

tory explains the high frequency of segregating progenies.

The Hardy-Weinberg equilibrium may be violated. Trees in a mature forest are sometimes found to be more heterozygous than expected. Plustrees as used in this study are selected for their good performance and may be more heterozygous than expected from gene frequencies. Some epistatic action might be able to cause distortion like the observed.

#### Overall segregations

For selfings 27 +: 130 is found in segregating progenies, if the obvious deviator H 1010 is excluded, and this is in acceptable agreement with expected 3:1.

For outcrosses 107:98 is found, which is in acceptable accordance with an expected mixture of 1:1 and 3:1.

#### Concluding Remarks

Despite several such factors as: (1) The deficit of individuals giving only offspring "+" and  
(2) The strange behaviour of S 3244 and H 1010

which rules out that simple monohybrid inheritance is a general rule, there is still the general accordance of individual segregations with expectation and the many cases where selfed parents 0 gave exclusively progeny 0 strongly indicates that in many genetic environments the character behaves as a simple dominant Mendelian one.

Although good fit is found in many families, still significant exceptions are found, and this emphasises the risks in assuming the general validity of simple Mendelian se-

gregation just because it is found in some crosses, as is frequently done.

That such a complicated character as isoabienol often behaves as a simple Mendelian character demonstrates that forest tree breeding should probably not assume all valuable genes to behave according to the rules of quantitative genetics.

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## Genetic Variation in the Time of Transition from Juvenile to Mature Wood in Loblolly Pine (*Pinus taeda* L.)

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#### Abstract

Wood samples were collected from a 25-year old loblolly pine progeny test in east Texas. Specific gravity and tracheid length were determined for two-ring segments from the pith to ring 22. Values for each property were plotted against age to determine the age of transition from juvenile to mature wood. The mean ages of transition were 11.45 and 10.30 years for specific gravity and tracheid length respectively. There was no correlation between the age of transition for specific gravity and tracheid length. Narrow sense heritabilities estimated on a family mean basis for age of transition of each property were sufficiently high to suggest moderate gains are possible. Genetic correlations between the age of transition for each charac-

ter and height and diameter of the trees at age 20 were negative, suggesting that fast growth may be related to early age of transition. Genetic and phenotypic correlations between age of transition and whole core specific gravity and tracheid length were negative.

**Key words:** specific gravity, tracheid length, juvenile wood, mature wood, loblolly pine, heritability, transition age.

#### Zusammenfassung

In einem 25 Jahre alten *Pinus taeda*-Nachkommen-schaftstest in Ost-Texas wurden Holzproben entnommen und das spezifische Gewicht sowie die Tracheiden-Länge jeweils für 2 Ring-Segmente vom Kern bis zu Ring 22 bestimmt. Diese Werte wurden für jede Eigenschaft dem Alter nach aufgezeichnet, um den Übergang vom Holz der Jugendphase zu demjenigen der Altersphase zu bestimmen. Das Mittel des Überganges lag für das spezifische Gewicht

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bei 11,45 und für die Tracheidenlänge bei 10,39 Jahren. Hierbei war keine Korrelation zwischen dem Alter des Überganges für das spezifische Gewicht und dem für die Tracheidenlänge zu erkennen. Für das Alter des Überganges jeder Eigenschaft auf der Basis der Familienmittelwerte waren die Schätzwerte für die Heritabilitäten im engeren Sinne genügend hoch, um einen mäßigen Gewinn für möglich halten zu können. Zwischen dem Alter des Überganges für jede Eigenschaft und der Höhe sowie dem Durchmesser der Bäume im Alter 20 waren die Korrelationen negativ, was darauf schließen läßt, daß Schnellwüchsigkeit zu einem Übergang in frühen Jahren in Beziehung stehen kann. Genetische und phänotypische Korrelationen zwischen dem Alter des Überganges und dem spezifischen Gewicht des Gesamtkernes und der Tracheidenlänge waren negativ.

### Introduction

Loblolly pine (*Pinus taeda* L.) is the primary timber species grown in the southern United States due to its extensive range, good growth characteristics, and desirable wood properties. The species is well suited to short rotation forestry because of rapid early growth exhibited during the sapling stage. Genetic improvement and silvicultural practices are designed to further reduce rotation length while increasing productivity. As the rotation age is reduced, however, the relative proportion of juvenile wood in the harvest increases.

Juvenile wood which is formed near the pith throughout the bole of a tree is significantly different from wood produced in the outer rings, termed mature wood. Juvenile wood characteristically has low specific gravity, short tracheids, large fibril angle, and a lack-luster appearance when compared with mature wood (ZOBEL *et al.* 1972, PEARSON and GILMORE 1971, BENDTSEN 1978). Specific gravity, tracheid length and fibril angle have been identified as key indicators of wood quality for various end products because of their impact on strength, pulping quality and shrinkage (MITCHELL 1965, WAHLGREN and SCHUMANN 1972, McELWEE 1963). Thus the relative proportions of juvenile and mature wood reaching a manufacturer significantly influences the quality of the finished product.

The relationship between wood properties and wood age (distance from the pith) in loblolly pine has been described as a trend characterized by rapidly increasing specific gravity and tracheid length with age, levelling off at 7 to 15 rings from the pith (ZOBEL and McELWEE 1958, SAUCIER and TARRAS 1969, McMILLIN 1948, PEARSON and GILMORE 1980). BENDTSEN (1978) stated that it is possible for one character such as cell length to reach maturity before another character such as cell wall thickness. ZOBEL and McELWEE (1958) indicated that both specific gravity and tracheid length, plotted against age produce curves of similar form.

Heritabilities reported for specific gravity and tracheid length in juvenile wood of loblolly pine are relatively high. Heritability estimates for specific gravity of trees from three to eight years of age range from .56 to 1.0 (STONECYPHER and ZOBEL 1966, VAN BUIJTENEN 1962, GOGGANS 1964, STONECYPHER *et al.* 1973). Heritability estimates for tracheid length from trees of the same age range were reported by GOGGANS (1964) and STONECYPHER *et al.* (1973) to be .44 and .97 respectively. Thus it should be possible to develop trees with more desirable juvenile wood properties than is generally found in young trees if there is significant genetic variation in the population. ZOBEL and BLAIR (1976) reported, however, that high density juvenile wood did not have comparable physical properties to mature wood. An alter-

native to breeding for trees with high specific gravity, long-fibred juvenile wood may be to breed trees for a shorter juvenile wood production phase.

The objective of this study was to examine the possibility of breeding loblolly pine for a reduced juvenile wood phase. Genetic variation in the time of transition from juvenile to mature wood was estimated for a population of loblolly pine from east Texas.

### Materials and Methods

Twelve millimeter increment core samples were collected in December 1981, from a 25-year old loblolly pine open-pollinated progeny test in east Texas. The test was planted at two locations with 16 families randomized within each of three blocks at location one, near Rusk, and two blocks at location two, near Nacogdoches<sup>1)</sup>. The parent trees had been selected from throughout east Texas for high or low specific gravity extremes. Each family consisted of a row of 24 trees in each block when the plantations were established. The rows have subsequently been thinned to an average of nine trees per row at location one and 12 trees per row at location two. The 15 families that were sampled for this study had at least five surviving trees in each of two blocks at each location. One radial increment core was taken from the north side of each of five trees per family from each block at a height of 1.4 meters above the ground. Cores were examined for branch or knotwood and were used only if they consisted entirely of clear wood.

Each core was divided into two-ring segments beginning at the pith. Prior to specific gravity determination, extractives were removed using a modified ASTM (1970) procedure described by GOGGANS (1962) and a modified soxhlet extractor apparatus described by BOWNE *et al.* (1977). Specific gravity was determined by the maximum moisture content method described by SMITH (1954). A small section of latewood was removed from the second ring of each two year segment for determination of tracheid length. The sample was macerated following a procedure described by BUXTON (1967) and the fibers were stained with safrannin 0 dye. Thirty whole tracheids per segment sample were selected at random and measured to the nearest .05 mm.

### Analysis

The time of transition from juvenile to mature wood was estimated separately for specific gravity and tracheid length. Initially it was assumed that both specific gravity and tracheid length, when plotted against age, would produce a curve as shown in Figure 1 (ZOBEL and McELWEE 1958).

Thus the point of transition could be identified by fitting two regressions to the data for each tree and finding the

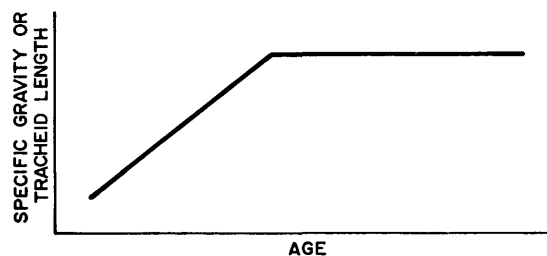


Figure 1. — Expected form of the transition from juvenile to mature wood in loblolly pine. Adapted from ZOBEL and McELWEE (1958).

<sup>1)</sup> The material was made available by the Western Gulf Forest Tree Improvement Cooperative, the Texas Forest Service and Texas A & M University.

point of interaction for the two lines with best fit (smallest error sum of squares).

All data did not conform to the expected pattern, however, and the most reasonable value resulting from a combination of three methods was used as the age of transition. The first method involved fitting two regressions, without forcing an intersection of the lines. This was done eight times for each tree with each iteration dividing the samples into two groups beginning with rings less than or equal to age four in the juvenile group and rings greater than age four in the mature group up to rings less than or equal to age 18 in the juvenile group and rings greater than age 18 in the mature group. Increments were by two years. The age of transition was estimated as the age at which the second group (mature wood) began for the model with best fit determined by the smallest error sum of squares.

A second method was applied in cases where the best fit using method one resulted in the mature group having negative slope. This occurred in about 15% of the cases. Method two differed from method one in that the slope of the mature group was held constant at zero, with the assumption that the mature wood values fluctuate around the constant mean. In several cases where the best fit resulted in the juvenile group having negative slope and the mature group having a positive slope, the time of transition was estimated by visual examination of the data points plotted over age. The ages estimated by the regression methods were checked against the plots to ensure that the regression model used was the most reasonable with respect to the data.

Specific gravity and tracheid values for each segment were averaged over all families and each was plotted against age to yield an average curve. Phenotypic correlations using Pearson's product moment method (Statistical Analysis System 1979) and genetic correlations (FALCONER 1980) were computed for the following pairs of characters:

1. Age of transition for specific gravity with age of transition for tracheid length
2. Age of transition for each trait with the value of that trait at transition.
3. Age of transition with height and diameter of the trees at age 20.
4. Age of transition for specific gravity with parent tree specific gravity<sup>2</sup>).
5. Specific gravity at the point of transition with parent tree specific gravity.

The mean age of transition for each trait was calculated for each family. Analyses of variance were computed for age of transition for each trait using the following models for locations pooled and by location respectively.

$$y_{ijk1} = u + l_j + r_{ij} + f_k + (fl)_{ik} + p_{ijk} + w_{ijk1} \quad (1)$$

$$y_{ik1} = u + r_j + f_k + p_{jk} + w_{jk1} \quad (2)$$

where  $y_{ijk1}$  = the  $i^{\text{th}}$  tree in the  $k^{\text{th}}$  family in the  $j^{\text{th}}$  replicate of location  $i$

$y_{jk1}$  = the  $j^{\text{th}}$  tree in the  $k^{\text{th}}$  family in replicate  $j$

$u$  = the general mean

$l_j$  = the location effect

$r_{ij}$ ,  $r_j$  = the replicate effect

$f_k$  = the family effect

$(fl)_{ik}$  = the family x location interaction effect

$p_{ijk}$ ,  $p_{jk}$  = the plot effect

$w_{ijk1}$ ,  $w_{jk1}$  = the within plot error

Variance components were estimated from the analysis of variance and family mean and individual tree heritabilities were calculated for age of transition for each character and for specific gravity at the point of transition. Standard errors associated with the heritability estimates were approximated (KENDALL and STUART 1958). The estimated heritabilities were based on the assumption that the open-pollinated families consisted of half-sibs. Heritabilities were calculated as follows:

$$h_f^2 = \frac{\sigma_f^2}{\sigma_f^2 + 1/2 \sigma_{f1}^2 + 1/4 \sigma_{fr(1)}^2 + 1/20 \sigma_e^2} \quad (3)$$

$$h_i^2 = \frac{4\sigma_f^2}{\sigma_f^2 + \sigma_{f1}^2 + \sigma_{fr(1)}^2 + \sigma_e^2} \quad (4)$$

Where  $h_f^2$  = estimated narrow sense heritability by family mean

$h_i^2$  = estimated narrow sense heritability by individual tree

$\sigma_f^2$  = family variance component

$\sigma_{f1}^2$  = family x location interaction variance component

$\sigma_{fr(1)}^2$  = family x replicate in location variance component

$\sigma_e^2$  = among progeny variance component

Expected individual tree breeding values were calculated independently for specific gravity and tracheid length for the three trees having the shortest juvenile phase in each of the two families with the shortest average juvenile phase. Expected breeding values were calculated as follows (FALCONER 1980).

$$E(B. V.) = [(1-r)/(1-t)]Pw + [(1+(n-1)r)/(1+(n-1)t)]Pf \quad (5)$$

Where E(B. V.) = Expected breeding value

$r$  = genetic correlation between individuals

$t$  = intraclass correlation; in this case, 1/4 additive variance divided by total variance

$Pw$  = deviation of individual from family mean

$n$  = number of individuals in each family

$Pf$  = deviation of family from population mean.

An expected breeding value provides a means for estimating the deviation of an individual's future progeny from the population mean. In the above form it can be used to predict a response to combined family and individual tree selection.

## Results and Discussion

Individual plots for specific gravity and tracheid length over age varied considerably from the expected shape. The plots could be divided into four categories based on the configuration of the points (Figure 2). Forty-five percent of the specific gravity plots and 65% of the tracheid length plots fit the expected curve. Twenty-five percent of the specific gravity plots showed a discontinuity or a very abrupt change from juvenile to mature wood and a large number of the plots for both traits, 16% of specific gravity and 29% of tracheid length, continued to increase consistently through ring 20. Due to the construction of the regression models, age 20 was used as the age of transition in the latter cases. In some cases, the rate of increase in

<sup>2</sup> Growth data from the trees at age 20 and parent tree specific gravity was made available by the Western Gulf Forest Tree Improvement Cooperative, the Texas Forest Service and Texas A & M University.

tracheid length abruptly slowed but a constant "mature" tracheid length was not attained. Here the age of transition was identified as the point where the rate of increase in tracheid length declined. Thirty-one specific gravity plots and nine tracheid length plots showed a tendency for decreasing values with age in the mature wood. This was assumed to be a random fluctuation around an actual slope equal to zero.

Specific gravity, averaged over all trees, was plotted over age and produced a sigmoid curve, with a period of juvenile wood extending to age six, a transition period of rapidly increasing specific gravity extending from age six to approximately age 14 and mature wood from age 14 to age 22 (Figure 3). Average tracheid length, when plotted over age (Figure 4) yielded a picture that was similar to the expected shape with rapidly increasing tracheid length from age two to age 10 and a more gradual increase in length from age 10 through age 22.

Phenotypic and genetic correlations were computed for a number of pairs of characters, and are presented in Table 1. Phenotypic and genetic correlations between age of transition for specific gravity and the age of transition for tracheid length were very low. The data indicate that there is not a specific age where all wood properties express maturity. The onset of mature wood production in a loblolly pine tree must be considered relative to the wood property of interest. Phenotypic correlations for the age of transition with height and diameter of the trees at age 20 were not significant at the .05 level for either specific gravity or tracheid length. Genetic correlations were strong and negative, however, indicating that selection for fast growing trees may have the effect of shortening the juvenile phase of wood specific gravity and tracheid length. Phenotypic correlations were significant and positive between the age of transition for each wood property and the value of that property at the point of transition, but genetic correlations were less than .10. This would suggest

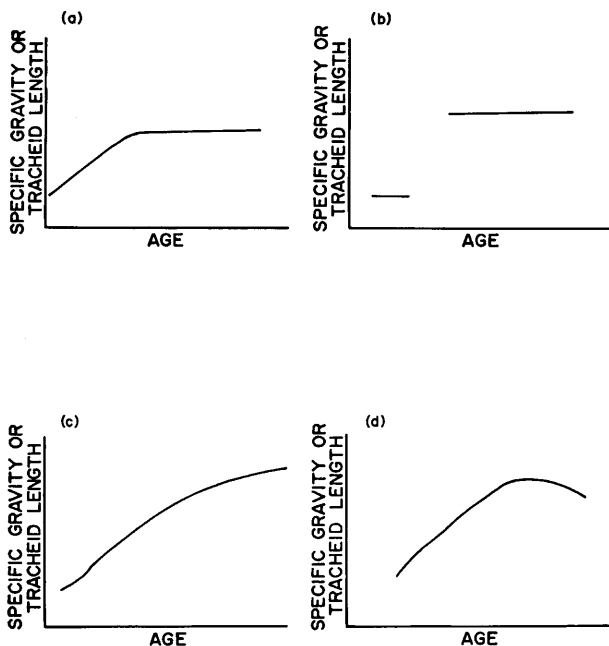


Figure 2. — Generalized shapes of the plots of specific gravity and tracheid length over age: (a) 45% of specific gravity, and 65% of tracheid length plots, (b) 25% of specific gravity and 1% of tracheid length plots, (c) 16% of specific gravity and 29% of tracheid length plots, and (d) 10% of specific gravity and 3% of tracheid length plots.

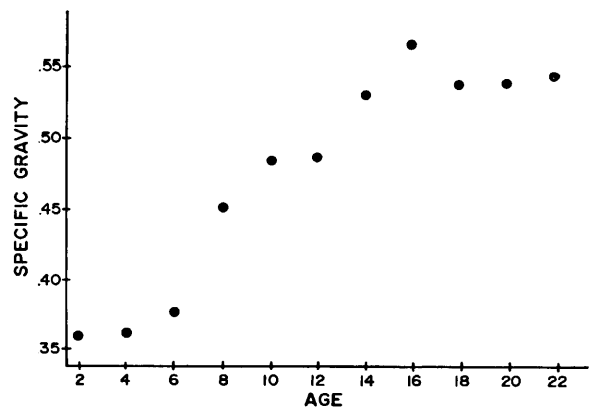


Figure 3. — Specific gravity averaged over 300 trees plotted against age.

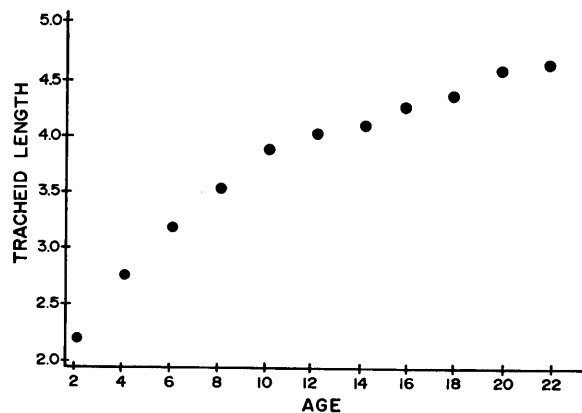


Figure 4. — Tracheid length averaged over 300 trees plotted against age.

that selection for early maturity should not have a negative effect on mature values for specific gravity or tracheid length.

There was no correlation between the age of transition for specific gravity and the parent tree specific gravity. Thus the mode of selection of the parents should not cause bias in heritability estimates for age of transition for specific gravity. The age of transition for specific gravity was negatively correlated with whole core specific gravity. The phenotypic correlation ( $r_p$ ) was  $-.12$  and the genetic correlation ( $r_A$ ) was  $-.68$ . Mature wood specific gravity had a positive phenotypic correlation ( $r_p = .13$ ) but a negative genetic correlation ( $r_A = -.22$ ) with the time of transition. The time of transition for tracheid length was negatively correlated with whole core tracheid length ( $r_p = -.25$ ) and with mature tracheid length ( $r_p = -.08$ ). The correlations are low but indicate a tendency for the whole core or mature wood specific gravity and tracheid length to increase as age of transition decreases.

The mean age of transition for specific gravity was 11.5 years (Table 2). The minimum age was four years and the maximum age was 20 years. The mean age of transition for tracheid length was 10.4 years with a minimum of six years and a maximum of 20 years. The wide range in the age of transition for both properties indicates broad phenotypic variability. The mean specific gravity at the age of transition was .53 and the mean tracheid length at transition was 4.09. Family means ranged from 9.8 to 13.0 for age of transition of specific gravity (Table 3). Family means for age of transition for tracheid length ranged from 8.7 to 12.3 years. Texas family 4041001 had the earliest age of

Table 1. — Phenotypic ( $r_p$ ) and genetic ( $r_A$ ) correlations among age of transition for specific gravity (SG Age) and tracheid length (TL Age), the values of the parameters at the point of transition (SG, TL), specific gravity of the parent trees (PSG) and height (Ht20) and diameter (Dia20) of the trees at age 20.

	TL Age	SG	TL	PSG	Ht20	Dia20
SG Age						
$r_p$	.03	.51*	.06	-.04	-.10	-.06
$r_A$	-.12	.07	.00		-1.37	-.61
TL Age						
$r_p$		.02	.56*	.07	-.09	-.03
$r_A$		.10	.00		-.43	.01
SG						
$r_p$			-.04	.26*	-.25*	-.26*
$r_A$			.00		-1.08	-1.07
TL						
$r_p$				-.02	.11	.04
$r_A$					.00	.00

\* significant at the P = .05 level

transition for both specific gravity and tracheid length.

Analysis of variance results are presented in Table 4. Although the among family variance pooled over locations was not significant at the .05 level for specific gravity transition age, it was the closest to significance among the sources of variance. There was significant family  $\times$  location interaction for transition age of tracheid length, resulting from several changes in family ranking between the two locations. When each location was analyzed separately the family variation was significant at each location.

Variance components were estimated and narrow sense heritabilities were calculated on a family mean ( $h^2_f$ ), and an individual tree ( $h^2_i$ ) basis for age of transition for specific gravity over locations, and age of transition of tracheid length both over locations and by individual locations. Heritabilities with associated estimates of standard errors are presented in Table 5. The heritability estimate for specific gravity at the age of transition may be biased upward since there was a significant phenotypic correlation between this trait and parent tree specific gravity. The heritability estimate for tracheid length at the age of transition was negative and is therefore assumed to be close to zero.

Family mean heritability estimates for age of transition for both characters appear sufficiently high to allow moderate gains through family selection or combined selection based on family and individual tree heritabilities. Expected breeding values were calculated for the three individuals having the shortest juvenile wood phase in the two top ranked families for each property. The mean expected breeding value for the three top individuals for specific gravity from the families ranked first and second were

Table 2. — Means, standard deviations (S.D.) and maximum and minimum values for age of transition for specific gravity (SG Age) and tracheid length (TL Age), and values of each parameter at transition.

Character	Mean	S. D.	Max	Min
SG Age	11.45	3.20	20	4
SG	.53	.06	.73	.40
TL Age	10.39	3.61	20	6
TL	4.09	.48	5.54	2.94

Table 3. — Family mean ranking for age of transition for specific gravity (SG Age) and tracheid length (TL Age).

SG Age	Family	TL Age	Family
9.8	4041001	8.7	4041001
10.1	4401034	9.0	4021002
10.8	4061001	9.4	4051002
10.8	4051002	9.6	4051001
10.9	4021001	9.8	4061003
11.1	4011001	9.8	4021004
11.4	4051001	10.0	4031002
11.4	4031001	10.2	4061001
11.4	4021003	10.7	4031001
11.6	4031002	10.9	4201001
11.9	4201001	11.0	4021001
12.2	4021002	11.2	4011001
12.6	4031004	11.5	4401034
12.8	4061003	11.7	4021003
13.0	4021004	12.3	4031004

Table 4. — Analysis of variance for age of transition for specific gravity, (a), tracheid length over locations, (b), and for tracheid length by locations, location 1, (c), and location 2, (d).

Source	d. f.	(a) Specific gravity		(b) Tracheid length	
		F	P>F	F	P>F
Location	1	0.48	0.56	1.81	0.31
Replication	2	1.38	0.25	2.81	0.06
Family	14	1.80	0.14	1.53	0.22
Family x location	14	0.82	0.65	2.37	0.03
Family x rep(location)	28	1.22	0.21	0.47	0.99
Error	240				

Source	d. f.	(c) Location 1		(d) Location 2	
		F	P>F	F	P>F
Replication	1	0.00	1.00	13.20	0.00
Family	14	3.08	0.02	2.89	0.03
Family x replication	14	0.50	0.93	0.44	0.95
Error	120				

Table 5. — Family mean and individual tree heritability estimates for specific gravity at the age of transition (SG) and for the age of transition for specific gravity (SG Age) and tracheid length (TL Age in loblolly pine wood with associated standard errors (s.e.).

Character	$h^2_f$	s. e.	$h^2_i$	s. e.
SG				
Over locations	.52	.11	.30	.04
SG Age				
Over locations	.36	.38	.12	.06
TL Age				
Over locations	.34	.57	.11	.14
Location 1	.51	.15	.37	.20
Location 2	.45	.16	.31	.22

4.10 and 3.45 respectively. Thus, theoretically, progeny produced from a mating of one of the three trees from the first family with the population at random could be expected to have a juvenile wood phase 2.05 years shorter for specific gravity than the population mean. If these three trees were mated with the three in the second ranked family, the progeny could be expected to have a juvenile wood phase lasting 3.77 years less than the population mean of 11.43 years.

The mean expected breeding values for age of transition of tracheid length for the three best trees in the two top

ranked families were 4.37 and 4.48 respectively, implying a possible reduction in juvenile wood phase among progeny of a cross between these two groups of trees of 4.42 years.

The selection intensities implied by the above estimates are improbably high, but it serves to demonstrate that considerable gains could be made. It is important to realize that the reported heritability estimates are based on the assumption that all of the open pollinated progeny are half-sibs. Further, the assumptions that there are no correlations among pollen parents and no correlations between pollen and seed parents, are implicit in the genetic models. Any or all of these assumptions may be violated when open pollinated progeny are used to estimate half-sib covariances, with the probable result that heritabilities will be slightly over-estimated (SQUILLACE 1974, NAMKOONG 1966).

### Conclusion

The age of transition from juvenile wood to mature wood in loblolly pine can be estimated only with reference to a particular wood property, such as specific gravity or tracheid length. When each character is considered independently, there is evidence of additive genetic variance influencing the time of transition among loblolly pine of east Texas. Estimated family mean heritabilities of transition age for specific gravity (.36) and tracheid length (.34—.51) are sufficiently high to suggest moderate gains can be achieved by selection on a family mean basis or by combined selection based on family mean and individual tree information.

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## Experimentally Synthesized Allotetraploids in Eucalyptus

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### Summary

Colchicine induced allotetraploidy in the genus *Eucalyptus* has been reported, which perhaps seems to be the first report of its kind in this genus. Allotetraploids (*E. tereticornis* × *E. grandis*, 4n = 44) were compared with diploids (F<sub>1</sub> *E. tereticornis* × *E. grandis* 2n = 22) for various morphological traits. The allotetraploids have quite distinct leaves, flowers, fruits, seeds etc. as compared to diploids and have exhibited vigour in certain traits. Allotriploids were also synthesized by crossing allotetraploids with diploids using *E. tereticornis* and *E. grandis* as pollen parents. Allotriploids have registered faster rate of growth as com-

pared to diploids and tetraploids at nursery stage and are under study for their future growth behaviour and other traits of economic value. This biotechnique could be utilized for the production of fast growing allopolyploids and genetically improved prototypes for different uses.

**Key words:** Induced Allotetraploids, Induced Allotriploids, Inter-specific F<sub>1</sub> hybrid - *Eucalyptus grandis*. HILL ex MAIDEN, *E. tereticornis* Sm.

### Zusammenfassung

In der Gattung *Eucalyptus* wird über eine durch Cholchizyn induzierte Allotetraploidie berichtet, die vielleicht die erste dieser Art in dieser Gattung ist, über die berichtet wird. Allotetraploide (*E. tereticornis* × *E. grandis* mit

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