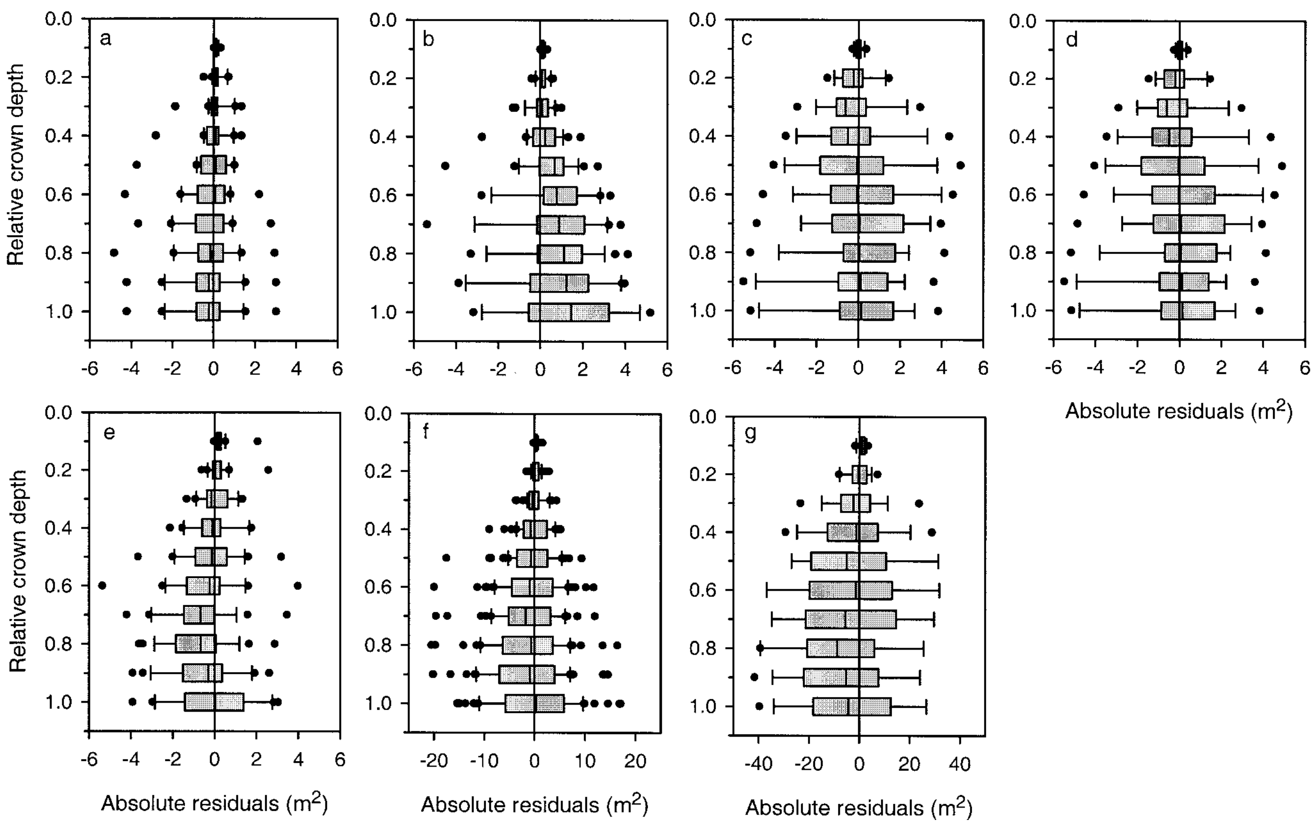

Figure 2. Boxplots of the absolute cumulative residuals (observed–predicted) of the total leaf area per 0.1 intervals of relative crown depth. Predicted values determined with relative leaf area predicted with the S_B function for the crown segment times the predicted leaf area per tree. The horizontal bars represent the 10th, 25th, 50th, 75th, and 90th percentiles, respectively. Individual points are extreme values. Data for loblolly pine trees are (a) unfertilized 4-year-old trees, (b) fertilized 4-year-old trees, (c) unfertilized 10-year-old trees, (d) fertilized 10-year-old trees, (e) 12-year-old trees sampled during the winter, (f) 15-year-old trees, and (g) 36-year-old trees.

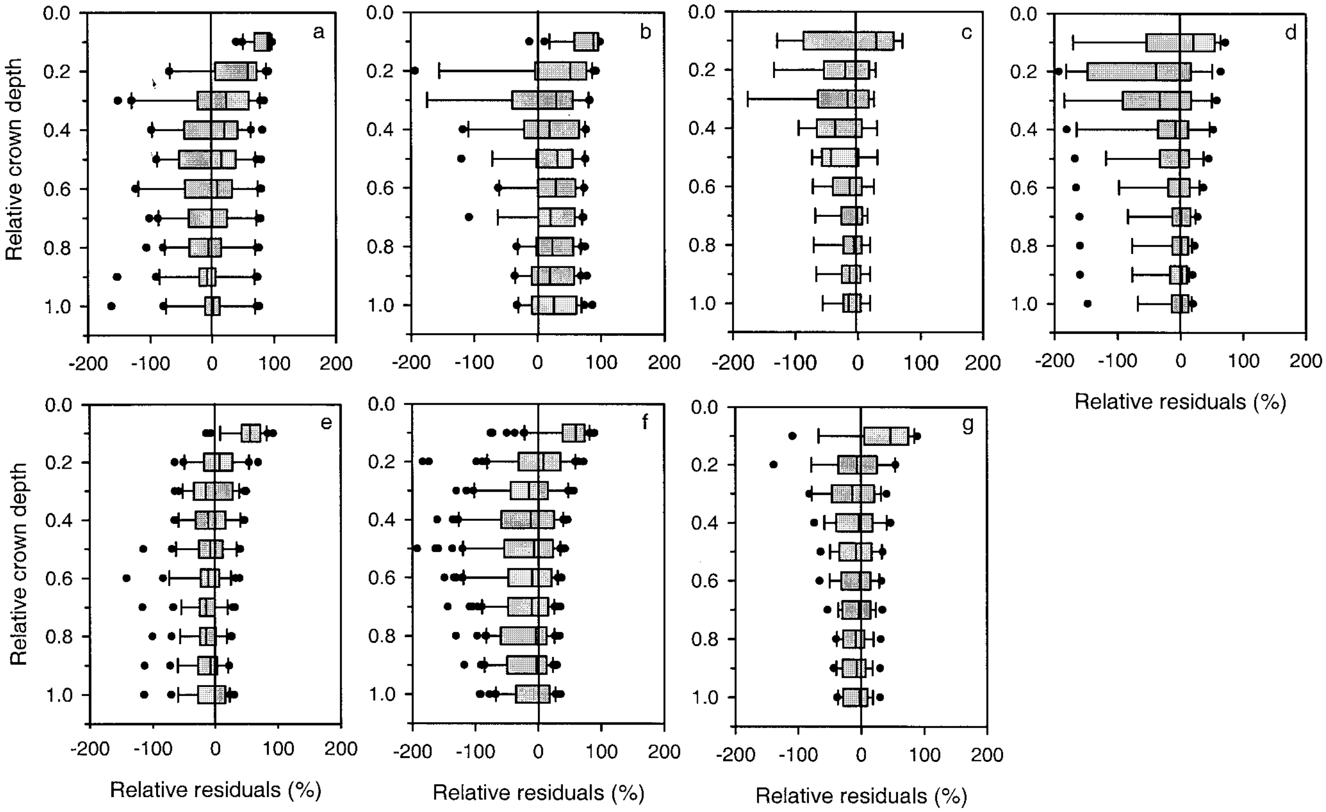

Figure 3. Boxplots of the residuals for the cumulative, absolute values of leaf area expressed as a percentage of the actual cumulative leaf area at 0.1 intervals of canopy depth. Data for loblolly pine trees are (a) unfertilized 4-year-old trees, (b) fertilized 4-year-old trees, (c) unfertilized 10-year-old trees, (d) fertilized 10-year-old trees, (e) 12-year-old trees sampled during the winter, (f) 15-year-old trees, and (g) 36-year-old trees.

Table 4. Mean and standard deviation (SD) values of parameter estimates for the S_B distribution that describe the vertical distribution of relative leaf area for individual loblolly pine trees

		γ		δ	
Group*	n[†]	Mean	SD	Mean	SD
1	18	−0.38	0.56	0.99	0.39
2	25	−0.50	0.38	1.14	0.48
3	9	0.01	0.30	1.04	0.26
4	18	0.10	0.37	1.20	0.21
5	24	0.12	0.39	0.90	0.22
6	60	−0.22	0.30	1.04	0.29
7	18	0.13	0.23	1.17	0.18

The parameters γ and δ were obtained for each tree by fitting the S_B distribution for each tree.
*Groups: (1) unfertilized 4-year-old trees, (2) fertilized 4-year-old trees, (3) unfertilized 10-year-old trees, (4) fertilized 10-year-old trees, (5) 12-year-old trees sampled during the winter, (6) 15-year-old trees, (7) 36-year-old trees.
[†]Sample size.

evident for these trees. However, the data used in this study were from trees selected to represent the range of tree sizes within a stand; consequently, the sample did not represent the actual distribution of tree sizes within the stands that would be important in detecting differences in leaf area distribution at the stand level.

Conclusions

These results support the hypothesis that the S_B function with parameters calculated with the two-percentile method adequately describes the vertical distribution of leaf area for a wide variety of loblolly pine stands growing in the western Gulf region of the United States. Statistics for the residuals between cumulative leaf area predicted by the S_B function and measured through destructive harvest indicate close correspondence between the two estimates with only small prediction biases. In addition, the values of γ and δ appear to correspond to differences in stand density and age of the various groups of data. Predictions of the foliage distribution for an individual tree are associated with considerable variation, however, due to the incongruities between a smooth mathematical function and the inherently irregular distribution of foliage along the stem. Nonetheless, the S_B

function with parameters calculated with the simple two-percentile method produces reliable descriptions of both relative and absolute leaf area distributions for these loblolly pine stands.

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