Genetic Variation in the Microfibril Angle of Loblolly Pine From Two Test Sites

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ABSTRACT: *In recent years, several studies have examined the effect of microfibril angle (MFA) on wood quality. However, little research has been conducted upon the genetic mechanisms controlling MFA. In this study, we examined the heritability of MFA in loblolly pine,* Pinus taeda *L., and its genetic relationships with height, diameter, volume, and specific gravity. Increment cores were collected at breast height from 20 to 25 progeny from each of 12 to 17 crosses (among 11 parents) in two modified partial-diallels in different locations in southern Arkansas. Specific gravity was measured on segments containing rings 1 through 5 and on segments containing rings 6 through 20. MFA was measured on the earlywood and latewood sections of rings 4, 5, 19, and 20. Rings 4 and 5 were chosen as representative of core wood and rings 19 and 20 as representative of outer wood. Analyses of variance revealed statistically significant genetic and environmental influences on MFA. Significant general combining ability (GCA), specific combining ability (SCA), and SCA × block effects indicated that there are both additive and nonadditive genetic influences on MFA. Individual-tree, narrow-sense heritability estimates were variable, ranging from 0.17 for earlywood (ring) 4 MFA to 0.51 for earlywood (ring) 20 MFA. Genetic correlations between MFA, specific gravity, and the growth traits were nonsignificant due to large estimated standard errors. South. J. Appl. For. 28(4):196–204.*

Key Words: *Pinus taeda*, microfibril angle (MFA), heritability, genetic correlation, specific gravity.

Improving wood quality through tree improvement has become more important than ever. The average rotation length for a southern pine plantation has decreased significantly in recent years. Because of the shorter rotations, core wood now accounts for a higher proportion of harvested wood than it has in the past. Studies have shown that core wood has both lower strength and lower density than outer wood (Pearson and Gilmore 1980, Schniewind and Gammon 1986, Megraw et al. 1999). Studies also have shown that core wood has greater longitudinal shrinkage than outer wood, making it more prone to defect (Meylan 1968, Megraw et al. 1998).

Differences in core and outer wood properties are in part explained by differences in the angle of their wood microfibrils. This angle is commonly referred to as the microfibril angle (MFA) and is measured as the angle at which the fibers in the secondary cell wall deviate from the longitudinal axis of the cell. Megraw et al. (1999) found that the MFA in core wood can be 10 to 20° higher than the MFA in outer wood and higher angles have been associated with lowered strength characteristics (Ifju and Kennedy 1962, Cave and Walker 1994, Evans and Ilic 2001).

MFA has a significant influence on paper and solid wood properties. For example, stretch is greater in pulp sheets containing fibers with higher MFAs than in pulp sheets containing fibers with lower MFAs (Watson and Dadswell 1964, Horn and Setterholm 1988). Stretch is also greater in paper made from core wood pulp than in paper made from outer wood pulp (Watson and Dadswell 1964). This is

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important because sheets with greater stretch require additional adjustments during conversion to avoid distortion (Watson and Dadswell 1964). When MFA is large (>30 to 35°), longitudinal shrinkage increases dramatically in lumber (Meylan 1968, 1972). This is important because lumber with high longitudinal shrinkage is prone to defects such as crook (Megraw et al. 1998). Furthermore, breaking strength (Cave 1969), tensile strength, and stiffness all decrease as the MFA increases (Ifju and Kennedy 1962, Cave and Walker 1994, Evans and Ilic 2001). Along with specific gravity, MFA accounts for 93% of the variation in the modulus of elasticity (MOE) of loblolly pine (Megraw et al. 1999). This is important because MOE indicates the amount of stress and strain a beam can withstand before internal damage occurs.

MFA could be used as a selection criterion for breeding efforts specializing in wood quality. However, an understanding of the genetic variability of MFA is required before it can be incorporated into any selection scheme, and few studies have examined the genetic mechanisms influencing MFA. Jackson (1964) discovered a significant correlation in loblolly and slash pines (*P. elliottii* Engelm.) between the MFA of female parent trees and that of their open- and control-pollinated progeny. Decades later, Donaldson (1993) found significant variation in MFA among progeny groups of radiata pine, and Donaldson and Burdon (1995) found high clonal repeatability for MFA. Through QTL analysis, Sewell et al. (2000) have shown that both additive and nonadditive genes influence MFA in loblolly pine. Yet, the degree to which MFA is heritable and the genetic associations between MFA and other traits in loblolly pine have not been determined.

The first objective of this study was to estimate the amount of genetic variability in MFA in loblolly pine. Second, because loblolly pine is a commodity species and selecting for one trait often has an effect on another trait, an additional objective was to examine the relationship between MFA and other commercially important traits, in particular height, diameter, and specific gravity.

Materials and Methods

Study Locations

Two loblolly pine progeny tests, GP065 and GP258, established by Georgia Pacific Corporation (now managed by Plum Creek Timber Company) were sampled in this study. These tests were chosen because they had good survival and long-term data were available from each test. GP065 and GP258 were established in 1974 and 1968, respectively, to evaluate the combining abilities of Western Gulf Forest Tree Improvement Program (WGFTIP) select trees. Breeding was conducted using a complementary, modified partial-diallel mating design in which open-pollinated (op) families are replicated in multiple locations to evaluate the breeding population and control-pollinated (cp) progeny are planted in a single location for use as the selection population (Table 1; Byram 2000). GP065 contained 11 op families and 36 cp crosses; GP258 contained 6 op families and 22 cp crosses. Both tests were planted in Ashley County, AR on fine, silty loam soils with good internal drainage. Progeny were distributed among 10 blocks at GP065 and 5 blocks at GP258 using a randomized complete block design. Ten-tree row-plots (10 progenies per cross) were used at GP065 and 6 × 6-tree block-plots (36 progenies per cross) were used at GP258. Initial spacing was 2.4 m × 2.4 m at both sites. At the time of sampling, GP065 was 20 years old and had been systematically thinned after age 15 to remove trees in positions 1, 4, 6, and 9. GP258 was 25 years old and had been thinned twice from below (once after age 15 and once after age 20).

Wood Core Samples

Increment cores were collected from both test sites. Cores were taken bark-to-bark at breast height (1.37 m) and were approximately 9 mm in diameter. Progeny from 17 cp crosses (among seven parents) were sampled in GP065 and progeny from 12 cp crosses (among six parents) were sampled in GP258. Within sites, crosses were selected to maximize the number of half-sib progeny from each parent and the number of full-sib families between parents. Two of the 11 parents had half-sib progeny at both tests. Approximately 20 trees per cross (two trees per block) were sampled at GP065 and approximately 25 trees per cross (five trees per block) were sampled at GP258. In all, 335 trees were sampled in GP065 and 297 trees were sampled in GP258. At GP258, cores also were collected from an unimproved checklot (comprised of a bulk collection of open-pollinated seed). All of the parent trees used in the crosses sampled were selected in southern Arkansas, except for one parent represented in GP065, which was selected in southern Mississippi.

Each core was divided into three pieces: a single center piece containing the pith and growth rings 1 through 5 (5–0-5), and two radial pieces containing growth rings 6 through 20 from the pith. Specific gravity was measured on each core section individually using the maximum moisture content method of Smith (1954). Measurements from the two radial pieces were weighted using the length of each piece and then averaged to obtain a single specific gravity value for rings 6 through 20. Similarly, measurements from the center and two radial pieces were weighted based on their lengths and averaged to obtain a total specific gravity value. Rings 1 through 5 will be referred to as core wood and rings 6 through 20 as outer wood.

Rings 4 and 5 and rings 19 and 20 were chosen to estimate core and outer wood MFA, respectively. Each ring was separated using a razor blade. Then, to measure the variation in MFA within individual growth rings (Megraw et al. 1998), pieces of the earlywood and latewood portions of each ring were also separated. All ring separations were conducted based on ocular evaluation of the rings. No exclusions were made based on the presence of compression wood. MFA measurements were taken by Dr. Robert Megraw (Weyerhaeuser Company (retired), Department of Forest Science, Texas A&M University, College Station, TX 77843-2585) on the earlywood and latewood 4, 5, 19,

Table 1. Modified partial-diallel mating designs used by the Western Gulf Forest Tree Improvement Program; each unique number represents a single parent tree, each X represents a cross made, X* indicates a cross that was sampled for this study.

a. at Test GP065

		Males													
		1	2	3	4	5	6	10	11	15	16	17	20	21	OP
	2														X
	3		X		X										X
	4			X											X
	5														X
	6									X*	X	X*	X*		X
	9	X			X	X		X	X				X	X	X
Females	10									X*	X	X*	X		X
	13						X*	X*				X*	X*		X
	16						X*	X*		X*		X	X		X
	17						X	X		X*	X*		X		X
	20						X	X*			X*	X*			X
	Check														X
Population								*Selection*							*Eval*

b. at Test GP258

		Males									
		6	7	8	10	11	12	14	18	19	OP
	6							X			X
	8	X*			X	X		X*	X*		X
	10			X*				X*	X	X	X
Females	14	X*			X				X		X
	18	X*			X*	X		X*			X
	19		X		X*		X	X*	X*		X
	Check										X*
Population						*Selection*					*Eval*

and 20 samples using the X-ray diffraction technique described in Megraw et al. (1998). MFA measurements are identified by their corresponding within-ring position (earlywood, latewood) and ring number (4, 5, 19, 20) and are reported in degree deviations from the longitudinal axis of the cell.

Growth Measurements

Height and diameter at breast height (dbh) measurements were taken at several ages in each test prior to the collection of core samples. At GP065, growth data were collected from all trees at ages 5, 10, 15, and 20. At GP258, growth data were collected from all trees at ages 15 and 20, while only the interior 16 trees of each plot were measured at age 10. Volumes at ages 10, 15, and 20 were expressed as mean annual increment (cubic meters per hectare per year) from the growth data. Only data from trees with MFA and specific gravity measurements were used in subsequent analyses.

Statistical Analyses

Analyses of variance were conducted using a modification of DIALL (Schaffer and Usanis 1969), and the Simple Interactive Statistical Analysis (SISA) (Uitenbroek, D.G., www.home.clara.net/ sisa/signif.htm. Accessed Feb. 22, 2003). A statistical model containing block, general combining ability (GCA), specific combining ability (SCA), and the SCA × block interaction was used to estimate genetic and environmental effects for microfibril angle. Variation due to the GCA × block interaction was pooled with the error because it was not significant for any of the traits studied. The model used in the analyses was:

$$Y_{ijkl} = \mu + B_i + G_j + G_k + S_{jk} + SB_{ijk} + e_{(ijk)l} \quad (1)$$

where Y_{ijkl} is the observation on the $ijkl^{\text{th}}$ tree, μ is the population mean, B_i is the effect due to the i^{th} block, G_j and G_k are the effects due to the general combining ability of the j^{th} and k^{th} parent, respectively, S_{jk} is the effect due to the specific combining ability of the j^{th} by k^{th} cross, SB_{ijk} is the effect due to the SCA × block interaction, and $e_{(ijk)l}$ is the within-plot residual error term. All variables were treated as random effects. Sums of squares and F-test statistics were calculated using DIALL and significance levels were calculated using SISA. DIALL was also used to generate variance and covariance components and coefficients for estimating individual-tree narrow-sense heritabilities and genetic correlations. Individual-tree narrow-sense heritability was calculated using the equation for the WGFTIP partial diallel as reported in van Buijtenen and Yeiser (1989):

$$h^2_{(\text{individual tree})} = \frac{4\sigma_g^2}{2\sigma_g^2 + \sigma_s^2 + \sigma_{sb}^2 + \sigma_e^2} \qquad (2)$$

where σ_g^2 is the variance component for GCA, σ_s^2 is the variance component for SCA, σ_{sb}^2 is the variance component for SCA × block and σ_e^2 is the variance component for the within plot residual error. Standard errors for the heritability estimates were approximated according to the methods of Gordon et al. (1972).

Additive genetic correlations were estimated as follows:

$$r_{A_{xy}} = \frac{\sigma_{A_{xy}}}{\sqrt{\sigma^2_{A_x} * \sigma^2_{A_y}}} \qquad (3)$$

where $\sigma_{A_{xy}}$ is the additive genetic covariance of traits x and y (estimated as 4 times the covariance component for GCA_{xy}), and $\sigma^2_{A_x}$ and $\sigma^2_{a_y}$ are the additive genetic variances of traits x and y, respectively (estimated as 4 times the variance components for GCA_x and GCA_y). Standard errors were approximated according to the methods of Scheinberg (1966) and used to determine the significance of the genetic correlations. Correlations greater than two standard errors from zero were deemed significant.

Results

Exploratory data analysis of GP065 revealed that latewood 19 and earlywood 20 MFA measurements were intermediate to earlywood 19 and latewood 20 MFA measurements. Pair-wise *t* tests based on individual tree measurements showed that latewood 19 and earlywood 20 MFA values were significantly different from earlywood 19 and latewood 20 MFA values but not from each other at the $\alpha = 0.05$ level (data not shown). It appeared that some of the latewood 19 samples were contaminated with earlywood fibers and some of the earlywood 20 samples were contaminated with latewood fibers. Several of the sampled trees from GP065 had very narrow growth rings and clean separation of the earlywood and latewood within rings 19 and 20 proved to be impossible with our methods. Thus, the latewood 19 and earlywood 20 measurements from GP065 were excluded from further analyses. To minimize the risk of contamination among additional samples, earlywood 19 measurements from 82 trees with narrow growth rings were also excluded.

Contamination was not a problem at GP258, where latewood 19 MFA was significantly different from earlywood 19, earlywood 20, and latewood 20 MFAs. On average, the difference between latewood 19 and latewood 20 MFAs was less than a degree. However, average differences between the outer wood early- and latewood MFAs ranged from 4.5 to 5.7°. Earlywood 19 and earlywood 20 MFAs

Table 2. Site means (with standard deviations) and the range of full-sib family means for wood quality and growth traits in loblolly pine at two progeny tests in south Arkansas.

	Test GP065		Test GP258	
	Site mean	Range of family means	Site mean	Range of family means
Earlywood 4 MFA[a]	41.4 (3.6)	38.8–43.7	39.1 (4.3)	37.0–41.8
Latewood 4 MFA	43.0 (4.2)	39.6–45.8	41.4 (4.4)	38.9–44.9
Earlywood 5 MFA	41.2 (3.8)	38.2–44.0	38.9 (4.0)	36.7–40.9
Latewood 5 MFA	41.6 (4.7)	37.0–45.4	40.9 (4.5)	37.9–44.2
Earlywood 19 MFA	31.3 (5.1)	28.1–33.7	25.4 (7.8)	20.2–32.0
Latewood 19 MFA[b]			21.3 (8.3)	13.3–26.6
Earlywood 20 MFA[b]			25.7 (7.8)	18.3–31.2
Latewood 20 MFA	20.8 (8.40)	16.1–26.8	20.1 (8.4)	12.4–25.7
Core wood sp. gr.[c]	0.40 (0.03)	0.37–0.42	0.43 (0.03)	0.41–0.46
Outer wood sp. gr.[c]	0.50 (0.03)	0.46–0.55	0.52 (0.03)	0.48–0.54
Total sp. gr.[c]	0.45 (0.03)	0.42–0.49	0.48 (0.03)	0.46–0.50
Height 5 (m)[d]	2.5 (0.7)	2.1–3.0		
Diameter 5 (cm)[d]	3.2 (1.4)	2.2–3.9		
Height 10 (m)	8.1 (1.0)	7.4–9.0	8.9 (1.0)	7.7–10.1
Diameter 10 (cm)	14.0 (2.4)	11.5–15.9	14.3 (1.9)	12.6–16.0
Volume 10 (m^3/ha/yr)	7.4 (3.0)	4.7–10.0	8.3 (3.0)	5.6–11.3
Height 15 (m)	13.8 (1.1)	13.0–14.7	13.9 (1.0)	12.9–14.9
Diameter 15 (cm)	19.5 (3.1)	16.3–22.0	20.1 (2.1)	18.9–22.0
Volume 15 (m^3/ha/yr)	20.5 (7.1)	13.8–27.0	21.7 (5.4)	17.7–27.3
Height 20 (m)	17.8 (1.3)	16.8–18.9	18.1 (1.2)	16.7–19.4
Diameter 20 (cm)	23.6 (3.9)	19.4–26.9	24.5 (2.6)	22.8–27.0
Volume 20 (m^3/ha/yr)	29.2 (10.5)	19.2–38.6	31.4 (7.9)	25.3–40.4

[a] All microfibril angle measurements are reported in degree deviations from the longitudinal axis of the cell.

[b] Latewood 19 and earlywood 20 MFA measurements from GP065 were excluded due to corrupt samples (see *Results*).

[c] Core wood specific gravity is the specific gravity of the center piece of the core containing rings 1 through 5 (5-0-5); outer wood specific gravity is the weighted average of the two radical pieces containing rings 6 through 20; total specific gravity is the weighted average of the center and two radial pieces; weights based on the length of each piece.

[d] Height 5 and diameter 5 were not measured in GP258.

were not significantly different from each other (average difference of less than 0.3°).

Latewood MFAs in the core wood were significantly different between rings 4 and 5 at both sites (average differences of 1.5 and 0.5° at GP065 and GP258, respectively). They also were significantly different from core earlywood MFAs at both sites (average differences of 0.4 to 1.7° and 2.0 to 2.2°, respectively). Earlywood 4 and 5 MFAs, however, were not significantly different from each other at either site (average differences of 0.2° at both sites).

A wide range of MFA values was observed among full-sib families at both progeny tests (Table 2). At both sites, latewood MFAs in the core wood were greater than earlywood MFAs and tended to be more variable than earlywood MFAs. The converse was true in the outer wood where earlywood MFAs were greater than latewood MFAs. MFAs in general were greater at GP065 than at GP258.

Core wood and total specific gravity measurements were slightly higher at GP258 than at GP065. However, outer wood-specific gravity measurements were similar at the two sites. Age-10 height measurements were greater at GP258 than at GP065 due to a severe tip moth (*Rhyacionia frustrana* Comstock) infestation at GP065 but age-15 and age-20 height measurements were similar at the two sites. On average, diameter measurements were almost identical at both sites at all ages but the range of family means and the variances about those means were greater at GP065 than at GP258. As a result, trees with small diameters were present in all of the families in GP065.

Analyses of variance identified significant genetic and environmental effects ($\alpha = 0.1$; Table 3) for almost all of the MFA measurements taken. An α level of 0.1 was used for these analyses because of the unbalanced sample size and small number of degrees of freedom for GCA and SCA effects, and because the presence of compression wood adds error variation (Megraw et al. 1998). At GP065, GCA effects were statistically significant for earlywood 4 and 5 MFAs and for latewood 4, 5, and 20 MFAs. SCA effects were only significant for latewood 5 MFAs but SCA × block effects were statistically significant for earlywood 4 and 5 MFAs and for latewood 4, 5, and 20 MFAs. At GP258, GCA effects were statistically significant for earlywood 4, 19, and 20 MFAs and for all of the latewood MFAs and SCA effects were significant for latewood 5 and latewood 20 MFAs. SCA × block effects were significant for earlywood and latewood 4 MFAs where mean squares were similar in magnitude to those for SCA.

Individual-tree narrow-sense heritability estimates were low to moderate for all MFA measurements (Table 4). At GP065, they ranged from 0.21 for latewood 20 MFA to 0.41 for earlywood 4 MFA. At GP258, they ranged from 0.17 for earlywood 4 MFA to 0.51 for earlywood 20 MFA.

Table 3. Analyses of variance for earlywood and latewood 4, 5, 19 and 20 microfibril angle.

	Test GP065	df	Prob > F	Test GP258	df	Prob > F
Ew 4[a]	Block	9	0.0014	Block	4	0.8764
	GCA[b]	6	0.0011	GCA[b]	5	0.0987
	SCA[b]	10	0.4464	SCA[b]	6	0.2729
	S × B[b]	143	0.0164	S × B[b]	44	0.0562
Lw 4[a]	Block	9	0.3455	Block	4	0.3639
	GCA	6	0.0035	GCA	5	0.0091
	SCA	10	0.3368	SCA	6	0.5532
	S × B	143	0.0423	S × B	44	0.0116
Ew 5	Block	9	0.0110	Block	4	0.2276
	GCA	6	0.0054	GCA	5	0.1276
	SCA	10	0.2646	SCA	6	0.2817
	S × B	143	0.0147	S × B	44	0.2661
Lw 5	Block	9	0.0400	Block	4	0.0087
	GCA	6	0.0190	GCA	5	0.0504
	SCA	10	0.0525	SCA	6	0.0664
	S × B	143	0.0625	S × B	44	0.3202
Ew 19	Block	9	0.3260	Block	4	0.0163
	GCA	6	0.1540	GCA	5	0.0210
	SCA	10	0.2059	SCA	6	0.1412
	S × B	131	0.3476	S × B	44	0.3959
Lw 19[c]	Block			Block	4	0.3780
	GCA			GCA	5	0.0122
	SCA			SCA	6	0.1076
	S × B			S × B	44	0.9042
Ew 20[c]	Block			Block	4	0.7646
	GCA			GCA	5	0.0043
	SCA			SCA	6	0.2643
	S × B			S × B	44	0.6532
Lw 20	Block	9	0.7171	Block	4	0.4722
	GCA	6	0.0065	GCA	5	0.0562
	SCA	10	0.6764	SCA	6	0.0724
	S × B	143	0.0037	S × B	44	0.2075

[a] Ew = earlywood MFA, Lw = latewood MFA.

[b] GCA = general combining ability, SCA = specific combining ability, S × B = SCA × Block.

[c] Lw 19 and Ew 20 MFA measurements from GP065 were excluded due to corrupt samples (see *Results*).

Table 4. **Individual-tree, narrow-sense heritability estimates (with standard errors) for microfibril angle, specific gravity, height, diameter, and volume in loblolly pine at two test sites.**

	Test GP065 indiv. tree	Test GP258 indiv. tree
Earlywood 4 MFA	0.41 ± 0.18	0.17 ± 0.13
Latewood 4 MFA	0.34 ± 0.16	0.40 ± 0.19
Earlywood 5 MFA[a]	0.33 ± 0.16	
Latewood 5 MFA	0.30 ± 0.17	0.32 ± 0.19
Earlywood 19 MFA[b]		0.39 ± 0.20
Latewood 19 MFA[c]		0.39 ± 0.19
Earlywood 20 MFA[c]		0.51 ± 0.21
Latewood 20 MFA	0.21 ± 0.11	0.31 ± 0.19
Csg[d]	0.33 ± 0.20	0.35 ± 0.18
Oasg[d]	0.72 ± 0.24	0.72 ± 0.22
Tsg[d]	0.60 ± 0.25	0.58 ± 0.22
Height 5[e]	0.24 ± 0.12	
Height 10	0.26 ± 0.14	0.90 ± 0.25
Diameter 10	0.47 ± 0.20	0.73 ± 0.24
Volume 10	0.42 ± 0.19	0.77 ± 0.26
Height 15	0.41 ± 0.17	0.62 ± 0.31
Diameter 15	0.54 ± 0.20	0.51 ± 0.24
Volume 15	0.56 ± 0.21	0.56 ± 0.27
Height 20	0.25 ± 0.15	0.58 ± 0.29
Diameter 20	0.59 ± 0.21	0.58 ± 0.24
Volume 20	0.57 ± 0.21	0.60 ± 0.26

[a] No significant genetic effects detected at GP258 for earlywood 5 MFA.

[b] No significant genetic effects detected at GP065 for earlywood 19 MFA or diameter 5.

[c] Latewood 19 and earlywood 20 MFA measurements from GP065 were excluded due to corrupt samples (see *Results*).

[d] Csg = core wood specific gravity, Oasg = outer wood average specific gravity, Tsg = total specific gravity.

[e] Height 5 was not measured in GP258.

Additive genetic correlations between MFA, specific gravity, height, diameter, and volume are presented in Tables 5 and 6. Core wood MFAs were positively correlated with outer wood MFAs at both sites but the correlations were mostly nonsignificant. The only significant correlations were at GP258 between core latewood and outer earlywood (Table 5b). The majority of genetic correlations between MFA and specific gravity were not significant at either site (Table 5) nor were the majority of correlations between the wood quality traits and the growth traits (Table 6).

Discussion

The range of MFA values observed in this study was slightly greater than those reported by Donaldson (1992, 1993, 1997) and Megraw et al. (1998). Donaldson (1997) found MFAs ranging from 30 to 50° in core wood and from 15 to 25° in outer wood of *P. radiata*. Megraw et al. (1998) observed mean MFA values above 35° in growth rings 1 through 5 and MFAs from 20 to 35° in rings 6 through 20 in loblolly pine (at 1.22 m). In this study, core wood MFA values (estimated using rings 4 and 5) ranged from 21 to 54° at GP065 and from 22 to 54° at GP258. Outer wood MFA values (estimated using rings 19 and 20) ranged from 7 to 43° at GP065 and from 5 to 46° at GP258. The differences between these values and those reported in other studies do not appear to be a result of selection on the parents or thinning in the progeny tests since the mean MFAs of the unimproved checklot were intermediate to those of the families in GP258, the site that was silviculturally thinned. Instead, the wider range of MFA values reported in this study is probably due to a much larger sample size and the presence of compression wood in the cores. Over 650 trees were sampled in this study while only 5 to 15 trees were sampled by Donaldson (1992, 1993, 1997) and approximately 100 trees were sampled by Megraw et al. (1998). Both Donaldson (1992, 1993, 1997) and Megraw et al. (1998) excluded samples with compression wood because compression wood can have a higher MFA. No exclusions

Table 5. **Estimates of the genetic correlations (with standard errors) between microfibril angle and specific gravity (Significant correlations, $P \leq 0.05$, marked with *).**

a. At Test GP065

	Ew 4	Lw 4	Ew 5	Lw 5	Lw 20	Csg	Oasg
Lw 4[a]	0.94* (0.12)						
Ew 5[a]	1.02* (0.01)	0.86* (0.34)					
Lw 5	1.00* (0.07)	0.95* (0.10)	0.94* (0.11)				
Lw 20	0.56 (1.88)	0.25 (3.26)	0.67 (1.43)	0.75 (1.22)			
Csg[b]	0.44 (3.45)	0.14 (4.42)	0.49 (3.97)	0.59 (4.11)	0.78 (2.10)		
Oasg[b]	0.03 (3.45)	−0.27 (3.03)	0.04 (3.72)	0.10 (4.16)	0.34 (3.03)	0.88* (0.26)	
Tsg[b]	0.13 (3.68)	−0.17 (3.63)	0.12 (4.03)	0.22 (4.41)	0.45 (2.91)	0.94* (0.07)	0.98* (0.01)

b. At Test GP258

	Ew 4	Lw 4	Lw 5	Ew 19	Lw 19	Ew 20	Lw 20	Csg	Oasg
Lw 4	1.01* (0.18)								
Lw 5	1.01* (0.16)	1.08* (0.11)							
Ew 19	0.68 (2.09)	0.93* (0.45)	0.90* (0.32)						
Lw 19	0.77 (1.71)	0.83 (0.71)	0.89 (0.59)	1.02* (0.19)					
Ew 20	0.70 (2.17)	0.89 (0.53)	0.97* (0.45)	1.08* (0.12)	0.92* (0.12)				
Lw 20	0.95 (3.27)	1.01 (1.06)	1.02 (0.85)	1.19 (0.81)	1.06* (0.09)	1.00* (0.10)			
Csg	−0.39 (4.47)	−0.64 (1.61)	−0.59 (2.53)	−0.63 (2.13)	−0.52 (2.67)	−0.55 (2.16)	−0.60 (2.77)		
Oasg	−0.32 (4.23)	−0.55 (1.95)	−0.56 (2.19)	−0.89* (0.33)	−0.75 (0.83)	−0.76 (0.69)	−0.88* (0.37)	0.69 (1.17)	
Tsg	−0.36 (4.09)	−0.60 (1.63)	−0.58 (2.10)	−0.82 (0.70)	−0.68 (1.26)	−0.69 (1.09)	−0.81 (0.85)	0.90* (0.17)	0.94* (0.06)

[a] Lw = latewood MFA, Ew = earlywood MFA.

[b] Csg = core wood specific gravity, Oasg = outer wood average specific gravity, Tsg = total specific gravity.

Table 6. Estimates of the genetic correlations (with standard errors) between wood quality and growth traits (Significant correlations, $P \leq 0.05$, marked with *).

a. At Test GP065

	MFA					Specific Gravity		
	Ew 4[a]	Lw 4[a]	Ew 5	Lw 5	Lw 20	Csg[b]	Oasg[b]	Tsg[b]
Ht 5[c]	0.09 (3.46)	0.51 (1.91)	−0.00 (3.80)	0.27 (3.41)	−0.20 (3.71)	−0.43 (3.19)	−0.70 (1.01)	−0.57 (1.90)
Ht 10	−0.01 (3.65)	0.44 (2.36)	−0.12 (3.97)	0.15 (3.99)	−0.26 (3.60)	−0.55 (2.54)	−0.77 (0.68)	−0.66 (1.39)
D 10[c]	0.54 (1.65)	0.85* (0.29)	0.48 (2.07)	0.65 (1.29)	−0.03 (3.71)	−0.38 (3.14)	−0.69 (0.94)	−0.60 (1.55)
Vol 10[c]	0.39 (2.42)	0.76 (0.66)	0.32 (2.90)	0.50 (2.11)	−0.14 (3.76)	−0.46 (2.81)	−0.75 (0.69)	−0.65 (1.34)
Ht 15	0.02 (3.23)	0.46 (2.06)	−0.09 (3.43)	0.15 (3.55)	−0.50 (2.40)	−0.70 (1.56)	−0.81 (0.53)	−0.75 (0.93)
D 15	0.35 (2.46)	0.73 (0.75)	0.28 (2.88)	0.47 (2.22)	−0.23 (3.38)	−0.58 (2.09)	−0.80 (0.50)	−0.73 (0.96)
Vol 15	0.24 (2.82)	0.65 (1.09)	0.16 (3.22)	0.36 (2.75)	−0.35 (3.04)	−0.62 (1.85)	−0.82 (0.46)	−0.74 (0.90)
Ht 20	0.12 (3.85)	0.53 (2.30)	−0.11 (4.50)	0.20 (4.18)	−0.48 (3.74)	−0.66 (1.63)	−0.76 (0.86)	−0.72 (1.19)
D 20	0.22 (2.89)	0.66 (1.13)	0.12 (3.33)	0.35 (2.83)	−0.37 (3.02)	−0.59 (2.00)	−0.78 (0.60)	−0.70 (1.12)
Vol 20	0.15 (3.06)	0.60 (1.40)	0.04 (3.46)	0.28 (3.13)	−0.43 (2.78)	−0.61 (1.83)	−0.77 (0.62)	−0.69 (1.11)

b. At Test GP258

	MFA							Specific gravity		
	Ew 4	Lw 4	Lw 5	Ew 19	Lw 19	Ew 20	Lw 20	Csg	Oasg	Tsg
Ht 10	0.00 (5.13)	0.03 (4.82)	−0.16 (4.08)	−0.14 (4.67)	0.14 (4.37)	−0.11 (6.35)	0.02 (7.60)	−0.68 (1.40)	−0.10 (4.30)	−0.43 (2.97)
D 10	0.47 (3.16)	0.50 (2.61)	0.30 (3.38)	0.27 (3.92)	0.45 (2.69)	0.34 (3.91)	0.46 (4.04)	−0.74 (0.94)	−0.20 (3.77)	−0.50 (2.39)
Vol 10	0.38 (4.02)	0.38 (3.49)	0.18 (3.97)	0.15 (4.50)	0.36 (3.32)	0.20 (4.94)	0.33 (5.38)	−0.73 (1.12)	−0.14 (4.09)	−0.46 (2.72)
Ht 15	0.02 (7.23)	−0.17 (4.75)	−0.18 (5.40)	−0.18 (4.97)	0.35 (4.82)	−0.15 (4.69)	0.27 (5.98)	−0.24 (4.55)	−0.18 (4.27)	−0.29 (3.88)
D 15	0.64 (3.03)	0.46 (2.63)	0.44 (3.38)	0.34 (3.73)	0.72 (1.60)	0.38 (3.44)	0.75 (2.85)	−0.55 (2.32)	−0.34 (3.18)	−0.48 (2.42)
Vol 15	0.56 (4.57)	0.33 (3.64)	0.33 (4.52)	0.25 (4.46)	0.69 (2.23)	0.29 (4.14)	0.69 (3.72)	−0.49 (2.88)	−0.32 (3.49)	−0.45 (2.77)
Ht 20	0.06 (7.04)	−0.13 (4.76)	−0.09 (5.58)	−0.13 (4.96)	0.42 (4.42)	−0.06 (4.77)	0.37 (6.01)	−0.27 (4.45)	−0.14 (4.33)	−0.26 (4.00)
D 20	0.74 (2.09)	0.57 (1.88)	0.58 (2.36)	0.46 (2.90)	0.81 (0.93)	0.49 (2.63)	0.84 (1.96)	−0.53 (2.32)	−0.37 (2.88)	−0.48 (2.30)
Vol 20	0.68 (3.34)	0.45 (2.81)	0.49 (3.46)	0.37 (3.71)	0.80 (1.40)	0.42 (3.36)	0.81 (2.83)	−0.48 (2.83)	−0.33 (3.28)	−0.45 (2.70)

[a] Ew = earlywood MFA, Lw = latewood MFA.

[b] Csg = core wood specific gravity, Oasg = outer wood average specific gravity, Tsg = total specific gravity.

[c] Ht = height, D = diameter, Vol = volume.

were made based on the presence of compression wood in this study.

At both sites, MFA was greatest in ring 4 and lowest in ring 20. Similar pith-to-bark decreases in MFA were noted in previous studies of *P. taeda* and *P. radiata* (Bendtsen and Senft 1986, Donaldson 1992, 1993, Megraw et al. 1998). In both species, the relationship between MFA and ring position has been shown to be a curvilinear decline. In the core wood, MFA was greater in the latewood than in the earlywood. The converse was true in the outer wood. That is, outer earlywood MFAs were greater than outer latewood MFAs. This same pattern was noted by Megraw et al. (1998). In that study, latewood MFAs were greater than earlywood MFAs until ring 7 (at 1.22 m). After ring 7, earlywood MFAs exceeded latewood MFAs.

Results of the analyses of variance were comparable across sites. GCA was significant for most of the MFA measurements, indicating that there are additive genetic effects influencing MFA. The only MFA measurement for which GCA was not significant at GP065 was earlywood 19. Though attempts were made to minimize the contamination of earlywood 19 measurements by excluding trees with narrow growth rings, the presence of latewood fibers in the remaining earlywood 19 samples may have increased the error variance and thus biased the results of the analysis of variance (ANOVA). The 82 earlywood 19 measurements excluded were not distributed equally among families. Parents lost between 16 and 31 observations each and crosses lost between 2 and 8 observations each. Loss of degrees of freedom due to unequal sample sizes and to the exclusion of samples could also have biased the results.

In addition to additive genetic effects, it appears that nonadditive genetic effects also influence MFA. This is consistent with the QTL work of Sewell et al. (2000). At both test sites, the SCA effect was significant for some latewood measurements and the SCA × block effect was significant for some core wood measurements. The significance of the SCA × block interaction suggests that nonadditive genes coding for MFA may be sensitive to changes in the environment. Large changes in full-sib family rank across blocks supports this result (data not shown). However, the significance of the SCA × block interaction may simply be a product of within-plot variation or the fact that there were a large number of degrees of freedom for the SCA × block effect, especially at GP065.

Individual-tree, narrow-sense heritability estimates for the MFA measurements were low to moderate. The true heritability of MFA in loblolly pine may be lower than reported in this study. Because there were no full-sibling families common to both sites, the significance of genetic × environment interactions could not be tested. Should a significant genetic × environment interaction exist, the heritabilities reported in this study would overestimate the true heritability of MFA. On the other hand, the true heritability of MFA may be much higher than reported here but the limited sample size available, small number of degrees of freedom involved, and added error variation from compression wood may have caused an underestimate. This may be the case for specific gravity, which is generally considered to be highly heritable. Megraw (1985) reported that it is not uncommon to see narrow-sense heritability estimates for specific gravity exceeding 0.5. In our study, narrow-sense heritability estimates for core wood specific gravity reached only 0.33 to 0.35. However, it should be noted that specific gravity measurements were taken on unextracted increment cores that were collected at maturity. The presence of resins and other extractives in the core portion could also have lowered the estimates of core wood heritability.

Genetic correlations between MFA measurements were moderate to high even though most were nonsignificant (Table 5). The fact that all correlations were positive has important implications for tree improvement. If the direction of the true correlations is in fact positive, measurement and selection on a subset of core wood MFAs could indirectly improve/decrease the MFA throughout the core wood and improve core wood quality. This is especially important now that core wood accounts for a greater proportion of the wood harvested from southern pine plantations. Should the positive correlations between core and outer wood MFAs also represent the true direction of the correlations, early selection on core wood MFA could have a beneficial effect on outer wood MFAs as well and result in improvements in the wood quality of the whole tree. On the other hand, should correlations between core and outer wood MFAs prove to be nonsignificant, early selection on core wood MFAs would not affect outer wood MFAs. This also could be beneficial because improvements could be made in core wood MFAs without causing a corresponding change in outer wood MFAs and a more uniform distribution of MFAs could be achieved from pith to bark. This would mean boards cut across multiple rings would have more uniform shrinkage properties and would be less prone to crook.

A genetic correlation between MFA and growth rate also would have important implications for tree improvement. Studies have shown that tracheid length decreases with increased diameter growth rate because the length of the cambial initials decreases (Megraw 1985). Studies also have shown that MFA increases as tracheid length decreases (Megraw 1985). Although these studies were based on phenotypic data, this implies that trees with a greater diameter may have a greater MFA than smaller trees of the same age. The significant, positive genetic correlation between latewood 4 MFA and diameter growth at age 10 in GP065 supports this deduction (Table 6a). However, because the majority of correlations between MFA and diameter were not precisely estimated, caution should be used in interpreting the results of this research as proof of a positive genetic relationship between MFA and diameter growth.

Positive genetic correlations between MFA and growth traits are unfavorable because they indicate that selection for increased volume growth can result in increased MFA. Negative relationships between height, diameter, or volume and MFA would be more favorable for a tree improvement program because they imply that simultaneous improvement in all of the traits is possible. Negative correlations were observed at both sites but all had large standard errors, indicating that they may not be reliable estimates. Additional research is needed to precisely estimate genetic correlations between MFA and growth traits.

Negative genetic correlations between MFA and total core-specific gravity also would be favorable for a tree improvement program. They imply that progenies with high specific gravity also will have low MFA and that breeding for improvements in specific gravity, which is less expensive to measure and has a higher heritability than MFA, will indirectly produce desirable changes in the MFA. The genetic correlations between MFA and total specific gravity were imprecisely estimated and not significantly different from zero. Estimates from the two sites were almost always opposite in sign, either because the genetic samples were different or simply by chance (Table 5). Therefore, it is not possible to draw inferences from the trends.

Specific gravity is highly heritable and studies by Talbert et al. (1983) suggest that large gains in specific gravity can be made through selection. However, selection for specific gravity is rarely undertaken in existing loblolly pine breeding programs because of the overwhelming importance of growth characteristics. Likewise, MFA is not used because there is a lack of genetic data and there is a high cost associated with its measurement. If new breeding programs were designed to focus on wood quality rather than solely on faster growth, the results of this study suggest that both traits could be incorporated into selection strategies. However, depending on the direction of the true correlation between the traits, indirect selection for MFA and simultaneous gains in both specific gravity and MFA may be infeasible. Therefore, the development of selection indices with proper weights for each trait will be necessary before specific gravity and MFA can be incorporated into a breeding program. Better estimates of genetic correlations between MFA and specific gravity will be required before proper selection weights can be assigned to each trait.

Future Research Needs

This study was meant to provide an initial look at the genetic influences on MFA and its relationship with specific gravity, height and diameter. Additional work is necessary to understand the implications of including MFA as a selection criterion. For example, more parents and families need to be examined to increase the reliability of the results. Many of the genetic correlations were low and had extremely large estimated standard errors, which caused them to be nonsignificant. Sewell et al. (2000) and Brown et al. (2003) identified QTLs for specific gravity and for MFA that mapped less than 10 to 20 cm apart, suggesting a genetic relationship between the two traits may exist. With additional sampling, correlations, such as those between MFA and specific gravity, may prove to be significant. Also, the heritability of MFA and its relationship with specific gravity and growth needs to be examined throughout the tree, not just at breast height. Megraw (1985) noted that the core wood MFA in a given ring can be 15% greater at the base of the tree than in the same ring position further up the bole and that as a result, the relationship between specific gravity and MFA is different in the base than in the rest of the bole. Furthermore, the experiment needs to be replicated across sites so that environmental influences and genetic by environmental interactions can be identified. Specific gravity has been shown to vary by site (Byram and Lowe 1988) and can express a genotype × environment interaction (Jett et al. 1991). The presence of statistically significant block and SCA × block effects within locations suggests that there may also be significant environmental influences on MFA as well.

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