HERITABILITY ESTIMATES FOR LOBLOLLY PINE WOOD SPECIFIC GRAVITY BASED ON CONTROL-POLLINATED GENETIC TESTS

W. J. Lowe and T. D. Byram'

Abstract. Specific gravity is an important wood quality trait that affects both the quality and quantity of pulp and solid wood properties. To determine the heritability and age-age relationships for specific gravity, increment cores were collected at DBH (1.4 m) from four control-pollinated loblolly pine genetic tests that were at least 20 years old. These tests contained 93 families representing 23 different parents. Unextracted specific gravity was determined on core segments that included the first five years from the pith, rings six to 20 years and the total core. The estimates of general combining ability were significant for all age segments in each test; however, none of the estimates for specific combining ability were significant. Family heritability estimates for the first five years from the pith averaged 0.58 and ranged from 0.38 to 0.75 among the four genetic tests. For the six to 20-year core segments, family heritability estimates averaged 0.73 and ranged from 0.62 to 0.79. The coefficient of genetic prediction between the two age segments averaged 0.50. Selection at age five for specific gravity would be approximately 68 percent as efficient as direct selection to increase age six to 20-year specific gravity.

Keywords: *Pinus taeda* L., density, coefficient of genetic prediction.

INTRODUCTION

Specific gravity is an important wood quality trait that affects the forest products industry. Increasing specific gravity can impact both the quantity and/or quality of pulp and solid wood products. Both selection (van Buijtenen 1962, McKinley et al. 1982, Talbert et al. 1982, Williams and Megraw 1994) and silvicultural treatments (Megraw 1985, Zobel and van Buijtenen 1989) can influence wood specific gravity.

Wood specific gravity for loblolly pine *(Pinus taeda* L.) has been reported to be under moderate to high genetic control (review Zobel and van Buijtenen, 1989, pp. 259-261). However, most of these studies were based on open-pollinated genetic tests of relatively young ages (ten years or less). Talbert et al. (1982) reported ten-year results from a control-pollinated loblolly pine genetic test. They concluded that juvenile wood specific gravity was under strong additive genetic control ($h^2 = 0.84$) and that a genotype by environment interaction was of little importance. The lack of any meaningful genotype by environment interaction for loblolly pine wood specific gravity was confirmed by Byram and Lowe (1988) and Jett et al. (1991).

Wood specific gravity has not been commonly used as a selection criteria in developing breeding populations for loblolly pine in the southeastern United States. The lack of juvenile-mature relationships and different economic importance for various products have hindered the incorporation of

'Associate Geneticist, Texas Forest Service and Assistant Professor, Department of Forest Science, Texas Agricultural Experiment Station; and Assistant Geneticist, Western Gulf Forest Tree Improvement Program, Texas Forest Service, College Station, TX 77843-2585.

wood specific gravity into selection criteria. Recently, increased consideration is being given to the development of breeding populations that include specific gravity as a selection criteria. Reliable juvenile mature relationships are needed to incorporate wood specific gravity into a breeding strategy. Williams and Megraw (1994) reported moderate to high positive age-age relationships for loblolly pine using several techniques.

The objectives of this study were to determine the heritability pattern and age-age relationship of wood specific gravity for the first 20 years in control-pollinated genetic tests of loblolly pine and evaluate the efficiency of early selection.

MATERIAL AND METHODS

Samples were collected from four control-pollinated loblolly pine genetic tests located in Ashley County, Arkansas. The genetic tests ranged from 25 to 33 years in age. All of the tests were established using a randomized complete-block design with families planted in block plots. The number of replications varied from three to six and the number of seedlings planted for each control-pollinated family per replication ranged from 9 to 64 among the tests. All of the tests had been thinned at least once.

Unextracted wood specific gravity was determined on 11 mm diameter bark to bark increment cores that were collected at DBH (1.4 m). Knots, resin pockets or other visible abnormalities were avoided. The cores were divided into two age segments: 1) the first five years from the pith, and 2) 6 to 20 years. The maximum moisture content procedure as described by Smith (1954) was used to determine specific gravity for each age class. Specific gravity was also determined for the total core. Approximately 20 cores were collected from each control-pollinated family in each test. A total of 93 families representing 23 different parents were sampled. The number of crosses ranged from three to twelve per parent utilizing a partial-diallel mating scheme in each genetic test.

Variance components, including general combining ability (GCA) and specific combining ability (SCA) were estimated using DIALL (Schaffer and Usanis 1969). Heritability and the coefficient of genetic prediction were determined on a family basis. Family heritability was calculated as (van Buijtenen 1976):

$$h^2_{fam} = \frac{\sigma^2_{GCA}}{\sigma^2_{GCA} + \sigma^2_{SCA} + \sigma^2_e / r}$$

Where σ^2_{GCA} is the general combining ability variance, σ^2_{SCA} is the specific combining ability variance, σ^2_e is the error variance, and r is the harmonic mean of the number of replications. Nonsignificant ($p \leq .25$) and negative estimates were set to zero.

Baradat (1976) defined the coefficient of genetic prediction (CGP) between two traits as follows:

$$CGP = \frac{Cov(xy)}{P(x)\,P(y)}$$

Where Cov(xy) is the additive genetic covariance between x and y; P(x) and P(y) are the phenotypic standard deviation of x and y, respectively.

Pearson correlation coefficients were calculated among GCA estimates for

parents that occurred in more than one test (SAS Institute 1989).

RESULTS AND DISCUSSION

The DIALL analysis for each test indicated significant effects for GCA ($p > .05$) for all of the age classes but no significant SCA for any of the classes (Table 1). The lack of significance of SCA for the first five year core segments supported the conclusion of Talbert et al. (1982) that non-additive variation was unimportant in the inheritance of juvenile wood specific gravity for loblolly pine. The same pattern of genetic variation (no significant SCA) was evident in this study for both the whole core (20 years) and older age segment (6-20 years). This study supports the conclusion that wood specific gravity is mainly influenced by additive genetic effects.

Table 1. Variance components[1] for wood specific gravity by genetic test and age class.

Variance Component[2]	Test Number 102	103	123	258
A. First Five-Years.				
Replications	0.008	0.071	0.004	0.023
GCA	0.235	0.038	0.100	0.103
SCA	0.005	0.000	0.000	0.000
Error	0.222	0.360	0.398	0.250
h^2_{fam} (S. E.)	0.75(.34)	0.38(.27)	0.50(.32)	0.67(.36)
B. Age 6 to 20 Years.				
Replications	0.126	0.006	0.018	0.035
GCA	0.156	0.126	0.212	0.120
SCA	0.008	0.000	0.008	0.000
Error	0.135	0.198	0.478	0.179
h^2_{fam} (S. E.)	0.75(.34)	0.79(.40)	0.62(.37)	0.77(.40)
C. Total Core.				
Replications	0.047	0.047	0.002	0.016
GCA	0.151	0.086	0.149	0.086
SCA	0.000	0.000	0.003	0.000
Error	0.108	0.212	0.287	0.162
h^2_{fam} (S. E.)	0.81(.36)	0.71(.37)	0.66(.38)	0.73(.37)

'All variance components were multiplied by 1000.

[2]All estimates of GCA were significant at the 5 percent level of confidence. None of the SCA estimates were significant at the 25 percent level of confidence.

Family heritability estimates for the first five year core segments averaged 0.58 and ranged from 0.38 to 0.75 among the four tests (Table 1). These estimates were smaller than the estimate of 0.84 reported by Talbert et al (1982) for juvenile wood. Because unextracted specific gravity was determined on older trees in this study, differential resin deposits may have contributed to reducing the heritability estimates. Heritability estimates ranging from 0.55 to 0.76 for extracted specific gravity at age three were reported by Williams and Megraw (1994). Again, their estimates tend to be slightly larger than those obtained in this study; however, their estimates were based on extracted samples.

Average heritability estimates for the 6 to 20 year segment and the total core increased to 0.73 (range 0.62 to 0.79) and 0.73 (range 0.66 to 0.81) among the four tests, respectively. These heritability estimates are biased upwards because they are based on single genetic tests, and the genotype by environment interaction cannot be determined. This bias should not be a major factor because genotype by environment interactions are reported to be negligible for wood specific gravity in loblolly pine (Byram and Lowe 1988, Jett et al. 1991, and Williams and Megraw 1994). These heritabilities indicate that loblolly pine wood specific gravity is under strong genetic control and can easily be manipulated in a breeding program.

The CGP values between the first five year and the 6 to 20 year core segments ranged from 0.44 to 0.52 among the four tests and average 0.50 (Table 2). These estimates indicated that approximately 68 percent of the gain made by direct selection for wood specific gravity on the 6 to 20 year core segment could be made by selecting for specific gravity in the five year core. The effect of a common environment could have biased these estimates. Average values for the CGP's increased to 0.60 and 0.70 when the specific gravity for the first five year core segment and the 6 to 20 year core segment were compared to the total core specific gravity. Repeated measurements on a sample collected from a single tree contain biases because of a common environment and an autocorrelation effect. The GCP values for both age segments with the total core specific gravity are inflated because of these biases.

Table 2. Coefficients of genetic prediction (CGP) for wood specific gravity among age classes by genetic test.

	Test Number			
Traits	102	103	123	258
First 5 Years and 6 to 20 Years	0.51	0.51	0.52	0.44
First 5 Years and Total Core	0.69	0.51	0.57	0.61
6 to 20 Years and Total Core	0.72	0.74	0.64	0.69

Although represented by different crosses, seven parents were in common between tests 102 and 103. Correlation coefficients among specific gravity GCA estimates for parents in both tests were significant for all age classes (Table 3). This is important because the GCA estimates for wood specific gravity for the common parents were based on a different set of crosses in each genetic test. Furthermore, These correlations are free from both the biases of autocorrelation and a common environment because the cores were collected from different genetic tests.

Table 3. Correlation coefficients among wood specific gravity GCA estimates for seven common parents among age classes in genetic tests 102 and 103.

	Test 102		
Test 103	First Five Years	Years 6 to 20	Total Core
First five years	0.82*	0.93**	0.96**
Years 6 to 20	0.76*	0.94**	0.94**
Total Core	0.82*	0.93**	0.96**

*Significant at the five percent level of confidence.
**Significant at the one percent level of confidence.

The large positive correlations among parents across genetic tests indicate that the bias due to a common environment should not be a major factor inflating the CGP values. Both the CGP values and correlations indicate that selection based on juvenile wood specific gravity would be effective in changing mature wood specific gravity in loblolly pine. The results of this study support the conclusions of Williams and Megraw (1994) describing the efficiency of early selection for wood specific gravity. The large positive correlations among GCA estimates for parents in different genetic tests support the reported lack of any meaningful genotype by environment interaction (Byram and Lowe 1988, Jett et al. **1991).**

SUMMARY

Four control-pollinated loblolly pine genetic tests greater than 20 years in age were sampled to determine the inheritance pattern of wood specific gravity and explore age-age correlations. Eleven mm diameter increment cores were collected bark to bark at DBH (1.4 m) on the sample trees. Unextracted wood specific gravity was determined on the first five rings from the pith, rings 6 to 20, and the total core. The results of the study were as follows:

1. Loblolly pine wood specific gravity was mainly controlled by additive genetic effects. Average family heritability across the four genetic tests was 0.58 for the first five year core segments and 0.73 for both age segments 6 to 20 and the total core specific gravity.

2. Specific combining ability was not important in the inheritance of wood specific gravity for any age class.

3. Early selection would be an efficient procedure to improve mature wood specific gravity in loblolly pine. According to this study, selection on juvenile specific gravity (five years from the pith) would be 68 percent as efficient as direct selection in improving specific gravity at age 6 to 20 years.

ACKNOWLEDGEMENTS

The authors gratefully acknowledge Georgia-Pacific Corporation for maintaining the genetic tests used in this study. Also, appreciation is expressed to Boise Cascade Corporation, Champion International Corporation, Georgia-Pacific Corporation, International Paper Company and Temple-Inland Forest

Products for additional financial support for this project. We also thank C. Williams for her helpful review.

LITERATURE CITED

Baradat, P. 1976. Use of juvenile-mature relationships and information from relationships in combined multitrait selection. Proc. IUFRO Joint Meeting on Advanced Generation Breeding. Bordeaux, France. pp. 121-138.

Byram, T. D. and W. J. Lowe. 1988. Specific gravity variation in a loblolly pine seed source study in the western gulf region. For. Sci. 34(3):798-803.

Jett, *J.* B., S. E. McKeand, and R. *J.* Weir. 1991. Stability of juvenile wood specific gravity of loblolly pine in diverse geographic areas. Can. *J.* For. Res. 21:1080-1085.

McKinley, C. R., W. J. Lowe and *J.* P. van Buijtenen. 1982. Genetic improve ment of wood specific gravity in loblolly pine *(Pinus taeda* L.) and its relation to other traits. Proc. TAPPI Research and Development Division Conf. pp. 153-158.

Megraw, R. A. 1985. Wood quality factors in loblolly pine. TAPPI Press, Atlanta, GA 89 p.

SAS Institute, Inc. 1989. SAS/STAT Guide Release 6.03, Ed. SAS Institute Inc., Cary, NC, 1028 p.

Schaffer, H. E. and R. A. Usanis. 1969. General least squares analysis of diallel experiments. A computer program - DIALL. Genet. Dept. Res. Rep. No. 1, NC State Univ., Raleigh, NC, 61 p.

Smith, D. M. 1954. A comparison of maximum moisture content and water displacement methods for determination of specific gravity. USDA, For. Prod. Lab, Rep. 2033, 4 p.

Talbert, *J.* T., F. E. Bridgwater, *J.* B. Jett and S. Jahromi. 1982. Genetic parameters of wood specific gravity in a control-pollinated loblolly pine progeny test. Proc. TAPPI Research and Development Division Conf. pp. 179-182.

van Buijtenen, *J.* P. 1962. Heritability Estimates of wood density in loblolly pines. TAPPI 45:602-605.

van Buijtenen, J. P. 1976. Mating designs. Proc IUFRO Joint Meeting on Advanced Genetic Breeding. Bordeaux, France. pp 11-27.

Williams, C. G. and R. W. Megraw. 1994. Juvenile-mature relationships for wood density in *Pinus taeda.* Can. J. For. Res. 24:714-722.

Zobel, B. *J.* and J. P. van Buijtenen. 1989. Wood variation: Its causes and control. Springer-Verlag, Berlin, Heidelberg. 363 p.