Genetic variation of juvenile wood properties in a loblolly pine progeny test

ROBERT SYKES, FIKRET ISIK, BAILIAN LI, JOHN KADLA, AND H-M. CHANG

ABSTRACT: Genetic variation was studied in several juvenile wood traits of loblolly pine (*Pinus taeda L.*). Transition wood (Ring 8) had higher α-cellulose content, average fiber length, and coarseness but lower lignin content than juvenile wood (Ring 3). For all of these traits, genetic variation increased from juvenile wood to transition wood. Fourteen loblolly pine full-sib families differed significantly for α-cellulose content, average fiber length, and coarseness but not for lignin content. Weak individual and family heritabilities were found for α-cellulose content, average fiber length, and coarseness for the juvenile wood. The heritability estimates for the transition wood were moderately high. Positive genetic correlations of wood density were found with α-cellulose content, average fiber length, and coarseness. These traits could be genetically improved by selection based on wood density.

Application: Genetic testing and selection could improve cellulose yield, fiber length, fiber coarseness, and reduce lignin content in Loblolly pine.

The demand for timber production and pulp in the southeast of the United States has increased greatly, with harvesting on public lands decreasing in other areas of the United States [1]. As urban sprawl increases and rural land is converted into urban areas, less and less land is available for wood production. If we are to meet the demand for wood in the United States, the remaining timberland must be managed efficiently through intensive silvicultural practices and genetic improvement [2].

This study was undertaken to quantify the genetic variation of important juvenile wood quality traits of loblolly pine. Our specific objectives were to:

- Determine genetic variation in α-cellulose content, average fiber length, coarseness, and lignin content
- Study genetic variation of earlywood and latewood and estimate genetic parameters
- Examine correlations among these chemical and morphological wood traits.

This information would benefit the tree improvement program and the pulp and paper industry by allowing silviculturists to select and plant trees with desirable traits. Trees with uniform and genetically improved juvenile wood properties would allow mills to process wood more efficiently and economically.

BACKGROUND

Intensive silvicultural practices and genetic improvement of trees have increased forest plantation productivity significantly in the southeast U.S. for loblolly pine (*Pinus taeda L.*) [3]. Improved growth has allowed rotation ages to be reduced to about 20–25 years for intensively managed loblolly pine plantations from about 40–50 years in natural stands. Consequently, the percent of juvenile wood from plantations has increased [4]. Compared to mature wood, juvenile wood has lower density, shorter tracheid length, and higher lignin content [5, 6]. As a result, the increased use of juvenile wood has led to reduced yields and higher pulping costs [7].

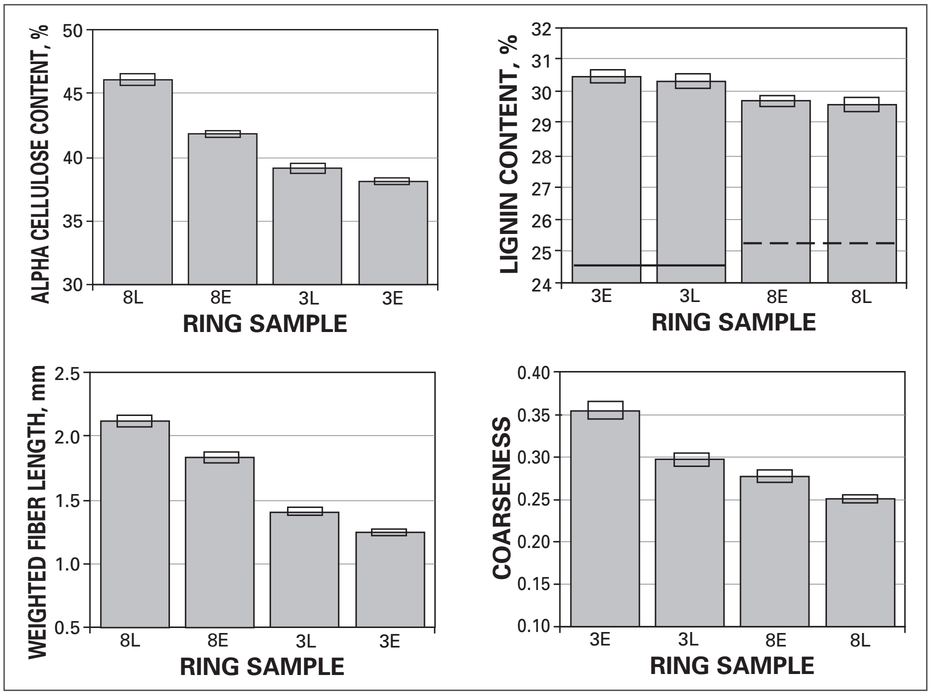
In most studies on wood properties, researchers have concentrated on the genetic control of wood density [8–10]. Zobel and Sprague compiled a list of heritabilities that ranged from 0.20 to 1.00 for loblolly pine specific gravity [11]. Heritability is the extent to which phenotypes are determined by the genes transmitted from parents. It measures the strength of inheritance for a given trait in a population [6]. Genetic control has also been studied in regard to the age of transition from juvenile to mature wood for loblolly pine. Loo *et al*. [12] reported that loblolly pine families produce juvenile wood through the first 6 years, with a transition period between 6 and 14 years, and mature wood production beyond 14 years. Szymanski and Tauer reported similar results for transition age [7], and Hodge and Purnell reported the average transition age for slash pine as occurring at 9.4 rings from the pith [9].

Genetic variation in juvenile wood properties in loblolly pine is important in improving the quality and uniformity of solid and chemical wood products. Specific gravity, cellulose content, lignin content, average fiber length, and coarseness are key properties that affect the quality and quantity of wood produced either in plantations or in natural stands. Favorable juvenile wood properties may be obtained through a breeding program if there is significant genetic variation among families and populations. Large genetic variations in holocellulose content, α-cellulose content, average fiber length, and lignin content have been reported in juvenile wood for loblolly pine and other species [13–18]. This genetic variation allows the breeder to select trees with desirable and uniform juvenile wood properties that will increase yield, improve product properties, and lower pulping costs [19].

MATERIALS AND METHODS

Material and data collection method

Fourteen full-sib families generated by a six-parent, half-diallel mating design were tested in the piedmont region of South Carolina. A randomized complete block design with six replications was used in the field. Each full-sib family was laid out in plots consisting of six trees in a row for each replication. Wood core samples were collected from 11-year-old trees from one site in Florence County, SC. Wood samples of 12-mm-increment cores were taken from each tree at breast



1. Least squares means and 95% confidence intervals of average fiber length, α-cellulose content, coarseness, and lignin content for earlywood and latewood of juvenile (3E and 3L) and transition wood (8E and 8L).

height (about 1.30 m) with a drill powered by a generator. We avoided taking wood cores with visible limbs, curves, resin pockets, compression wood, or rust infections. The samples were placed into sealed plastic storage bags, which were stored on ice in coolers to retain moisture while the material was being collected.

The bark and cambium were removed from the wood cores, and the cores were split at the pith into two halves. Chemical analyses was carried out with microanalytical techniques developed by Yokoyama *et al*. [20]. These techniques allow us to rapidly characterize the fiber components and morphology of loblolly pine in a large number of samples. The techniques involved are extractive removal, holocellulose preparation, determinations of α-cellulose and lignin content, and analyses of average fiber length and coarseness. Nonvolatile extractives greater than 95% were removed from the increment core by four successive two-day acetone extractions [20]. Extractives were removed from all cores by the successive acetone method. The increment cores were soaked in water overnight before ring samples were taken.

To study chemical properties of juvenile wood (Ring 3) and transition wood (Ring 8), we took within-core samples from Rings 3 and 8. Using a microtome, we cut thin wafers from earlywood and latewood from both Ring 3 and Ring 8. At least 300–500 mg were taken for each sample, and the samples were oven-dried for 12 h.

Statistical analyses

Averages of earlywood and latewood traits within each ring were compared through T-tests. An analysis of variance was conducted to compare full-sib families by the GLM procedure of SAS [21, 22]. To analyze the data, we used a linear mixed model for diallel analysis [23], which included the fixed effect of replication as well as the random effects of general combining ability (GCA), specific combining ability (SCA), and their interactions. We estimated the variance components of random effects, which measure the magnitude of variation, by using the SAS PROC MIXED procedure developed for diallel analysis [23].

We estimated the coefficients of variation for general and specific combining abilities by dividing the square roots of the estimates by their means. Means for family least squares were estimated with 95% confidence intervals. Earlywood and latewood of both juvenile and transition wood were compared for each wood trait. Using variance components from the mixed model, we estimated individual (h^2_i), half-sib family (h^2_{hs}), full-sib family (h^2_{fs}), and within full-sib family (h^2_{wfs}) heritabilities. The following equations were used.

$$h_i^2 = \frac{4\sigma^2_{GCA}}{2\sigma^2_{GCA} + \sigma^2_{SCA} + \sigma^2_{plot} + \sigma^2_E} \quad (1)$$

$$h_{hs}^2 = \frac{\sigma^2_{GCA}}{\left(p\sigma^2_{GCA} + \sigma^2_{SCA} + \frac{\sigma^2_{plot}}{b} + \frac{\sigma^2_E}{bn}\right)\left(\frac{1}{p-1}\right)} \quad (2)$$

$$h_{fs}^2 = \frac{2\sigma^2_{GCA}}{2\sigma^2_{GCA} + \sigma^2_{SCA} + \frac{\sigma^2_{plot}}{b} + \frac{\sigma^2_E}{bn}} \quad (3)$$

$$h_{wfs}^2 = \frac{2\sigma^2_{GCA}}{\left(\frac{b-1}{b}\right)\sigma^2_{plot} + \left(\frac{bn-1}{bn}\right)\sigma^2_E} \quad (4)$$

where

s^2_{GCA} = genetic variance
s^2_{SCA} = dominance variance
s^2_{plot} = SCA × replication variance
s^2_e = error variance
p = number of parents in the diallel
b = number of blocks
n = number of trees per family per replication.

Product-moment correlations and genetic correlations were estimated among these traits and with wood density [24]. Wood density was determined by the standard volumetric method. Standard errors of heritabilities and genetic correlations were calculated using the Delta Method [25] and ASREML software [26].

RESULTS

Differences of earlywood and latewood, rings and families

Latewood had significantly greater α-cellulose content, average fiber length, and coarseness than earlywood had in Ring 3, as shown in **Fig. 1**. The differences between latewood and earlywood for α-cellulose content, average fiber length, and coarseness were more pronounced in Ring 8 than in Ring 3. Latewood of Ring 8 had greater α-cellulose content, longer average fiber length, and greater coarseness than earlywood had. The average fiber length for latewood of Ring 8 was 13.4% longer than earlywood of the same ring. Earlywood and latewood of Ring 8 were not different for lignin content.

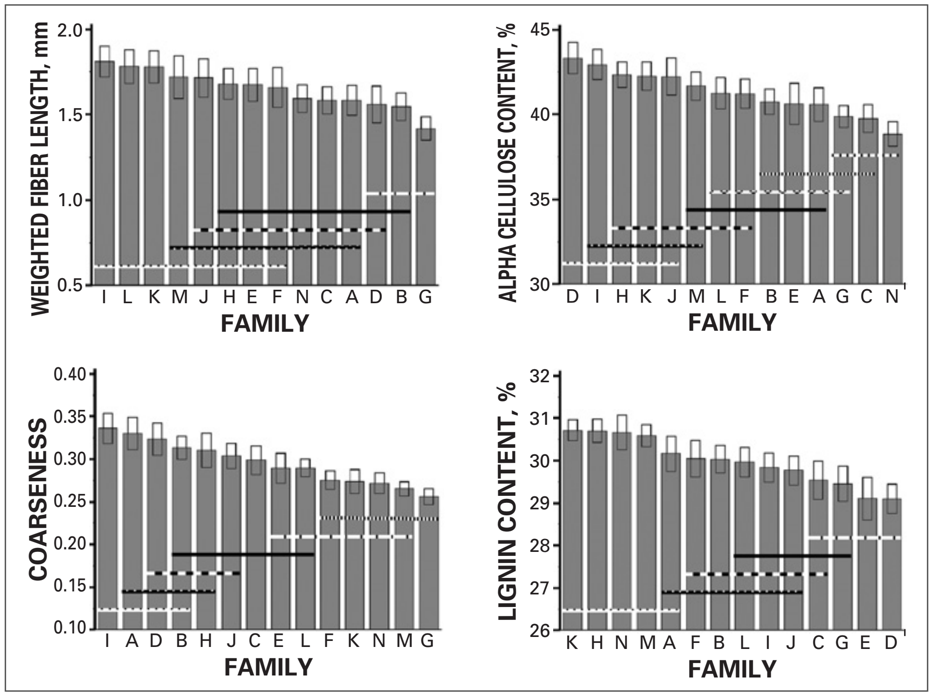
Families differed significantly for all the chemical and morphological wood properties at the probability level of <0.001 (data not presented). The interactions of family by earlywood or latewood within a ring were not significant. Family means for average fiber length ranged from 1.42 (Family I) to 1.81 mm (Family G), as shown in **Fig. 2**. For coarseness, there was considerable variation among families. Family I had the greatest coarseness, whereas Family G had the lowest values. Families I and G were consistent in ranking for average fiber length and coarseness. Family means for α-cellulose content ranged from 38.8% to 43.3%, with Family D having the highest value and Family N the lowest. Very little variation was found among families for lignin. Family E had the lowest lignin content (29.1%), while Family K had the highest lignin content (30.7%).

Phenotypic and genetic parameters

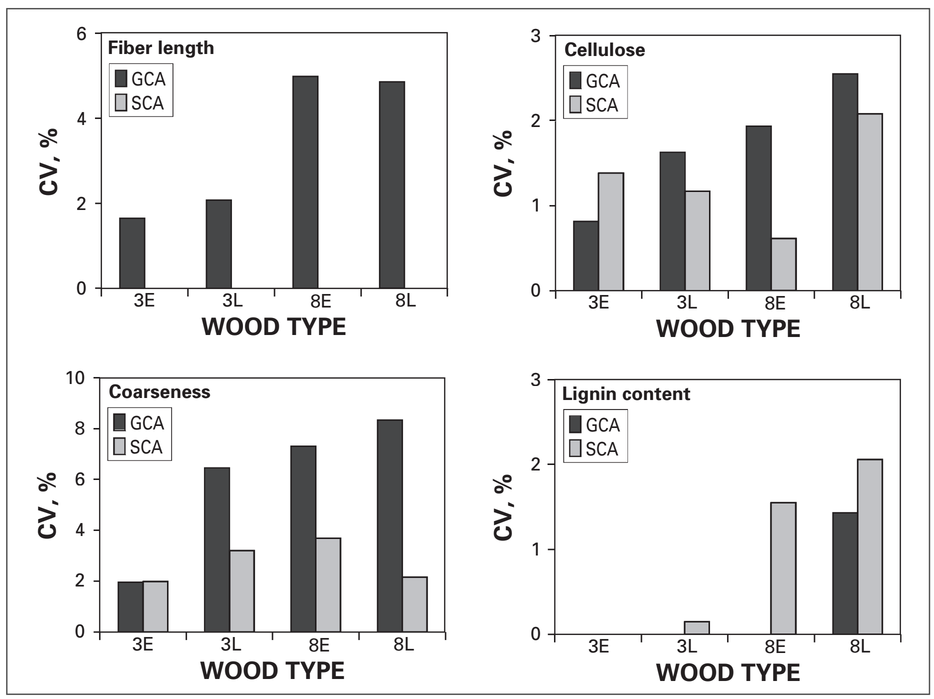
Coefficients of genetic variation for fiber length, cellulose content, coarseness, and lignin content were generally large, as **Fig. 3** shows. In general, additive genetic effects (GCA variance) accounted for the greater variation for fiber length, coarseness, and cellulose content than did the dominance genetic effects (SCA variance). The coefficient of variation of SCA for fiber length was essentially zero for earlywood and latewood of juvenile and transition wood.

The coefficient of variation of GCA was greater than that of SCA for average fiber length, α-cellulose content, and coarseness for latewood of Ring 3 and Ring 8. There was no genetic variance for lignin in juvenile wood, but the coefficient of variation of SCA for transition wood was higher than that of GCA for both earlywood and latewood. In general, GCA variance increased from earlywood to latewood of the same ring and from Ring 3 to Ring 8. However, the coefficient of variation of SCA was inconsistent from one ring to another.

Moderately high family heritabilities were estimated for α-cellulose content, average fiber length, and coarseness. Weak individual and within full-sib family heritabilities were observed for earlywood of Ring 3. Heritabilities could not be estimated for lignin content for earlywood and latewood of Ring 3 because of the lack of GCA variance. Family heritabilities were higher than individual heritabilities for all traits. Latewood heritabilities for Ring 3 were higher than earlywood heritabilities. In contrast to Ring 3, heritabilities for earlywood and latewood of Ring 8 were similar but higher



2. Rankings of 14 full-sib family means (Families A–N) and 95% confidence intervals for average fiber length, α-cellulose content, coarseness, and lignin content. Families with the same line are not significantly different.



3. Coefficients of variation (CV) for estimates of general combining ability (GCA) and specific combining ability (SCA) for average fiber length, α-cellulose content, coarseness, and lignin content in earlywood and latewood of Rings 3 and 8 (3E, 3L, 8E, and 8L).

	AVG. FIBER LENGTH	α-CELLULOSE CONTENT	COARSENESS	LIGNIN CONTENT	DENSITY
Avg. fiber length	—	0.37±0.48	0.99±0.01	-0.39±0.66	0.95±0.25
α-cellulose content	0.52[b]	—	0.40±0.45	-0.99±0.01	0.56±0.51
Coarseness	0.13[a]	0.33[b]	—	0.57±0.51	0.32±0.55
Lignin content	–0.03	–0.10	-0.11	—	—[c]
Density	0.10	0.13[a]	0.12	–0.04	—

[a]Significant at the 0.05 level. [b]Significant at the 0.001 level. [c]Genetic correlation not estimable. The number of observations used ranged from 183 to 242.

I. Genetic correlations (above diagonal) and phenotypic correlations (below diagonal) among average fiber length, α-cellulose content, coarseness, lignin content, and wood density for transition wood (Ring 8).

for all traits. Among all the traits studied, coarseness and α-cellulose content had the highest heritabilities, whereas lignin was more controlled by nongenetic effects.

The chemical and morphological wood properties had higher heritabilities for transition wood than for juvenile wood. For example, the family heritability for α-cellulose content was 0.38 for juvenile wood, whereas it was 0.55 for transition wood. Heritabilities for α-cellulose content and coarseness were similar and higher than those of average fiber length, both for Ring 3 and Ring 8. Heritabilities for lignin were essentially zero for Ring 3 but were moderate for Ring 8. When data from both rings were combined, the heritabilities were lower for all traits than the heritabilities derived from the data for one ring alone.

Average fiber length had a high genetic correlation with wood density (r_g = 0.95), as shown in **Table I**. Positive and moderate genetic correlations were observed between wood density, cellulose content, lignin content, and coarseness. The α-cellulose content had a high negative genetic correlation with lignin content. Lignin content was also negatively correlated with fiber length. The genetic correlation between average fiber length and coarseness was positive and high (r_g = 0.99). Genetic correlations could not be estimated for Ring 3 because of a lack of genetic variation.

The wood density of the wood core was phenotypically correlated with cellulose content but not with other traits. Phenotypic correlations between average fiber length, coarseness, and α-cellulose content were significant. None of the traits had significant phenotypic correlation with lignin content.

DISCUSSION

Wood properties

The chemical and morphological wood properties evaluated in this study are important in pulp and paper production. The content of α-cellulose content relates to the amount of pulp that is obtained from wood. The higher the α-cellulose content in a tree, the more pulp the tree will produce [27]. Increasing the amount of cellulose content in wood will reduce pulping costs and increase the efficiency of the pulp and paper mill.

Average fiber length also plays an important role. Either long fibers or short fibers may be favored, depending on the product being manufactured. Long fibers give paper greater tensile strength and tear strength for products such as cardboard and paper bags [28]. Short fibers are favored for products such as fine printing paper, where surface smoothness is important.

Coarseness is related to the thickness of the fiber wall. The thicker the fibers, the higher the coarseness values. Lower coarseness values result in better fiber collapse, tighter fiber bonds, and the formation of dense paper with a smooth surface. Trees with higher coarseness values yield pulp with higher bulk, which is beneficial to paper products that require higher absorbance and/or higher bending stiffness.

One of the most important properties in wood is lignin content. To separate the wood fibers, lignin must be removed [29]. However, the chemical breakdown of lignin is an expensive process, and reducing the lignin content in wood could save processing costs for the pulping industry.

Results of this study in relation to wood traits

Latewood had greater cellulose content, longer average fiber length, and greater coarseness than earlywood of the same rings. Juvenile wood of Ring 3 appeared to be less desirable for these chemical wood traits than wood of Ring 8, which is considered to be transition wood rather than mature wood for loblolly pine (*7*). Cellulose content, fiber length, and coarseness increased from juvenile wood to transition wood. Genetic selection based on latewood of the transition ring could be an effective way to manipulate chemical and morphological wood properties.

We found considerable genetic variation between earlywood and latewood for all of the wood traits except lignin content. Some of the genetic variance for cellulose content, fiber length, and coarseness was explained by additive genetic effects (CV of GCA, Fig. 3). Additive genetic variation in cellulose content was higher than that found by Jett *et al*. [30]. Lignin had little to no GCA variance for both juvenile and transition wood (Fig. 3).

To genetically improve cellulose content and average fiber length, controlled crosses or vegetative propagation techniques should be used to capture nonadditive genetic variance (*6*). Dominance genetic effects (SCA) explained about 50% of total genetic variance for these two traits in transition wood. Lowering lignin content through breeding will involve considerable effort and cost. In this study with limited sample size, selecting the family with the lowest lignin content would cause less than a 2% reduction in lignin as compared to selecting the family with the highest lignin content (Fig. 2).

Cellulose content had a high genetic correlation with wood density, suggesting that increasing the wood density would increase cellulose content (Table I). Similarly, coarseness and fiber length had positive genetic relationships with density. Because wood density can be measured more easily, it may be possible to use wood density as a selection criterion by which to improve other traits indirectly. However, wood density correlated positively with lignin in this study, and selecting for higher wood density might also increase lignin content.

Latewood fibers are thicker and longer than earlywood fibers, and they result in higher values for α-cellulose content and coarseness [31].

We observed a high, positive genetic correlation (0.99) between fiber length and coarseness, indicating that long fiber is associated with a thicker fiber wall.

Heritabilities

Family heritabilities were moderate to high for all chemical and morphological traits, except for the lignin content of juvenile wood, which could not be estimated. Genetic parameters estimated from this study may be biased as a result of the small population (6 parents and 14 full-sib families) because of the genetic drift. Since one field test was measured, heritabilities may be over estimated due to possible genotype by environment interaction. Nevertheless, these moderate estimates suggest that genetic improvement for cellulose content and fiber length could be realized through genetic improvement. Heritabilities for fiber length from this study were similar to those found by Loo *et al.* (*12*) for loblolly pine. Loo *et al.* reported 0.31 and 0.37 for individual heritabilities and 0.45 and 0.51 for family heritabilities for transition wood at two sites. Increasing the cellulose content will result in the production of more paper per cubic meter of wood.

Heritabilities of transition wood may be more meaningful than those of juvenile wood, because they are closer to the age (age six) at which most selections are made for the North Carolina State University Industry Tree Improvement Coop [3]. As transition wood is formed, the wood properties become more uniform, which may contribute to more accurate estimates of genetic parameters. Juvenile wood (Ring 3) seems to be more affected by environmental conditions such as moisture content and resin. For example, the expression of genetic differences for lignin content was observed in transition wood but not in juvenile wood. At Ring 8, genetic differences for lignin appeared to be more important.

Caveats and considerations

The combined measure of a whole wood core may not provide meaningful information on genetic variation on these traits. By averaging over rings, the genetic variation of earlywood and latewood, cannot be determined. This information is important for selection if one component has higher genetic variation (such as a wood trait in latewood at Ring 8). For example, if latewood of ring 8 has considerably higher genetic variation than earlywood, then measuring traits in latewood would be more efficient in improving the trait.

Other considerations should be taken into account before chemical and morphological wood properties are used in a tree-breeding program. The costs for sampling each tree from a progeny test and processing wood samples for chemical analysis in the lab can be prohibitively expensive. New methods for measuring chemical traits that are cheaper and less time-consuming need to be developed. One such method is the use of a near infrared reflectance (NIR) machine to scan the sample to predict the wood properties. The technology has been used on other species, such as eucalyptus, but not for loblolly pine.

The operational use of trees with genetically improved wood properties also poses a problem. Many forest industry companies are selling their land bases for various reasons. The largest gains can be obtained by using the best families with the desired wood properties, if family information in plantations are well documented. While this approach may be simple on industry land, that is not where all the wood is harvested. Private landowners currently provide much of the wood that is used in pulp and paper mills. Genetic differences among families for chemical wood traits provide an opportunity for family forestry. Planting in family blocks will allow the industry to grow individual families for the specific chemical properties needed, but company land bases will need to be maintained.

CONCLUSIONS

Considerable genetic variation was detected for all chemical and morphological traits in this loblolly pine progeny test. Heritabilities were moderate to high for all traits, indicating potential for genetic improvement. High positive genetic correlations between cellulose content, fiber length, and wood density suggested that simultaneous improvement of chemical wood properties and wood density may be possible. Further studies with large population sizes are on the way to confirm the genetic variation and develop breeding strategies for improving these wood quality traits.

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INSIGHTS FROM THE AUTHORS

Intensive silviculture has reduced rotation ages, which has led to increased amounts of juvenile wood. To improve the pulping properties of plantation wood, it is necessary to assess the genetic variation of wood traits that affect paper properties.

In this study, our procedure of using small, nondestructive wood samples was unique. Most studies in the past have required large wood samples and have been destructive to trees. To work on such small samples, we had to develop microanalytical methods, which was the most difficult aspect of our study. These newly developed procedures can be used to screen progeny trees in large-scale tests. In our future studies, more wood samples from other sites will be examined to determine the site effects on wood properties.

In most of the traits measured, we found large genetic variation. The large differences in genetic traits means that we can use selective breeding to bring out the traits we want in the progeny. The idea is to improve the pulping quality of loblolly pine, but the uniformity of the pulp properties will also improve, which will also be beneficial to mills.

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