

# Inheritance and Correlations of Juvenile Characteristics in Loblolly Pine (*Pinus taeda* L.)

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## Introduction

Improvement of forest trees requires information about the variation and the inheritance patterns of the desirable traits. Knowledge of characteristics such as the inheritance of juvenile wood properties, growth characteristics, and resistance to fusiform rust of loblolly pine (*Pinus taeda* L.) is of vital importance and of major economic value to tree improvement in the southeastern United States.

It is commonly accepted (ZOBEL et al., 1965; ZOBEL and McELWEE, 1958; DADSWELL, 1960) that the portion of the stem which is close to the pith (juvenile wood) possesses distinctly different cellular structure and properties, than wood closer to the bark. Such juvenile wood has lower specific gravity, shorter tracheids, thinner cell walls, less cellulose, more hemicellulose, greater fibril angle and a greater amount of compression wood than does mature wood.

Although juvenile wood has many disadvantages, it was not considered to be too important in the past because it constituted only a small portion of the total volume of timber grown under long rotations. In recent years, however, because of the high cost of land and establishing new plantations, high rates of interest, and demands for cellulose, there is a strong movement towards shorter rotations for pine (ZOBEL, 1970). As the rotation age is lowered, the proportion of juvenile wood increases and becomes more and more important in determining the quality of the end product.

Investigations in loblolly pine have shown that a strong negative correlation ( $r = -0.835$ ) exists between stand age and percent juvenile wood (ZOBEL et al., 1965). For example, a 48 year-old stand contained 8 percent juvenile wood, while another stand on a similar site but 18 years old had 47 percent juvenile wood by volume. This indicates that with rotations 20 years or less juvenile wood will constitute a major portion of the volume utilized. Since quantity and quality of the end product is determined to a great extent by specific gravity, low values for this characteristic in juvenile wood are important.

Occasional loblolly trees are observed with high juvenile wood specific gravity. If this is inherited strongly enough it could be of considerable importance, so a study was initiated to determine the possibility for developing strains of loblolly pine with more desirable juvenile wood specific gravity. The data presented here are from a 5 year-old open pollinated progeny test of loblolly pine in a study by International Paper Company and North Carolina State University to determine the inheritance of juvenile wood properties.

The objectives were:

1. To investigate the possibility of developing strains of loblolly pine with more suitable juvenile wood specific gravity than is normally produced.
2. To determine the magnitude of any correlations which might exist between wood growth and form.
3. To estimate heritability values for the characteristics studied.

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## Materials and Methods

### Experimental Design and Materials

The progeny test of loblolly pine (*Pinus taeda*) in which the present study was made is located near Georgetown, South Carolina, and has been established cooperatively by International Paper Company and North Carolina State University. Detailed description of the parent trees, and planting design was given earlier (ZOBEL et al., 1965; ZOBEL, 1970).

Data were collected for the harvested trees (June, 1970) as well as from the trees left growing to study the following characteristics:

#### Only From Cut Trees

1. Specific gravity of the wood
2. Tracheid length of the wood
3. Moisture content of the wood
4. Total tree height
5. Bark thickness at breast height
6. Total stem volume

#### From All Trees, Cut Plus Left

1. Diameter at breast height (DBH)
2. Straightness of stem
3. Crown form
4. Fusiform (*Cronartium fusiforme*) infection.

### Field Procedures and Measurements

#### Scoring

All trees of the progeny were evaluated for fusiform rust infection by assigning numerical values as follows:

No infection = 1, branch infection = 2, stem infection above 4.5 feet = 3, combination of condition in category 2 and 3 = 4, stem infection below 4.5 feet = 5.

Crown form and straightness were scored. Crowns were judged on the basis of branch diameter, branch angle, branch length and general conformation while straightness was rated on lean, sinuosity, and crook. Scores range from 1 to 6; the best crown and best straightness rated a score of 1 while the worst were scored 6. All such subjective scoring was done by the same individual within each replication.

#### Harvested Trees

A total of 355 trees were cut (three trees within each row plot, or 12 for all four replications). Total height was measured to the nearest 0.1 foot. Two bark readings 180° apart on the stem were taken at breast height and averaged.

Two full cross sectional disks were taken at approximately 5 and 10 feet above ground level. The cross-sections were to 1 to 1.5 inches thick and were free of knots, compression wood, disease and other factors which might bias wood properties.

The volume of the felled trees was derived by using the formula constructed by PERRY and ROBERTS (1964) for loblolly pine seedlings.

In the laboratory forty tracheids were measured from the

5th ring in the first 5 foot disks and specific gravity and moisture content were also estimated by usual methods.

### Statistical Procedures

#### Analysis of Variance-Covariance Technique

Although the initial design of the progeny test was a balanced randomized complete block with 34 families, 4 replications and 3 trees within a plot, missing trees within plots and whole missing plots created difficulties in the estimation of heritability values and genetic correlations. To avoid this, nine families with complete missing plots were deleted from the analyses. The data for the remaining 25 families (unbalanced because of missing trees within plots) were analysed as in *Appendix Table 1*. From these the components of variance and covariance were estimated.

To make biological interpretations of the components the assumptions described by STONECYPHER (1966) and DUDLEY and MOLL (1960) were accepted. The variance among families was interpreted as one quarter of the additive genetic variance and the narrow sense heritability ( $h^2$ ) was calculated on an individual basis. The standard error of the components of variance was computed using the method proposed by ANDERSON and BANCROFT (1952) (formula, as *equation 1, in the Appendix*). The genetic correlations were estimated by the formula in *App., equation 2*.

#### Parent-Offspring Relationships

Regression of offspring on parent was used to estimate heritability for specific gravity and tracheid length. In the open pollinated test the heritability is estimated by twice the offspring on parent regression coefficient (*App., equation 3*). The standard error of the heritability estimates is essential to assess the precision of the estimates and was estimated by the formula (*App., equation 4*) given by FALCONER (1960).

#### Robertson and Lerner Approach

The percentage of infected trees per plot was computed and heritability was obtained using the method (*App., equation 5*) outlined by ROBERTSON and LERNER (1949). This method which enables computation on an individual tree basis, was used by GODDARD and ARNOLD (1966) and BLAIR (1970) to estimate heritability value of resistance to fusiform rust.

## Results and Discussion

### Variation Among Families

The overall means for the characteristics studied their range, standard deviations, coefficients of variation and number of trees per mean are listed in *Table 1*.

#### Wood Properties

From the analyses of the data significant differences among families were found for all wood characteristics (specific gravity, tracheid length, moisture content). The difference between the highest and the lowest specific gravity families of 0.057 (*Table 1*) indicates that the former family produced 3.56 lbs. per cubic feet (57 kg per cubic meter) more wood at 5 years of age than did the lowest specific gravity family; this was surprisingly large difference at this age. For tracheid length, the greatest difference among family means was 0.39 mm which is large enough to affect quality of paper made from juvenile wood.

The variation among families in moisture content was quite large, with a range of 221% to 177%. This indicates that 100 pounds of dry wood can be obtained, from 321 pounds of green wood from the highest moisture content family or from 277 pounds of green wood from the lowest moisture content family. Differences of this magnitude between families of the same age growing under similar environments appear to be genetically controlled. The variation found lends weight to the statement by KELLISON and ZOBEL (1971) that, the variation in moisture content cannot be ignored when wood is bought on a green weight basis.

#### Bark Thickness

Great variability was observed among individual loblolly pine trees of the same age growing under the same environmental conditions (FEDERICK, 1970). In the present study variations from family to family were quite large but these were not statistically significant. The mean family bark thickness ranged from 0.18 inches to 0.28 inches; the overall mean was 0.24 inches. Part of the observed differences in bark thickness were associated with differences in tree diameter, but it was not necessary to adjust to a common diameter since the F-value among families was not significant for the non-adjusted data.

*Table 1.* — Overall means, standard deviation, coefficient of variation, and number of trees for characteristics of the 5 year-old open pollinated progeny test.

Characteristic	Mean	Range	Units	Standard deviation	Coefficient of variation %	No. of trees
Specific gravity	0.326	0.299—0.356		0.023	7.06	355
Tracheid length	2.27	2.01—2.40	mm.	0.148	6.52	355
Moisture content	200.00	177—221	%	20.35	10.18	355
Bark thickness	0.24	0.18—0.28	in.	0.063	26.25	355
Total height	18.2	13.1—20.0	ft.	2.3	12.64	355
Diameter ((DBH)	3.0	2.4—3.4	in.	0.68	22.37	803
Volume	0.554	0.317—0.749	ft. <sup>3</sup>	0.227	40.97	355
Straightness	4.2	3.3—5.5	score	1.07	25.47	803
Crown form	3.7	3.1—4.8	score	0.81	21.71	803
Fusiform infection	1.6	1.0—2.7	score	1.34	81.21	803
Fusiform infection in square root plus one	1.6	—	score	0.35	22.01	803
Fusiform infection <sup>1)</sup>	25.6	3.6—62.9	%	21.76	84.93	125
Fusiform infection in Arcsin transformation	0.27	—	%	0.242	89.62	125

<sup>1)</sup> The analysis of percentage of infected by fusiform, is based on 125 plot means, each plot containing 6 trees.

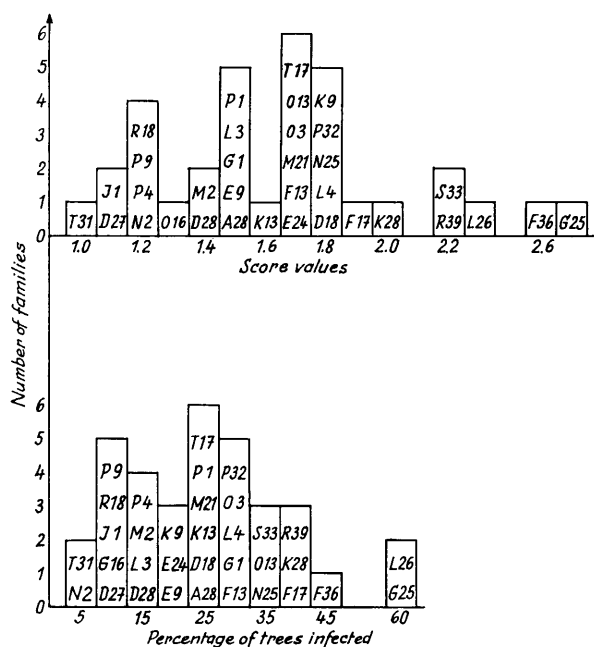


Figure 1. — Distribution of families infected with fusiform rust, based on percentage of trees infected and score values (percentage and score values are strongly correlated with  $r = 0.90$ ).

#### Other Characteristics

Results obtained from the analysis of fusiform rust data confirms the considerable variability which exists among families. The difference between the most and least susceptible ones was found 3.6 to 62.9 percent or in score units, 1.0 to 2.7.

The distribution of individual family means in score units and percentage of infected trees is illustrated in Figure 1.

Significant differences among families were also found for crown form and stem straightness. For growth, only diameter had a significant F-value while the among families differences for height and volume were not significant, in spite of very large differences among their means.

#### Parent-Offspring Relationship

Extracted specific gravity and tracheid length values of the juvenile wood from the parents (7 rings from the pith) were obtained in previous studies. These were compared with the unextracted weighted specific gravity of the whole bole and the tracheid length of the last ring of the 5 year-old open pollinated progeny.

#### Specific Gravity

The unextracted specific gravity of the trees of each family were averaged and regressed on their parent values. It was not necessary to extract the resinous materials from the progeny because as STONECYPHER and ZOBEL (1966) have reported this only results in a small uniform change in young trees. Thus, it is possible to compare the extracted juvenile wood specific gravity of the parents with the unextracted specific gravity of their 5 year-old progeny.

The slope of the regression line (regression coefficient), was significant at the 0.01 level ( $F = 29.78^{**}$ ), indicating that as specific gravity of the juvenile wood of the parent changes a given amount, the specific gravity of their progeny increase or decrease a proportional amount. This is indicative of good inheritance of specific gravity. The parent juvenile wood was plotted against family specific

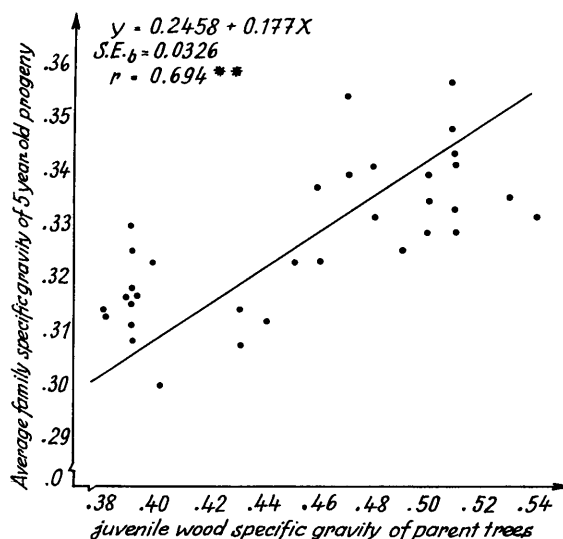


Figure 2. — Relationship of specific gravity of the juvenile wood of the parent trees (7 rings from the pith) to the juvenile wood of their 5 year-old progeny.

gravity (Figure 2); the equation which fits the data is also shown.

The phenotypic correlation between parent juvenile wood specific gravity and their 5 year-old progeny ( $r = 0.694^{**}$ ) was significant at the 0.01 level (Table 2). Thus 48 percent ( $r^2 = 0.48$ ) of the total variation of the progeny specific gravity was associated with parent juvenile wood specific gravity. The magnitude of the phenotypic correlation ( $r = 0.694$ ) is in close agreement with the 0.68 reported by ZOBEL (1970), between the same parents and their three year-old progeny. The values of the regression coefficient and phenotypic correlations found in this study support the hypothesis that progeny from the high juvenile wood parents produce higher juvenile wood specific gravity than do the progeny from low specific gravity parents.

Table 2. — Correlation coefficient ( $r$ ) and coefficient of determination ( $r^2$ ) between parent and 5 year-old open pollinated progeny for juvenile wood specific gravity and tracheid length.

Combination	$r$	$r^2$
Parent juvenile wood specific gravity with their 5 year-old progeny	0.694**	0.481
Parent juvenile wood tracheid length with their 5 year-old progeny	0.175 <sup>ns</sup>	0.025

\*\* Statistically significant at the 0.01 level.

ns Statistically non-significant at the 0.05 level.

#### Tracheid Length

The tracheid length of all trees of each family were averaged and regressed on the juvenile wood tracheid lengths of their parents. The analysis indicated that the slope of the regression line was not significant at the 0.05 level ( $F = 0.805$ ), indicating that the tracheid lengths of the fifth ring are not closely related to their parent juvenile wood tracheid length. As an example, the mean tracheid length of families P-32 and M-21 was 2.40 mm although parent P-32 had juvenile wood tracheid length 2.25 mm and the parent of M-21 family had 3.97 mm.

#### Heritability Estimates from Analysis of Progeny Data

Narrow sense heritability on an individual tree basis has been estimated for all traits by analysis of variance, values

Table 3. — Components of variance<sup>1)</sup>, standard error of the components and heritability estimates for 10 characteristics.

Characteristic	$\sigma_f^2$	S. E. ( $\sigma_f^2$ )	$\sigma_{rf}^2$	$\sigma_w^2$	$h^2$
Specific gravity <sup>2)</sup>	0.059	0.68	0.057	0.387	0.47
Tracheid length	5.104	5.42	5.217	10.880	0.97
Moisture content	80287.000	213.00	35140.000	286540.000	0.80
Total height	595.530	72.85	1371.330	3452.600	0.44
Diameter (DBH)	31.093	10.10	34.399	403.568	0.26
Volume	3.703	6.50	9.827	39.021	0.28
Bark thickness	0.276	1.79	0.780	2.888	0.28
Straightness	169.070	20.50	47.800	811.266	0.66
Crown form	54.810	13.70	106.491	534.021	0.31
Fusiform infection (score)	75.630	17.80	100.480	1662.610	0.17
Fusiform infection (score) in square root plus one	6.778	5.230	14.445	113.399	0.20
Percentage of infected trees (ROBERTSON and LERNER method)					0.26

<sup>1)</sup> All components of variance and standard error  $\times 1000$ .

<sup>2)</sup>  $\sigma_f^2$  estimate of component of variance among families; S. E. ( $\sigma_f^2$ ) standard error of the  $\sigma_f^2$ .

$\sigma_{rf}^2$  estimate component of variance of replications by families interaction.

$\sigma_w^2$  within plot variance;  $h^2$  narrow sense heritability on individual basis.

are shown in Table 3. The standard error of the variance among families, which can be used as an indicator of the accuracy by which the heritability values have been estimated are also presented in Table 3. It was found that for characteristics which were based on 804 observations (trees) the standard error of the components of the among family variance ( $\sigma_f^2$ ) was quite low while for those based on only 355 observations (trees) the standard error was relatively high. An exception was for the moisture content which had a low standard error even when based on 355 trees.

#### Heritability of Wood Properties

The parent trees of the studied progeny were selected for uniformity of juvenile wood specific gravity and therefore one of the necessary assumptions (parents are random members of the population) for making biological interpretations of the derived components of variance was not valid. Such bias tends to exaggerate heritability (SQUILLACE and BENGTSON, 1961), because the estimated family component of variance ( $\sigma_f^2$ ) becomes too high. Analysis of such data for specific gravity gave an overestimated heritability value  $h^2 = 1.1$ . An  $h^2$  value of 1.0 for specific gravity has been reported by VAN BUIJTENEN (1962) in six year-old open pollinated progeny of loblolly pine, whose parents were selected for high and low specific gravity.

In order to obtain an estimation of heritability of specific gravity in which the non-random distribution of the parent trees would be taken into consideration, the method of SQUILLACE and BENGTSON (1961) was applied. They estimated the heritability of gum yield in slash pine (*Pinus elliotii*) progeny from parents selected for high and average gum yield.

It is commonly accepted (MOLL and ROBINSON, 1966; ROBERTSON, 1969; BULMER, 1971; KROW and KIMURA, 1970) that the change in genetic variance resulting from selection decrease as the number of loci which affect the character increase and eventually tend to become zero. For a complex wood characteristic such as specific gravity in which many genes are involved the above assumption seems to be valid. Therefore the parent trees were grouped into high and low specific gravity classes and analyses were performed on their progeny separately. The two analyses were pooled and from the combined analysis a heritability value of 0.47 was obtained. Heritability of the magnitude of 0.50 for specific gravity in loblolly pine, has often been reported (STONECYPHER *et al.*, 1964; GOGGANS 1964).

Heritability values of tracheid length and moisture content were estimated as 0.97 and 0.80, respectively, which indicate that genetic control for these characteristics is strongly additive. High heritability value of the magnitude 0.97 for tracheid length of the 5th ring of loblolly pine has also been reported by GOGGANS (1964).

#### Heritability of Fusiform Rust Resistance

Heritability of resistance to disease was computed on an individual tree basis based on score, using components of variance, and from proportion of trees infected using ROBERTSON and LERNER'S method which adjusts for percentage data. Heritability estimated from score evaluations was 0.17 when raw data were used, and 0.20 when data were transformed using the Arcsin method. When percentage data of infected trees was used the heterogeneity chi-square of infected trees was computed (according to SNEDECOR, 1956). This value was applied in ROBERTSON and LERNER'S formula, with a heritability value of 0.26 being obtained. Values of 0.20 and 0.199 were also reported by BLAIR (1970) and GODDARD and ARNOLD (1966) for young loblolly and slash pine, respectively.

#### Other Heritability Values

Heritability of total height, diameter (DBH), and total bole volume were found to be 0.44, 0.26, and 0.28, respectively. These results are in general agreement with those reported in the literature and show that height is more strongly genetically controlled than diameter. The heritability of bark thickness ( $h^2 = 0.28$ ) is also in close agreement with the 0.33 reported by FEDERICK (1970) for young loblolly pine and indicates that bark thickness is moderately inherited.

For the complex characteristics crown form and straightness a subjective evaluation was made; analyses of the data gave heritability of 0.33 and 0.66 respectively. Because for the straightness an early evaluation is feasible (GODDARD and STRICKLAND 1964) the high heritability estimated here indicates that selection for this characteristic should result in rapid improvement.

#### Heritability Estimated from Regression of Offspring on Parents

Heritability values for specific gravity and tracheid length were estimated from the regression of offspring on parents. Although this method is simple in computation

interpretation of the values estimated are more difficult. Wood of different ages of parent and offspring cannot be directly compared in a regression analysis, because such wood may be quite different at different ages and could be considered as two independent characteristics. This difficulty was overcome by comparing only the juvenile wood of parents (7 rings from the pith) with that of their 5 year-old open pollinated progeny; the 2 year difference between parent and offspring should cause little bias.

Another difficulty, even in wood of exactly the same age, is the different environments under which wood of parent and progeny was formed (ZOBEL, 1964; SQUILLACE, 1967); therefore heritability values reported here can only be applied to selection under conditions existing for the natural stands of the parents. This may explain the relative low heritability values of 0.355 for specific gravity and 0.06 for tracheid length, compared with 0.47 and 0.97, respectively, from analysis of progeny data (Table 4). Thus when selection is made under natural environmental conditions of the parents the expected gain is 35.5 percent of the selection differential for specific gravity and 6 percent for tracheid length for young trees.

The higher  $h^2$  values based upon analyses of progeny data is the result of the lower phenotypic variances. The environment of the site where the progeny were grown was rather uniform and, therefore, the phenotypic variance in the denominator of the heritability formula was reduced, resulting in higher  $h^2$  values. These values can only be applied when selection is done on plantations growing under uniform sites.

Table 4. — Heritability values obtained from offspring-parent regression compared with those obtained by progeny analysis

Characteristic	Regression Offspring-Parent	Progeny Data Analysis
Specific gravity	0.355 ± 0.064	0.47
Tracheid length	0.061 ± 0.068	0.97

#### Relationships Between Characteristics of the Progeny

Progress from selection is dependend on the nature and extend of interrelationships which exist between different characteristics. A measure of the degree of interrelationship is given by the magnitude of phenotypic and genetic correlations.

The components of variance among families, the genetic correlations, phenotypic correlations, and coefficients of determination of 26 combinations of characteristics are presented in Table 5. The genetic correlation of 3 out of 26 combinations (straightness with crown form, specific gravity with bark thickness, height with volume) have been overestimated ( $r_g > 1.0$ ). This is the result of the relatively high error associated with the components of variance of these characteristics. Only those relationships between traits that are of special importance are dicussed below.

#### Relationship Between Specific Gravity — Growth Characteristics — Tracheid Length

The relationship between specific gravity and growth is of great importance because of the economic value of both characteristics. Based on observations of 355 trees, a positive phenotypic correlation coefficient ( $r = 0.242^{**}$ ) was found between specific gravity and volume. Although the coefficient indicates that the faster growing trees have

Table 5. — Estimates of family components of covariance<sup>1)</sup> ( $\sigma_{fii}$ ) genetic correlations ( $r_g$ ), phenotypic correlations ( $r$ ), and coefficients of determination ( $r^2$ ) between the characteristics of 5 year-old open pollinated progeny.

Relationship	$\sigma_{fii}$	$r_g$	$r^2$	$r^2$	D.F.
Specific gravity with moisture content	33.488	-0.509	-0.873**	0.762	353
Specific gravity with tracheid length	-0.103	-0.188	-0.175*	0.031	353
Specific gravity with volume	0.213	0.464	0.242**	0.058	353
Specific gravity with total height	1.332	0.228	0.271**	0.073	353
Specific gravity with diameter (DBH)	0.234	0.017	0.231**	0.053	353
Specific gravity with bark thickness	0.155	1.22	0.267**	0.071	353
Height with moisture content	-2064.400	-0.299	-0.341**	0.116	353
Height with tracheid length	43.380	0.787	0.208**	0.043	353
Height with bark thickness	7.215	0.568	0.637**	0.637	353
Height with (DBH)	118.000	0.867	0.741**	0.549	353
Volume with bark thickness	0.470	0.747	0.721**	0.520	353
Diameter (DBH) with bark thickness	2.032	0.691	0.704**	0.496	353
Height with volume	47.030	3.117	0.847**	0.717	353
Diameter (DBH) with volume	14.893	1.00	0.896**	0.803	353
Diameter (DBH) with crown form	20.267	0.488	0.276**	0.08	803
Diameter (DBH) with straightness	21.990	0.302	0.128**	0.02	803
Diameter (DBH)with fusiform (score)	10.352	0.209	0.275**	0.07	803
Moisture content with bark thickness	-64.880	-0.438	-0.337**	0.113	803
Moisture content with volume	-143.300	-0.265	-0.348**	0.121	353
Moisture content with diameter (DBH)	-165.767	-0.329	-0.341**	0.116	353
Tracheid length with bark thickness	0.255	0.210	-0.024ns	0.000	353
Tracheid length with diameter	7.025	0.554	0.047ns	0.002	353
Tracheid length with volume	3.816	0.006	0.080*	0.006	353
Straightness with crown form	100.465	1.03	0.58**	0.336	803
Straightness with fusiform (score)	7.524	0.067	0.043ns	0.002	803
Crown form with fusiform	9.797	0.153	-0.020ns	0.000	803

<sup>1)</sup> All estimates of covariances × 1000.

<sup>2)</sup> \*\*Statistically significant at the 0.01 level.

\*Statistically significant at the 0.05 level.

ns Statistically non-significant at the 0.05 level.

higher specific gravity, only 5.8 percent of the variation in specific gravity is related to growth.

The average family volume was plotted against the average family specific gravity (Figure 3); it is clear that a fast growing family may have high or low specific gravity. Therefore, it is possible in a selection program to combine fast growth with either high or low specific gravity depending upon the product desired.

The relationship between specific gravity and tracheid length was also studied. Slight negative phenotypic and genetic correlations were found ( $r = -0.175^*$ ,  $r_g = -0.188$ ), indicating that the two traits are essentially inherited independently. Families with high specific gravity may have either long or short tracheids (Figure 4), and it is possible to breed for specific gravity and still maintain the desirable tracheid length.

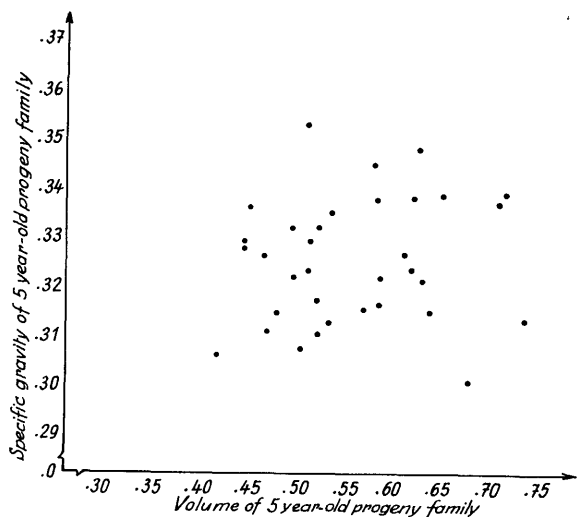


Figure 3. — Relationship of volume in cubic feet to the weighted specific gravity, of 5 year-old progeny family average.

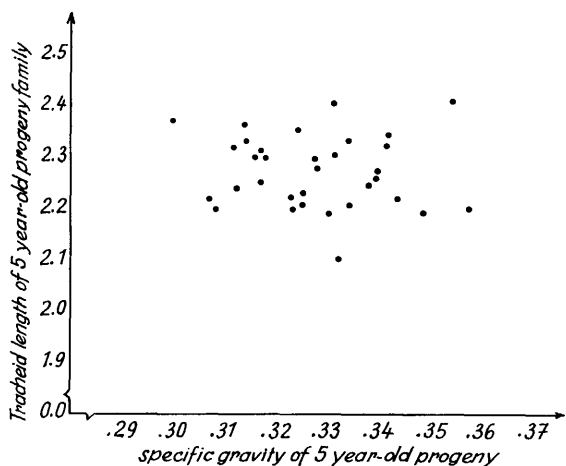


Figure 4. — Relationship of juvenile wood specific gravity (5 year-old) to the juvenile wood tracheid length (5th ring from the pith).

Although significant differences in tracheid length have been found among the families, they have not been associated with the growth rate of the trees. Correlations between tracheid length and stem volume, diameter (DBH), and total height resulted in only the correlation between total height and tracheid length ( $r = 0.208^{**}$ ), being highly significant, although the relationship is very small ( $r^2 = 4.3$ ). Similar weak correlations between these characteristics in loblolly pine have been reported by ZOBEL (1961, 1970).

### Summary and Conclusions

An investigation of 10 characteristics was conducted in a 5 year-old open pollinated progeny test of loblolly pine. The study was located near Georgetown, South Carolina, at International Paper Company, Eight Oaks Seed Orchard. The progeny test included 34 families replicated in four blocks of 12 tree rows. The data were collected from 355 cut and 816 uncut trees. Specific gravity, tracheid length, moisture content, total height and bark thickness were measured on the cut trees. Both cut and uncut trees were evaluated for straightness, crown form, fusiform rust infection and diameter (DBH).

Phenotypic and genetic correlations between the characteristics as well as heritability values were estimated.

Positive phenotypic and genetic correlations were found between specific gravity and growth characteristics. The phenotypic correlations, based on 353 degrees of freedom, for specific gravity and volume ( $r = 0.242^{**}$ ), specific gravity by height ( $r = 0.271^{**}$ ), and specific gravity by diameter ( $r = 0.231^{**}$ ) were significant at the 0.01 level. However, the "r" values were of small magnitude and practical speaking, a meaningful relationship between them is nearly non-existent. Slight but significant negative correlations (genetic and phenotypic) were found between specific gravity and tracheid length; the phenotypic correlation was  $r = -0.175^*$ . No relationship was found between tracheid lengths and growth characteristics. Crown form and straightness were related ( $r = 0.58$ ), indicating that trees with straight stems tend to have better crown form.

The parent-offspring relationship of juvenile wood specific gravity and tracheid length was a major objective of the present study. Regression analyses of offspring on parent values showed the regression coefficient of specific gravity to be highly significant ( $F = 29.78^{**}$ ), and the coefficient of tracheid length to be non-significant ( $F = 0.807$ ). Correlation coefficients were also computed between offspring-parent for specific gravity with  $r = 0.694^{**}$ , and between offspring-parent tracheid length  $r = 0.157^{ns}$ . Results indicate the possibility of developing young trees with high specific gravity by selecting parents with high juvenile wood specific gravity.

Heritability values from analyses of progeny data ranked from 0.17 (fusiform infection) to 0.97 (tracheid length). Heritability values for specific gravity by progeny analysis was 0.47 while from offspring-parent regression 0.335. Tracheid length  $h^2$  for progeny analysis was 0.97 but dropped to 0.06 for offspring-parent regression. Therefore, it appears that juvenile wood tracheid length is strongly affected by the environment and selection under natural stands for juvenile wood tracheid length will give little improvement; on the other hand, selection to change juvenile wood specific gravity is feasible even when it takes place in natural stands. Under plantation conditions, in which the environment is rigidly controlled, both characteristics will respond well to selection.

The size of the offspring-parent correlation coefficient and the high heritability of juvenile wood specific gravity, combined with the weak relationship between specific gravity and volume, indicate that it is feasible to develop a strain of loblolly pine with high specific gravity juvenile wood that also grows rapidly.

**Key words:** *Pinus taeda*, juvenile wood, specific gravity, tracheid length, inheritance, genetic correlation, phenotypic correlation, variances, moisture content, *Cronartium fusiforme*.

### Literature Cited

- ANDERSON, R. L., and A. T. BANCROFT: *Statistical Theory in Research*. McGraw-Hill Company, Inc., New York, 1952. — BLAIR, L. R.: Quantitative inheritance of resistance to fusiform rust in loblolly pine. Ph. D. Thesis, Dept. of Forest Management, N. C. State Univ., Raleigh, 1970. — BULMER, G. M.: The effect of selection on genetic variability. *American Naturalist* 105 (943): 201—211 (1971). — CROW, J. F., and M. KIMURA: *An introduction to population Genetics Theory*. Harper and Row, New York, 1970. — DADSWELL, E. H.: *Tree Growth-Wood Property Inter-relationships*. Proc. of a special field institute in forest biology. School of Forest Resources, N. C. State Univ., Raleigh, 1960. — DUDLEY, W. J., and R. H. MOLL: Interpretation and use of estimates of heritability and genetic variances in plant breeding. *Crop Science* 9: 257—261 (1969). — FALCONER, R. S.: *Introduction to Quantitative Genetics*. The Ronald Press Co., New York, 1960. — GODDARD, R. E., and J. T. ARNOLD: Screening select slash pines for resistance to fusiform rust by artificial inoculation, pp. 431—435. In H. D. GERHOLD, E. J. SCHREINER, R. E. McDERMOTT, and J. A. WINIESKI (Eds.), *Breeding Pest-Resistant Trees*. Pergamon Press, New York, 1966. — GODDARD, R. E., and R. K. STRICKLAND: Crooked stem form in loblolly pine. *Silvae Gen.* 13: 155—157 (1964). — GOGGANS, J. F.: Correlation and heredity of

certain wood properties in loblolly pine (*Pinus taeda* L.). Tappi 47: 318–322 (1964). — KELLISON, R. C., and B. J. ZOBEL: Wood and Fiber Properties in Five Southern Hardwood Species. Proc. 25th Annual Meeting of For. Prod. Research Society, Pittsburg, Pa. pp. 17 (1971). — MOLL, H. R., and H. F. ROBINSON: Observed and expected response in four selection experiments in maize. Crop Science 6: 319–324 (1966). — PEDERICK, A. L.: Variation and inheritance of stem form and bark thickness in young loblolly pine. Tech. Rept. No. 41, School of Forest Resources, N. C. State Univ., Raleigh, 1970. — FERRY, T. O., and A. Y. ROBERTS: Volume formulas for loblolly pine seedlings in the vicinity of Raleigh, North Carolina. Jour. Forestry 62: 186–187 (1964). — ROBERTSON, A.: The theory of animal breeding. Proc. XII Intern. Congr. Genetics (3): 371–377, 1969. — ROBERTSON, A., and I. M. LERNER: The heritability of all or none traits: Variability of poultry. Genetics 34: 385–411 (1949). — SNEDECOR, G. W.: Statistical Methods. Iowa State Univ., Press, Ames, Iowa, 1956. — SQUILLACE, E.: Selection of superior trees. Proc. of Ninth South. Conf. on For. Tree Improvement, 7–9, 1967. — SQUILLACE, E. A., and G. W. BENGTON: Inheritance of gum yield and other characteristics of slash pine. Proc. of Sixth South. Conf. on For. Tree Improve-

ment, 85–96, 1961. — STONECYPHER, R. W.: The loblolly pine heritability study. Southlands Experiment Forest Tech. Bul. No. 5. International Paper Co., Bainbridge, Georgia, 128 pp., 1966. — STONECYPHER, R. W., and B. J. ZOBEL: Inheritance of specific gravity in five-year-old seedlings of loblolly pine. Tappi 49: 303–305 (1966). — STONECYPHER, R. W., F. C. CECH, and B. J. ZOBEL: Inheritance of specific gravity in two and three-year-old seedlings of loblolly pine. Tappi 47: 405–407 (1964). — VAN BUITENEN, J. P.: Heritability estimates of wood density in loblolly pine. Tappi 45: 602–605 (1962). — ZOBEL, B. J.: Inheritance of wood properties in conifers. Silvae Gen. 10: 65–70 (1961). — ZOBEL, B. J.: Breeding for wood properties in conifers. Unasylva 18: 89–103 (1964). — ZOBEL, B. J.: Developing trees in the southeastern United States with wood most desirable for paper. Tappi 53: 2320–2325 (1970). — ZOBEL, B. J., and R. L. McELWEE: Natural variation in wood specific gravity in loblolly pine, and a analysis of contributing factors. Tappi 41: 158–161 (1958). — ZOBEL, B. J., J. RALSTON, and J. H. ROBERTS: Wood yield from loblolly pine stands of different age, site, and stand density. Tech. Rept. No. 26, School of Forest Resources, N. C. State Univ., Raleigh, 1965.

## Appendix

App. Table 1. — Form of analysis used for estimating components of variance, covariance and heritability values in a 5 year-old open pollinated progeny test.

Source of variation	D. F.	Expected M.S. <sup>a)</sup>	Expected M.C.P. <sup>b)</sup>
Replications	$r-1$		
Families	$f-1$	$\frac{\sigma_w^2}{k} + \sigma_{rf}^2 + r\sigma_f^2$	$\frac{\sigma_{w_{ij}}}{k} + \sigma_{rf_{ij}} + r\sigma_{f_{ij}}$
Families × replications	$(r-1)(f-1)$	$\frac{\sigma_w^2}{k} + \sigma_{rf}^2$	$\frac{\sigma_{w_{ij}}}{k} + \sigma_{rf_{ij}}$
Within plot	$\sum_{i=1}^{127} (n_i-1)$	$\sigma_w^2$	$\sigma_{w_{ij}}$

a)  $\sigma_w^2$  = Variance due to differences among trees within plots

$\sigma_{rf}^2$  = Variance due to interaction of families and replications

$\sigma_f^2$  = Variance due to differences among families =  $\frac{1}{4} \sigma_A^2 \cdot (\sigma_A^2 = \text{additive genetic variance})$

$k$  = Harmonic mean of plants per plot

$f$  = Number of families

$\sigma_f^2 + \sigma_{rf}^2 + \sigma_w^2 = \sigma_p^2$  = Total phenotypic variance

$\frac{4\sigma_f^2}{\sigma_f^2 + \sigma_{rf}^2 + \sigma_w^2}$  = Heritability on an individual basis.

b)  $\sigma_{w_{ij}}$  = Covariance among trees within plots of  $i$  and  $j$  traits

$\sigma_{rf_{ij}}$  = Covariance due to interaction of families and replications of the  $i$  and  $j$  traits

$\sigma_{f_{ij}}$  = Covariance due to families for traits  $i$  and  $j$ .

### Standard Error of the Component of Variance

$$\text{S.E.}(\sigma^2) = \sqrt{\frac{2}{C^2} \left[ \sum \frac{V_i^2}{f+2} \right]} \quad (1)$$

Where:

S.E.(\(\sigma^2\)) = Standard error of the variance component

$C$  = Coefficient of the component of variance

$\sum V_i^2$  = The sum of the squared mean squares involved in the computation of  $\sigma^2$

$f_i$  = The degrees of freedom for each mean square.

### Genetic Correlation

$$r_{g_{ij}} = \frac{\sigma_{f_{ij}}}{\sqrt{\sigma_{f_i}^2 \times \sigma_{f_j}^2}} \quad (2)$$

Where:

$r_{g_{ij}}$  = Genetic correlation between the  $i$  and  $j$  characteristics

$\sigma_{f_{ij}}$  = Estimated genetic covariance among the half sib families of the combination of  $ij$  characteristics

$\sigma_{f_i}^2$  = Half sib variance of the  $i$ th characteristic

$\sigma_{f_j}^2$  = Half sib variance of the  $j$ th characteristic.

### Heritability of the Regression of Offspring on Parent

$$b = \frac{\text{Cov(OP)}}{\sigma_p^2} = \frac{\frac{1}{2}(\sigma_A^2)}{\sigma_p^2} = \frac{1}{2}(h^2) \quad (3)$$

Where:

$b$  = Regression coefficient of offspring on parent

Cov(OP) = Covariance of offspring and parents

$\sigma_A^2$  = Additive genetic variance

$h^2$  = Narrow sense heritability on an individual basis.

### Standard Error of Heritability Obtained from the Regression of Offspring on Parent

$$\text{S.E.}(b) = \sqrt{\frac{1}{N-2} \left[ \frac{\sigma_y^2}{\sigma_x^2} - b^2 \right]} \quad (\text{FALCONER 1960}) \text{ and due to half sib relationship:}$$

$$\text{S.E.}(h^2) = 2 [\text{S.E.}(b)] \quad (4)$$

Where:

S.E.(b) = Standard error of the regression coefficient  
N = The number of paired observations of x and y variables which is equivalent to the number of families in the experiment  
 $\sigma_y^2$  = Variance of y variable  
 $\sigma_x^2$  = Variance of the x variable.

*Heritability of Robertson and Lerner Approach*

$$h^2 = \frac{x^2 - (N-1)}{rN_0} \quad (5)$$

Where:

$h^2$  = Heritability on an individual basis  
 $x^2$  = The heterogeneity Chi-square in the 2 x N table formed by the percent infected data  
N = Number of families  
r = The genetic relationship between members of a family  
 $N_0 = n_i - \frac{\sum n_i^2}{\sum n_i} - (N - 1)$

Where:

n = the number of individuals of one family.

## Blühstimulation\*)

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Seit es Züchtung mit Waldbaumarten gibt, besteht das Problem, die Zeit zu verkürzen, bis Jungpflanzen erstmals fruktifizieren oder auch die Zeitspanne zwischen zwei Samenjahren zu verringern. In einem Waldbestand besteht dieses Problem nicht, bzw. frühes und reichliches Fruktifizieren ist dort sogar unerwünscht, da bekannt ist, daß durch die Fruktifikation der Holztrag vermindert wird. So hat die Forstwissenschaft viel später als z. B. die Landwirtschaft begonnen, die Vorgänge bei der Fruktifikation der Waldbäume mit der Blickrichtung auf eine Förderung derselben zu erforschen.

Trotzdem konnten, vor allem aufgrund der Erfahrungen der allgemeinen Pflanzenphysiologie, schon bald zahlreiche wertvolle Erkenntnisse gewonnen werden. Zum Beispiel ist heute weitgehend bekannt, welche Witterungsverhältnisse die Fruktifikation fördern und wie die morphologischen Entwicklungsschritte von der Befruchtung bis zur Samenreife ablaufen. Noch nicht hinreichend bekannt ist aber, durch welche Vorgänge im einzelnen eine Pflanze mannbar wird und was geschehen muß, damit sie vom rein vegetativen Wachstum in ihre reproduktive Phase übergeht.

Einen Überblick über diesen Problemkreis soll mein Referat geben, wobei ich zunächst einige Definitionen nennen darf, die zwar nicht allgemeingültig sind, die aber doch im Rahmen dieses Referates zur Klärung erlaubt sein mögen.

Der Begriff Blühstimulation soll ein sehr weites Gebiet, nämlich alle Maßnahmen erfassen, die die physiologischen und morphologischen Vorgänge in der reproduktiven Entwicklungsphase der Pflanze fördern. Blühstimulation ist also ein Oberbegriff, der noch weiter unterteilt werden muß. Für diese Unterteilung bieten sich die einzelnen Schritte bei der Bildung und Entwicklung der Blüten an. Unter bestimmten Voraussetzungen werden ja die Vegetationspunkte oder Apices der mannbaren Pflanzen vom vegetativen Wachstum umgestimmt zur Bildung

reproduktiver Organe. Dieser Vorgang heißt Blüteninitiation oder Blühinduktion und das Ergebnis Blütenprimordien oder Infloreszenzanlagen. Bald nach der Blühinduktion wird die Infloreszenzanlage bei Arten mit eingeschlechtlichen Blüten, wie z. B. den meisten unserer Nadelbaumarten, geschlechtlich determiniert. Wenn die Ernährungsverhältnisse günstig sind, z. B. bei hohem P/N-Verhältnis, dann entwickelt sich die Infloreszenzanlage zu einer Blüte oder einem Blütenstand. Nach der Befruchtung bildet sich aus der weiblichen Blüte unter günstigen Umweltbedingungen und bei guter Stickstoffernährung der reife Samen.

Nach den bisherigen Erfahrungen ist es nun relativ einfach, eine Pflanze, an der bereits Blütenprimordien gebildet sind, dazu zu bringen, daß möglichst viele dieser Blütenprimordien sich entwickeln, und zwar durch zeitlich gezielte Düngungsmaßnahmen. Weitaus schwieriger ist es, an Jungpflanzen, und die in Samenplantagen meist verwendeten Pfropflinge sind ja physiologisch zumindest verjüngte Pflanzen, oder an nicht blühwilligen Pflanzen, z. B. zwischen den Mastjahren, Blüten zu induzieren und diese dann, soweit notwendig, gezielt sexuell zu determinieren. Untersuchungen über Blühstimulation lassen sich also grundsätzlich in vier Untergruppen eingliedern:

1. Untersuchungen über Blühinduktion,
2. Untersuchungen über sexuelle Determination,
3. Untersuchungen über die Voraussetzungen der Blühreife oder der Mannbarkeit,
4. Untersuchungen über Verfahren zur Steigerung des Samenertes.

Im allgemeinen ist aber eine klare und eindeutige Zuordnung der Forschungsergebnisse zu einzelnen dieser Untersuchungsgruppen nur schwer möglich. Dies gilt besonders für die Ergebnisse bei der Anwendung mechanischer Verfahren zur Steigerung der Fruktifikation, die ursprünglich vom Obstbau entwickelt wurden. Diese Methoden gehen alle von dem gleichen Grundgedanken aus, nämlich daß im Kronenbereich möglichst viele Stoffwechselprodukte angereichert werden sollen, bzw. daß die sog. apikale

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