AN INDIVIDUAL-TREE MEASURE OF GROWING STOCK AND STAND DENSITY

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ABSTRACT

Implicit in the concepts of growing stock and stand density is that they are functionally related to the number and size of the trees in a stand. If they are additive, they should be a function of the size and number of trees within a stand. To test this idea, data from a slash pine (*Pinus elliotii*) spacing and thinning study were fit to the nonlinear regression model $\frac{i_v}{i_h} = \beta_0 D_0^{\beta_1} + \epsilon$ where i_v = periodic annual increment of stem volume, i_h = periodic annual increment of stem height, D_0 = initial stem diameter at breast height, and β_0 and β_1 are parameters to be estimated. Previous research indicates that $\Sigma \frac{i_v}{i_h}$ is proportional to Dq^xN, the general mathematical form of Reineke's stand density index. Since Dq^xN can be closely approximated by $\sum D_0^x$, the relationship should also extend to single trees. The value of $\beta_0 D_0^{\beta_1}$ will indicate the value of a single tree to total growing stock or stand density. Results show that the power function fits the data well with little bias due to initial spacing and age. For these data the value of a single slash pine tree in terms of $\frac{i_v}{i_h}$ is $8.5 \times 10^{-4} D_0^{1.8}$. This result may be useful in furthering our understanding of how tree structure affects growth and also in determining the appropriate mix of stem diameters in uneven-aged stand structure.

INTRODUCTION

Each tree occupies space in a forest, contributes to forest growth, and competes with other trees for more space. The total space occupied increases with tree growth and tree density. Since the raw materials and resources for growth are distributed in space, the total space occupied by the trees is an important trait characterized in different ways depending on the function under consideration. For example, stand density refers to competition and growth limitations (Curtis 1970). Growing stock also refers to growth but from a yield perspective. Long (1985) related the two concepts through Langsaeter's curve whereby stand growth increases with growing stock or stand density as site occupancy increases to a maximum and individual-tree growth decreases with increased tree occupancy. While the relationship between tree occupancy and total stand growth varies between saturating to linear, the effect of increasing competition on individual tree growth is consistently negative (Dean and Baldwin 1996).

Stand growth, stand density, growing stock, and tree occupancy are naturally additive variables. Consider stand density. Reineke's stand density index (SDI) is $N\left(\frac{Dq}{25}\right)^x$ where N is tree density, Dq is quadratic mean diameter, and x is 1.6. This equation is approximately equal to $\Sigma\left(\frac{Dq}{25}\right)^x$ summed over trees per hectare (Ducey and Larson 2003). According to these equations, each tree's contribution to stand density is proportional to d.b.h.^{x}, where d.b.h. is diameter at breast height. However, adding another tree to the population has been thought to have a diminishing effect, especially with regards to competition.

Dean and others (2013) reported a standwise metric of tree growth that is consistently additive and proportional to the general form of Reineke's SDI, $N\left(\frac{Dq}{25}\right)^x$ with x ranging from 1.55 to 1.80 depending on the species. This transforms Reineke's SDI from an abstract measure of occupancy to a concrete measure of stand growth. Specifically, periodic increment

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in stem volume divided by periodic increment in height growth ($\frac{i_v}{i_h}$) can be treated as a marginal height cost as discussed in Dean and others (2023). Its relationship with stem diameter is a consequence of the thickness of the growth layer needed to physically and physiologically support an additional meter of height. Since both total marginal height cost and SDI are additive, the contribution of a single tree to the overall growing stock or stand density should be given by the following power function:

$$\frac{i_v}{i_h} = \beta_0 D_0^{\beta_1} + \epsilon \quad (1)$$

where

i_v = periodic annual increment of stem volume

i_h = periodic annual increment of stem height

D_0 = initial stem diameter at breast height

β_0 and β_1 = parameters to be estimated

ε = the error in the model

The objective of this study was to fit individual-tree data to this regression model to determine whether the results obtained at the stand level by Dean and others (2013) are simply the sum of equation (1) across the trees in a stand. If so, then equation (1) provides the contribution of an individual tree to the total growing stock and stand density.

METHODS

Data for this analysis came from a slash pine (*Pinus elliotii*) spacing and thinning study conducted in cooperation with the U.S. Department of Agriculture, Forest Service, Southern Research Station, and the Louisiana Department of Agriculture and Forestry in Pineville, LA. The study design and the effects of spacing and thinning on plot growth were reported by Baldwin and others (1995) and Schexnayder and others (2002), respectively. The study was laid out in a randomized complete block design. Storm damage created an unequal replication of treatments within blocks. Sixty-four trees were planted in each plot at seven spacings (1.2 m by 1.2 m, 1.2 by 1.8 m, 1.8 m by 1.8 m, 1.8 m by 2.4 m, 2.4 m by 2.4 m, 3.1 m by 3.1 m, and 4.3 m by 4.3 m). All plots were thinned to a 35 percent of maximum SDI when the trees were 17 years old. Diameter at breast height (d.b.h.) (1.37 m) and total height were measured on all trees at ages 15 and 17 years (before thinning); thereafter, trees were measured every year until age 23. Periodic annual increment of stem volume and height were calculated for a 2-year period: 15–17 (before thinning), 18–20, and 21–23 years. Individual-tree stem volume was calculated with the equation from Lohrey (1985)

$$\ln V = -5.42 + 2.08 \ln d.b.h. + 0.846 \ln H \quad (2)$$

where

V = stem volume in cubic feet

d.b.h. is in inches

H = total height in feet

Data were fit to equation (1). To avoid autocorrelation due to repeatedly measured data on the same tree, one tree was randomly selected from each combination of block and spacing across measurement ages to produce a data matrix consisting of block, spacing, tree, age, d.b.h., and $\frac{i_v}{i_h}$. This was repeated 100 times to produce 100 estimates of β_0 and β_1. On average, each resampled dataset contained 25 trees. Goodness of fit was evaluated on the basis of bias with respect to initial spacing and age with residual plots. Each residual is the difference between the predicted and observed values of $\frac{i_v}{i_h}$ for each tree in the replicate. Bias was also evaluated with the mean of the residuals and the mean absolute difference between the observed and predicted values.

The implicit hypothesis tested with this analysis is that $\frac{i_v}{i_h}$ is related to a common power function of stem diameter regardless of initial spacing, thinning history, or age. Analysis of variance was used to test for spacing and age effects with a randomized complete block design with replicates treated as a blocking effect. Spacing and age effects on the means of the residuals were tested with a Tukey's test with the root mean square errors for the interaction between replicate and spacing and between replicate and age, respectively.

RESULTS

The null hypothesis that the 100 estimates of β_1 were normally distributed could not be rejected with the Shapiro-Wilk test ($P = 0.79$) (fig. 1). The mean value of β_1 was 1.79 and the median value was 1.84. The null hypothesis that spacing and age had no effect on the fit of $\frac{i_v}{i_h}$ to the power function of d.b.h. was rejected for both effects (P <0.001). The mean values of the residuals grouped by spacing decreased from positive values for spacings closer than 2.4 m by 1.2 m to negative values for the wider spacings (table 1). Means comparison for age indicated that the means were significantly different for each age, starting negative for the 15- to 17-year age group to positive for the 21- to 23-year age group. While the mean of the residuals was significantly affected by initial spacing and age, these effects were not evident in scattergrams of the residuals plotted against the predicted values of $\frac{i_v}{i_h}$ (figs. 2 and 3). Within most spacings and age groups, a majority of the residuals were scattered around zero. The lack of significant bias in the fitted equation resulted in a close 1:1 relationship between predicted and observed plot sums of $\frac{i_v}{i_h}$ (fig. 4).

Table 1—Means testing for the effects of initial spacing and age grouping on the residuals of the fit of equation (1) to the 100 replications of the resampled slash pine data

	Group	n	Mean (m³/m)
Spacing (m)	1.2 by 1.2	89	0.0068a
	1.2 by 1.8	354	0.0062a
	1.8 by 1.8	366	0.0087a
	1.8 by 2.4	274	0.0030a
	2.4 by 2.4	482	-0.0039b
	3.1 by 3.1	478	-0.0054bc
	4.3 by 4.3	292	-0.0099c
Age group (years)	15–17	787	-0.0106a
	18–20	842	-0.0031b
	21–23	706	0.0148b

Means in a group followed by the same letter were statistically similar.

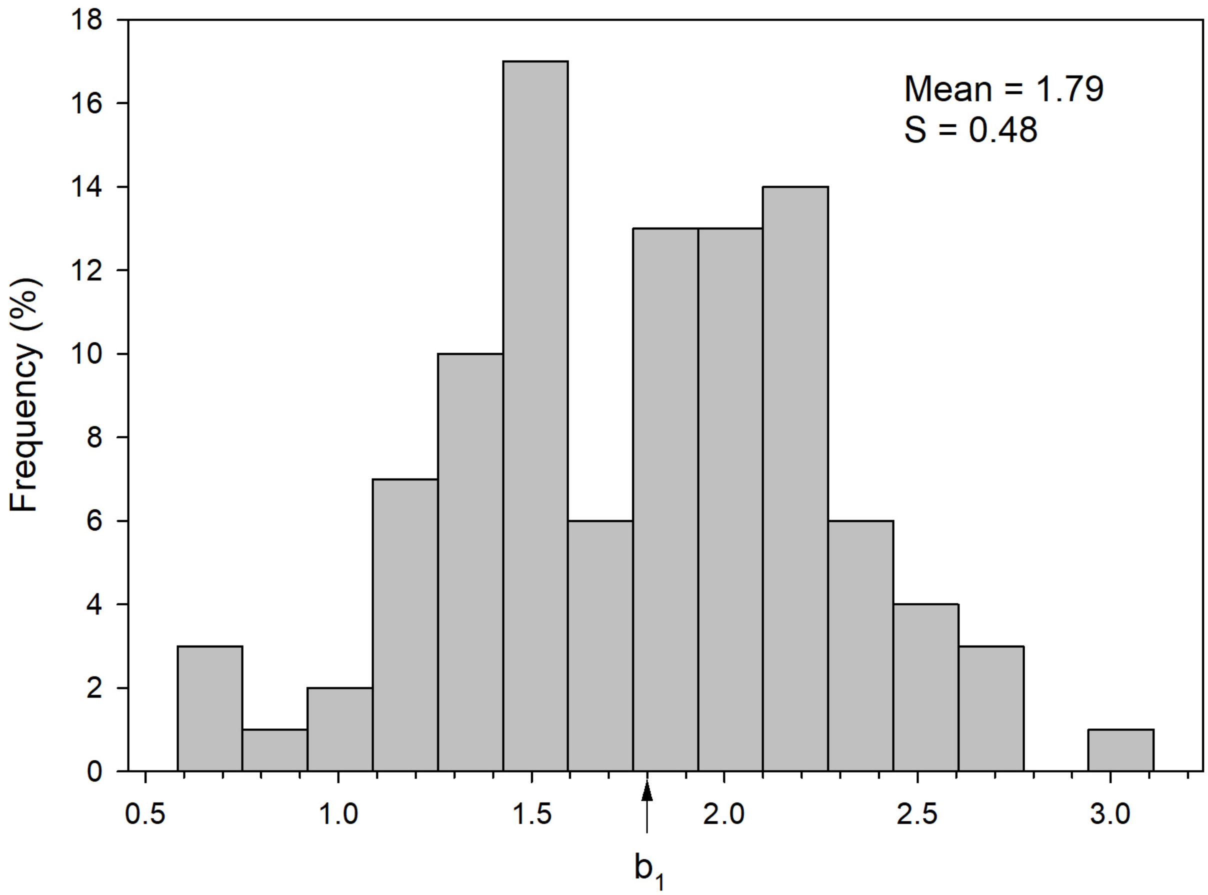

Figure 1—Histogram of the estimated values of β_1 for the nonlinear equation $\frac{i_v}{i_h} = \beta_0 D_0^{\beta_1} + \epsilon$ for 100 resampled datasets from the slash pine spacing and thinning study. Arrow shows the position of the mean value of β_1. S = standard deviation.

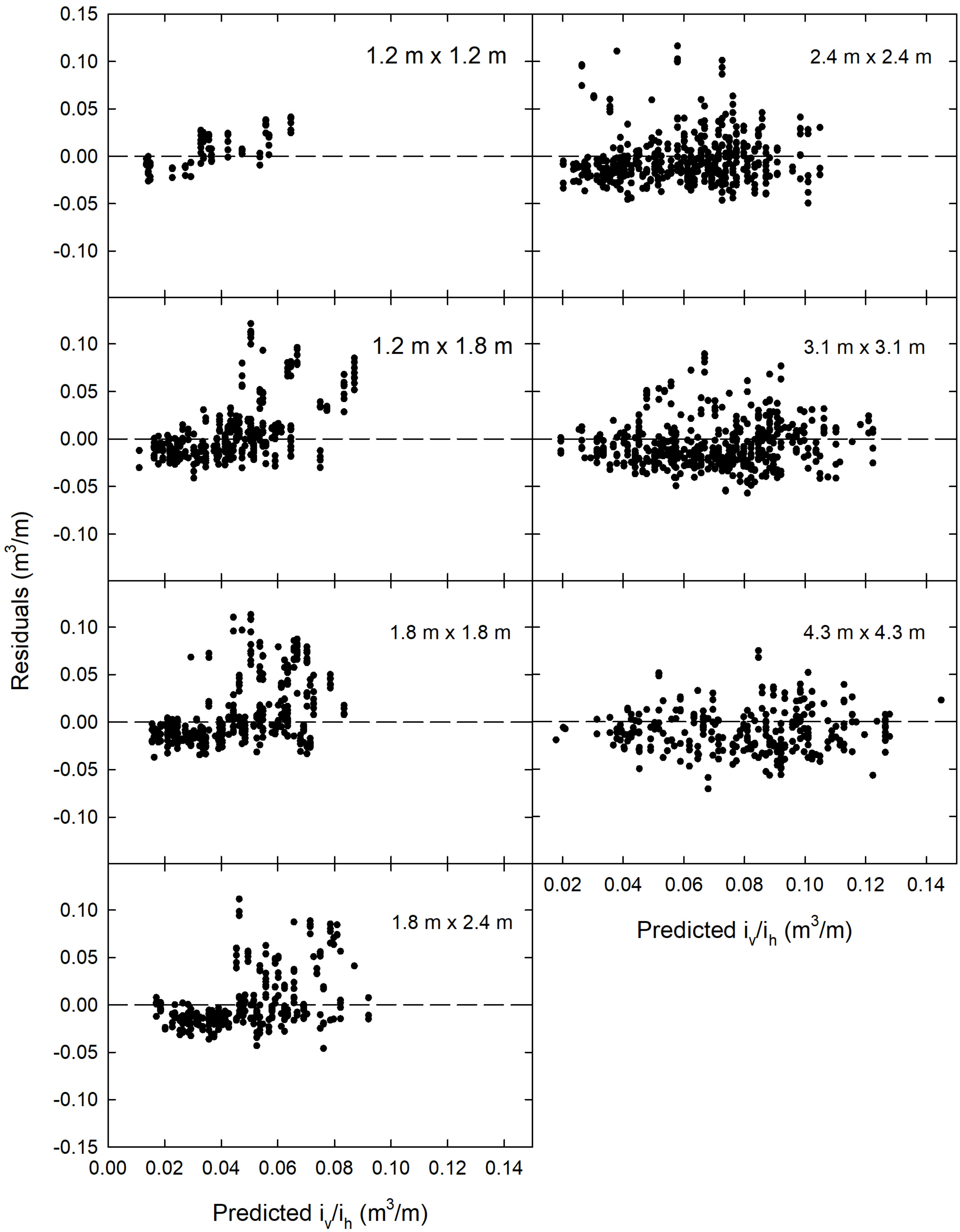

Figure 2—Residuals of fitting $\frac{i_v}{i_h} = \beta_0 D_0^{\beta_1} + \epsilon$ to the data from the slash pine spacing and thinning study by initial spacing.

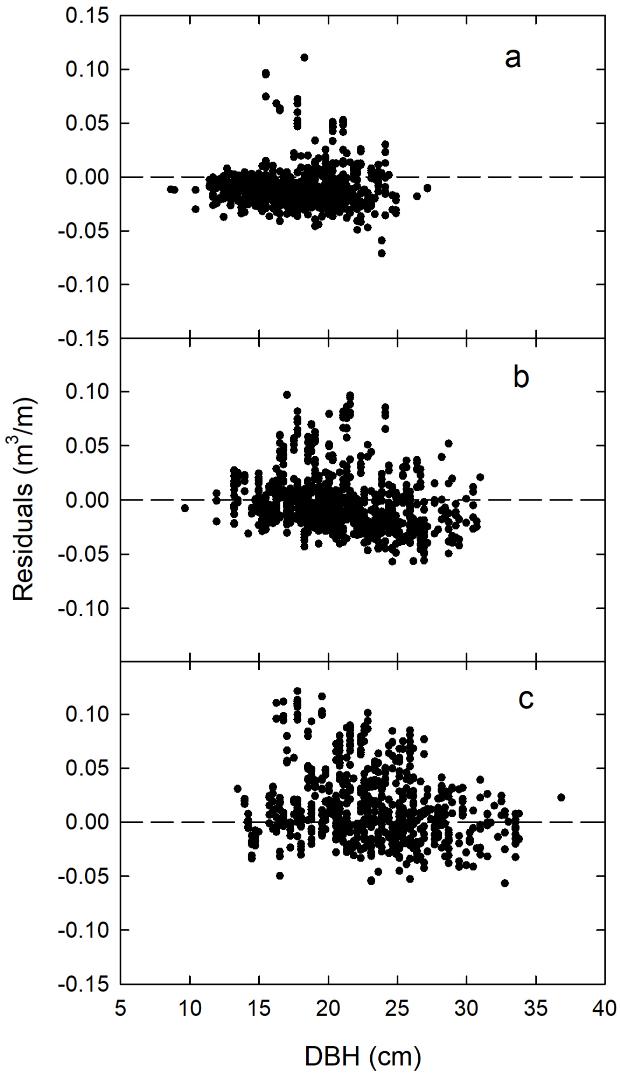

Figure 3—Residuals of fitting $\frac{i_v}{i_h} = \beta_0 D_0^{\beta_1} + \epsilon$ to the data from the slash pine spacing and thinning study by age group: (a) 15–17, (b) 18–20, and (c) 21–23.

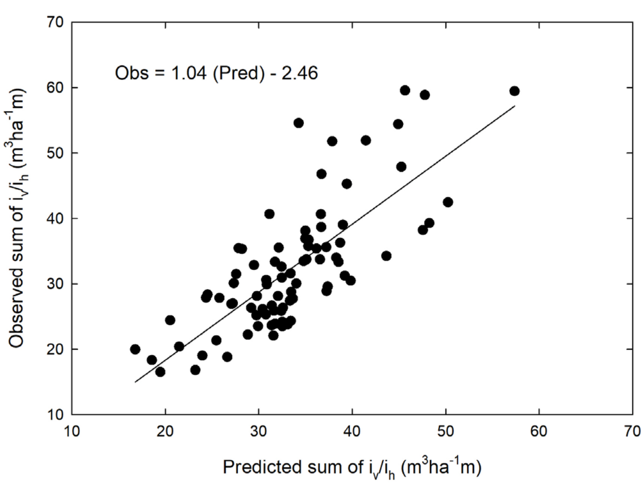

Figure 4—Observed plot sums of $\frac{i_v}{i_h}$ in relation to the plot sums predicted from the fit of equation (1) to the data from the slash pine spacing and thinning study.

DISCUSSION

Based on these results, each tree contributed $8.5 \times 10^{-4}\mathrm{d.b.h.}^{1.8}$ to the stand density or growing stock of a stand. Although analysis of variance indicated that initial spacing and age have significant effects on this relationship, from a practical perspective the effects were negligible and can be ignored without loss of accuracy. According to Dean and others (2021), the relationship between marginal height cost and stem diameter may be affected by live-crown ratio, which can be influenced by prethinning spacing. Schexnayder and others (2002) note some residual effect of initial spacing on the growth response of these trees to thinning.

The mean value of β_1 was significantly less than 2 ($t = 4$, $P < 0.001$), which would be the logical result of individual tree volume divided by tree height. This means that the ratio between stem volume increment and height increment is a fundamentally different relationship. As explained by Dean and others (2021), the predictable relationship between $\frac{i_v}{i_h}$ and d.b.h. seems to result from coordinated growth between height and stem volume where d.b.h. is the result of past height growth. The thickness of the growth layer needed to support additional height is manifest in stem diameter, and this increased girth is not simply proportional to the square of initial diameter.

The relationship between $\frac{i_v}{i_h}$ and d.b.h. may be a better method for setting target diameter distributions for uneven-aged stands compared to current methods that rely on the q factor, a somewhat arbitrary geometric mathematical progression. The q factor has a long and controversial history in creating the target structure in uneven-aged stands (Dean 2019) because it is more of an artifact of past disturbances rather than a biological constraint on development (Guldin 1991). Since the stand sum of $\frac{i_v}{i_h}$ is linearly related to stand density, equal proportions of the sum can be allocated across a range of diameter classes. This follows the same reasoning used by Long and Daniel

(1990) in allocating equal proportions of SDI to create the diameter distributions for Douglas-fir (*Pseudotsuga menziesii*). The number of trees allocated to each diameter class would be the expected value of $\frac{i_v}{i_h}$ calculated with the fitted values of equation (1) for each diameter class divided into the sum of $\frac{i_v}{i_h}$ allocated to that diameter class. If the periodic height increment for a diameter class is known, the periodic volume increment for that class can also be calculated. The total periodic volume increment for the stand would be the sum of the periodic volume increment across the diameter classes.

ACKNOWLEDGMENTS

I thank the U.S. Department of Agriculture, Forest Service, Southern Research Station and the Office of Forestry of the Louisiana Department of Agriculture and Forestry for their support and its cooperation in this study establishing and helping in data collection. This project was supported in part with McIntire-Stennis funds under LAB94512. This project was published with the approval of the Director of the Louisiana Agricultural Experiment Station as publication No. 2023-241-38936.

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