



# Variation in biomass distribution and nutrient content in loblolly pine (*Pinus taeda* L.) clones having contrasting crown architecture and growth efficiency



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## ABSTRACT

Loblolly pine (*Pinus taeda* L.) is well adapted across an extensive range of sites, is responsive to silvicultural treatments, and has undergone genetic improvement through traditional tree breeding programs, with selection based primarily on rapid growth and disease resistance. Loblolly pine clones with contrasting crown architecture provide an opportunity to better understand the mechanistic relationships among stem growth, biomass partitioning, and component nutrient content. We assessed inventory data from four clones which exhibited a range of crown widths. Using a subset of three clones, we measured crown sizes, crown volume, biomass allocated to components (foliage, branches, stemwood and bark), and component nutrient concentration and content to assess variation in allocation and growth efficiency. Clonal variation in biomass distribution patterns helped explain variation in growth efficiency between the narrow crown clone (ARB-1) and wide crown clone (ARB-4). Clone ARB-1 was more efficient at producing stem biomass increment per unit foliar biomass and unit foliar nutrient content than clone ARB-4; this was consistent with the concept of a crop ideotype. This study provides new information useful for improving our understanding of the relationships among crown structure, biomass distribution patterns, growth efficiency, and tree productivity, and may help guide clonal tree population management.

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## 1. Introduction

The development of intensive management practices in forest plantations in the southeastern United States has made the region the woodbasket of the world (Wear and Greis, 2002). Improvements in silvicultural technologies such as fertilization and competition control have greatly increased the productive potential of forest stands (Fox et al., 2007). Genetic improvement of loblolly pine (*Pinus taeda* L.) has also significantly contributed to large increases in plantation productivity, producing a wide variety of highly productive open-pollinated (half-sib) and full-sib families and, more recently, clones (McKeand et al., 2006; Fox et al., 2007). Deployment of trees in clonal blocks ("clonal forestry") has a number of potential benefits compared to more diverse genetic deployments, including increased stand uniformity, increased gain in growth and disease resistance, and improved wood quality (Bettinger et al., 2009). Few published studies have examined tree- or stand-level characteristics of clonal stock, however, and further research is needed to better understand the

dynamics of clonal stands compared to more traditional deployments (McKeand et al., 2003; Emhart et al., 2007; Aspinwall et al., 2011b).

A potentially useful approach for assessing clonal phenotypes is the ideotype model proposed by Donald (1968) for agronomic crops. Donald and Hamblin (1976) proposed three classes of ideotypes: isolation ideotypes that perform best in young stands when intraspecific competition is minimal; competition ideotypes that grow well through aggressive competition with their neighbors and are less efficient users of site resources (Cannell, 1978); and crop ideotypes that achieve high productivity through efficient use of resources and are less aggressive intra-specific competitors. It is reasonable to hypothesize that crop ideotypes should be ideal for intensively managed production systems (Dickmann, 1985).

Ideotypes offer a valuable model for evaluating variation in crown traits and tree and forest productivity (Dickmann et al., 1994; Nelson and Johnsen, 2008). It has been proposed that crop ideotypes would have more compact, narrow crowns, while competition ideotypes would have wider crowns (Cannell, 1978; Martin et al., 2005). Within the context of stand dynamics, crown traits may influence competitive interactions among trees. Many crown architectural traits are under genetic influence in southern

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pinces, and therefore may be incorporated into breeding programs if desired (McCrary and Jokela, 1998; Emhart et al., 2007).

Previous research has shown that soil nutrient availability is the primary factor limiting growth in southern pines in their native range (Fox et al., 2007). Previous studies with loblolly pine (McKeand et al., 2006; Tyree et al., 2009b; Stovall et al., 2011) and other tree species have shown genetic variation in nutrient traits (Beets and Jokela, 1994; Gonzalez and Fisher, 1997; Xu et al., 2003). How nutrient traits interact with crown traits and efficiency of growth has not been examined, however.

Typically, genetic experiments comprise single-tree plots or row plots not using operational management or fully representing ecosystem dynamics (Martin et al., 2001). Physiological variation and stand dynamics in larger, genetic block-plot studies may offer useful information for understanding genotype performance under operational conditions (Martin et al., 2005). The present study examines variation in tree- and stand-level stem growth, biomass partitioning, and component nutrient content in loblolly pine clones having contrasting crown architecture. We hypothesized that narrow-crowned clones would have greater stand-level efficiency in terms of stem biomass produced per unit foliage or biomass nutrient content, consistent with predictions for crop ideotypes. The study used the Varietal Architecture Investigations Examining Tree Interactions on Experimental Sites (VARIETIES) clonal block plot experiment installed near Starke, Florida. The goal of this study was to increase our understanding of the relationship between crown architecture and tree productivity, and to explore the causes of growth efficiency variation.

## 2. Materials and methods

### 2.1. Study area and experimental design

VARIETIES is a clonal block plot experiment established in 2009 near Starke, Florida (29°56'50"N, 82°6'29"W). The study was established as a split-plot, randomized complete block experiment with four replicates. The whole-plot treatment was planting spacing (wide, 2.7 m × 3.7 m, 1000 trees/ha, and narrow, 1.5 m × 3.7 m, 1802 trees/ha), with split-plots planted with genetic entries of four clones (ARB-1, ARB-2, ARB-3, ARB-4) and one full-sib family. An additional genetic entry consisted of the four clones planted in mixture. The different genetic entry split-plot sizes were 7 × 7 tree plots (280 m<sup>2</sup> for and 490 m<sup>2</sup> for narrow and wide spacing, respectively). In this study, only the clonal genotypes growing in pure plots were analyzed, and all biomass sampling and scaling up calculations were performed only on the wide planting spacing treatment.

### 2.2. Inventory measurements

An age 3 year inventory conducted in December, 2011 included measurements of tree height (H, m), diameter at breast height (DBH, cm), crown length (CL, m) and crown width (CW, m) measured in two directions for all genotypes in the study. Stem volume index (SV = DBH<sup>2</sup> × H, dm<sup>3</sup>), crown volume (CV, m<sup>3</sup> and approximated as a paraboloid), relative crown width (CW/H, m/m) and an index of stem volume growth efficiency (SV/CV, dm<sup>3</sup>/m<sup>3</sup>) and crown shape ratio (CL/CW, m/m) were derived from primary measurements.

### 2.3. Biomass sampling

Based on an analysis of the inventory data, three contrasting clones were chosen for measurement of biomass distribution: ARB-1, ARB-2, and ARB-4. ARB-1 and ARB-4 had the narrowest

and widest average CW/H, respectively, and also had contrasting SV/CV (Table 1). In addition, we chose to measure biomass distribution for ARB-2 because this clone had the greatest productivity of all clones in the study (Table 1). For each clone, we chose eight trees distributed across the full range of tree DBH for destructive harvest. Harvested trees were chosen from among all four replicate plots for each clone in the wide planting spacing treatment. The destructive harvest was carried out on March 13 and March 16–19, 2012. Each sample tree was cut at the base and separated into stem and branch + foliage components. Branches with foliage attached (foliated branches, FB) and branches without foliage attached (NFB) were weighed separately. The total green weight of stem, branch, and branch + foliage components was measured in the field. Subsampling in the field enabled scaling of field green weights to component dry weights as follows. Subsample disks of stem were weighed green in the field, separated into stem wood and bark components which were also weighed green, and then bagged for laboratory drying. Non-foliated branch subsamples were weighed green in the field and then bagged for laboratory drying. Foliated branch subsamples were weighed green, separated into branch and foliage components that were also weighed green, then bagged for laboratory drying. Subsamples were then dried in the lab at 70 °C to a constant weight. Due to field and/or data recording errors, data were discarded for two trees from each of clones ARB-1 and ARB-4. As a result, the final sample size for clones ARB-1, ARB-2, and ARB-4 was 6, 8, and 6 trees, respectively.

Additional subsamples of stem wood, bark, branch, foliated branches, non-foliated branches, and foliage were collected from a small, medium, and large biomass harvest tree from each clone. The subsamples were chipped and ground in a Wiley Mill to pass through a 1 mm stainless steel sieve. The subsamples were sent to an independent laboratory (Micro-Macro International, Athens, Georgia, USA) for nutrient analysis as follows. About 0.5 g of ground tissue samples was first dry ashed in a muffle furnace and then the samples were brought up to volume with aqua regia (3:1 HNO<sub>3</sub>: HCl). The extracts were then analyzed using inductively coupled plasma atomic emission spectroscopy (ICP-AES; MMI Labs, Athens, GA, USA). Total N was analyzed in a CNS analyzer (LECO Corporation, St. Joseph, MI, USA) using the Dumas Method.

### 2.4. Data analysis

Data from destructively harvested trees were used to create allometric functions describing distributions of stem wood, stem bark, branches, and foliage for each of the three clones. Allometric relationships were fitted by regressing age 3 year individual tree component biomass against total individual tree biomass using a log–log regression approach. The generic model was:

$$\ln(y) = \beta_0 + \beta_1 x + \varepsilon,$$

**Table 1**

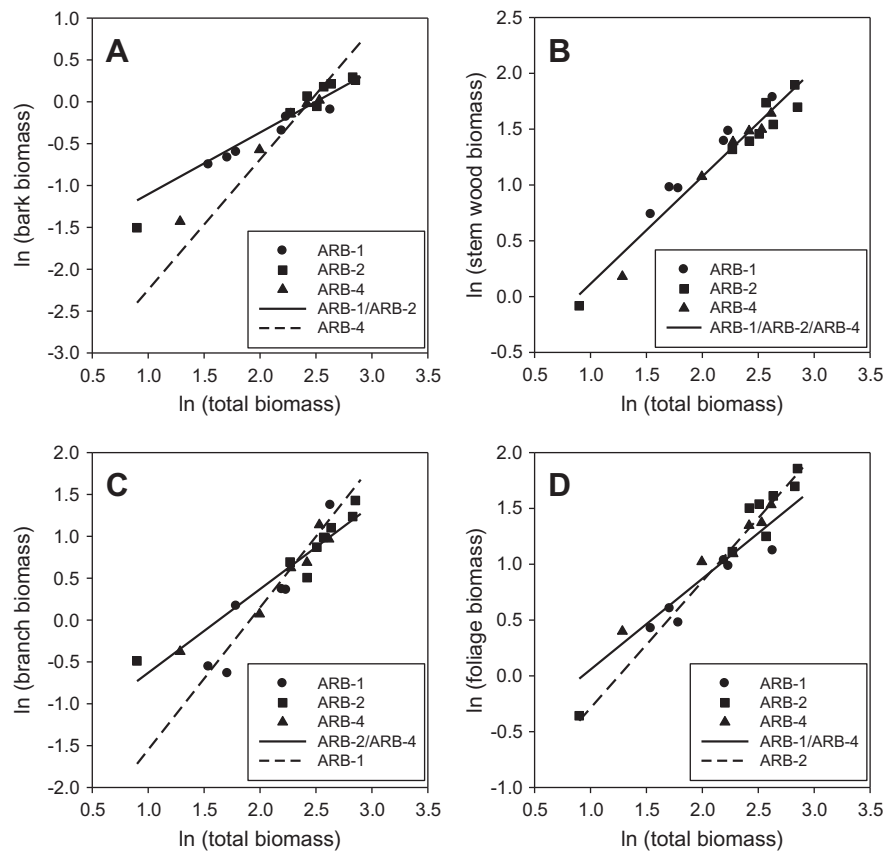
Age 3 year tree-level means from analysis of variance for stem volume (SV, dm<sup>3</sup>), crown volume (CV, m<sup>3</sup>), crown width (CW, m), relative crown width (CW/H, m/m) and stem volume growth efficiency (SV/CV, dm<sup>3</sup>/m<sup>3</sup>) for four clones in the VARIETIES experiment near Starke, FL.

Clone	SV <sup>a</sup>	CV	CW	CW/H	SV/CV
ARB-4	15.32 b	5.70 b	1.96 b	0.580 c	2.45 b
ARB-3	12.44 b	4.54 b	1.81 b	0.551 b	2.58 b
ARB-1	14.34 b	4.87 b	1.81 b	0.515 a	2.78 ab
ARB-2	24.22 a	7.61 a	2.17 a	0.555 bc	3.08 a
p-Value	<0.001	<0.001	<0.001	<0.001	0.001

<sup>a</sup> Values within a column followed by a different letter are statistically different ( $p < 0.050$ ) based on a Tukey's test for comparison of means.

**Table 2**  
Parameter estimates and standard errors (SE) for the relationships between age 3 year biomass components for three clones in the VARIETIES experiment near Starke, FL. Relationships are of the form  $\ln(y) = \beta_0 + \beta_1 * \ln(\text{Total})$ , where y is the predicted component biomass (kg),  $\beta_0$  and  $\beta_1$  are the intercept and slope parameters, respectively, and Total is the total tree biomass (kg). Data were combined for clones when the analysis in Table 8 showed no significant difference in the slopes or intercepts for those clones.  $R^2$  values are for the log-transformed regressions.

Component	Clones	Slope (SE)	Intercept (SE)	R <sup>2</sup>	MSE	p-Value
Stem	All	0.961 (0.05)	−0.846 (0.12)	0.946	0.015	<0.001
Bark	ARB-1/ARB-2	0.737 (0.06)	−1.840 (0.13)	0.938	0.011	<0.001
	ARB-4	1.557 (0.10)	−3.803 (0.23)	0.982	0.014	<0.001
Branches	ARB-2/ARB-4	1.004 (0.08)	−1.630 (0.19)	0.926	0.026	<0.001
	ARB-1	1.698 (0.31)	−3.246 (0.63)	0.886	0.077	0.005
Foliage	ARB-1/ARB-4	0.815 (0.10)	−0.759 (0.22)	0.867	0.022	<0.001
	ARB-2	1.135 (0.09)	−1.424 (0.21)	0.966	0.020	<0.001



**Fig. 1.** Log–log plots of bark biomass (A), stem wood biomass (B), branch biomass (C), and foliage biomass (D) vs. total biomass for three loblolly pine clones in the VARIETIES experiment near Starke, FL. Parameter estimates and regression statistics are presented in Table 2.

where  $\ln(y)$  is the natural log-transformed biomass component (stem, branch, bark and foliage in kg),  $x$  the natural log-transformed total biomass (in kg),  $\beta_0$  and  $\beta_1$  are the regression coefficients to estimate, and  $\varepsilon$  is the residual error term. A similar equation was fitted to determine the relationship between a given biomass component and a measure of tree size based on the explanatory variable  $x = \text{DBH}^2 * H$ .

Analysis of covariance was used to evaluate differences in component biomass distribution among clones using an F-test. When there were no significant differences in a particular equation among clones, a regression model was fitted that combined one or more clones. All statistical analyses were performed with SAS v. 9.3 (SAS Institute, 2011) using the procedure GLM and comparisons of parameters between clones were done using Tukey's tests. All statistical tests were done at a significance level of 5%.

Allometric equations were used to calculate stand-level component biomass from inventory measurements using the following back-transformed equation:

$$y = CF * \exp(\beta_0 + \beta_1 \text{ DBH}^2 * H),$$

where  $y$  is the biomass component (stem, branch, bark and foliage in kg),  $\beta_0$  and  $\beta_1$  are the estimated regression coefficients, and  $CF$  is a logarithmic bias correction factor with  $CF = \exp(\text{MSE}/2)$ , where  $\text{MSE}$  is the mean square error (Baskerville, 1972).

The final equations were used to calculate stem biomass increment (SBI, kg/ha/yr) between ages 2 and 3. Plot-level component nutrient contents were calculated by multiplying the average clonal nutrient concentration for each component by the estimated component biomass derived from the allometric equations. As an

**Table 3**

Parameter estimates and standard errors (SE) for the relationships between age 3 year biomass components for three clones in the VARIETIES experiment near Starke, FL. Relationships are of the form  $\ln(y) = \beta_0 + \beta_1 * \ln(\text{DBH}^2 * H)$ , where  $y$  is the predicted component biomass (kg),  $\beta_0$  and  $\beta_1$  are the intercept and slope parameters, respectively, DBH is diameter at breast height (cm) and  $H$  is tree height (m). Data were combined for clones when the analysis in Table 9 showed no significant difference in the slopes or intercepts for those clones.

Component	Clones	Slope (SE)	Intercept (SE)	R <sup>2</sup>	MSE	p-Value
Stem	ARB-1	0.997 (0.18)	−8.613 (1.80)	0.881	0.023	0.006
	ARB-2/ARB-4	0.644 (0.02)	−5.165 (0.19)	0.989	0.004	<0.001
Bark	ARB-1/ARB-2	0.513 (0.07)	−5.343 (0.68)	0.829	0.032	<0.001
	ARB-1/ARB-4	0.869 (0.06)	−9.014 (0.56)	0.959	0.014	<0.001
	ARB-2	0.452 (0.03)	−4.613 (0.27)	0.979	0.004	<0.001
	ARB-4	0.908 (0.04)	−9.395 (0.45)	0.990	0.008	<0.001
All Branches	ARB-1	1.721 (0.49)	−16.806 (4.90)	0.750	0.169	0.026
	ARB-2/ARB-4	0.607 (0.07)	−5.426 (0.72)	0.857	0.052	<0.001
Foliage	ARB-1/ARB-2	0.761 (0.09)	−6.573 (0.91)	0.854	0.058	<0.001
	ARB-2/ARB-4	0.507 (0.11)	−4.058 (1.08)	0.683	0.053	0.001
	ARB-2	0.715 (0.09)	−5.987 (0.98)	0.903	0.056	<0.001
	ARB-4	0.452 (0.06)	−3.347 (0.58)	0.937	0.013	0.002
Total	ARB-1	1.031 (0.19)	−8.152 (1.92)	0.875	0.026	<0.001
	ARB-2/ARB-4	0.618 (0.03)	−3.918 (0.33)	0.967	0.011	<0.001
Foliated Branches	ARB-1/ARB-2	0.500 (0.23)	−5.793 (2.28)	0.288	0.363	0.048
	ARB-1/ARB-4	0.840 (0.28)	−9.118 (2.75)	0.478	0.341	0.013
	ARB-2	0.426 (0.18)	−5.097 (1.84)	0.481	0.199	0.566
	ARB-4	0.748 (0.20)	−8.250 (1.99)	0.777	0.150	0.020
Non-foliated Branches	ARB-1	1.941 (0.97)	−19.631 (9.57)	0.501	0.643	0.116
	ARB-2/ARB-4	0.622 (0.08)	−5.859 (0.82)	0.831	0.066	<0.001

**Table 4**

Biomass accumulation (kg/ha) and fractional biomass ratios of foliage, stemwood, bark, branches, foliated branches (FB), non-foliated branches (NFB), and total aboveground biomass among three different clones of loblolly pine at age 3.

Clone	Foliage <sup>a</sup>	Foliage Fraction	Stemwood	Stemwood Fraction	Bark	Bark Fraction	Branches	FB	FB Fraction	NFB	NFB Fraction	Total
ARB-1	1,712 a	0.30 a	2,562 a	0.44 b	513 a	0.09 a	923 a	385 a	0.07 b	611 a	0.11 b	5,664 a
ARB-2	3,394 b	0.34 b	3,703 b	0.37 a	924 b	0.09 a	2,008 b	510 b	0.05 a	1,527 b	0.15 a	9,935 b
ARB-4	2,607 c	0.36 c	2,682 a	0.37 a	518 a	0.07 b	1,477 c	394 a	0.05 a	1,116 c	0.15 a	7,272 a
p-Value	<0.001	<0.001	0.002	<0.001	<0.001	<0.001	<0.001	0.004	<0.001	<0.001	<0.001	<0.001

<sup>a</sup> Values within a column followed by a different letter are statistically different ( $p < 0.050$ ) based on a Tukey's test for comparison of means.

index of foliar efficiency or nutrient use efficiency, we calculated efficiency ratios as SBI divided by foliar biomass or foliar content of different elements. Analysis of variance was used to compare plot-level traits using SAS v. 9.3 (SAS Institute, 2011). Because only one planting spacing treatment (wide) was used, the experiment was analyzed as a randomized complete block design.

### 3. Results

#### 3.1. Biomass distribution

All of the clones chosen for this study were highly productive, and this was reflected in the inventory data (Table 1). These results showed similar growth performance among clones, with the exception of clone ARB-2. Clone ARB-2 had a significantly greater age 3 stem volume ( $24.22 \text{ dm}^3$ ,  $p < 0.001$ ) compared to the other three clones (Clone ARB-1 =  $14.34 \text{ dm}^3$ , clone ARB-3 =  $12.44 \text{ dm}^3$  and clone ARB-4 =  $15.32 \text{ dm}^3$ ).

Clone ARB-2 (2.17 m) had significantly wider absolute CW than the other clones ( $p < 0.001$ ). However, when CW was normalized by total tree height, clone ARB-1 had the narrowest CW/H ratio ( $0.515$ ,  $p < 0.001$ ), while ARB-2 and ARB-4 had the widest CW/H ( $0.555$  and  $0.580$ , respectively). Clone ARB-2 had 50% greater stem volume than the other clones in the study, and significantly greater SV/CV than clones ARB-4 and ARB-3 (Table 1,  $p = 0.001$ ).

Log–log regressions of component biomass versus total biomass were analyzed to determine if there were differences among clones

in the distribution of component biomass (Table 8). Linear regressions fitted the data well, with  $R^2$  values greater than 0.85 (Table 2). For stem, there were no differences among clones in either the slope or the intercept of the relationship between stem biomass ( $p < 0.001$ ) and total biomass ( $p < 0.001$ ). For bark, clone ARB-4 had a significantly greater slope and a significantly more negative intercept than the other two clones ( $p < 0.001$ ). Clone ARB-1 had a significantly greater slope and a significantly lower intercept in the relationship between branch biomass ( $p = 0.005$ ) and total biomass ( $p = 0.006$ ) compared to the other two clones. For foliage, clone ARB-2 had a significantly greater slope and a lower intercept than the other two clones ( $p = 0.004$ ). After observing the contrast for slopes and intercepts for all the variables among clones (Table 8), we combined data for clones with no differences to derive appropriate component regression equations (Table 2, Fig. 1) (see Table 3).

#### 3.2. Component biomass

The analysis of component biomass accumulation showed some differences among clones. ARB-2 had greater total aboveground biomass accumulation than the other two clones ( $p < 0.004$ ) (Table 4). For example, the total aboveground biomass estimates for clone ARB-1, ARB-2 and ARB-4 were  $5664 \text{ kg/ha}$ ,  $9935 \text{ kg/ha}$  and  $7272 \text{ kg/ha}$ , respectively. For the components foliage ( $p < 0.001$ ), branches ( $p < 0.001$ ) and non-foliated branches ( $p < 0.001$ ) all clones were statistically different. Clone ARB-4 had



**Table 5**

Mean macroelement concentrations (g/kg) in foliage, bark, stemwood, non-foliated branches (NFB) and foliated branches (FB). Standard deviations are presented in parentheses.

Component	Clone	N*	P	K	Ca	Mg	S
Foliage	ARB-1	12.9 a (1.51)	0.9 a (0.02)	4.4 a (0.86)	2.2 a (0.81)	0.9 a (0.11)	0.9 a (0.06)
	ARB-2	12.9 a (0.21)	0.9 a (0.04)	3.4 a (0.40)	2.2 a (0.25)	1.1 a (0.07)	0.8 a (0.58)
	ARB-4	14.9 b (0.67)	1.1 b (0.08)	4.9 a (0.42)	2.5 a (0.61)	1.0 a (0.13)	1.3 a (0.40)
p-Value		0.066	0.003	0.250	0.816	0.176	0.381
Bark	ARB-1	5.0 a (0.61)	0.4 a (0.05)	3.3 a (0.92)	1.3 a (0.13)	0.7 a (0.03)	0.3 a (0.06)
	ARB-2	5.3 a (0.31)	0.5 ab (0.03)	4.0 a (0.44)	1.0 a (0.16)	0.5 b (0.06)	0.3 a (0.06)
	ARB-4	5.8 a (0.57)	0.5 b (0.07)	3.7 a (0.45)	1.8 b (0.18)	0.6 ab (0.12)	0.5 b (0.06)
p-Value		0.226	0.107	0.446	0.004	0.038	0.047
Stemwood	ARB-1	2.1 a (0.21)	0.2 a (0.02)	0.8 a (0.18)	0.5 a (0.01)	0.2 a (0.02)	0.1 a (0.06)
	ARB-2	2.3 a (0.31)	0.2 a (0.04)	1.0 a (0.20)	0.6 b (0.03)	0.2 ab (0.02)	0.1 a (0.06)
	ARB-4	2.1 a (0.12)	0.2 a (0.005)	1.1 a (0.07)	0.6 b (0.03)	0.3 b (0.03)	0.2 a (0.06)
p-Value		0.512	0.641	0.237	0.003	0.077	0.729
NFB	ARB-1	2.4 a (0.45)	0.2 a (0.03)	0.9 a (0.21)	1.3 a (0.05)	0.3 a (0.03)	0.2 a (0.12)
	ARB-2	2.9 a (0.59)	0.2 a (0.03)	1.1 a (0.08)	1.7 ab (0.40)	0.4 a (0.06)	0.2 a (0.10)
	ARB-4	2.5 a (0.29)	0.2 a (0.03)	1.0 a (0.21)	1.9 b (0.26)	0.4 a (0.05)	0.1 a (0.10)
p-Value		0.361	0.144	0.488	0.088	0.251	0.533
FB	ARB-1	5.3 a (0.79)	0.5 a (0.03)	2.1 a (0.20)	1.8 a (0.81)	0.7 a (0.11)	0.4 a (0.06)
	ARB-2	5.1 a (0.89)	0.5 ab (0.07)	2.2 a (0.24)	1.8 a (0.34)	0.6 a (0.10)	0.4 a (0.10)
	ARB-4	5.9 a (0.55)	0.5 a (0.06)	2.2 a (0.23)	2.0 a (0.20)	0.7 a (0.04)	0.4 a (0.06)
p-Value		0.399	0.243	0.340	0.832	0.547	0.579

\* Within each element/component combination, values followed by a different letter are statistically different ( $p < 0.050$ ) based on a Tukey's test for comparison of means.

greater biomass (2607 kg/ha of foliage, 1477 kg/ha of branches and 1116 kg/ha of non-foliated branches) than clone ARB-1 (1712 kg/ha of foliage, 923 kg/ha of branches and 611 kg/ha of non-foliated branches). Clone ARB-2 stemwood ( $p < 0.004$ ), bark ( $p < 0.001$ ) and foliated branches ( $p < 0.010$ ) were significantly different than the other two clones, but ARB-1 and ARB-4 were similar. Clone ARB-1 had the lowest total biomass in all the components compared with the other 2 clones.

Foliage biomass as a fraction of total biomass differed statistically among clones ( $p < 0.001$ ), with clone ARB-4 having a greater fraction (0.36,  $p < 0.002$ ) than clone ARB-1 (0.30,  $p < 0.001$ ) (Table 4). Clone ARB-1 had significantly greater fractions of total biomass in stem (0.44,  $p < 0.001$ ) and foliated branches (0.07,  $p < 0.001$ ) than the other two clones, but had a smaller fraction of total biomass in non-foliated branches (0.11 vs. average of 0.15 for the other two clones,  $p < 0.001$ ). Clone ARB-4 had a significantly smaller fraction of biomass in bark (0.07,  $p < 0.001$ ) compared to the other two clones (average 0.09,  $p = 0.211$ ).

### 3.3. Component nutrient concentration and content, stem biomass increment, and efficiency ratios

In many cases at age 3, clone ARB-4 had greater macronutrient concentrations and contents than clones ARB-1 and ARB-2 (Tables 5 and 10). For example, ARB-4 had greater foliar N concentrations (14.9 g/kg,  $p = 0.066$ ) than the other two clones (12.9 g/kg), and

also had greater foliar P concentrations (1.1 g/kg for ARB-4, vs. about 0.9 g/kg for ARB-1 and ARB-2,  $p = 0.003$ ). Moreover, the ARB-4 component foliage contents (N (38.9 kg/ha,  $p < 0.110$ ), P (2.9 kg/ha,  $p < 0.519$ ), K (12.7 kg/ha,  $p < 0.239$ ) and Ca (6.5 kg/ha,  $p < 0.065$ ), were greater than those of clone ARB-1 (22 kg/ha, 2 kg/ha, 8 kg/ha and 4 kg/ha, respectively,  $p < 0.001$ ).

Micronutrient concentration patterns were similar to macronutrient concentrations in that clone ARB-4 often had greater values than clone ARB-1 (Table 6). For foliage, clone ARB-4 had greater B concentration (14 mg/kg,  $p < 0.288$ ) than clone ARB-1 (10 mg/kg). For the component micronutrient content we did not observe significant differences in any component among the clones (Table 11).

Stem biomass increment (SBI) from ages 2–3 years for clone ARB-2 (2920 kg/ha/yr) was significantly greater than clone ARB-1 (2,310 kg/ha/yr) and clone ARB-4 (2066 kg/ha/yr) (Table 7). The efficiency ratios of SBI/Folbio, SBI/Foliar N and SBI/Foliar P showed consistent variation among the three clones ( $p < 0.001$ ), with ARB-1 showing approximately twice the efficiency of ARB-4, and ARB-2 with intermediate values.

## 4. Discussion

Genetic variation in productivity among different loblolly pine genotypes has been shown in some studies to be related to variations in dry matter partitioning patterns (Bongarten and Teskey, 1987; Li et al., 1991a; Chmura et al., 2007). For example, at the family level, McCrady and Jokela (1996, 1998) found that differences in volume production among different open-pollinated loblolly pine families were associated with variation in crown traits, such as foliage and branch biomass production. Bongarten and Teskey (1987) showed that variation in dry matter allocation among seed sources was associated with productivity in some cases, but that these relationships varied with growth environment (e.g. drought vs. well-watered treatments). Aspinwall et al. (2012) suggested that quantifying whole-tree allometric relationships in contrasting genotypes may provide a better understanding of the primary component traits which regulate phenotypic variability in whole-plant growth and productivity. In the current study, we hypothesized that variation in growth and different measures of growth efficiency in contrasting loblolly pine clones were associated with variation in allometry.

### 4.1. Genetic variation in biomass distribution and nutrient traits

In our study, all clones exhibited the same stem wood biomass to total biomass ratio, which is consistent with other allocation studies in loblolly pine clones (Stovall et al., 2012) and families (Bongarten and Teskey, 1987). The lower allocation of biomass to branches by narrow-crowned clone ARB-1 may contribute to the greater efficiency (measured as both SV/CV and SBI/Folbio) for this clone. Clone ARB-2 had lower foliage biomass allocation compared to the other two clones, but had intermediate levels of efficiency, implying a greater net photosynthetic gain for this clone. A number of studies have shown variation in photosynthetic rate among loblolly pine genotypes (e.g. McGarvey et al., 2004), although this has not always been consistent (e.g. Aspinwall et al., 2011). Further measurements would be required to confirm this for the clones in this study. Stovall et al. (2013) examined clonal variation in biomass partitioning to a number of above- and below-ground components in 10 loblolly pine clones, and found significant genetic variation in most of them. Stovall et al. (2013) suggested that the variety of biomass partitioning patterns observed among clones of loblolly pines indicates an opportunity to choose clones with rapid stem growth rates and a range of other advantageous features. In the current study, clone ARB-1 could be an example of a

**Table 6**

Mean microelement concentrations (mg/kg) in foliage, bark, stemwood, non-foliated branches (NFB) and foliated branches (FB). Standard deviations are given in parentheses.

Component	Clone	B	Cu	Fe	Mn	Mo	Zn
Foliage	ARB-1	9.8 a (0.94)	1.7 a (0.52)	27.7 a (1.63)	31.6 a (0.58)	0.1 a (0.20)	18.7 a (3.40)
	ARB-2	12.4 ab (2.55)	1.9 a (0.58)	25.8 a (3.16)	38.2 a (13.97)	0.02 a (0.03)	13.4 a (4.68)
	ARB-4	13.9 b (0.83)	1.7 a (0.73)	31.3 a (5.16)	43.9 a (28.96)	0.1 a (0.03)	12.3 a (2.01)
p-Value		0.058	0.929	0.243	0.730	0.611	0.135
Bark	ARB-1	8.9 a (0.59)	2.6 a (0.55)	19.3 a (2.50)	24.5 a (5.64)	0.3 a (0.47)	29.3 a (1.14)
	ARB-2	9.6 ab (0.37)	2.2 a (0.46)	30.1 a (16.43)	25.3 a (5.47)	0.1 a (0.12)	27.6 a (3.46)
	ARB-4	10.2 b (0.79)	2.1 a (0.90)	31.9 a (287.85)	18.6 a (3.71)	0.4 a (0.57)	43.8 a (37.90)
p-Value		0.0976	0.670	0.525	0.277	0.808	0.633
Stemwood	ARB-1	2.9 a (0.26)	2.2 a (0.56)	11.9 a (4.12)	10.4 a (2.48)	0.2 a (0.03)	8.8 a (0.67)
	ARB-2	3.2 a (0.22)	1.9 a (0.43)	15.1 a (3.91)	10.5 a (0.43)	0.2 a (0.15)	8.0 ab (0.46)
	ARB-4	3.3 a (0.10)	1.6 a (0.37)	10.6 a (1.63)	7.5 a (1.29)	0.1 a (0.09)	7.6 b (0.29)
p-Value		0.224	0.324	0.321	0.113	0.509	0.072
NFB	ARB-1	4.4 a (0.37)	2.3 a (0.49)	10.0 a (0.84)	16.2 a (3.24)	0.0 a (0.00)	10.7 a (2.94)
	ARB-2	5.9 b (0.68)	1.9 a (0.32)	19.5 b (3.52)	22.1 a (8.88)	0.2 b (0.09)	10.5 a (2.89)
	ARB-4	5.2 ab (0.50)	1.9 a (0.25)	14.0 a (0.96)	13.6 a (3.89)	0.04 a (0.06)	7.9 a (1.05)
p-Value		0.034	0.432	0.005	0.275	0.014	0.349
FB	ARB-1	7.3 a (0.72)	3.2 a (1.31)	19.1 a (2.95)	27.7 a (1.79)	0.1 a (0.10)	16.4 a (4.59)
	ARB-2	7.7 a (0.83)	2.1 a (0.74)	19.6 a (3.80)	33.1 a (6.45)	0.04 a (0.06)	12.1 a (2.57)
	ARB-4	7.9 a (0.64)	2.1 a (0.86)	18.0 a (3.21)	28.7 a (11.85)	0.1 a (0.06)	11.8 a (2.15)
p-Value		0.684	0.346	0.851	0.682	0.462	0.238

\*Within each element/component combination, values followed by a different letter are statistically different ( $p < 0.050$ ) based on a Tukey's test for comparison of means.**Table 7**

Average foliage biomass (kg/ha), foliar nitrogen content (Foliar N, kg/ha), foliar phosphorus content (Foliar P, kg/ha), stem biomass increment from age 2–3 years (SBI, kg/ha/yr) and ratios of SBI/Foliage biomass, SBI/Foliar N and SBI/Foliar P.

Clone	Foliage biomass <sup>a</sup>	Foliar N	Foliar P	SBI	SBI/foliage biomass	SBI/Foliar N	SBI/Foliar P
ARB-1	1,712 a	22.09 b	1.50 b	2,310 a	1.35 a	104.59 a	1,547.65 a
ARB-2	3,394 b	43.79 a	2.98 a	2,920 b	0.86 b	66.85 b	982.95 b
ARB-4	2,608 c	38.86 a	2.85 a	2,066 a	0.79 c	53.10 c	724.50 c
p-Values	<0.001	<0.001	<0.001	0.002	<0.001	<0.001	<0.001

<sup>a</sup> Within a column, values followed by a different letter are statistically different ( $p < 0.050$ ) based on a Tukey's test for comparison of means.

clone with desirable traits of high stem volume production and high production efficiency. While we did not examine heritability of traits in this study, others have shown that crown traits are heritable in loblolly pine clones (Emhart et al., 2007), and so might be amenable to selection in breeding programs.

There was intriguing and consistent variation in both component nutrient concentration and content among the clones in our study. Clone ARB-4 had greater N and P foliar concentrations than the other two clones, and had a greater foliar B concentration than clone ARB-1. Variation in other elements was less conclusive, but in most cases where differences existed (e.g. bark S concentration), ARB-4 had the greatest component nutrient concentrations. Because clone ARB-4 also produced relatively high levels of foliage biomass, its foliar N and P contents were also quite high, and were greater for all measured macro-elements than clone ARB-1, which produced the smallest relative foliage biomass quantities and (generally) lower foliar nutrient concen-

trations of all the clones. A relatively small number of studies have examined genetic variation in nutrient traits in gymnosperms, including loblolly pine clones (Stovall et al., 2011) and Douglas-fir (*Pseudotsuga menziesii*) families (Hawkins, 2007). Xue et al. (2013) found that nutrient traits in *Pinus radiata* clones were more heritable than growth traits, suggesting that nutrient-related traits could be considered in tree breeding programs. However, research on the genetic architecture of nutrient traits is sorely lacking, and nutrient traits are likely independently inherited (Beets and Jokela, 1994; Garcia et al., 1997; Xu et al., 2003), so substantial additional research would be necessary before breeding for those traits could be seriously considered. In addition, genotype x environment interaction for nutritional traits has been demonstrated for both *P. radiata* (Hawkins et al., 2010) and *P. taeda* (Tyree et al., 2009a) clones, which highlights the importance of incorporating multiple sites and treatments for making wider genetic inferences.

**Table 8**

Analysis of the log–log relationships between age 3 year component biomass and total biomass for three clones in the VARIETIES experiment near Starke, FL.

Equation	Clone	Slope <sup>a</sup>	SE	Intercept	SE	R <sup>2</sup>	MSE
Stemwood: $\ln(\text{Stem}) = \beta_0 + \beta_1 * \ln(\text{Total})$	ARB-1	0.96 a	0.048	−0.71 a	0.099	0.99	0.002
	ARB-2	1.00 a	0.068	−1.02 a	0.165	0.974	0.012
	ARB-4	1.06 a	0.064	−1.12 a	0.142	0.986	0.005
Bark: $\ln(\text{Bark}) = \beta_0 + \beta_1 * \ln(\text{Total})$	ARB-1	0.65 a	0.074	−1.75 a	0.152	0.95	0.005
	ARB-2	0.69 a	0.044	−1.67 a	0.107	0.976	0.005
	ARB-4	1.56 b	0.104	−3.80 b	0.232	0.982	0.014
Branches: $\ln(\text{Branch}) = \beta_0 + \beta_1 * \ln(\text{Total})$	ARB-1	1.69 a	0.305	−3.25 a	0.625	0.886	0.077
	ARB-2	0.94 b	0.097	−1.46 b	0.237	0.941	0.024
	ARB-4	1.09 b	0.164	−1.85 b	0.367	0.916	0.034
Foliage: $\ln(\text{Foliage}) = \beta_0 + \beta_1 * \ln(\text{Total})$	ARB-1	0.71 a	0.122	−0.66 a	0.249	0.896	0.123
	ARB-2	1.14 b	0.087	−1.42 b	0.214	0.966	0.019
	ARB-4	0.79 a	0.061	−0.61 a	0.137	0.977	0.005
Total: $\ln(\text{Total}) = \beta_0 + \beta_1 * \ln(\text{D}^2\text{H})$	ARB-1	1.03 a	0.194	−8.15 a	1.920	0.875	0.026
	ARB-2	0.64 b	0.048	−4.13 a	0.489	0.968	0.014
	ARB-4	0.57 b	0.047	−3.49 a	0.463	0.974	0.008
Foliage: $\ln(\text{Foliage}) = \beta_0 + \beta_1 * \ln(\text{Branch})$	ARB-1	0.33 a	0.126	0.71 a	0.087	0.637	0.043
	ARB-2	1.11 b	0.175	0.40 a	0.168	0.869	0.074
	ARB-4	0.66 ab	0.133	0.79 a	0.098	0.858	0.028

<sup>a</sup> Within a column, values followed by a different letter are statistically different ( $p < 0.050$ ) based on a Tukey's test for comparison of means.**Table 9**

Analysis of the log–log relationships between age 3 year component biomass and D2H for three clones in the VARIETIES experiment near Starke, FL.

Equation	Clone	Slope <sup>a</sup>	SE	Intercept	SE	R <sup>2</sup>	MSE
Stemwood: $\ln(\text{Stem}) = \beta_0 + \beta_1 * \ln(\text{DBH}^2\text{H})$	ARB-1	0.99 a	0.182	−8.61 a	1.804	0.881	0.023
	ARB-2	0.66 b	0.025	−5.33 b	0.253	0.992	0.003
	ARB-4	0.62 b	0.036	−4.92 b	0.353	0.987	0.004
Bark: $\ln(\text{Bark}) = \beta_0 + \beta_1 * \ln(\text{DBH}^2\text{H})$	ARB-1	0.66 ab	0.163	−6.92 ab	1.609	0.802	0.018
	ARB-2	0.45 a	0.026	−4.61 a	0.272	0.979	0.004
	ARB-4	0.91 b	0.044	−9.39 b	0.446	0.990	0.008
Branches: $\ln(\text{Branch}) = \beta_0 + \beta_1 * \ln(\text{DBH}^2\text{H})$	ARB-1	1.72 a	0.496	−16.81 a	4.904	0.750	0.169
	ARB-2	0.59 b	0.095	−5.21 b	0.965	0.866	0.054
	ARB-4	0.61 b	0.129	−5.49 b	1.277	0.848	0.062
Foliage: $\ln(\text{Foliage}) = \beta_0 + \beta_1 * \ln(\text{DBH}^2\text{H})$	ARB-1	0.76 ab	0.172	−6.69 ab	1.698	0.829	0.020
	ARB-2	0.71 a	0.095	−5.99 a	0.977	0.903	0.056
	ARB-4	0.45 b	0.058	−3.35 b	0.580	0.937	0.013
Total: $\ln(\text{Total}) = \beta_0 + \beta_1 * \ln(\text{DBH}^2\text{H})$	ARB-1	1.03 a	0.194	−8.15 a	1.920	0.875	0.026
	ARB-2	0.64 b	0.048	−4.13 b	0.489	0.968	0.014
	ARB-4	0.57 b	0.047	−3.49 b	0.463	0.974	0.008
Fbranches: $\ln(\text{Fbranch}) = \beta_0 + \beta_1 * \ln(\text{DBH}^2\text{H})$	ARB-1	0.95 a	0.199	−8.38 a	1.968	0.851	0.027
	ARB-2	0.67 ab	0.078	−5.42 ab	0.797	0.925	0.037
	ARB-4	0.49 b	0.054	−3.60 b	0.533	0.955	0.011
NFbranches: $\ln(\text{NFbranch}) = \beta_0 + \beta_1 * \ln(\text{DBH}^2\text{H})$	ARB-1	1.94 a	0.969	−19.63 a	9.568	0.501	0.643
	ARB-2	0.64 b	0.106	−5.98 b	1.077	0.859	0.067
	ARB-4	0.55 b	0.134	−5.26 b	1.332	0.809	0.067

<sup>a</sup> Within a column, values followed by a different letter are statistically different ( $p < 0.050$ ) based on a Tukey's test for comparison of means.

#### 4.2. Ideotypes and growth efficiency

Ideotypes have long been discussed in the forestry literature as a potential approach for identifying traits for genetic selection, and as a tool for better understanding the mechanisms underlying productivity (Martin et al., 2001). The crop ideotype is cited as a potential target because it has a narrow crown suitable for growth in dense plantations. Conversely, the competition ideotype will perform better in older or more widely spaced stands (Martin et al., 2005). It has been hypothesized that narrow-crowned crop ideotypes may be more efficient in terms of biomass productivity. In order to effectively deploy crop ideotypes, investigation of silvicultural methods and their interactions with biomass partitioning patterns and other traits (Nelson and Johnsen, 2008) will be required. Emhart et al. (2007) suggested that variation in crown traits and growth efficiency offers opportunities for ideotype-based clonal selection. In this study, clone ARB-1 had significantly narrower crowns than the other two clones, and we hypothesized that it might show traits consistent with a crop ideotype. Narrow-crowned “crop ideotypes” could have improved stemwood

growth efficiency through several mechanisms, including altered allocation of biomass to different components, elevated leaf area productivity (perhaps due to increased photosynthesis rates), increased efficiency of nutrient uptake or utilization (Colbert et al., 1990; Long and Smith, 1992; Xiao et al., 2003). We found evidence of all three mechanisms in clone ARB-1. While altered below-ground carbon allocation is another plausible hypothesis for varied efficiency, we did not address belowground growth in this study. Clone ARB-1 had a narrower crown than clone ARB-4, which was in turn manifested at the stand scale as a relative decrease in allocation to branch biomass in that clone. Hence, clone ARB-1 allocated less biomass to branches and foliage and, therefore, could allocate more biomass to stemwood, making this clone a good candidate crop ideotype.

Clone ARB-1 and ARB-4 produced similar levels of stem wood biomass (Table 4), but clone ARB-1 had significantly lower nutrient concentration and content for several elements in most biomass components (see Tables 5 and 6). When expressed as stem volume increment per unit foliar N or foliar P content, clone ARB-1 was more efficient than either clone ARB-2 or ARB-4. This difference

could point to the possibility of finding or breeding clones with elevated nutrient use efficiency, which could lead to greater stem wood production with fewer costly nutrient inputs. Nutrient-use efficiency has often been defined in terms of biomass production per unit of nutrient uptake (Gholz et al., 1985; Elliott and White, 1993); this definition could help to evaluate nutrient utilization and production efficiency (Xiao, 2000). N use efficiency could be an important selection trait for increasing loblolly pine productivity because many pine sites in the southeastern U.S. are deficient in N and P (Jokela et al., 1988). In this study, clones ARB-1 and ARB-4 had similar levels of stem productivity, although clone ARB-1 reached its level of stem growth with less foliar biomass and less foliar N and P content (Table 7). This suggests that clone ARB-1 was more efficient at producing stem wood biomass per unit foliar biomass and unit foliar nutrient than clone ARB-4. This is also consistent with the hypothesis of ARB-1 being a crop ideotype. There is some evidence that nitrogen use efficiency is under genetic control in loblolly pine (Li et al., 1991b), which points to the possibility of finding or breeding clones with elevated nutrient use efficiency, which could lead to greater stem wood production with fewer costly nutrient inputs. As this study only focused on juvenile growth patterns, further investigations are needed to determine if the concept of ideotype persists across sites and at different ages and stages of stand development.

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## Appendix A

See Tables 8–11.

**Table 10**

Average component macronutrient content (kg/ha) in foliage, bark, stemwood, non-foliated branches (NFB) and foliated branches (FB) among different clones of loblolly pine at age 3.

Clone	Component	[N] <sup>*</sup>	[P]	[K]	[Ca]	[Mg]	[S]
ARB-1	Foliage	22.1 b	1.5 b	7.6 b	3.8 b	1.5 a	1.5 a
ARB-2		43.8 a	2.9 a	11.7 a	7.5 a	3.7 b	2.7 b
ARB-4		38.9 a	2.9 a	12.7 a	6.5 a	2.5 c	3.4 c
p-Value		<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
ARB-1	Bark	2.6 a	0.2 a	1.7 a	0.7 b	0.4 a	0.15 a
ARB-2		4.9 b	0.4 b	3.7 b	0.9 a	0.5 b	0.28 b
ARB-4		3.0 a	0.3 c	1.9 a	0.9 a	0.3 a	0.26 a
p-Value		<0.001	<0.001	0.006	0.001	<0.001	<0.001
ARB-1	Stem	5.4 a	0.4 a	2.2 a	1.3 a	0.6 a	0.3 a
ARB-2		8.5 b	0.7 b	3.9 b	2.3 b	0.9 b	0.4 b
ARB-4		5.6 a	0.5 a	2.9 c	1.6 a	0.8 c	0.5 c
p-Value		<0.001	<0.001	<0.001	0.002	<0.001	<0.001
ARB-1	NFB	1.5 a	0.1 a	0.6 a	0.8 a	0.2 a	0.1 a
ARB-2		4.4 b	0.4 b	1.7 b	2.5 b	0.6 b	0.3 b
ARB-4		2.8 c	0.2 c	1.2 c	2.1 c	0.4 c	0.1 a
p-Value		<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
ARB-1	FB	2.0 a	0.18 a	0.8 a	0.7 a	0.3 a	0.15 a
ARB-2		2.6 b	0.24 b	1.1 b	0.9 b	0.33 b	0.20 b
ARB-4		2.3 ab	0.21 ab	0.9 a	0.8 a	0.3 a	0.16 a
p-Value		0.023	0.003	0.012	0.059	0.004	0.047
ARB-1	TOTAL	33.5 a	2.4 a	12.8 b	7.3 a	2.9 a	2.3 b
ARB-2		64.3 b	4.7 b	22.0 a	14.2 b	5.9 b	3.9 a
ARB-4		52.5 c	4.0 c	19.5 a	11.9 c	4.3 c	4.5 a
p-Value		<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

<sup>\*</sup> Within a column, values followed by a different letter are statistically different ( $p < 0.05$ ) based on a Tukey's test for comparison of means.

**Table 11**

Average of component micronutrient content (mg/ha) in foliage, bark, stemwood, non-foliated branches (NFB) and foliated branches (FB) among different clones of loblolly pine at age 3.

Clone	Component	[B] <sup>*</sup>	[Cu]	[Fe]	[Mn]	[Mo]	[Zn]
ARB-1	Foliage	16.8 a	2.8 a	47.5 a	54.0 a	0.2 a	32.1 a
ARB-2		41.9 a	6.3 a	87.5 a	129.7 a	0.1 a	45.5 a
ARB-4		36.3 a	4.5 a	81.6 a	114.4 a	0.2 a	32.0 a
p-Value		<0.001	<0.001	<0.001	<0.001	<0.001	0.001
ARB-1	Bark	4.6 a	1.3 a	9.9 a	12.6 a	0.2 a	15.0 a
ARB-2		8.9 a	2.1 a	27.8 a	23.4 a	0.1 a	25.5 a
ARB-4		5.30 a	1.1 a	16.5 a	9.6 a	0.2 a	22.7 a
p-Value		<0.001	<0.001	<0.001	0.002	<0.001	<0.001
ARB-1	Stemwood	7.7 a	5.7 a	30.4 a	26.6 a	0.5 a	22.5 a
ARB-2		11.8 a	7.0 a	55.8 a	38.8 a	0.6 a	29.7 a
ARB-4		8.9 a	4.3 a	28.3 a	20.1 a	0.2 a	20.5 a
p-Value		0.001	<0.001	<0.001	<0.001	0.002	0.001
ARB-1	NFB	2.7 a	1.4 a	6.1 a	9.9 a	0.00 a	6.6 a
ARB-2		9.1 a	3.0 a	29.7 a	33.7 a	0.32 a	16.0 a
ARB-4		5.8 a	2.1 a	15.7 a	15.2 a	0.04 a	8.8 a
p-Value		<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
ARB-1	FB	2.8 a	1.2 a	7.3 a	10.7 a	0.05 a	6.3 a
ARB-2		3.9 a	1.2 a	9.9 a	16.2 a	0.03 a	6.7 a
ARB-4		3.1 a	0.8 a	7.2 a	11.7 a	0.03 a	4.7 a
p-Value		0.042	0.001	0.001	0.274	0.026	0.004
ARB-1	TOTAL	34.6 a	12.5 a	101.2 a	113.7 a	0.9 a	82.5 a
ARB-2		75.6 b	19.6 a	210.7 b	241.8 b	1.2 a	123.4 a
ARB-4		59.4 ab	12.8 a	149.4 ab	171.0 ab	0.7 a	88.6 a
p-Value		<0.001	<0.001	<0.001	0.001	0.001	<0.001

<sup>\*</sup> Within a column, values followed by a different letter are statistically different ( $p < 0.05$ ) based on a Tukey's test for comparison of means.



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