VARIATION IN LOBLOLLY PINE RING MICROFIBRIL ANGLE IN THE SOUTHEASTERN UNITED STATES

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ABSTRACT

The effect of physiographic region on microfibril angle (MFA) in loblolly pine (*Pinus taeda* L.) in the southern United States was evaluated. MFA was determined at 1.4, 4.6, 7.6, 10.7, and 13.7 m up the stem of 59 trees, representing five physiographic regions. A nonlinear mixed-effects model was developed to test for regional differences in the initial value of MFA, the rate at which MFA changes with ring number from pith, and the lower bound of MFA achieved. Our results suggest that the parameters of interest differ significantly by region. It was found that MFA differs significantly between the South Atlantic, Gulf, and Hilly regions, compared to the North Atlantic and Piedmont regions. The initial value of MFA was found to be smaller in the Piedmont compared to all other regions. Similarly, the rate at which MFA changes with ring number was found to be significantly smaller in the North Atlantic and Piedmont regions. A test of the lower bound of MFA indicates that the Piedmont region has a significantly larger lower asymptote. These results combined indicate that overall, MFA values are larger in the North Atlantic and Piedmont regions.

Keywords: Clustered data, loblolly pine, repeated measures, random-effects, wood properties.

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INTRODUCTION

Microfibril angle (MFA), defined as the angle between the cellulose fibrils and the fiber axis, has a significant effect on both the mechanical properties and dimensional stability of wood (MacDonald and Hubert 2002). MFA is inversely correlated with specific gravity (SG), stiffness or modulus of elasticity (MOE), modulus of rupture (MOR), and tangential shrinkage (Megraw et al. 1999). The stiffness of Sitka spruce (*Picea sitchensis*) was found to increase 2.5 times as MFA declined from 40 to 15 degrees (Brazier et al. 1985). Microfibrils shrink transversely, and large MFAs imply increased longitudinal shrinkage of the tracheid and subsequently increased longitudinal shrinkage of the wood (Lundgren 2004). Megraw et al. (1999) found that both longitudinal shrinkage and MFA are dependent on position in the tree, and are highest within inner rings at the base of the tree. MFA is also highly correlated with stretch, stiffness, and strength properties of paper, with high MFA values resulting in low tear strength of paper (Lundgren 2004; Uprichard et al. 1994; Megraw 1985; Kellogg et al. 1975; Watson and Dadswell 1964).

Wood properties of loblolly pine typically change from the pith toward the bark in a nearly asymptotic manner, with initially rapid change followed by little if any change occurring beyond rings 16–20 from pith (Burdon et al. 2004). MFA decreases from the first earlywood cell to the last latewood cell (Cave and Walker 1994). The decrease in MFA with age takes place at a slower rate near the base of the tree than it does at upper heights. For a given number of rings from the pith, this results in higher MFAs at the butt and breast height regions than at several meters in height and above (Megraw 1985).

MFA in loblolly pine is large near the pith and decreases rapidly out to 10 or more rings from the pith, and then continues dropping, regardless of height, but at a much slower rate until such time as it essentially stabilizes. From measurements at the base, 1 and 2 m in height, Megraw et al. (1999) found that the average MFA values of 24 loblolly pine trees decreased with increasing ring number all the way out through ring 20. At heights of 3 m and above, MFA was found to decrease to ring 10 where it essentially stabilized near 10 degrees for all rings thereafter.

Similar trends have been observed by Jordan et al. (2005a) and He et al. (2006) when examining earlywood and latewood MFA in loblolly pine from Southeast Texas, with MFA being initially large near the pith and then decreasing rapidly out to approximately 15 rings, where it eventually stabilizes between 9 and 13 degrees. They also found that the quasi-asymptotic lower bounds of MFA were larger in earlywood than in latewood, and the lower bounds increased with increasing disk height.

Jordan et al. (2005b) reported significant height, region, and height by region interaction effects in whole disk cross-sectional MFA in the southern United States. They found no significant differences across the North Atlantic and Piedmont regions, at any height except 1.4 m. No differences at any height were detected when comparing cross-sectional MFA between the South Atlantic, Gulf, and Hilly regions. Since MFA was found to be similar in the North Atlantic and Piedmont regions, and the South Atlantic, Gulf, and Hilly regions, joint comparisons of the two groups indicated that on average, whole disk MFA was significantly larger in the North Atlantic and Piedmont regions compared to the South Atlantic, Gulf, and Hilly regions by an amount of approximately 5.9, 1.8, 1.8, 2.2, and 1.8 degrees at heights of 1.4, 4.6, 7.6, 10.7, and 13.7 m, respectively.

Repeated measures data arise in numerous forestry related experiments and occur when multiple measurements of essentially the same response variable are taken on each of several (or many) "subjects" (e.g., trees, plots, etc.). Often the repeated measurements on each unit are taken through time, but can also occur along other dimensions such as space; e.g., multiple MFA measurements within the same tree at different heights. A variety of approaches have been developed for analyzing repeated measures data, including a univariate repeated measures analysis of variance (RM-ANOVA), or a multi-

variate analysis of variance (MANOVA) (Davis 2002). A more modern approach to repeated measures analysis utilizes linear mixed-effects models. This more flexible methodology subsumes the previous two more traditional approaches and allows a middle ground or compromise choice for the covariance among repeated measures, which can be chosen empirically to fit the data.

Oftentimes, repeated measurement data reflect an underlying nonlinear functional relationship between at least one of the predictor variables and the responses within individuals (Lindstrom and Bates 1990; Vonesh and Chinchilli 1997). For example, growth data typically exhibit a sigmoidal relationship between size and time, or, in the current context, MFA changes nonlinearly with height in a given tree. Generalizations of mixed-effect models to accommodate such nonlinear relationships among repeated measurement data are known as nonlinear mixed-effect models (NLMMs) and have gained considerable popularity in the forestry sciences in recent years (Gregoire and Schabenberger 1996; Hall and Bailey 2001; Zhao et al. 2005; Jordan et al. 2005b). The objectives of the previous cited authors' uses of NLMMs are to understand between subject (stands/plots/trees) variation in the response variables used, and to determine whether some of this variation can be attributed to differing silvicultural regimes, physiographic regions, or other covariates.

The objective of this research is to investigate how MFA changes with age (ring number) and disk height, and to determine how these relationships differ across five distinct physiographic regions in the Southeastern United States. This goal is pursued through the development of a suitable NLMM that describes these patterns while accounting appropriately for the hierarchical grouping structure and spatial correlation within the available data.

MATERIALS AND METHODS

Fifty-nine loblolly pine trees from 20 stands were sampled across the Southeastern United States for MFA analysis. Plantations were sampled in the South Atlantic Coastal Plain, North Atlantic Coastal Plain, Piedmont, Gulf Coastal Plain, and Hilly Coastal Plain regions (Fig. 1). The stands were located on land owned by forest products companies, and included only stands with similar silvicultural history: 1) site preparation with no herbaceous weed control; 2) no fertilization at planting except phosphorus on phosphorus-deficient sites; 3) stand density of at least 617 trees per hectare at the time of sampling. Trees larger than 12.7 cm in diameter were inventoried on three 0.04-hectare plots to determine stand stocking and diameter distribution. A sample of three trees was chosen for MFA analysis proportional to the diameter distribution of each stand to represent a range of tree sizes in the stand. Regional attributes are summarized in Table 1.

The trees selected for analysis were felled and cross-sectional disks 2.54 cm thick were cut at 1.4, 4.6, 7.6, 10.7, and 13.7 m up the stem. Two radial strips 1.27 cm square were cut from each disk and dried at 50 degrees Celsius. One strip was sawn into a 2-mm-thick radial strip for X-ray densitometry for measurement of radial growth and SG at 0.0060-cm intervals. The second strip was sawn into a 2- × 7-mm strip for MFA analysis. MFA was determined by Silviscan® using X-ray diffraction at 0.10-cm intervals on the radial surface. The MFA data were then assigned to an annual ring based on the radial measurements collected on the strip analyzed by X-ray densitometry. Details of sample

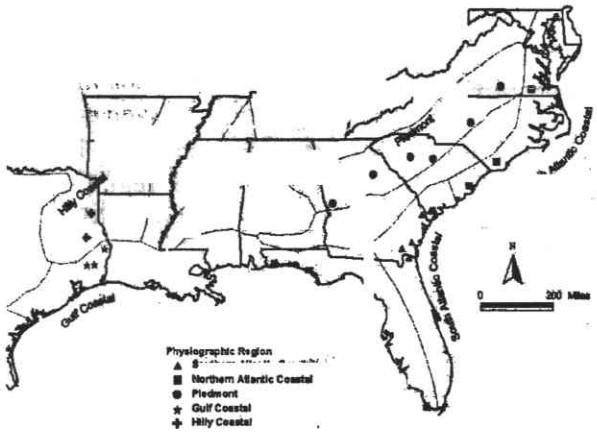


FIG. 1. Plot of the 20 stands selected for cross-sectional microfibril analysis.

TABLE 1. *Range and average (in parentheses) tree size characteristics for 59 loblolly pine trees sampled for microfibril angle analysis.*

Region	Trees sampled	DBH (cm)	Total Height (m)	Age (years)	MFA (degrees)
S. Atlantic	15	15.5–32.2 (23.9)	17.7–25.3 (22.2)	21–24 (22.3)	7.8–47.0 (16.3)
N. Atlantic	9	16.8–28.7 (22.7)	15.5–21.9 (19.0)	21–24 (22.7)	9.5–41.3 (19.5)
Piedmont	17	15.7–36.1 (25.6)	15.1–19.9 (18.2)	21–25 (23.5)	8.7–50.7 (19.0)
Gulf	9	14.5–24.9 (18.8)	12.6–18.7 (16.8)	20–27 (23.7)	8.4–38.2 (16.5)
Hilly	9	14.0–29.2 (21.1)	11.4–21.7 (17.6)	20	8.2–33.7 (16.6)

preparation and use of the X-ray densitometer and diffractor can be found in Harding (1995) and Evans (1998).

A plot of mean MFA versus ring by height level for each region is given in Fig. 2. At all heights, MFA is large near the pith and decreases rapidly. MFA appears to stabilize in the range of 10–15 degrees at heights of 4.6, 7.6, and 10.7 m respectively. At 1.4 m in height, MFA appears to be leveling off in the Gulf, Hilly, and South Atlantic regions, as opposed to the North Atlantic and Piedmont regions. Mean MFA is significantly larger across all ring numbers at 1.4 m compared to all other heights, especially so in the Piedmont and North Atlantic regions. Above 1.4 m MFA is generally indistinguishable, although mildly larger values can be observed at 4.6 and 13.7 m compared to 7.6 and 10.7 m in height. Also, average MFA values appear to be generally larger in the Piedmont and North Atlantic regions compared to the Gulf, Hilly, and South Atlantic regions. A plot of observed MFA versus ring by height level and region for all sample trees is given in Fig. 3. The curves seen in Fig. 3 have a similar shape, but differ among individuals, suggesting that mixed-effects modeling techniques could be employed to account for between tree variation.

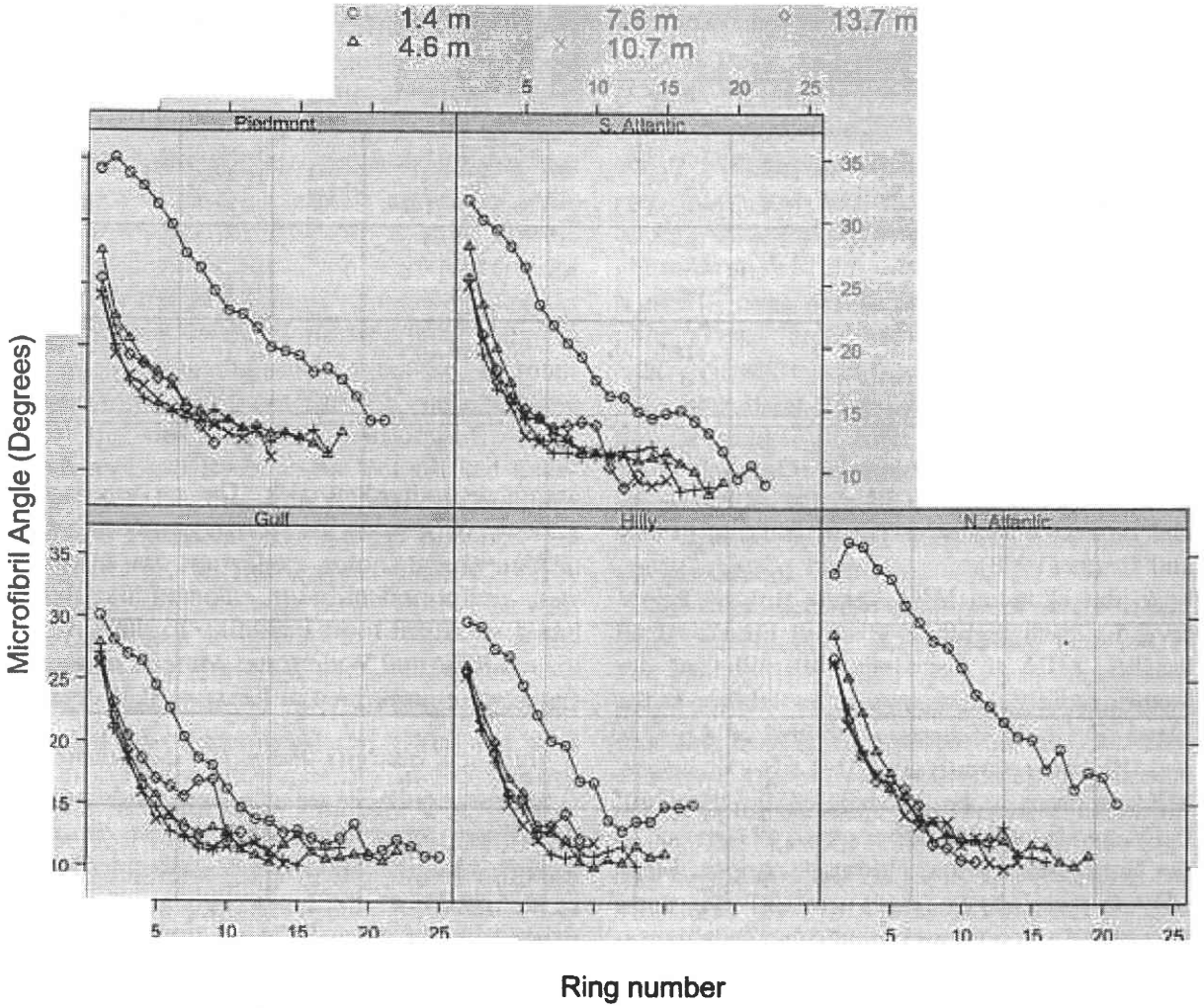
The data used in this analysis are grouped according to a hierarchical (nested) structure. Disks are nested within trees, which in turn are nested within stands. Each sample disk has repeated measures, with the number of observations dependent on the number of rings observed within an individual disk. The models in this paper were fit using the NLME library in S-Plus (2006). Model choice, evaluation, and inference were performed utilizing standard likelihood-based statistical tools including likelihood ratio tests (LRTs) and Wald tests. All tests of significance were performed at the $\alpha = 0.10$ level.

Statistical analysis and model development

Several nonlinear models were evaluated for describing the trends of MFA and we chose the modified Logistic model as described by Jordan et al. (2005a) as the basic tool to describe the dependence of mean MFA on ring number and height. The basic model can be expressed as

$$f(Ring) = \frac{\gamma_0}{1 - e^{\gamma_1 Ring}} + \gamma_2 \qquad (1)$$

where $f(Ring)$ is the mean response function of MFA, *Ring* is ring number from pith, γ_0 corresponds to an initial value parameter (equal to two times the y-intercept), γ_1 is the rate parameter which controls how quickly MFA decreases with increasing distance from the pith, and γ_2 is the lower asymptote. Here, *Ring* is treated as the primary covariate in the logistic function, but to also account for the dependence of MFA on height and on the individual characteristics of the particular disk, tree, and stands from which the data were drawn, we modeled the parameters γ_0, γ_1, and γ_2 as linear functions of ln(height) and random disk, tree, and stand effects. Similarly, regional effects may be included in the model by adding indicator variables.



Plot of mean microfibril angle versus ring number by height level and region.

More specifically, let y_{ijkl} denote MFA at the lth measurement location (ring) on the kth disk (height) in the jth tree of the ith stand ($i = 1 \ldots M$, $j = 1 \ldots M_i$, $k = 1 \ldots M_{ij}$, $l = 1 \ldots n_{ijk}$). Then the model can be expressed as

$$y_{ijkl} = \frac{\gamma_{00ijk} + \gamma_{01ijk} \ln(ht_{ijk})}{1 + \exp[\{\gamma_{10ijk} + \gamma_{11ijk} \ln(ht_{ijk})\} Ring] + [\gamma_{20ijk} + \gamma_{21ijk} \ln(ht_{ijk})] + \varepsilon_{ijkl}} \quad (2)$$

where,

$$\begin{pmatrix} \gamma_{00ijk} \\ \gamma_{01ijk} \\ \gamma_{10ijk} \\ \gamma_{11ijk} \\ \gamma_{20ijk} \\ \gamma_{21ijk} \end{pmatrix} = \begin{pmatrix} (\beta_{001}R_1 + \beta_{002}R_2 + \beta_{003}R_3 + \beta_{004}R_4 + \beta_{005}R_5 + b_{0i} + b_{0ij} + b_{0ijk}) \\ (\beta_{01}) \\ (\beta_{101}R_1 + \beta_{102}R_2 + \beta_{103}R_3 + \beta_{104}R_4 + \beta_{105}R_5 + \beta b_{1i} + b_{1ij} + b_{1ijk}) \\ (\beta_{11}) \\ (\beta_{201}R_1 + \beta_{202}R_2 + \beta_{203}R_3 + \beta_{204}R_4 + \beta_{205}R_5 + b_{2i} + b_{2ij} + b_{2ijk}) \\ (\beta_{21}) \end{pmatrix}$$

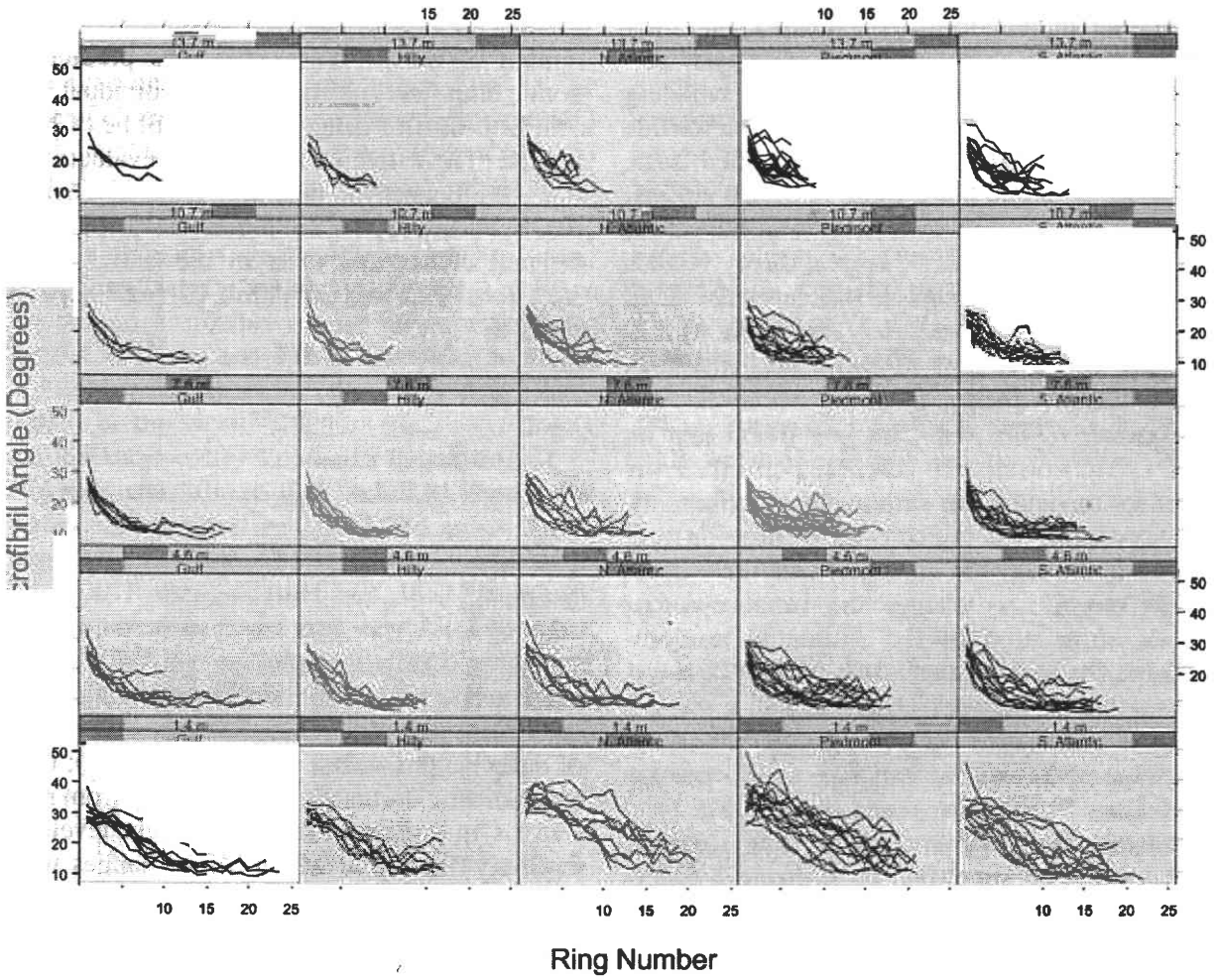


FIG. 3. Plot of observed microfibril angle versus ring number by height level and region.

$\boldsymbol{\beta}$ are the fixed-effects parameters, $\mathbf{b}$ are random-effects, R_1, R_2, R_3, R_4, and R_5 are 0/1 indicators for whether the region is the South Atlantic, North Atlantic, Piedmont, Gulf, or Hilly region, respectively. We assume

$$\mathbf{b}_i = \begin{pmatrix} b_{0i} \\ b_{1i} \\ b_{2i} \end{pmatrix} \sim N(0, \boldsymbol{\Psi}_1), \quad \mathbf{b}_{ij} = \begin{pmatrix} b_{0ij} \\ b_{1ij} \\ b_{2ij} \end{pmatrix} \overset{i.i.d}{\sim} N(0, \boldsymbol{\Psi}_2), \quad \mathbf{b}_{ijk} = \begin{pmatrix} b_{0ijk} \\ b_{1ijk} \\ b_{2ijk} \end{pmatrix} \sim N(0, \boldsymbol{\Psi}_3), \quad \boldsymbol{\varepsilon}_{ijk} \sim N(0, \sigma^2 \mathbf{I}_{ijk})$$

No constraints other than assuming they are positive-definite symmetric matrices are put on $\boldsymbol{\Psi}_1$, $\boldsymbol{\Psi}_2$ and $\boldsymbol{\Psi}_3$. It may be useful to restrict $\boldsymbol{\Psi}_1$, $\boldsymbol{\Psi}_2$ and $\boldsymbol{\Psi}_3$ to special forms of variance-covariance matrices for computational stability and speed. Although fairly general, Eq. (2) is somewhat restrictive because of the assumption $Var(\boldsymbol{\varepsilon}_{ijkl}) = \sigma^2 \mathbf{I}_{ijk}$, or conditional independence and homoscedasticity of the within-subject errors. A more flexible form of Eq. (2) can be specified with $\boldsymbol{\varepsilon}_{ijkl} \sim N(\mathbf{0}, \sigma^2 \boldsymbol{\Lambda}_{ijk})$, where $\sigma^2 \boldsymbol{\Lambda}_{ijk}$ is an $n_{ijk} \times n_{ijk}$ intrasubject covariance matrix. Correlation can now be accounted for through the subject-specific random-effects, or through specification of an appropriate intrasubject covariance matrix ($\sigma^2 \boldsymbol{\Lambda}_{ijk}$).

A plot of the residuals indicated that even with the inclusion of the random-effects, heteroscedasticity still exists in the model, violating the assumption $\varepsilon_{ijkl} \sim \sigma^2 \mathbf{I}_{ijk}$. To account for this feature, we utilized a power of the fitted value variance function. For a more thorough review, readers are referred to Vonesh and Chinchilli (1997). In the context of normal-theory mixed-effects models, correlation structures are often used to model the correlation among the within-subject errors. A host of correlation structures are available to account for the within-disk autocorrelation. For our data, we found that an *AR*(1) autocorrelation function performed the best for modeling the within-subject errors.

Accounting for regional differences, heteroscedasticity, and the correlation of the within-disks errors, may change the variance-covariance correlation of the estimated random-effects. Upon closer inspection of Eq. (2), it was found that the between-stand variability was adequately accounted for with the addition of the regional covariates, the variance, and correlation structures. It was also found that the tree-level random-effects' variance-covariance structure (Ψ_2) could be simplified by utilizing a block-diagonal structure. Similarly, Ψ_3 was simplified by eliminating the b_{0ijk} random-effect due to the small variance estimate.

With the variance-covariance matrices, within-group errors, and autocorrelation functions specified, it is now possible to test regional effects on MFA. Two possible approaches can be employed for testing the significance of fixed-effects parameters based upon regional covariates: 1) LRTs can be used for the comparison of nested models with differing mean structures; 2) use of approximate Wald t and F tests to test the significance of the regional parameters. We chose the use of Wald tests for deciding which regional parameters should be included in the model. The use of LRTs has been shown to be "anticonservative" resulting in smaller P-values, and as the number of fixed-effects being removed becomes large, the inaccuracy in the reported P-values can be considerable (Pinheiro and Bates 2000).

The main focus of this study is identifying possible regional differences in MFA, *not* development of the most parsimonious prediction model; thus the significance of individual parameter estimates using the t test will be of limited use. The F test will be used to evaluate the joint significance of potential regional covariates. Specifically, we are interested in testing if regional differences exist in the initial value (γ_{00}), rate (γ_{10}), and asymptote parameters (γ_{20}) found in Eq. (2).

RESULTS

The estimated parameter values from Eq. (2) are shown in Table 2. It can be seen that the initial value of MFA was larger in the North Atlantic region, compared to the South Atlantic, Piedmont, Gulf, and Hilly regions. The initial value of MFA was also found to decrease with increasing disk height ($\hat{\beta}_{01} = -8.7540$). MFA was found to be substantially larger at ring number 1 from pith at 1.4 m in height compared to all other heights across all regions (Fig. 2); thus such a drastic decrease of initial values from ring 1 at 1.4 m compared to larger height levels is sensible. The rate at which MFA changes with ring number (γ_{10}) is also presented in Table 2; MFA decreases at a slower rate in the North

TABLE 2. *Fixed-effects parameter estimates and corresponding standard errors from Eq. (2).*

Parameter	Region	Parameter	Estimate	Standard Error
Initial value	S. Atlantic	β_{001}	56.4924	1.8899
γ_{00}	N. Atlantic	β_{002}	58.7544	2.2689
	Piedmont	β_{003}	50.9169	1.8328
	Gulf	β_{004}	55.4605	2.3080
	Hilly	β_{005}	55.2198	2.2351
ln(ht)		β_{01}	−8.7540	0.7596
Rate γ_{10}	S. Atlantic	β_{101}	0.0879	0.0147
	N. Atlantic	β_{102}	0.0316	0.0168
	Piedmont	β_{103}	0.0448	0.0131
	Gulf	β_{104}	0.1146	0.0197
	Hilly	β_{105}	0.0793	0.0181
ln(ht)		β_{11}	0.2147	0.0084
Lower	S. Atlantic	β_{201}	7.6900	0.6996
asymptote	N. Atlantic	β_{202}	8.2668	0.7377
γ_{20}	Piedmont	β_{203}	9.7031	0.6077
	Gulf	β_{204}	8.3132	0.7296
	Hilly	β_{205}	7.2457	0.7259
ln(ht)		β_{21}	1.8557	0.2134

Atlantic and Piedmont regions, compared to the South Atlantic, Gulf, and Hilly regions, which are reasonable assumptions given Fig. 2. The rate of change of MFA increases with increasing disk height, leading to higher values of MFA at 1.4 m compared to larger height values in all regions. Above 1.4 m, MFA decreases rapidly across all regions, on the order of approximately five times faster when moving from 1.4 to 4.6 m in height. Estimates of the lower asymptotic bound indicate that MFA converges to larger values in the Piedmont ($\hat{\beta}_{203}$ = 9.7031) compared to the North Atlantic ($\hat{\beta}_{202}$ = 8.2668), Gulf ($\hat{\beta}_{204}$ = 8.3132), South Atlantic ($\hat{\beta}_{201}$ = 7.6900), and Hilly ($\hat{\beta}_{205}$ = 7.2457) regions. The parameter estimates also suggest that the lower bound of MFA increases with increasing disk height ($\hat{\beta}_{21}$ = 1.8557). A plot of population-predicted MFA values versus ring number by height and region can be obtained by setting the random-effects estimates in Eq. (2) equal to zero, and substituting the corresponding fixed-effects values. We constructed a plot of estimated MFA at heights of 1.4, 4.6, 7.6, 10.7, and 13.7m by region (Fig. 4). Figure 4 closely follows the trends of MFA as shown in Figs. 2 and 3, with higher values of MFA being observed at 1.4 m, followed by a rapid decrease in MFA with increasing height and ring number from pith.

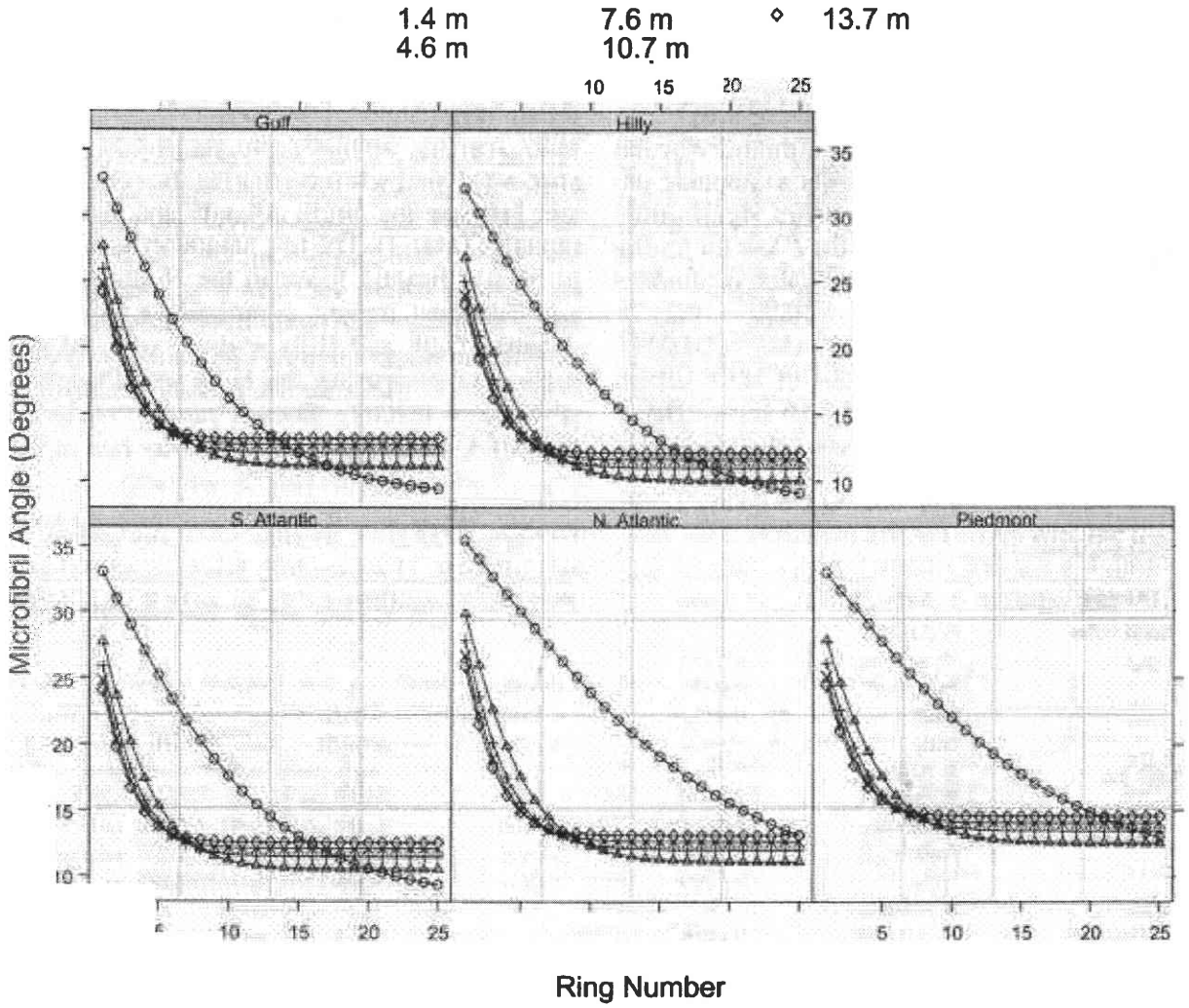


FIG. 4. Plot of estimated microfibril angle versus ring number by height level and region.

Estimates of the variance-covariance components for the trees and disk random-effects respectively, are

$$Var(b_{ij}) = Var\begin{pmatrix} b_{0ij} \\ b_{1ij} \\ b_{2ij} \end{pmatrix} = \hat{\Psi}_2$$

$$\begin{pmatrix} 9.6658 & 0 & -3.3717 \\ 0 & 0.038 & 0 \\ -3.3717 & 0 & 2.4775 \end{pmatrix}$$

$$Var(b_{ijk}) = Var\begin{pmatrix} b_{0ijk} \\ b_{1ijk} \\ b_{2ijk} \end{pmatrix} = \hat{\Psi}_3$$

$$\begin{pmatrix} 0 & 0 & 0 \\ 0 & 0.0004 & -0.0046 \\ 0 & -0.0046 & 0.0603 \end{pmatrix}$$

with a residual error ($\hat{\sigma}$) estimate of 0.2615.

We are now interested in determining whether the initial value, rate, and lower asymptotic parameters found in Table 2 differ significantly across regions. The value of the *F* test for testing the hypothesis of equal initial value parameters across regions, $\beta_{001} = \beta_{002} = \beta_{003} = \beta_{004} = \beta_{005}$, was found to be 3.68 (*P*-value = 0.0054), indicating that the initial value of MFA differs across regions at the $\alpha = 0.10$ level. The *F* statistics and *P*-values for testing the hypothesis of equal rate ($\beta_{101} = \beta_{102} = \beta_{103} = \beta_{104} = \beta_{105}$) and lower asymptote parameters ($\beta_{201} = \beta_{202} = \beta_{203} = \beta_{204} = \beta_{205}$), were found to be $F = 4.38$ (*P*-value = 0.0016) and $F = 3.81$ (*P*-value = 0.0043), respectively. These findings indicate that both the rate and lower asymptote parameters differ across regions.

Since the joint *F* tests indicated that significant differences among the parameters exist across regions, we then constructed a table containing all pairwise parameter comparisons (Table 3). The *P*-values for testing differences in the initial value parameter by region indicate significant differences exist between the Piedmont and all other regions at the $\alpha = 0.1$ level. These findings suggest that MFA at ring 1 is significantly lower in the Piedmont region compared to all other regions. The rate at which MFA changes among regions was not found to differ between the South Atlantic, Gulf, and Hilly regions. Similarly, no significant difference was found when comparing the rate parameter between the North Atlantic and Piedmont regions (Table 3). The rate parameter was found to be significantly lower in the North Atlantic and Piedmont regions compared to the South Atlantic, Gulf, and Hilly regions, with the exception of comparing the Hilly and Piedmont (P-value = 0.1007). Thus, it can be concluded that MFA decreases at a much faster rate in the

TABLE 3. *P-values of all pairwise comparisons for testing regional differences in the initial value, rate, and lower asymptote parameters.*

Parameter	Region	S. Atlantic	N. Atlantic	Piedmont	Gulf	Hilly
nitial value	S. Atlantic	1				
γ_{00}	N. Atlantic	0.3336	1			
	Piedmont	0.0039	0.0006	1		
	Gulf	0.6774	0.2351	0.0622	1	
	Hilly	0.5886	0.1837	0.0620	0.9310	
Rate γ_{10}	S. Atlantic	1				
	N. Atlantic	0.0070	1			
	Piedmont	0.0161	0.5100	1		
	Gulf	0.2421	0.0008	0.0017	1	
	Hilly	0.6899	0.0431	0.1007	0.1634	
ower	S. Atlantic	1				
asymptote	N. Atlantic	0.4419	1			
γ_{20}	Piedmont	0.0013	0.0531	1		
	Gulf	0.4151	0.9571	0.0667	1	
	Hilly	0.5514	0.2282	0.0009	0.2146	

South Atlantic, Gulf, and Hilly regions compared to the North Atlantic and Piedmont regions. No significant differences were detected in the lower asymptote parameter between the North Atlantic, South Atlantic, Gulf and Hilly regions. However, the lower asymptote in the Piedmont was found to be significantly different (larger) than all other regions.

We also tested for overall differences in the response curves of MFA between regions. For example, the test of the hypothesis that the response curves of MFA in the Gulf and Hilly regions are equal is given as $(\beta_{004}\ \beta_{104}\ \beta_{204})^T = \beta_{005}\ \beta_{105}\ \beta_{205})^T$. Results of the F tests for comparing overall region responses are presented in Table 4. Table 4 indicates that no significant differences in the response curves of MFA were found when comparing the South Atlantic, Gulf, and Hilly regions. Comparing the North Atlantic and Piedmont to the South Atlantic, Gulf, and Hilly regions indicated significant differences between all comparisons. Also, a significant difference in response curves was found when comparing the North Atlantic and Piedmont regions. These findings suggest that overall, the general patterns of MFA are similar between the South Atlantic, Gulf, and Hilly regions, with the North Atlantic and Piedmont regions exhibiting statistically distinct differences.

DISCUSSION AND CONCLUSIONS

In this study we utilized a NLMM approach for testing regional differences in MFA in loblolly pine. Estimates of the random-effects indicated that inter-stand variability was negligible, suggesting that MFA varies consistently between stands. However, since only three trees were selected for analysis from each stand, the inter-stand variation may in reality be inter-tree variability. Not to suggest that there isn't stand to stand variability, but the same families planted in two different places will often have different height/ring MFA averages. Much the same can be said for having only nine trees total sampled from each of three out of the five regions. MFA in loblolly pine is highly influenced by growth rate and therefore sensitive to the various environmental factors that go into growth rate. This implies that it will require sampling of many trees to know whether one is actually seeing regional differences, and not "luck of the draw" variation due to edaphic or weather-related factors. Inspection of $\hat{\Psi}_2$ (disk) and $\hat{\Psi}_3$ (tree) variance-covariance matrices indicates more variation exists among trees compared to disks within trees. We expect that disk-level variables (e.g. disk height) accounted for the majority of variation in MFA from disk to disk. However, the large variance estimates associated with $\hat{\Psi}_2$ indicate that potential tree-level covariates such as DBH, total height, or crown-characteristics could be helpful in explaining inter-tree variation.

It was found that MFA differs significantly between the South Atlantic, Gulf, and Hilly regions, compared to the North Atlantic and Piedmont regions, which are consistent with the findings of Jordan et al. (2005b). MFA was found to be overall larger in the North Atlantic and Pied-

TABLE 4. *Results of joint F tests for testing regional differences in overall response curves of MFA.*

Null hypothesis	Description	*P*-value
$(\beta_{001}\ \beta_{101}\ \beta_{201}) = (\beta_{002}\ \beta_{102}\ \beta_{202})$	S. Atlantic = N. Atlantic	0.0053
$(\beta_{001}\ \beta_{101}\ \beta_{201}) = (\beta_{003}\ \beta_{103}\ \beta_{203})$	S. Atlantic = Piedmont	0.0003
$(\beta_{001}\ \beta_{101}\ \beta_{201}) = (\beta_{004}\ \beta_{104}\ \beta_{204})$	S. Atlantic = Gulf	0.5970
$(\beta_{001}\ \beta_{101}\ \beta_{201}) = (\beta_{005}\ \beta_{105}\ \beta_{205})$	S. Atlantic = Hilly	0.7555
$(\beta_{002}\ \beta_{102}\ \beta_{202}) = (\beta_{003}\ \beta_{103}\ \beta_{203})$	N. Atlantic = Piedmont	0.0050
$(\beta_{002}\ \beta_{102}\ \beta_{202}) = (\beta_{004}\ \beta_{104}\ \beta_{204})$	N. Atlantic = Gulf	0.0012
$(\beta_{002}\ \beta_{102}\ \beta_{202}) = (\beta_{005}\ \beta_{105}\ \beta_{205})$	N. Atlantic = Hilly	0.0046
$(\beta_{003}\ \beta_{103}\ \beta_{203}) = (\beta_{004}\ \beta_{104}\ \beta_{204})$	Piedmont = Gulf	0.0015
$(\beta_{003}\ \beta_{103}\ \beta_{203}) = (\beta_{005}\ \beta_{105}\ \beta_{205})$	Piedmont = Hilly	0.0016
$(\beta_{004}\ \beta_{104}\ \beta_{204}) = (\beta_{005}\ \beta_{105}\ \beta_{205})$	Gulf = Hilly	0.3612

mont regions (Fig. 4). MFA was found to decrease slowest in the North Atlantic region at all height levels. The majority of differences in MFA appear to be attributable to differences between MFA at 1.4 meters compared to larger height values, where MFA is substantially larger in the North Atlantic and Piedmont regions (Fig. 2) compared to the South Atlantic/Gulf/Hilly regions. This study also suggests that MFA eventually converges to similar lower asymptotic values across all regions excluding the Piedmont.

The regional differences as observed in this paper may be attributable to any number of genetic or environmental factors. The finding of higher MFA values in the North Atlantic and Piedmont regions is consistent with lower SG values found in the North Atlantic and Piedmont regions compared to the South Atlantic, Gulf, and Hilly regions Clark and Daniels (2004). With the South Atlantic region receiving more summer rainfall and an extended growing season, trees in this area have a greater percentage of latewood and conversely lower MFA values. Lower MFA values in the Gulf and Hilly regions may be attributed to site quality. Trees from the Gulf and Hilly regions were found to be on average 0.7 cm smaller in diameter and 2.1 m shorter in height than the trees in the North Atlantic and Piedmont regions. Slow growth could produce a reduction in earlywood, resulting in lower MFA values. Regional weather patterns or site quality differences are not the sole factor influencing MFA. Initial stocking density and the number of trees per acre at the time of sampling could have influenced the size of the juvenile core, resulting in higher MFA at low planting densities and low MFA values at high planting densities.

As opposed to SG, less work has been done on MFA because of the tedious nature of the methods available including time in measurement or sample preparation, and the indirect X-ray diffraction method, which requires a more expensive technology (Deresse and Shepard 1999). The number of sample trees used in this analysis is small, and may not be adequate enough to truly characterize regional differences in MFA. However, these findings are unique and appear to be consistent with previous research. Even though this paper found that MFA varies significantly across region, ring number, and height, what is not so apparent is the question of whether the differences in MFA values observed here actually constitute a significant difference in the structural strength and integrity of solid wood and pulp products. Although the patterns of the curves exhibited in Fig. 4 vary by region, they are similar to some extent. However, are these differences large enough to constitute a significant difference in the end-use product? Intuition tells us that one may expect to see differences in the structural quality of products if comparisons are made between 1.4 and 10.7 m. But, does one really expect that an average difference of 3.7 degrees between the South Atlantic and Piedmont regions at 1.4 m will have a significant effect on both the mechanical properties and dimensional stability of wood? Also, would a difference of 3.7 degrees translate into marked differences in MOE and MOR, the standard for which solid wood products are judged? To our knowledge no such studies have been performed, leaving a large gap in the accurate quantification of wood properties. It is thus readily apparent that research needs to be conducted to evaluate and quantify these differences.

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