WOOD DENSITY ASSESSMENT OF DIVERSE FAMILIES OF LOBLOLLY PINE USING X-RAY DENSITOMETRY

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Abstract:--A direct scanning x-ray densitometer was used to measure juvenile wood density characteristics for two 10-year-old plantings of a genetics trial that included 52 open-pollinated families from four provenances of loblolly pine. Both volume production and wood density differed greatly for the two sites. Genetic parameters were estimated for basal area weighted whole-core density, earlywood and latewood density, and percent latewood. All traits were under high genetic control and exhibited strong family differences. Family mean whole-core densities ranged from 441 kg/m^3 to 507 kg/m^3. Site effects had a major affect on all these traits measured accounting for 42% to 73% of total variation, but significant genotype x environment interaction was not detected.

Linear regression models (density = ring number) were fit for individual tree annual earlywood, latewood, and ring densities to determine the rate of change in the traits over the first 10 years. Provenance differences were marginally significant ($p<0.10$) for the slope of the regression line for earlywood density and ring density. The individual tree narrow sense heritabilities for slope ranged from 0.05 to 0.15.

Keywords: Densitometry, *Pinus taeda,* Regression, Heritability, Correlation

INTRODUCTION

Gains in growth rate and quality traits generated by cooperative tree improvement programs have resulted in large increases in plantation productivity and the value of harvested trees (Talbert, et al. 1985). In addition, Jett and Talbert (1982) estimated that cooperators in the North Carolina State University-Industry Cooperative Tree Improvement Program that selected first generation orchard clones on the basis of average or above average wood density achieved a 2.6% gain in the wood density of the resultant improved plantation trees.

Several authors including Jett and Talbert (1982), Zobel and van Buijtenen (1989), and Zobel and Jett (1995) have reported that benefits beyond growth and form improvement can be realized by including wood density in selection strategies for advanced generations. Only a few programs (e.g., Anonymous 1995) have actually incorporated wood density into selection indices. To do so will require additional information describing the genetic and environmental variation of wood density. This paper describes the variation of wood density and related traits for 52 families representing four provenances of loblolly pine.

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MATERIALS AND METHODS

Plant Material

Wood samples for this study were taken from two of the remaining six installations of a loblolly pine provenance–progeny study jointly established by members of the North Carolina State University-Industry Cooperative Tree Improvement Program and the University of Florida Cooperative Forest Genetics Research Program (Table 1). The original objective of the plantings was to determine if two of the southern sources of loblolly pine (Marion County, Florida and Gulf Hammock, Florida) could be incorporated into a single coastal loblolly pine breeding population spanning from South Carolina to Mississippi (Anonymous 1988; Anonymous 1994).

The trials were planted in 1982 and included representative open-pollinated families from four geographic provenances (Figure 1) of loblolly pine: 1) Georgia–South Carolina Atlantic Coastal Plain (ACP), 2) Marion County (MC), Florida, 3) Gulf Hammock (GH) area of Florida located in Levy and Dixie Counties, and 4) Lower Gulf (LG) region of Mississippi and Alabama. These provenances are distinguished largely by geographic separation and the soil types (Vasquez 1993) on which they developed. The seeds for these plantings were produced in provenance-specific first generation open-pollinated seed orchards.

Table 1. Summary of location information.

Test Location	FL	AL
Latitude (N)	31°38'	31°54'
Longitude (W)	81°37'	86°45'
Elevation (ft.)	23	449
Mean Annual Rainfall (in.)	54	56
Mean Annual Temp. (°F)	68	68
Soil Series	Leon	Orangeburg
Soil Drainage Class	Very Poorly	Well
Mean Tree Height (ft.)	34	55
Mean Tree Diameter (in.)	5.4	7.1

Note: Tree growth values reflect age 10 years measurements.

The locations and replications used in the present study were selected based on family representation of the four provenances as affected by mortality and level of rust infection. Every effort was made to attain balance in the dataset. Analysis of 10-year growth data was used to identify three of the five replications at each location having the greatest environmental uniformity.

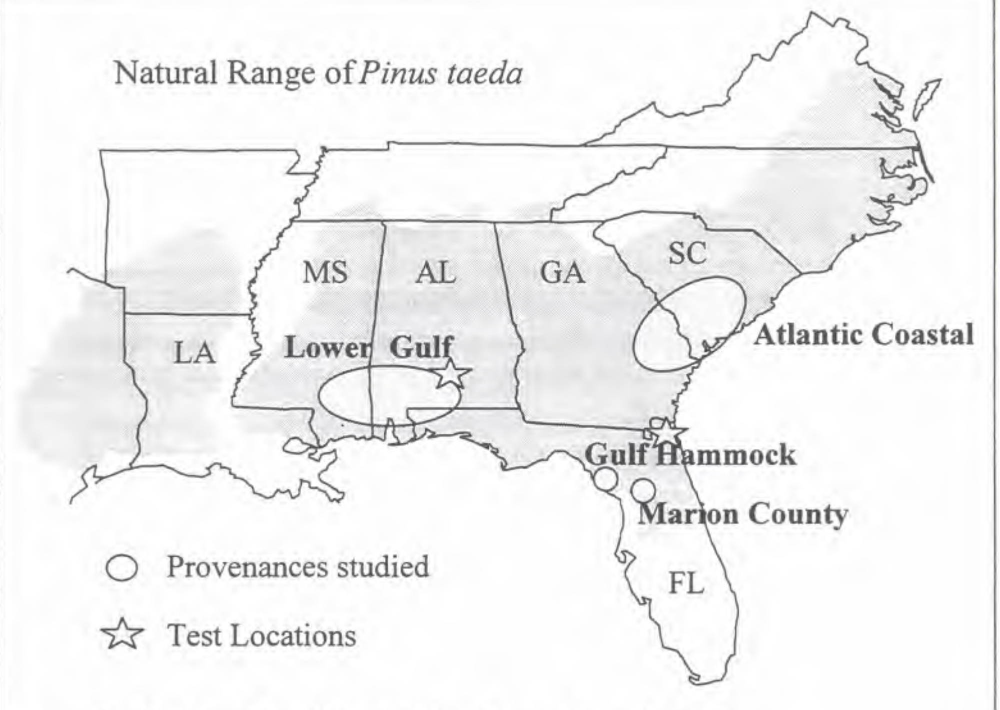

Figure 1. Origin of families and location of genetic tests

Sampling Procedure

Bark-to-bark 12mm increment cores were extracted from up to five dominant or codominat trees from each family in the three replications sampled from each location. Cores were extracted at breast height with minor allowances to avoid the confounding influence of compression wood caused by limbs and fusiform rust *(Cronartium quercuum* [Berk] Miyabe ex Shirai f. sp. *fusiforme).* Trees that were suppressed or had excessive stem rust were not sampled.

Each core was divided at the pith and ovendry weight - green volume unextracted specific gravity was determined (Zobel and van Buijtenen 1989) for one of the radial cores. Results from the analysis of these data (from four test sites) was reported by Belonger et al. (1996). The opposing half of the core was prepared for density data collection using the direct scanning x-ray densitometer housed in the tree improvement laboratory at North Carolina State University. Details of sample preparation methods and use of the densitometer can be found in Harding (1996).

Statistical Analysis

In general, the analyses were directed toward an evaluation of the variation available among the families. Since all families studied are well adapted to the Atlantic Coastal and Gulf Coastal Plains within the natural range of loblolly pine, they were viewed as a single population in terms of deployment. However, the full model for the test design used in this investigation is shown below as it was used to estimate total variation in wood density traits and for provenance level analyses. The varcomp procedure of SAS (SAS Institute Inc. 1988) was used to estimate variance components.

$$Y_{ijklm} = \mu + L_i + B(L)_{ij} + P_l + PL_{li} + PB(L)_{lji} + F(P)_{kl} + LF(P)_{ikl} + F(P)B(L)_{ijk} + \varepsilon_{ijklm}$$

Where: Y_{ijklm} = individual observation for the kth half-sib family of the lth provenance in the jth block of the ith location; μ = fixed experimental mean; L_i = random effect of the ith location; $B(L)_{ij}$ = random effect of the jth block nested within the ith location; P_l = random effect of the lth provenance; PL_{li} = interaction effect of the lth provenance with the ith location; $PB(L)_{lbi}$ = interaction effect of the lth provenance with the jth block within the lth location; $F(P)_{kl}$ = random effect of the kth half-sib family of the lth provenance; $LF(P)_{ikl}$ = interaction effect of the ith location with the kth half-sib family of the lth provenance; $F(P)B(L)_{kpji}$ = interaction effect of the kth half-sib family of the lth provenance with in the jth block nested within the ith location; ε_{ijklm} = within plot residual error term.

Genetic Parameter Estimates

Individual tree heritabilities were calculated according to Falconer (1989) assuming the trees of a given family are related as half-siblings (Squillace 1974) using the formula:

$$h_i^2 = \frac{G}{P} = \frac{4\sigma^2{}_F}{\sigma^2{}_F + \sigma^2{}_{FL} + \sigma^2{}_{BF(L)} + \sigma^2{}_e}$$

Where: h_i^2 = individual tree heritability estimate; G = additive genetic variance; P = phenotypic variance among individuals; $\sigma^2{}_F$ = family variance component; $\sigma^2{}_{FL}$ = variation due to the interaction of families with locations; $\sigma^2{}_{BF(L)}$ = variation due to the interaction of families and blocks within locations; $\sigma^2{}_e$ = within plot variance.

[he genetic correlation between traits was estimated as:

$$r_{Ga,b} = \frac{COV_{Fa,b}}{\sqrt{\sigma^2{}_{Fa} * \sigma^2{}_{Fb}}}$$

Where: $COV_{Fa,b}$ = family covariance between traits a and b = $(\sigma^2{}_{Fa+b} - \sigma^2{}_{Fa} - \sigma^2{}_{Fb}) / 2$, and $\sigma^2{}_{Fa+b}$, $\sigma^2{}_{Fa}$, $\sigma^2{}_{Fb}$ = family variance for traits a+b, a, and b, respectively.

Standard errors of heritability and genetic correlation estimates were computed using methods of Becker (1992).

Regression Approach

Loblolly pine is known to have two distinct phases of wood production: juvenile and mature (Zobel and van Buijtenen 1989; Clark and Saucier 1991). The period of juvenility (Figure 2) normally lasts from the time wood is produced at the pith for about 10 growing seasons. During that time the rate of increase in ring density and latewood density is very similar and nearly linear. Earlywood density shows very little change over time and has a slope near zero.

Simple linear regression was used to characterize the density profile for earlywood, latewood, and average ring density. Regressions were run on individual tree data following the model:

$$\text{Density (Y)} = b_0 + b_1(\text{ring number from pith})$$

Variation associated with the first year of growth was eliminated by removing the first growth ring from the analysis as is common in such studies. The first ring from the pith is generally omitted due to the occasional presence of knots and resin pockets and because the pith of the tree is not always included in the core.

The regression coefficients (intercept and slope) were analysis using the general linear model and varcomp procedures of SAS (SAS Institute Inc. 1988) to evaluate effect differences and to estimate variance components.

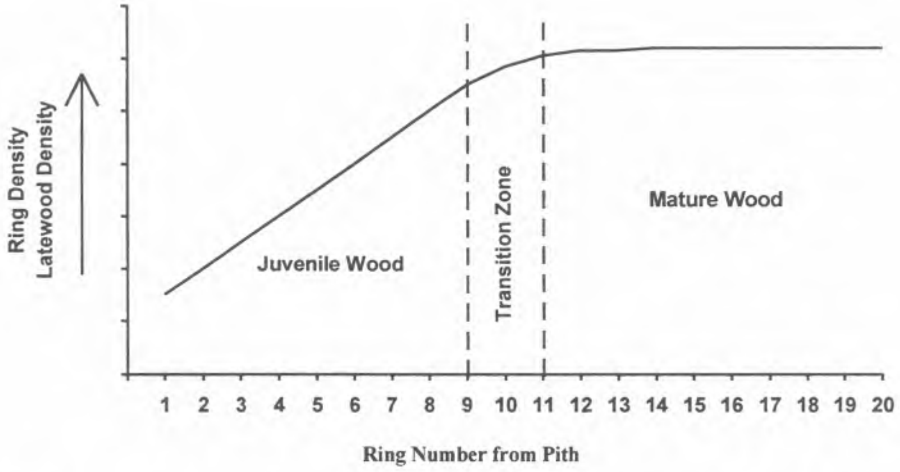

Figure 2. Generalization illustrating the change in wood density with age and the linear aspect of juvenile wood formation. The slope of the "juvenile wood" portion of the curve was calculated for each individual tree.

RESULTS AND DISCUSSION

Contribution to Total Variation

Whole-core Densities

Ring density in this study was most affected by environmental influences, namely test location, accounting for 73% of the total variation. This agrees with findings by Belonger et al. (1996) following analysis of the gravimetric data from four of the six provenance/progeny trials. Similar results have been reported by numerous authors (Zobel and van Buijtenen 1989). Site effects accounted for more than 50% of total variation for the four major density related traits except latewood density (42.1%). Location means for all density related traits studied are shown in Figure 3. Latewood percentage showed the largest difference (29.4%) comparing the two sites.

Provenance level contributions to total variation were near equal for the four major traits and each was less than 2%. No provenance contribution was detected for earlywood density. The greatest contribution from family effects were found for earlywood and latewood densities, 4.0% and 4.1% respectively. There was no evidence of GxE as provenances and families were very stable across the two sites that differed greatly in productivity (Florida = 6.1 ft^3/tree; Alabama = 2.5 ft^3/tree).

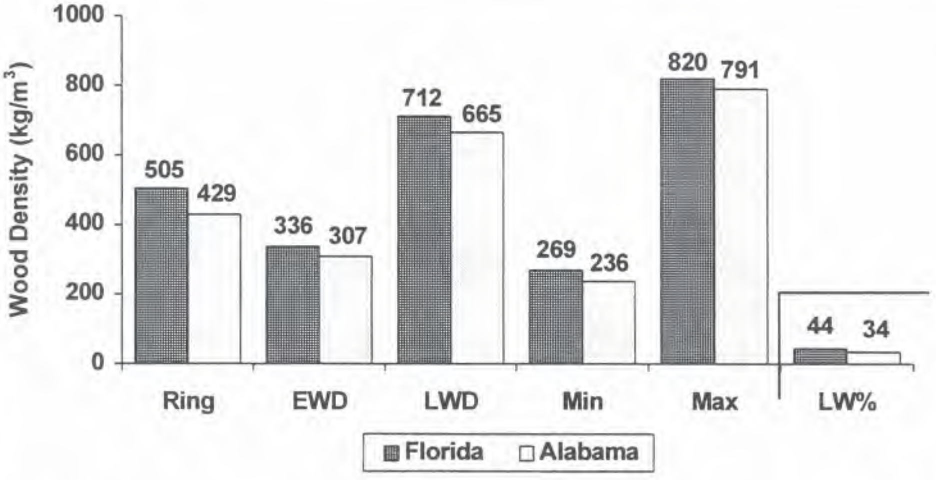

Figure 3. Comparison of wood density traits by location. (Ring=avg. density; EWD=avg. earlywood density; LWD=avg. latewood density; Min=minimum density; Max=maximum ring density; LW%=latewood percentage)

Regression Analysis

Contributions to the variation in the intercept and slope coefficients for the regression of wood density on ring number contrasted dramatically with each other (Table 2). The range in values for the contribution to the intercept approximated those for whole core densities except that test location had a smaller impact and the tree to tree variation was higher. The location and tree to tree variation values stand out when comparing the values for the intercept to those for the slope of the regression line. It's reasonable for the contributions of the intercept terms to approximate those for the whole core densities since the intercept could be used as a surrogate for the mean whole core values.

The lack of contribution of test location to variation in the slope of the regression line suggests that the environment in which trees are grown has minimal impact on year to year increase in ring and latewood densities during the juvenile period of wood formation. This is true if the assumption regarding the linear relationship of wood density to ring number for the growth period studied is correct.

Table 2. Percent contribution of environmental and genetic effects to total variation in the ntercept and slope terms for the regression of wood density on ring number from pith. Loc=location; Rep=replication; Prov=provenance; Fam=family.)

	Intercept			Slope		
Provenance	Ring	Earlywood	Latewood	Ring	Earlywood	Latewood
Loc	49.0	34.4	28.2	0.0	0.0	0.0
Rep(Loc)	1.2	5.2	0.6	9.8	4.4	0.0
Prov	3.5	0.5	0.0	1.7	1.9	0.3
Prov*Loc	0.0	0.0	2.1	0.0	0.0	0.0
Prov*Rep(Loc)	2.1	0.8	4.3	3.8	2.0	4.6
Fam(Prov)	1.2	1.3	3.4	0.6	1.7	0.7
Loc*Fam(Prov)	0.0	0.0	0.0	0.5	1.2	0.0
Rep(Loc) *Fam(Prov)	3.2	6.9	1.9	3.0	0.0	4.6
Within plot	39.7	50.9	59.6	80.6	88.8	89.7

Genetic Effects and Parameter Estimates

Whole-core Densities

Provenance means for wood density and growth traits are shown in Table 3. These results agree with Jett et al. (1991) and Byram and Lowe (1988) who reported that faster growing southern sources of loblolly pine have lower wood densities when grown with more northern sources on the same site. Belonger et al. (1996) reported a slight negative genetic correlation between wood density and growth for the same families studied here.

As reported elsewhere the relative proportion of earlywood to latewood (latewood percentage) is the primary determinant of overall ring density; especially after age five (Megraw 1985). In this study the two provenances with higher ring densities had latewood percentages 6.5% higher than the two less dense Florida sources. This is explained in part by the association between the cessation of height growth and the onset of latewood production at the provenance level (Jayawickrama et al. 1997). Because height growth of the more southern sources of loblolly pine extends longer into the fall, less latewood is produced prior to dormancy. The estimated genetic correlation between ring density and latewood percentage in the present study was 0.977 (0.008) which further illustrates the importance of this trait.

Individual tree narrow sense heritabilities were calculated for ring, earlywood, and latewood densities and latewood percentage and were 0.39, 0.32, 0.40, and 0.34, respectively. The heritabilities may be inflated by provenance effects, but reflect the amount of variation available to tree breeders within southern sources of loblolly pine.

Table 3. Provenance means for whole core density and growth traits at age 12 years. Sources joined by the same letter are not significantly different at p=0.05.

	Wood Density (kg/m³)					
Provenance	Ring	Earlywood	Latewood	Latewood %	Height (ft.)	DBH (in.)
Atlantic Coastal	479 a	321 a	693 a	41 a	45.3 a	6.6 a
Lower Gulf	480 a	321 a	697 a	40 a	42.7 b	6.3 a
Gulf Hammock	465 b	325 a	679 b	38 b	46.9 a	6.9 a
Marion County	463 b	320 a	685 ab	38 b	45.9 a	6.7 a

Regression Analysis

The linear regression of wood density on ring number produced a typical relationship among the three density traits (Figure 4). Families had significantly different intercept and slope terms as expected based on the contributions to their variation (Table 2).

Differences among provenances for the intercept term for ring density (p=0.022) were equivalent to those for whole core ring density (p=0.012). However, the level of significance for provenance effects on the intercept term for earlywood and latewood was reversed relative to the whole core traits. The intercept for latewood was not different among the four provenances (p=0.655), but source effects were marginally significant (p=0.064) for earlywood.

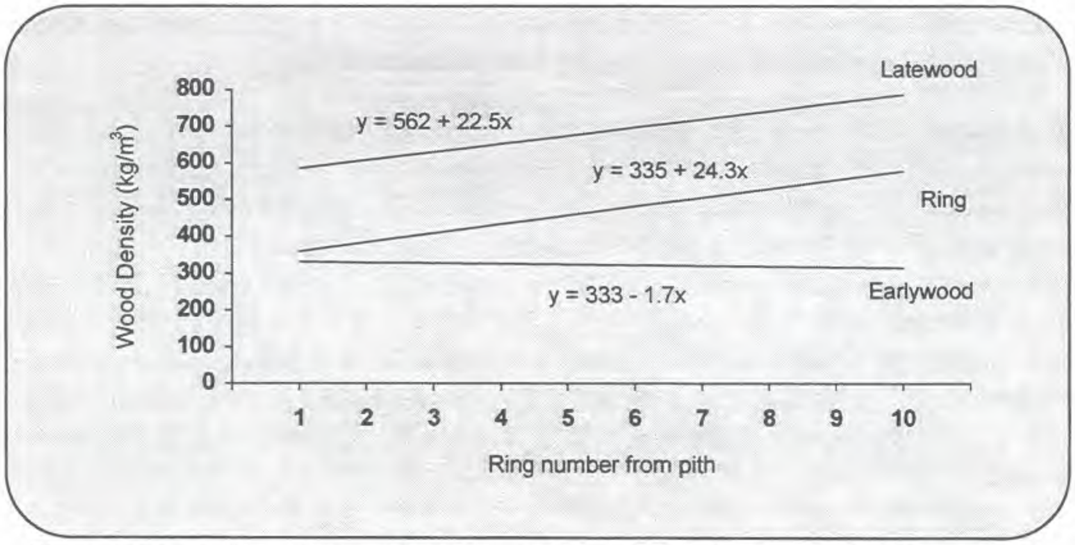

Figure 4. Linear change in wood density over time. The equations summarize the average effect of age from pith on wood density on an individual tree basis. (y=wood density, x=ring number.)

Family differences for the intercept term within the provenances were greatest for ring density and latewood density ($p<0.01$) and marginal for earlywood ($p=0.79$). No important GxE was detected at the provenance or family level.

The analysis of the slope term showed marginal provenance differences for ring density ($p=0.089$) and earlywood density ($p=0.064$), but no significant family effects. The Lower Gulf provenance had a higher average intercept and a smaller average slope compared to the other three provenances. As was the case throughout all analyses reported here no significant GxE was detected at the provenance or family level. The individual tree narrow sense heritabilities for the slope term were low for ring, earlywood, and latewood density were 0.10, 0.15, and 0.05, respectively.

The slopes of the regression lines indicate the rate of increase in wood density over time during the period of juvenile wood formation. In fact, analyses were not performed to clearly confirm this assumption and some families may have entered the transition zone while others may have begun to produce mature wood (Figure 2). Additional analyses (Belonger 1997) will investigate this relationship more closely.

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