

# Clonal variation in crown structure, absorbed photosynthetically active radiation and growth of loblolly pine and slash pine

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Received December 19, 2005; accepted April 14, 2006; published online December 1, 2006

**Summary** Crown structure, absorbed photosynthetically active radiation (APAR) and growth were analyzed in 300 replicated loblolly (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Engelm. var. *elliottii*) clones to: (1) quantify genetic variation in crown structural traits, growth and APAR at the species, family and clonal levels; and (2) estimate within-family genetic and environmental influences on measured variables. Species and family-within-species differences were found in some growth traits, crown size, leaf area, APAR and branch angle. Loblolly pine developed larger crowns, exposed more leaf area with an acute angle, and intercepted more radiation than slash pine. Significant differences among clones within-family were found for stem volume and crown architecture. Loblolly pine and slash pine within-family, individual-tree broad-sense heritabilities ranged from 0.00 to 0.41 for growth and crown structural traits and most were between 0.10 and 0.25 when estimated from a combined analysis across families. Genetic correlations of crown size, leaf area and APAR with volume increment generally ranged from 0.60 to 0.75. This knowledge of the genetic interactions among growth and crown structural traits improves our understanding of how crown morphology affects light interception and stand development, and ultimately how these attributes can be incorporated in the selection of families or clones for the development of new crop tree ideotypes.

**Keywords:** crown architecture, intercepted radiation, *Pinus taeda*, *Pinus elliottii* var. *elliottii*, quantitative genetics.

## Introduction

Crown structural characteristics, such as crown size and shape, branching frequency, branch diameter, branch angle, and leaf area, quantity and spatial distribution, influence the efficiency and magnitude of radiation interception and competitive interactions with other trees (Wang and Jarvis 1990, Stenberg et al. 1994, Vose et al. 1994, McCrady and Jokela 1996, 1998). As a result, crown architecture is an important determinant of both tree-level and stand-level productivity (Dalla-Tea and Jokela

1991, Stenberg et al. 1994, McCrady and Jokela 1996), and is central to an understanding of whole-tree physiology (Ford 1992, McGarvey et al. 2004). Crown traits such as branch diameter, branch angle and branch frequency are also important determinants of quality for many solid wood products (Bower et al. 2002).

The importance of crown structural traits is reflected in ideotypes, conceptual models of desirable tree phenotypes intended to guide plant genetic research and breeding programs (Donald 1968, Dickmann et al. 1994). For example, the published ideotypes for *Populus* (Dickmann 1985, Dickmann and Keathley 1996) and Scandinavian conifers (Kärki and Tigerstedt 1985) incorporate numerous crown structural variables. Species-level variation in crown structure has been examined for decades in an ecological context, with efforts focusing on understanding broad-scale patterns of crown structure and their relationships to habitat and life history (Horn 1971, Tomlinson 1987, Chen et al. 1994). Within-species, genetic variation in growth has been the subject of much research (White 1996), and forms the basis of most commercial tree improvement programs (White et al. 1993, McKeand and Bridwater 1998, Li et al. 2000). In contrast, the genetic architecture of crown structure has been much less intensively studied, and is seldom utilized in tree improvement programs (Martin et al. 2001).

Quantitative genetic analysis provides powerful tools for understanding within-species variation in quantitative traits such as crown structural variables. Genetic variation forms the basis for phenotypic change through selection, be it natural selection in wild populations or artificial selection in breeding programs. To understand whether a particular trait is subject to change by selection, it is necessary to know whether the trait varies significantly within the population, and whether the trait is heritable, or controlled by the plant's genes, as opposed to being controlled by the environment in which the plant is growing. The degree of trait variation can be determined by formal analysis of variance of traits in genetic experiments, and the degree of genetic control can be quantified by calculating heritability, the ratio of genetic variance to total pheno-

typic variance (Falconer and Mackay 1996). In addition, understanding whether pairs of traits are genetically correlated with each other gives insight into the control of traits by common genes, and can indicate whether genetic change in one trait will result in positive or negative changes in a second trait.

Quantitative genetic analysis of crown structural attributes in forest trees are relatively rare. Broad-sense heritabilities (used for vegetative propagation programs) for several structural and growth properties have been estimated for *Populus* and *Eucalyptus* (Wilcox and Farmer 1967, Weber et al. 1984, Borralho et al. 1992, Lambeth et al. 1994, Osorio 1999). Studies in *Populus*, *Eucalyptus*, loblolly pine and slash pine have identified positive genetic correlations between growth performance and branching patterns, and between growth performance and crown vigor (Wilcox and Farmer 1967, Lambeth et al. 1994, Lambeth and Huber 1997, Xiao 2000). The bulk of these analyses have investigated variation among half-sib or full-sib families, although some of the *Populus* and *Eucalyptus* studies have examined clonal variation. To our knowledge, there are no analyses of within-family clonal variation in crown structural traits of pine in the literature.

The objectives of this study were to: (1) quantify growth and crown structural variation among species, families and clones representing a range of growth performance in loblolly pine and slash pine; (2) integrate crown structural variables into a radiative transfer model to estimate variation in intercepted radiation for different genotypes for a given period of time and the relationship with growth rate; and (3) estimate within-family genetic control and environmental influence on crown structural attributes and growth. Martin et al. (2005) suggested that one reason ecophysiological research has failed to contribute to southern pine tree improvement programs is that researchers have focused on small spatial and short temporal scales that are too far removed in space and time from growth processes. Accordingly, we tested two hypotheses: (1) tree growth is genetically correlated with crown structural traits; and (2) traits that integrate information over space or time, or both are more highly correlated with growth than less integrated traits.

## Materials and methods

### *Site description and plant material*

The study area was located on lands managed by Rayonier in Bradford County (29°51' N, 82°12' W), Florida, USA. The climate is humid and subtropical with a mean annual temperature of 21 °C, and a mean annual rainfall of 1316 mm, with over 50% of the rainfall occurring in June through September. Periods of drought normally occur in the spring and fall. Mean annual rainfall during the period 1999–2001 was 967 mm compared with 1405 mm in 2002 (NOAA 2002). The soils are classified as Pomona and consist of deep, poorly drained soils that are formed in sandy and loamy marine sediments (sandy, siliceous, hyperthermic Ultic Alaquods). Slopes are 0 to 2 percent. In a typical soil profile, the spodic horizon occurs at 30–60 cm with an argillic horizon at 90–120 cm. The water table is typically at a depth of 15 to 45 cm for one to three

months and a depth of 25 to 100 cm for six months or more of most years (Soil Survey Staff 1998).

The study took place in an experimental plot containing 16 full-sib and half-sib loblolly pine and slash pine families planted in 337 m<sup>2</sup> family plots in January 1997. The experiment was designed as a randomized complete block with four replicates. For this study we used one full-sib loblolly pine family and four full-sib slash pine families. Each family plot contained 60 clones propagated as rooted cuttings from a single family, planted at 1.7 m × 3.4 m spacing (1730 trees ha<sup>-1</sup>). Cuttings were taken from donor hedges in the spring, and were rooted and grown in a greenhouse for six months before planting. Each of the four plots of the same family contained the same 60 genotypes, but with the ramets planted in different, randomly determined planting locations in the plot. In total we studied about 1200 trees: 60 trees per family plot × 5 families × 4 replications. Nitrogen (40 kg ha<sup>-1</sup> elemental N) and P (45 kg ha<sup>-1</sup> elemental) were applied in the form of diammonium phosphate in the establishment year and at age 3 years, and weeds were controlled with herbicide during site preparation (imazapyr, sulfometuron methyl) and in subsequent years (glyphosate) as necessary.

### *Growth and crown architectural traits*

Stem volume growth in the 2000, 2001 and 2002 growing seasons (ages 4, 5 and 6 years, respectively) was determined from dormant season measurements of tree diameter at 1.37 m height (DBH; m) and tree height (*H*; m). Outside-bark individual-tree stem volume (*V*; dm<sup>3</sup>) was calculated as (Hodge et al. 1996):

$$V = (0.25\pi(\text{DBH})^2 (1.37 + 0.33(H - 1.37)))1000 \quad (1)$$

Crown architecture was assessed by measuring length and width of the living crown and basal diameter of all living branches at the end of the 2001 and 2002 growing seasons. Branch angle was measured in four branches in the 2000 cohort of each tree with a protractor. Other traits derived from these records included total number of branches per tree, crown shape ratio (crown height/crown width), and branch-free stem height. Individual-tree leaf area at age 5 was calculated by summing individual branch leaf area estimated from regional allometric equations (McGarvey 2000). Regression equations were developed between crown size at age 5 (independent variable) and leaf area at age 5 (dependent variable) by family, and then leaf area at age 6 was predicted using crown volume at age 6 by family.

### *Estimation of absorbed photosynthetically active radiation by tree*

Total absorbed photosynthetically active radiation (APAR) was simulated for each study tree from January 1, 2002 to December 31, 2002, with hourly radiation data from a weather station at the site as input in the process model MAESTRA, a modification of the MAESTRO model (Wang and Jarvis 1990, Medlyn 2004). MAESTRA uses the method of Norman and Welles (1983) to calculate PAR at grid points within the

crown, taking into account the spatial distribution of foliage within the target crown and in adjacent tree crowns. Crown shape was assumed to be ellipsoidal. Vertical foliage distribution was specified by a  $\beta$  function developed for loblolly pine in North Carolina (Luo et al. 2001), and horizontal foliage distribution was assumed to be uniform. Simulations were run for each tree in each of the 20 study plots. For each tree, the location, crown radius in two directions, tree height, height to the base of the live crown and leaf area were specified. Tree locations, crown dimensions and leaf area of a two-tree-wide border surrounding each study plot were also specified. When study plots were located adjacent to non-study plots, crown dimensions and leaf area of border trees were predicted from measured height and diameter. Crown dimensions were assumed to increase linearly from March 1 to December 1.

This analysis implicitly assumes that all genotypes share the same branch size to branch leaf area allometry, and have the same vertical and horizontal foliage distribution functions. Although allometry and foliage distribution may vary by genotype, we did not have the resources to quantify these characteristics on the 1200 trees in our study. Therefore, our analysis focused on the influence of genotypic differences in crown volume, crown position (total tree height, height to base of live crown), crown shape (crown length/crown width), and leaf area (as influenced by number or size of branches or both) on annual APAR. In addition, because our modeling analysis explicitly incorporated the effects of adjacent trees on radiation interception by the target tree, our APAR estimate provides a "competition adjusted" metric that cannot be obtained by analysis of crown structure alone.

#### Statistical analysis

Growth, crown structural traits and APAR data were subjected to analysis of variance (ANOVA). PROC GLM in the SAS® System was used to test for significance of random effects (clone), and PROC MIXED was used to test the fixed effects (species and families). The linear model for the analyses was:

$$Y_{ijkl} = \mu + b_i + S_j + F_{k(j)} + c_{l(jk)} + bS_{ij} + bF_{ik(j)} + \varepsilon_{ijkl} \quad (2)$$

where  $Y_{ijkl}$  is the performance of the ramet of the  $l$ th clone within the  $k$ th family nested in the  $j$ th species in the  $i$ th replication;  $i = 1, 2, 3$  and 4 for replications;  $j = \text{slash, loblolly}$ ;  $k = 1, 2, 3, 4$  and 10 for families;  $l = 60$  identification numbers for 60 clones within each of the five families; and  $\mu =$  population mean,  $b_i =$  random variable of replication  $\sim$  NID  $(0, \sigma_b^2)$ ,  $S_j =$  fixed effect of species (slash or loblolly),  $F_{k(j)} =$  fixed effect of family nested within species,  $c_{l(jk)} =$  random variable of clone nested within-family and species  $\sim$  NID  $(0, \sigma_c^2)$ ,  $bS_{ij} =$  random variable for replication  $\times$  species interaction  $\sim$  NID  $(0, \sigma_{bS}^2)$ ,  $bF_{ik(j)} =$  random variable for replication  $\times$  family(species) interaction  $\sim$  NID  $(0, \sigma_{bF}^2)$ , and  $\varepsilon_{ijkl} =$  error term  $\sim$  NID  $(0, \sigma_\varepsilon^2)$ .

Because there was only one loblolly pine family in the study that met our criteria (vegetatively propagated, with 60 clones within a family), the effect of family within species was only tested for slash pine.

#### Genetic parameter estimation

For each species and family, two types of genetic parameters were estimated: within-family heritability ( $H_{WF}$ ) for each trait, and genetic and environmental correlations among traits. Within-family variance and covariance components were obtained using Multiple Trait Derivate-free Restricted Maximum Likelihood (MTDFREML) software (Boldman et al. 1995).

Within-family, individual-tree broad-sense heritability was calculated as:

$$H_{WF}^2 = \frac{\sigma_c^2}{\sigma_c^2 + s_e^2} \quad (3)$$

Theoretically, the broad-sense within-family heritability for full-sib families contains half the additive genetic variance, three-quarters of the dominance genetic variance and most of the epistatic genetic variance (Falconer and Mackay 1996). The standard error for heritability estimates was calculated as described by Dickerson (1962). The residual likelihood ratio test (Wolfinger 1996) was used to test heterogeneity of variances among slash pine families, and heritabilities were estimated separately for each family ( $\chi^2_{(6, 0.05)} = 12.6$ ), or pooled, as appropriate. In our study, all genetic parameters were estimated from data collected from one experimental site only; therefore, the clonal genetic variance contains the clone-environment interaction variance, and the estimated genetic parameters are biased upward if the interaction is non-zero (Hodge and White 1992).

Within-family genetic and environmental correlations among growth traits and crown structural variables were calculated as (Falconer and Mackay 1996):

$$r_{xy} = \frac{\sigma_{xy}}{\sigma_x \sigma_y} \quad (4)$$

where  $\sigma_{xy}$  is the covariance (clonal or residual) between two traits, and  $\sigma_x \sigma_y$  corresponds to the square root of the product of the clonal or residual variance within-family of each trait.

## Results

#### Genetic variation in stem and crown traits

We examined variation in cumulative stem volume, annual stem volume growth, and crown architectural and functional traits. Comparisons were made between species (loblolly pine and slash pine), among families within slash pine (four full-sib), and among clones within families (60 clones in each of the four slash pine families and one loblolly pine family).

By age 6, loblolly pine stem volume was almost 25% larger than mean slash pine stem volume ( $P = 0.0727$ , 31.42 versus 25.47 dm<sup>3</sup>), reflecting fairly consistent species-level differences in annual stem volume increment (Table 1). Within slash pine, there were consistent differences among families ( $P < 0.10$ ) in stem volume and stem volume increment, with the exception of the age 5–6 year increment (Table 1, Figure 1).

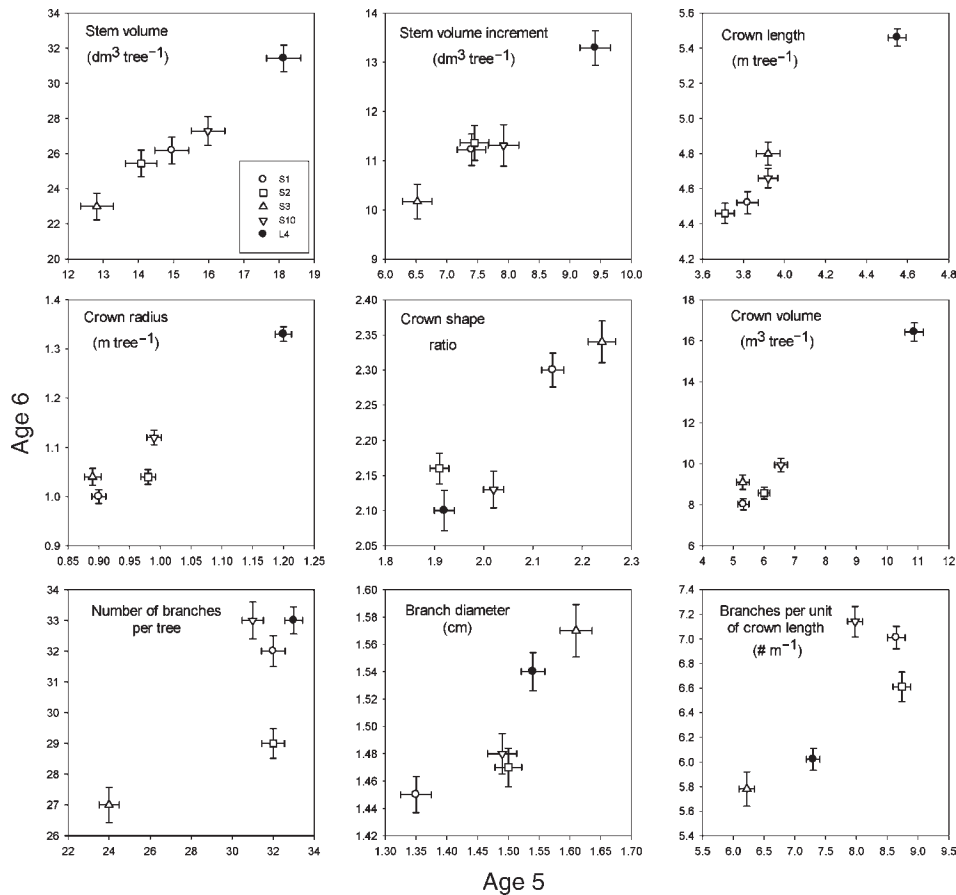


Figure 1. Family means and standard errors for individual-tree growth and crown structural traits for 5- and 6-year-old loblolly pine and slash pine families in north central Florida. Abbreviations: S1 = family slash 1; S2 = family slash 2; S3 = family slash 3; S10 = family slash 10; and L4 = family loblolly 4.

Within-family clonal variation in stem volume and stem volume increment was highly significant for all years ( $P < 0.0001$ ; Table 1).

There were species-level differences in several crown structural traits. Loblolly pine had longer and wider crowns at ages 5 and 6, resulting in species differences in crown volume of about 85% ( $P < 0.005$ ; Table 1). For a given crown length, slash pine crowns were slightly narrower than loblolly pine crowns, as quantified by the crown shape ratio (2.23 versus 2.10 at age 6 for slash pine and loblolly pine, respectively,  $P = 0.0519$ ; Table 1). Loblolly pine branches were displayed at a more acute angle than slash pine branches ( $51.1$  versus  $56.9^\circ$ , respectively,  $P < 0.01$ ; Table 1). For age 5–6 years, mean annual APAR, simulated with the MAESTRA radiative transfer model, was about 20% greater in loblolly pine ( $11,901$  MJ tree $^{-1}$ ) than in slash pine ( $9901$  MJ tree $^{-1}$ ,  $P = 0.0293$ ). Numbers of branches per crown, branch diameter, and number of branches per unit crown length did not differ significantly between species (Table 1).

Crown structure varied at the family level, with crown size and shape traits (length, radius, volume and crown shape ratio) varying significantly among the four slash pine families ( $P < 0.10$ ). Slash pine families also differed in numbers of branches, branch diameters (at age 5), numbers of branches per unit crown length, and branch angle (Table 1; Figure 1). There was no significant family-level variation in tree leaf area

( $P > 0.45$ ; Table 1) or annual APAR ( $P = 0.1041$ ; Table 1). Within families, there was significant clonal variation for all traits measured ( $P < 0.0001$ ; Table 1).

#### *Within-family individual-tree broad-sense heritabilities*

Within-family individual-tree broad-sense heritabilities ( $H_{WF}^2$ ) were low to moderate for stem volume and crown structural traits. In loblolly pine, several crown structural traits were moderately heritable, with crown radius at age 5, crown volume at age 6, leaf area at age 6, number of branches at age 5, and branch angle at age 5 having  $H_{WF}^2$  values between 0.20 and 0.27. Stem volume and stem volume growth traits had lower  $H_{WF}^2$ , ranging between 0.05 and 0.18 (Table 1).

For stem volume of slash pine at different ages,  $H_{WF}^2$  varied between 0.17 and 0.19, and crown structural traits showed similar ranges of variation (Table 1). When  $H_{WF}^2$  values were estimated separately by family because of heterogeneous variance components among slash pine families, there was a tendency for higher heritabilities in family S2 (Table 2). For example, crown radius at ages 5 and 6 showed  $H_{WF}^2$  of 0.41, and crown volume at ages 5 and 6 had moderate heritability values between 0.34 and 0.36.

#### *Within-family genetic and environmental correlations*

Within slash pine families, the genetic correlations between individual-tree stem volume increment (ages 5 and 6) were

Table 1. Significance values ( $P$  values), species means and pooled within-family heritabilities ( $H_{WF}^2$ ) for individual-tree growth and crown structural variables for 5- and 6-year-old loblolly pine and slash pine families in north central Florida. Values in parentheses are standard errors.

Trait	Code	Significance level by effect			Species mean		$H_{WF}^2$	
		Species	Family	Clone	Slash	Loblolly	Slash <sup>1</sup>	Loblolly
<i>Inventory</i>								
Volume age 4 (dm <sup>3</sup> tree <sup>-1</sup> )	V4	0.2240	0.0797	< 0.0001	7.13	8.72	–	0.05 (0.06)
Volume age 5 (dm <sup>3</sup> tree <sup>-1</sup> )	V5	0.1007	0.0451	< 0.0001	14.46	18.13	0.17 (0.04)	0.08 (0.07)
Volume age 6 (dm <sup>3</sup> tree <sup>-1</sup> )	V6	0.0727	0.0802	< 0.0001	25.47	31.42	0.17 (0.04)	0.18 (0.08)
Volume increment age 4–5 (dm <sup>3</sup> tree <sup>-1</sup> )	VI4-5	0.0455	0.0567	< 0.0001	7.32	9.41	0.19 (0.04)	0.12 (0.07)
Volume increment age 5–6 (dm <sup>3</sup> tree <sup>-1</sup> )	VI5-6	0.0754	0.3324	< 0.0001	11.02	13.29	–	0.18 (0.08)
<i>Crown structure</i>								
Live crown length age 5 (m)	CL5	0.0055	0.2358	< 0.0001	3.85	4.55	0.16 (0.04)	0.09 (0.07)
Live crown length age 6 (m)	CL6	0.0028	0.0812	< 0.0001	4.61	5.46	–	0.11 (0.07)
Crown radius age 5 (m)	CR5	0.0067	0.0106	< 0.0001	0.94	1.20	–	0.20 (0.08)
Crown radius age 6 (m)	CR6	0.0041	0.0233	< 0.0001	1.05	1.33	–	0.18 (0.08)
Crown shape ratio age 5	CSR5	0.1001	0.0012	< 0.0001	2.07	1.92	–	0.13 (0.07)
Crown shape ratio age 6	CSR6	0.0519	0.0095	< 0.0001	2.23	2.10	–	0.00 (0.00)
Crown volume age 5 (m <sup>3</sup> )	CV5	0.0039	0.0913	< 0.0001	5.80	10.88	–	0.19 (0.08)
Crown volume age 6 (m <sup>3</sup> )	CV6	0.0020	0.0723	< 0.0001	8.91	16.42	–	0.25 (0.09)
Leaf area age 5 (m <sup>2</sup> )	LA5	0.0450	0.4940	< 0.0001	33.11	44.07	0.12 (0.04)	0.08 (0.06)
Leaf area age 6 (m <sup>2</sup> )	LA6	0.1197	0.5562	< 0.0001	47.14	54.58	–	0.25 (0.09)
Number branches age 5	NB5	0.1214	0.0021	< 0.0001	30	33	–	0.27 (0.09)
Number branches age 6	NB6	0.1610	0.0225	< 0.0001	30	33	–	0.16 (0.07)
Branch diameter age 5 (cm)	BD5	0.5230	0.0793	< 0.0001	1.49	1.54	0.14 (0.04)	0.10 (0.07)
Branch diameter age 6 (cm)	BD6	0.3292	0.1584	0.0003	1.49	1.54	–	0.19 (0.08)
Number branches/crown length age 5	NBCL5	0.2087	0.0018	< 0.0001	7.90	7.30	–	0.11 (0.07)
Number branches/crown length age 6	NBCL6	0.1047	0.0136	< 0.0001	6.63	6.02	–	0.14 (0.07)
Branch angle age 5 (°)	BA5	0.0099	< 0.0001	< 0.0001	56.9	51.1	0.18 (0.04)	0.26 (0.08)
Light interception age 5–6 (MJ tree <sup>-1</sup> )	LI5-6	0.0293	0.1041	< 0.0001	9,901	11,901	0.17 (0.01)	0.17 (0.08)

<sup>1</sup> Values of  $H_{WF}^2$  for slash pine were estimated separately by family and are shown in Table 2.

positive and moderate to high with APAR between ages 5 and 6, crown size traits at age 5, and tree leaf area at age 5. Individual-tree stem volume increment had low positive or low negative

genetic correlations with crown shape ratio and branch angle at age 5 (Table 3). For loblolly pine family L4, individual-tree volume increment between ages 5 and 6 was moderate

Table 2. Ages 5 and 6 within-family individual-tree broad-sense heritability ( $H_{WF}^2$ ) for growth and crown structural traits in four slash pine families in north central Florida. Values in parentheses are standard errors.

Trait	$H_{WF}^2$			
	Family S1	Family S2	Family S3	Family S10
Stem volume (age 4)	0.16 (0.08)	0.22 (0.09)	0.08 (0.08)	0.00 (0.00)
Stem volume increment (age 5–6)	0.21 (0.08)	0.24 (0.09)	0.02 (0.07)	0.10 (0.07)
Crown length (age 6)	0.21 (0.08)	0.31 (0.10)	0.13 (0.08)	0.18 (0.08)
Crown radius (age 5)	0.11 (0.07)	0.41 (0.11)	0.12 (0.09)	0.09 (0.07)
Crown radius (age 6)	0.17 (0.07)	0.41 (0.11)	0.12 (0.08)	0.09 (0.08)
Crown shape ratio (age 5)	0.27 (0.09)	0.33 (0.10)	0.22 (0.10)	0.25 (0.09)
Crown shape ratio (age 6)	0.32 (0.09)	0.05 (0.07)	0.26 (0.10)	0.17 (0.08)
Crown volume (age 5)	0.13 (0.07)	0.34 (0.11)	0.10 (0.08)	0.10 (0.07)
Crown volume (age 6)	0.17 (0.08)	0.36 (0.10)	0.12 (0.08)	0.16 (0.08)
Leaf area (age 6)	0.13 (0.07)	0.34 (0.10)	0.15 (0.09)	0.16 (0.08)
Number of branches (age 5)	0.10 (0.07)	0.26 (0.09)	0.22 (0.10)	0.14 (0.08)
Number of branches (age 6)	0.26 (0.09)	0.15 (0.08)	0.14 (0.09)	0.10 (0.07)
Branch diameter (age 6)	0.09 (0.06)	0.08 (0.07)	0.03 (0.07)	0.02 (0.06)
Number of branches per unit of crown length (age 5)	0.00 (0.00)	0.12 (0.07)	0.27 (0.10)	0.03 (0.06)
Number of branches per unit of crown length (age 6)	0.04 (0.06)	0.01 (0.07)	0.24 (0.09)	0.05 (0.06)

ately genetically correlated with APAR between ages 5 and 6 ( $r_g = 0.64$ ), and with crown size traits at age 5 such as crown volume ( $r_g = 0.51$ ), crown radius ( $r_g = 0.47$ ), and crown length ( $r_g = 0.53$ ). Stem volume increment was positively, but less strongly correlated with leaf area at age 5 ( $r_g = 0.31$ ). As in slash pine, loblolly pine traits such as crown shape ratio and branch angle at age 5 had much weaker genetic correlations with stem volume growth (Table 3).

Environmental correlations are measures of microsite environmental fluctuation between two traits measured on the same ramets. In slash pine families, moderately to highly positive environmental correlations were found between volume increment and APAR for age 5–6 years, implying that microsites that enhanced APAR also enhanced stem growth. At the same time, positive environmental correlations were found between age 5–6 volume increment and crown size at age 5 (crown volume, crown radius and crown length), and between age 5–6 volume increment and leaf area, number of branches, and branch diameter at age 5 (Table 3). Finally, crown shape ratio and branch angle at age 5 had low positive or negative environmental correlations with age 5–6 volume increment, implying that microsites that favored growth did not affect crown shape ratio or branch angle. For loblolly pine, environmental correlations had similar tendencies as in slash pine, with moderate positive environmental correlations between age 5–6 volume increment and crown size (crown volume, crown radius, and crown length), leaf area and branch diameter at age 5 (Table 3).

Both APAR and crown volume at age 5 proved to be good integrators of crown characteristics for individual trees. In general, APAR and crown volume at age 5 had stronger ge-

netic correlations with stem volume growth than with any other crown traits.

## Discussion

At the species level, the one loblolly pine family studied tended to grow faster than the average of the four slash pine families at ages 5 and 6. At the same time, loblolly pine developed larger crowns with more acute branch angles and had more leaf area per tree at ages 5 and 6 than the slash pine families (Table 1). Xiao (2000) found similar species-level contrasts in juvenile loblolly pine and slash pine in north central Florida, where loblolly pine accumulated more crown volume per tree, allocated more biomass to branches and had greater amounts of leaf area than slash pine at ages 3 and 4. Stand-level studies have similarly confirmed the ability of loblolly pine to develop and retain higher amounts of leaf area than slash pine (Dalla-Tea and Jokela 1991, Martin and Jokela 2004).

Growth differences among slash pine families were subtle, probably because the families selected for this study were all chosen for superior growth potential. Despite the apparent similarities in stem volume growth rate, the four slash pine families differed in several crown architectural traits. Contrasting families had different arrangements and sizes of branches within the crown, and varied in crown shape ratio (Table 1, Figure 1), suggesting that any of a number of crown traits may be associated with high growth rate in southern pine families (see also McGarvey et al. 2004). In contrast, McCrady and Jokela (1996) concluded that, among the five loblolly pine

Table 3. Within-family genetic correlations among individual-tree volume increments between age 5–6 and crown structural variables at age 5, for slash (S1, S2, S3 and S10) and loblolly (L4) pine families in north central Florida. Values in parentheses are standard errors.

Trait	Stem volume increment (age 5–6 year)				
	Family S1	Family S2	Family S3	Family S10	Family L4
<i>Genetic correlations</i>					
Light interception (age 5–6)	0.70 (0.08)	0.74 (0.05)	0.62 (0.47)	0.67 (1.00)	0.64 (0.10)
Crown volume (age 5)	0.71 (0.11)	0.61 (0.10)	0.69 (0.78)	0.41 (0.33)	0.51 (0.14)
Leaf area (age 5)	0.64 (0.19)	0.64 (0.10)	0.35 (0.93)	0.61 (0.45)	0.31 (0.34)
Crown shape ratio (age 5)	0.39 (0.23)	–0.33 (0.23)	0.02 (0.72)	0.01 (0.37)	–0.20 (0.32)
Branch diameter (age 5)	0.51 (0.21)	0.75 (0.10)	0.40 (0.75)	0.02 (0.71)	0.16 (0.36)
Branch angle (age 5)	–0.05 (0.29)	0.01 (0.26)	0.01 (0.70)	–0.22 (0.45)	0.26 (0.25)
Number of branches (age 5)	0.43 (0.26)	0.41 (0.18)	–0.06 (0.75)	0.03 (0.41)	0.20 (0.24)
Crown radius (age 5)	0.55 (0.17)	0.66 (0.09)	0.42 (0.56)	0.20 (0.43)	0.47 (0.16)
Crown length (age 5)	0.77 (0.09)	0.55 (0.13)	0.37 (0.76)	0.31 (0.36)	0.53 (0.23)
<i>Environmental correlations</i>					
Light interception (age 5–6)	0.71 (0.03)	0.78 (0.03)	0.83 (0.03)	0.43 (0.07)	0.68 (0.04)
Crown volume (age 5)	0.69 (0.04)	0.70 (0.04)	0.76 (0.04)	0.60 (0.05)	0.58 (0.05)
Leaf area (age 5)	0.44 (0.06)	0.60 (0.05)	0.72 (0.07)	0.58 (0.05)	0.46 (0.06)
Crown shape ratio (age 5)	–0.10 (0.08)	0.09 (0.08)	0.03 (0.09)	0.01 (0.08)	–0.12 (0.08)
Branch diameter (age 5)	0.36 (0.07)	0.52 (0.06)	0.70 (0.05)	0.50 (0.06)	0.43 (0.06)
Branch angle (age 5)	–0.16 (0.08)	–0.06 (0.08)	–0.19 (0.09)	–0.24 (0.08)	0.01 (0.08)
Number of branches (age 5)	0.39 (0.06)	0.41 (0.07)	0.44 (0.07)	0.39 (0.07)	0.29 (0.07)
Crown radius (age 5)	0.62 (0.04)	0.62 (0.05)	0.74 (0.04)	0.58 (0.05)	0.56 (0.05)
Crown length (age 5)	0.52 (0.05)	0.64 (0.05)	0.76 (0.04)	0.57 (0.05)	0.49 (0.06)

families they studied, there were significant differences in height growth but none for most branching attributes.

Within-family clonal variation was highly significant for all growth and crown structural traits, reflecting a wide spectrum of clonal performance in growth and crown development at these ages. There are few reports in the literature on clonal variation in loblolly pine or slash pine growth. Paul et al. (1997) reported that height of loblolly pine clones varied significantly at different ages, but that DBH and volume did not. To our knowledge, no published studies have quantified clonal variation in crown characteristics in loblolly pine or slash pine, but these traits have been studied in other forest tree species. For example, Lambeth et al. (1994) found large differences among *Eucalyptus grandis* Hill ex Maiden clones in growth, branching and crown density. In *Populus*, clonal differences in branch characteristics and branching patterns were found that resulted in striking differences in crown form and architecture (Ceulemans et al. 1990). Syllaptic branches and the considerable leaf area that they carry have important implications for whole-tree light interception, and thus play a critical role in the superior growth and productivity of certain hybrid poplar clones. The considerable variation in branch characteristics implies a strong justification for including them in selection and breeding programs for *Populus* (Ceulemans et al. 1990). Wu (1994a) also reported significant clonal variation in *Populus* hybrids in crown structural traits at the leaf, branch and whole-tree levels.

Until recently, loblolly pine and slash pine breeding programs have focused on developing half-sib and full-sib families for commercial deployment (McKeand et al. 2003, Fox et al. 2004). This is in contrast to the situation with *Populus* and *Eucalyptus* species, which because of their ease of vegetative propagation, have had clonal breeding and deployment programs for some time (Fox et al. 2004). The demonstration of considerable within-family clonal variation in growth and crown characteristics (Table 1), and moderate within-family  $H^2$  for many traits (Tables 1 and 2) suggests that breeders will have flexibility in manipulating numerous crown structural traits in clonal breeding programs in the future, should that prove desirable.

Traditionally, most complex traits, such as growth rate and crown architecture, are thought to be polygenic (Falconer and Mackay 1996). This seems intuitive, given that growth rate and crown architecture are affected by many physiological parameters, phenological patterns, organ growth rates and also by environmental factors like competition interactions, seasonal variation in water availability, nutrient status, light intensity and duration, air and soil temperature, and pest and pathogen pressure. Our results agreed with the polygenic model in that crown architectural and growth traits had low to moderate within-family broad-sense heritabilities, and are therefore likely determined by the expression of many genes. It is possible that the low genetic variation is associated with the nature of the traits we measured and their role in determining fitness. Traits connected with fitness often show low heritability, because natural selection for these traits reduces genetic variation, whereas traits that are less intimately tied to fitness may

have higher genetic variability and so higher heritability (Falconer and Mackay 1996). Tree growth rate and crown size are potentially important components of fitness.

Broad-sense heritabilities estimated from our study are expected to be smaller than broad-sense heritability values usually reported in the literature, because we estimated them within full-sib families and half the additive genetic variation and three-quarters of the dominance variation as well as most of the epistatic variance occurs within full-sib families (Falconer and Mackay 1996). Considering this, our results were comparable with other clonal studies. Paul et al. (1997) reported an  $H^2$  of 0.14 for loblolly pine stem volume, whereas Borralho et al. (1992) estimated  $H^2$  values between 0.08 and 0.18 for height and sapwood area in *Eucalyptus globulus* Labill. For crown structural traits, reported  $H^2$  values range from 0.27 to 0.78 in *Eucalyptus grandis* and hybrid poplars (Lambeth et al. 1994, Wu 1994a).

Because no other studies have reported within-family clonal variation in growth and crown traits for pines, we can compare our results only with studies that investigated variation among families, which entails the calculation of narrow sense heritabilities. Narrow-sense heritability, which includes only the additive genetic variation, is necessarily smaller than broad-sense heritability for the same trait. For stem growth and crown structural traits, low to moderate narrow-sense heritabilities (0.0–0.62) have been reported in loblolly pine and slash pine at young ages (Lambeth and Huber 1997, Xiao 2000), as well as in other pine species such as *Pinus brutia* Ten., *P. radiata* D. Don and *P. sylvestris* L. (0.02–0.53; Espinel and Aragonés 1997, Haapanen et al. 1997, Isik and Isik 1999, Arregui et al. 1999).

We found that heterogeneity of the variance components among families, which resulted in significantly different within-family broad-sense heritabilities for many traits. Slash pine family S2 showed higher  $H_{WF}^2$  values compared with the other three slash pine families (Table 2). Higher within-family broad-sense heritability can reflect either a larger clonal variance component ( $\sigma_c^2$  in the numerator of  $H_{WF}^2$ ) or a smaller residual variance ( $\sigma_e^2$  in the denominator of  $H_{WF}^2$ ), or both. In slash pine family S2, in many cases both a larger proportion of clonal variance and smaller residual variance components were found compared with the other slash pine families, and resulted in larger  $H_{WF}^2$ . Smaller residual variances in family S2 corresponded also to a smaller interaction between clone and microsite for that particular family than the other slash pine families. It is possible that both parents of family S2 had a greater proportion of heterozygosity at gene loci determining crown size, producing more segregation among their progeny than in other slash pine families. If true, then even for polygenic traits, it is possible to find specific pairs of parents producing more variable offspring for growth or crown traits. These families might be useful for quantitative trait loci (QTL) mapping and gene discovery (Bradshaw and Stettler 1995, Wu and Stettler 1996, Wu 1998).

An understanding of the relationship between crown architecture and tree growth might provide a basis for predicting tree growth, and could aid in the search for genes involved in

growth and for developing new crop ideotypes (Kuuluvainen 1988, Dickmann and Keathley 1996, Martin et al. 2001). Evidence of positive phenotypic association between crown architecture and tree growth is common in many species, including loblolly pine and slash pine, with many authors reporting the importance of the amount of light intercepted by the canopy and its correlation with growth rate (Linder 1987, Cannell 1989, Dalla-Tea and Jokela 1991, McCrady and Jokela 1998, Will et al. 2001).

We found several crown architectural traits that were consistently genetically correlated with growth (Table 3), which accords with previous quantitative genetic analyses of crown architectural traits in other species (Wu 1994b, Espinel and Aragonés 1997, Haapanen et al. 1997, Isik and Isik 1999, Arregui et al. 1999), and production ecology work in loblolly pine and slash pine (e.g., McCrady and Jokela 1998, Martin and Jokela 2004). Our study, however, is the first to show that within-family clonal variation in these traits in slash pine and loblolly pine is, in many cases, under genetic control and therefore subject to selection. As we hypothesized, the more integrated measures of crown structure and function in this study, specifically APAR and crown volume, were consistently more strongly correlated with stem volume growth rate than the less integrative measures such as crown radius or length, number of branches, branch angle or mean branch diameter. Although APAR was a particularly comprehensive trait, providing a time- and space-integrated index of crown dimensional traits, leaf area, tree size and crown dimension of surrounding competitor trees, the relatively simple trait of crown volume was as strongly or almost as strongly correlated with stem volume growth as was APAR (Table 3).

Two crown traits consistently showed weak or nonexistent genetic relationships with growth: crown shape ratio and branch angle. Similar results were obtained by Lambeth and Huber (1997), who reported that branch angle (zero being the closest to horizontal) was weakly but negatively genetic correlated with growth rate ( $r_g = -0.24$ ) (bigger trees tending to have a flatter branch angle). In absolute terms, bigger trees tended to have wider crowns ( $r_g = 0.75$ ), and large branch diameter ( $r_g = 0.31$ ), but when adjustments were made for size, they tended to have smaller branches and narrower crowns for their size and fewer branches per meter of height than smaller families. Xiao (2003) reported that, for loblolly pine and slash pine families, crown shape ratio combined two important variables (crown height, crown width) that were statistically significant among taxa, but in ratio form appeared to have little ecological significance for growth performance in developing stands. Similarly, McCrady and Jokela (1996) observed significant intraspecific variation in crown shape ratio in young loblolly pine plantations, but they found no advantage of narrower crowns over wider crowns in height growth increment. The combination of moderate heritability and high clonal variation of branch angle (Table 1) with no correlation to growth rate (Table 2) suggests that clonal breeding programs could select clones with branch angles favorable for high wood quality without sacrificing volume gains.

In other species, such as *Pinus radiata*, *P. sylvestris*, *Populus* and *Eucalyptus grandis* significant positive genetic correlations were found among height, stem diameter, volume, crown diameter, and crown density and vigor. In contrast, genetic correlations between growth and branch diameter, and growth and branch angle were species specific and variable showing favorable or unfavorable correlations (Wu 1994b, Lambeth et al. 1994, Espinel and Aragonés 1997, Haapanen et al. 1997, Arregui et al. 1999).

In conclusion, we have presented the first analysis of within-family clonal variation of growth and crown structural attributes for loblolly pine and slash pine. Clones differed significantly for all traits measured, with several potentially commercially important traits (growth, crown dimensions and branch angle) having heritability and genetic correlations with other traits compatible with incorporation into clonal breeding programs. The spatially and temporally integrated APAR trait was the most highly genetically correlated with growth rate, but it was only slightly more highly correlated than the much simpler and easier to measure trait of crown volume.

#### Acknowledgments

Financial support for this research was provided by USDA Forest Service (Southern Research Station) and Forest Biology Research Cooperative-UFL; the study site was provided by Rayonier, Inc. Dave Nolletti, Sean Gallagher, Tim Walton and Jason Martin helped with field work. Thanks to Belinda Medlyn for providing documentation and access to the MAESTRA model.

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