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Genetic Variation Among Open-Pollinated Progeny of Eastern Cottonwood

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Improvement programs in eastern cottonwood (*Populus deltoides* BARTR.) are most frequently designed to produce genetically superior clones for direct commercial use. This paper describes a progeny test to assess genetic variability on which selection might be based.

Methods

Open-pollinated seed was collected in 1963 from 81 trees in natural stands along the Mississippi River between Clarksdale and Vicksburg, Mississippi. Twenty-nine of the trees were chosen for outstanding growth and form; the remaining 52 were randomly selected. Seeds were cleaned, then stored at 38° F and 25 percent relative humidity until sown on August 5. They were sown in subirrigated plant bands filled with a mixture of equal parts of sand, peat, and loam. In late August, seedlings were thinned to six per band, and two bands per family were transplanted to each plot in a nursery experiment that followed a 9 × 9 balanced lattice design with 10 replications; this design was carried into the outplanting.

Plants were lifted from the nursery in late February 1964, pruned to an 8-inch top, and bar-planted in the field with 2 inches of stem above the soil surface. A field plot consisted of a row of six trees randomly chosen from each nursery plot. Spacing was 4 × 4 feet. A two-row border was planted around the test site. The soil was Commerce loam underlain in some places by lenses of heavier soil. The trees were cultivated during the first growing season, and in the second growing season were irrigated twice in late summer. Survival averaged 97 percent.

Total height was recorded after the 1964 and 1965 growing seasons; diameter at 1 foot above soil surface was recorded in 1965. Incidence of leaf rust (*Melampsora medusae* THÜM.) was recorded for each plant in late October 1964. A rating of 0 indicated no rust while a 5 indicated heavy infection (100 percent of leaf surface covered with sori). Distribution of ratings was normal. Foliation date — the day on which the first leaves were ½ inch out of buds — was recorded on four replications in 1965 and 1966.

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Specific gravity of 8-inch-long stem sections from two trees per plot in 10 replications was determined by the maximum-moisture technique (SMITH 1954). Fiber length determinations (based on measurement of 50 fibres per sample) were made from samples taken adjacent to the cambium of two trees per plot in six replications.

Plot means were units in appropriate variance analyses of height, diameter, *Melampsora* rust rating, and foliation date (expressed as days from February 28 to foliation). In lattice analyses effective error mean square and adjusted treatment mean square (COCHRAN and COX 1957) were used in calculation of variance components. Within-plot variances for final height and diameter in 1965 were calculated for each plot. Estimates of within-plot variance for 1964 height, foliation date, and rust ratings were computed from data on individual trees in every tenth plot.

Individual-tree values were used in the analyses of fiber length and specific gravity. Plot means for specific gravity were also analyzed as for a lattice design, in order to determine the relative efficiency of the design with respect to this character. Efficiency of the lattice design relative to randomized blocks was determined with procedures outlined by COCHRAN and COX (1957).

Forms of variance analysis were:

	Expected mean squares	
Souce of variation	Plot mean analyses	Individual tree analyses
Families	$\frac{\sigma^2_w}{k} + \sigma^2_p + r\sigma^2_f$	$\sigma^2_w + k\sigma^2_p + rk\sigma^2_f$
Replications × families	$\frac{\sigma^2_w}{k} + \sigma^2_p$	$\sigma^2_w + k\sigma^2_p$
Within plots	$\frac{\sigma^2_w}{k}$	σ^2_w

Phenotypic and genetic correlation coefficients based on analyses of covariance were computed for diameter versus foliation date and diameter versus wood properties. A rank correlation analysis was used to study changes in family height rankings over time.

Results

Variation among families was statistically significant (0.05 level) for all characters measured. Summaries of means and variance components are given in *Tables 1 and 2*. Final mean family heights ranged from 14.5 to 17.7 feet, and diameters ranged from 1.4 to 1.9 inches. Mean heights

Table 1. — Summary of results.

Character	Test mean	Range of family means	Range of plant values	Percent of variance due to differences among families
1964 height (feet)	8.7	7.9—9.4	2.3—16.6	10.0
1965 height (feet)	15.8	14.5—17.7	4.9—26.6	5.9
1965 diameter (inches)	1.6	1.4—1.9	0.4—3.4	12.8
Melampsora rust rating	2.2	1.0—3.3	0.0—5.0	51.0
Foliation date				
1965 (days after 2/28)	38	33—44	33—47	86.6
1966 (days after 2/28)	35	22—42	21—43	91.6
Specific gravity	0.37	0.35—0.39	0.31—0.44	19.6
Fiber length (mm.)	0.90	0.85—0.97	0.62—1.11	3.1

Table 2. — Components of variance.

Character	Source of variation		
	Families	Replication × families	Within plot
Height			
1964	0.0625	0.2707	0.2905
1965	0.1271	1.2435	0.7733
Diameter			
1965	0.00576	0.01664	0.02266
Melampsora rust			
1964	0.2219	0.0645	0.1490
Foliation date			
1965	5.04	0.35	0.43
1966	26.81	0.31	2.16
Specific gravity	0.00009	0.00004	0.00033
Fiber length	0.00016	0.00147	0.00353

and diameters of progeny from phenotypically superior parents and randomly selected parents were identical, and ranges of family means for both groups were similar. Since all parents were random selections with respect to other characters studied, the two groups of progeny were considered as a single population. In this population 10 percent of the variance in height was associated with differences among families in 1964 and 5.9 percent in 1965. Slightly more of the diameter variance (12.8 percent) was due to familial differences. There were also major differences between family height rankings in 1964 and 1965; the rank correlation coefficient for the 2 years was 0.64.

In the lower Mississippi Valley, *Melampsora* rust occurs on cottonwood in late summer; it seldom kills trees but may reduce late-season growth. Average family rating for *Melampsora* rust infection varied from 1.0 to 3.3, a range indicating major differences in susceptibility among families. Fifty-one percent of the variance in ratings was due to these differences.

Familial variation in foliation date was broad and under strong genetic control. The sequence of foliation was the same in both 1965 and 1966; correlation coefficient of family sums for the 2 years was 0.96. Most of the variance in both years was associated with family differences (86.6 and 91.6 percent). This suggested rather simple genetic control over foliation time, and chi-square tests were therefore made to check the data for various segregation ratios. However, there were no discontinuous patterns of variation within families. A regression of mean offspring value on parent was statistically significant and had a coefficient of 0.38; 1963 foliation dates of the 52 randomly selected parents (Farmer 1966) and 1966 foliation dates for their progeny were used for this regression. Phenotypic and genetic correlation coefficients for final diameter × 1965 foliation date were respectively —0.16 and —0.53. Families foliating early thus were slightly larger than those foliating late.

Mean specific gravity was 0.37 and the range of family means was 0.35 to 0.39. About 20 percent of the population's variance in specific gravity was associated with family differences. The range of family means in fiber length was 0.85 to 0.97, and variance due to family differences was 3.1 percent. Phenotypic and genetic correlation coefficients for diameter × specific gravity and diameter × fiber length were:

	r_p	r_A
Diameter × specific gravity	—0.18	0.22
Diameter × fiber length	0.47	0.84

The efficiency of the lattice design relative to randomized blocks is given below for the four characters used in evaluation:

	Percent
Height	216
Diameter	164
Specific gravity	112
Resistance to rust	110

Discussion and Conclusions

The above estimates of genetic variance for juvenile growth and fiber length are lower than those noted by Farmer and Wilcox (1966) in an earlier study with slightly younger material. Because the sample was larger than in the previous study and was mostly selected randomly, the current estimates are believed to be more representative of the cottonwood population in the lower Mississippi Valley. The inheritance data for specific gravity, on the other hand, generally confirm results of the previous test, and data on resistance to *Melampsora* rust are similar to those obtained by Jokela (1966) for eastern cottonwood in Illinois. Familial variation in foliation dates has not been previously reported, but data support results from a study of variation in natural stands (Farmer 1966) and a clonal test (Wilcox and Farmer 1967).

Indications are that family selection for foliation date, rust resistance, and specific gravity will be very effective. Moreover, the very high broad-sense heritability (Wilcox and Farmer ~~1965~~ 1967) of these characters suggests that one can select directly from natural stands. As JOKELA (1966) noted, formal clonal testing may not be essential for evaluating juvenile resistance to rust. The moderate genetic correlation between foliation date and growth suggests that selection for early foliation may be profitable. Data from a clonal test (WILCOX and FARMER 1967) also support this conclusion. The relationship may be particularly important on droughty sites where early spring increment is the main component of growth.

Test data on inheritance of foliation dates are important from other viewpoints. First, the rather strong regression of half-sib progeny means over parent values indicates that a clonal seed orchard from field selections may be used to produce seedlings with highly predictable phenology. Second, the combination of wide variation and strong genetic control observed in this and other studies (FARMER 1966, WILCOX and FARMER 1967) suggests the existence of phenological divisions within the breeding population in the lower Mississippi Valley. Trees which for genetic reasons flower early in the season may never cross with late-flowering trees even though they are in the same stand. This breeding pattern may also affect the population structure with respect to other characters.

Since a relatively small amount of variance was associated with family differences in growth and fiber length, response to selection for these characters will be much less than for the others. This is further demonstrated by the fact that field selection of parents for growth was completely ineffective in terms of juvenile progeny performance. While selection from a test population will be more effective than field selection, appreciable year-to-year changes of family rankings in this test and of clone rankings in others (WILCOX and FARMER 1967) accentuate the need for sensitive long-term evaluation of growth.

The positive genetic correlation between growth and fiber length is similar quantitatively to that reported by FARMER and WILCOX (1966) and indicates that in the test population fiber length will respond positively to selection for diameter. However, this correlation has not been observed in preliminary clonal tests (FARMER and WILCOX 1968). Correlation coefficients for specific gravity $\times$ growth are too low to be of practical significance, as has been observed previously (FARMER and WILCOX 1966, FARMER and WILCOX 1968).

The effect of the 9×9 lattice design was similar to that observed in a clonal test with a triple lattice design (FARMER and WILCOX 1968). The greatest increase in efficiency over randomized blocks was observed in parameters of growth.

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