FOLIAGE DENSITY DISTRIBUTION AND PREDICTION OF INTENSIVELY MANAGED LOBLOLLY PINE

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Abstract—The pipe model theory says that foliage biomass is proportional to the sapwood area at the base of the live crown. This knowledge was incorporated in an effort to develop a foliage biomass prediction model from integrating a stipulated foliage biomass distribution function within the crown. This model was parameterized using data collected from intensively managed loblolly pine (*Pinus taeda* L.) plantations in the Lower Coastal Plain and Piedmont of Georgia and validated using litter trap data. Using readily obtained mensuration predictors—crown length and crown height, and diameter outside bark at the base of the live crown, this model can predict total foliage biomass and the foliage biomass for any piece of the crown.

INTRODUCTION

Continuous functions such as the Weibull (Bailey and Dell 1973) and Beta have been applied for predicting foliage biomass distribution within the crown (Baldwin and others 1997, Gillespie and others 1994, Vose 1988, Xu and Harrington 1998, Yang and others 1999). Predictors employed for this purpose are some tree and crown characteristics such as diameter at breast height (d.b.h., cm) and crown length (l, m). However, most of these studies were targeted to predict foliage biomass distribution on individual branches rather than tree level foliage and branch biomass prediction models, which restricts our ability to predict whole tree biomass and to evaluate morphological relationships among different tree components.

In this study, a foliage biomass prediction model was derived using a proposed distribution pattern in the crown, and a branch biomass prediction model was obtained based on a strong linear relationship between foliage and branch biomass. A key predictor, diameter outside bark at the base of the live crown (d.o.b., cm) was introduced to our prediction models because of a suggested relationship between foliage biomass and crown basal area; i.e., foliage biomass is proportional to the sapwood area at the base of the live crown from the pipe model theory (Causton 1985, Shinozaki and others 1964, Valentine and others 1994, Waring and others 1982). Other predictors employed were crown length (l, m) and crown height (ch, m). The impacts of cultural treatments were evaluated during parameterization using data collected from destructively sampled trees. Because the dependent variables involved are closely related and because foliage and branch biomass have high variability from site to site, a joint mixed-effects modeling approach was employed for parameter estimation to obtain consistent and unbiased estimates.

DATA COLLECTION AND DESCRIPTIVE ANALYSIS

Our data were collected from intensively managed loblolly pine (*Pinus taeda* L.) stands in the Piedmont (PID) and the Lower Coastal Plain (LCP) of Georgia. The Lower Coastal Plain installations had six blocks (two established in each year—1987, 1989, and 1993) and the Piedmont locations had five blocks (two established in 1988, two in 1990, and one in 1995) in which four 0.15-ha treatment plots were assigned one of four treatments: (1) complete vegetation control (controlling competing woody and herbaceous vegetation using herbicides [H]), (2) fertilization [F], (3) complete vegetation control and fertilization [HF], and (4) control [C] (Borders and Bailey 2001).

In the winter of 1999 (January), 192 trees were harvested from the Lower Coastal Plain installations for research on foliage, branch, and stem biomass. At each installation two blocks were 12 years old, two were 10 years old, and two were 6 years old at time of harvest. Similarly,160 sample trees were harvested from the Piedmont installations during the winter of 2000 (January) when the ages were 12, 10, and 5 years old, respectively.

For each fallen tree, we measured branch diameter at the base next to the bole and branch height from stump for all live branches. We also obtained green weight of all branches and foliage for each tree. A single live branch from each whorl was randomly sampled. For this sub-sample of branches, we measured total length, length to foliage from base of branch, green weight, and dry weight. In addition, for each of these sample branches, we took a composite subsample of 40 to 50 fascicles along the length of the branch. We determined the green weight, dry weight, and projected leaf area for each of these foliage samples.

In addition, we collected litterfall at approximately 6-week intervals between March 1999 and March 2001 from five 0.75-diameter round litter traps randomly placed in each plot. Litter collected from each plot was pooled and oven dried at 60 °C. Pine leaf litter was separated from the rest of the sample and weighed. Specific leaf area of the litter was determined individually for all plots using a subsample of litter. The amount that fresh needles shrank before abscission was determined empirically and used to convert litter area to that of fresh needles. Leaf biomass of fresh needles was then determined by multiplying leaf area by the inverse of specific leaf area of fresh needles. Specific leaf area of fresh needles was measured 7 times during the growing season and averaged to determine specific leaf areas for each location, age, and treatment combina-

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tion. At the time of harvest, the majority of year-old foliage had abscised. Therefore, the litter collected between March 1999 and March 2000 represents the foliage on the trees at the time of the harvest at the LCP installation (winter 1999), and the litter collected between March 2000 and March 2001 represents the foliage on the trees at the time of the harvest at the PID installation (winter 2000) (Will and others 2002).

MODEL DERIVATION

The approach employed is to derive a foliage prediction equation from its distribution function. In this approach, a mechanically reasonable model structure can be constructed based on the relationship between foliage biomass and crown characteristics. It was assumed that foliage biomass is uniformly distributed in cross-sectional areas of the crown with a distribution radius, *r*. The value of *r* should be zero at the top of the crown, should increase along crown until it reaches a maximum (r_{max}), and then decreases to the base of the live crown (r_b) where live branches still bear foliage. Note that the Maxima function (Keen and Spain 1992) can be used to represent foliage distribution within the crown well and its mathematical expression is:

$$r = \alpha h e^{-\beta h} \tag{1}$$

where h (m) is crown depth, and α and β are parameters.

The value of a unit virtual rotator of foliage biomass (unit length *dh*, m) in the cross sectional panel of the live crown can be obtained using the cylinder volume equation, $\pi r^2 dh$, and whole tree foliage biomass can be expressed with the following integration:

$$F_B = \int_0^l k r^2 dh = \int_0^l k(\alpha h e^{-\beta h})^2 dh = \int_0^l k\alpha^2 h^2 e^{-\gamma h} dh \tag{2}$$

where F_B is foliage biomass (kg), *l* crown length (m), $\gamma = 2\beta$, and *k* the transition coefficient.

The function under integration [on the utmost right hand side of equation (2)] is a Gamma distribution function with location parameter 0 (zero), power parameter 3, and exponential parameter $1/\gamma$ (Hogg and Craig 1995, p.132). The symbolic solution of equation (2) is:

$$F_B = \frac{k\alpha^2}{\gamma^3}(2 - \gamma^2 l^2 e^{-\gamma l} - 2\gamma l e^{-\gamma l} - 2e^{-\gamma l}) \tag{3}$$

which is equivalent to:

$$F_B = \frac{k\alpha^2}{\gamma^3}[2(1 - e^{-\gamma l}) - \gamma l(\gamma l + 2)e^{-\gamma l}] \tag{4}$$

According to the pipe model theory, foliage biomass can be estimated using the sapwood area at the base of the live crown. Kinerson and others (1974), Waring and others (1982), and Valentine and others (1994) pointed out that dry foliage biomass is highly correlated to the cross-sectional area at the base of the live crown (crown basal area), which can serve as a surrogate to the sapwood area.

We used analysis of covariance to detect impacts of cultural treatments on foliage biomass with d.o.b. or diameter at breast height (d.b.h., cm) as one of covariates where the most responsive factor was complete vegetation control for trees in the Piedmont, and fertilization for trees in the Lower Coastal Plain. When d.b.h. is used as a covariate, fertilization (F) is a significant factor (in the Lower Coastal Plain) and complete competing vegetation control (H) is not (in the Piedmont); when d.o.b. is a covariate, neither F nor H is a significant factor. The above analysis indicates that treatment impacts could be ignored during parameter estimation if d.o.b. is used as a predictor, which simplifies model structure and parameter estimation. Thus, d.o.b. rather than d.b.h. was used as a predictor of foliage biomass.

Our data also showed that unit foliage biomass (total tree foliage biomass divided by crown basal area) increased with crown height, C_h (m). It is also true that crown height is linearly related to tree age. Thus, crown height was chosen as a predictor of foliage biomass.

Reformulating equation (4) using d.o.b. and C_h to replace the coefficient *k*, a foliage biomass prediction model is obtained as:

$$F_B = \frac{\eta\, dob^{\beta} C_h^{\tau} \alpha^2}{\gamma^3}[2(1 - e^{-\gamma l}) - \gamma l(\gamma l + 2)e^{-\gamma l}]. \tag{5}$$

Re-parameterizing equation (5), the model can be written as:

$$F_B = \xi\, dob^{\beta} C_h^{\tau}[2(1 - e^{-\gamma l}) - \gamma l(\gamma l + 2)e^{-\gamma l}] \tag{6}$$

where ξ is a parameter and the others as defined as above.

We found a strong linear relationship between foliage biomass and branch biomass, which agrees with the description from Causton (1985). According to this discovery, we proposed a prediction model form for branch biomass (B_B, kg):

$$B_B = \zeta F_B \tag{7}$$

where ζ is the proportionality coefficient.

PARAMETER ESTIMATION

Foliage biomass prediction equation (6) is intrinsically nonlinear and needs to be fit using a nonlinear modeling technique. During parameter estimation, the mixed-effects modeling approach was chosen to obtain consistent and unbiased estimates. This approach has the capability to detect the impact of site on foliage biomass, which is usually considered a random impact due to the uncertainty of actions and interactions from external forces. Note that FB is an endogenous variable because it is the dependent variable in equation (6) and the independent variable in equation (7) (Borders and Bailey, 1986). To eliminate simultaneous equation bias, observed FB values were replaced with predicted values during fitting the branch biomass prediction equation. A joint model-fitting method, which addresses all dependent variables (FB and BB) simultaneously, was employed, and all dependent variables were stored in a one-column matrix (vector). With the use of an indicator (dummy) variable, the dependent variable matrix on the left-hand side is functionally related to the independent variable matrix on the right-hand side. This approach is similar to that introduced by Zhang and others (2002). Apiolaza and Garrick (2001) have also used a similar fitting approach.

In mixed-effects modeling terminology, subject denotes the entity with stipulated character. Data obtained from the same subject may exhibit correlation with each other, and it is defined as the within-subject correlation. There may also be relationships among different subjects that are defined as the among-subject correlation. To allow for correlation within subjects using the SAS nonlinear mixed-effects modeling algorithm, the repeated (RTYPE) option in a SAS macro for nonlinear mixed-effects modeling (Littell and others 1996) was evoked. Among-subject correlation can be modeled by invoking the option, RANDOM. Suspecting impacts from varying drainage and fertility conditions, or soil types for the sites involved, we adopted site as the subject with a total number of four sites (two in each region).

RESULTS

Impacts of cultural treatments on foliage biomass can be ignored during parameter estimation if d.o.b. is used as a predictor. It was also found that the slope parameters (ξ and ζ) are not significantly different (statistically) by region. Thus, both foliage and branch biomass models were fit using the same slope parameters for two regions (the PID and the LCP), and all estimates of parameters were found to be statistically significant (table 1). The estimates of random parameter (*u*) for the four sites show that site impacts in both regions are significantly different and cannot be ignored. Overall, the models fit our data well (table 2).

Residual analysis was done to evaluate the fit quality, and no obvious trends of the residual distribution were found.

Table 2—Fit statistics of the foliage and branch biomass prediction equations obtained using mixed-effects approach and statistics for goodness of fit

Fit statistics of mixed-effects fitting:	
-2 Res Log Likelihood	1904.5
AIC (smaller is better)	1910.5
BIC (smaller is better)	1908.6

Goodness of fit:

	SEE	*BIAS*	*ABIAS*
		kg/tree	
F_B	0.5976	0.0322	0.4830
B_B	1.3202	0.0229	1.1164

-2 Res Log Likelihood = the -2 Restricted Log Likelihood value; F_B = foliage biomass; B_B = branch biomass; SEE = standard error of estimate; BIAS = average bias; and ABIAS = absolute average bias.

Source: Littell and others 1996, pp. 139, 403-404), AIC the Akaike Information Criterion (Pinheiro and Betes 2000, pp. 10; BIC the Bayesian Information Criterion (Pinheiro and Betes 2000, pp. 10).

Validation of these prediction equations was not carried out directly because suitable independent data are not available. However, needle data collected from litter traps provided a pseudo set of validation data. Table 3 lists average foliage biomass on a tree basis for fertilized stands and unfertilized stands with all age classes in both regions for model

Table 1—Estimates obtained for foliage and branch biomass prediction models, where STD is the standard error, LCL and UCL the lower and upper 95 percent confidence limits

Parameter	Estimate	STD	LCL	UCL
Fixed				
$\hat{\xi}$	1.8290E-2	2.8000E-4	1.7740E-2	1.8840E-2
$\hat{\beta}$	1.7618	0.0628	1.6385	1.8851
$\hat{\gamma}$	1.3100	0.1572	1.0017	1.6188
$\hat{\tau}$	0.1116	0.0109	0.0901	0.1330
$\hat{\zeta}$	2.4269	0.0394	2.3496	2.5042
Random	**Estimate**	**STD**	**t-value**	**Pr > |t|**
$\hat{u}_1$	-0.1281	0.0374	-3.43	0.0006
$\hat{u}_2$	-0.0471	0.0406	-1.16	0.2465
$\hat{u}_3$	-0.1847	0.0646	-2.86	0.0044
$\hat{u}_4$	0.1909	0.0666	2.87	0.0043

Table 3—Comparisons of average predicted foliage biomass of a tree [F_B (kg)], average foliage biomass of a tree from destructive samples (DF_B, and litter trap collected foliage biomass of a tree [TFB_B (kg)] for most responded cultural treatments by age in both PID and LCP installations

	Age	Litter trap prediction TFB	Litter trap prediction FB	Destructive sampled DFB
	yr.	- - - - - - - - *kg/tree*	- - - - - - - -	
PID				
No H	5	1.44	1.04	1.15
	10	2.23	2.91	3.27
	12	4.10	3.42	3.48
H	5	1.38	2.36	2.54
	10	1.96	3.70	4.09
	12	2.68	3.85	4.05
LCP				
No F	6	3.08	3.08	2.98
	10	2.72	3.40	3.07
	12	2.56	3.41	3.10
F	6	3.33	3.25	3.06
	10	3.86	4.10	3.85

H = complete vegetation control; F = fertilization.

predictions (F_B, kg), litter trap collections (TF_B, kg), and destructively sampled data (DF_B, kg). The results showed that the difference between F_B and TF_B is somewhat larger than that between TF_B and DF_B. The larger difference may be due to the difference of collection times for litter trap data and destructively sampled data, collection methods, calculations and estimation methods, or impacts from other unobservable factors.

DISCUSSION

We derived a foliage biomass prediction model based on the Gamma distribution that can predict both total tree foliage biomass and the foliage biomass for any segment of the crown. This capability can improve estimates of tree and stand carbon gain, which is known to vary with foliage biomass as well as foliage position within crowns. The functional relationship between foliage biomass and diameter outside bark at the base of the live crown has been constructed according to the pipe model theory. Valentine and others (1994) suggested using a 'taper-based surrogate' consisting of a 'live crown ratio above breast height' that is the ratio of crown length to the distance between breast height and the top of tree, and d.b.h. squared to predict foliage biomass. Based on the same theory, Naidu and others (1998) employed d.b.h. as a predictor of foliage biomass. From our data, it was found the diameter at the base of the live crown was a better predictor of foliage biomass than d.b.h. or the surrogate suggested by Valentine and others (1994). However, if d.o.b. is not available via direct measurement it can be estimated indirectly using taper function and crown height. This estimate of d.o.b. then corresponds to the surrogate suggested by Valentine and others (1994).

We found that cultural treatments have significant impacts on foliage biomass growth. For instance, trees from complete vegetation control stands produced more foliage biomass than control or fertilized stands in the Piedmont, whereas fertilized trees produced the most foliage biomass in the Lower Coastal Plain. Also an interaction was found between age and the fertilization treatment in the Piedmont, which shows that the fertilized trees produced more foliage biomass than unfertilized trees at age 10 and above, but not at age 5 (Will and others 2002). The confounding between age and treatment complicates parameter estimation and even model structure. On the other hand, d.o.b. is a more robust predictor and is closely related to current crown status regardless of cultural treatment. Conversely, our analysis showed that the impacts of cultural treatments must be considered explicitly during parameter estimation if d.b.h. is used as a predictor.

A close linear relationship between foliage and branch biomass was described previously (Causton 1985) and confirmed by our data. Using a proportionality constant, branch biomass can be easily estimated using the prediction of foliage biomass, which significantly simplifies the structure of branch biomass prediction model.

We did not have a truly independent set of data with which to validate our models. However, we had estimates of foliage biomass that were obtained from litter trap data. In most instances, there was good agreement between the two estimates. In a few instances, however, we did find large differences between model predictions and litter trap data. The errors may be from different collection methods or seasonal variation between collection times.

Clearly, the model derived and presented above fits our crown data well. It should be emphasized that this model is not a purely statistical model but has a solid basis in the physical nature of tree crowns and is supported with the pipe model theory. Consequently, this model predicts foliage and branch biomass for various cultural treatments using dendrometric variables from individual trees that reflect crown differences by cultural treatment. This makes the model relatively general in that it is not necessary to parameterize separately by cultural treatment. For model application, one needs to measure diameter outside bark at the base of the live crown (d.o.b.), crown height, and total height. As a substitute, d.o.b. value can be predicted using stem taper function and predictors—d.b.h., total height, and crown height.

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