GENETIC PARAMETERS FOR TWO EASTERN COTTONWOOD POPULATIONS IN THE LOWER MISSISSIPPI VALLEY

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Abstract.--Genetic variances and heritabilities were compared between samples of two populations of eastern cottonwood tested on adjacent sites. Data for fourth-year growth and second-year survival yielded little difference between families in either population with most of the genetic variation associated with clones-within-families. Resultant estimates of additive genetic variance were low with much higher estimates of dominance variance. Consequently, narrow-sense heritabilities ranged from 0.00 to 0.27, and broad-sense heritabilities ranged from 0.01 to 0.45. A more efficient future test design includes smaller blocks and noncontiguous family and clonal plots.

Reforestation of eastern cottonwood (Populus deltoides Bartr.) has generally utilized clonal planting stock. Consequently, tree improvement efforts have been focused primarily on testing and selecting clones with little emphasis on recurrent selection programs. Without genetic recombination, a clonal selection program will eventually reach a plateau beyond which no further genetic gain can be obtained.

A recurrent selection program provides an opportunity for continuing advancement in gain over time; but to be efficient, breeders need estimates of genetic parameters for use in program planning. Estimates of additive genetic variance (Farmer and Wilcox 1966, Farmer 1970, Cooper and Randall 1973, and Ying and Bagley 1976), narrow-sense heritability (Farmer and Wilcox 1966), and dominance variance (Cooper and Randall 1973) have been published. However with the exception of one seven-year-old study (Ying and Bagley 1976), the reports have all described one and two--year-old data.

In this report, genetic parameter and heritability estimates are presented using second--year survival and fourth-year growth data from two populations of eastern cottonwood. Recommendations on future cottonwood test design are also made.

MATERIALS AND METHODS

Populations

Population 1.--Female parent trees were chosen in stands growing near Lake Albemarle, just north of Vicksburg, Mississippi. Criteria for

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selection included straightness and general appearance compared to neighboring trees. Open-pollinated seeds were collected and sown in a replicated nursery in July, 1971. The seedlings were cut back each following winter. In the spring of 1977, the best of the surviving trees were cloned and planted in another nursery. After being cut back in 1978, the clones with good survival and growth were again cloned and planted in a new nursery.

On February 15, 1980, clones were established in a field trial on Crown Zellerbach Corporation land near Fitler, Mississippi. The trial included 15 families with an average of 9.8 cloned individuals per family (range of 7 to 15; 147 clones total).

Population 2.--Female parent trees were chosen from stands in western Tennessee, 150 miles north of Stoneville, Mississippi. Using the same criteria as in Population 1. Open-pollinated seeds were collected, and seedlings were grown in a nursery in 1978 and cloned into a nursery in 1979.

The field study was planted on February 15, 1980 on a site adjacent to the test for Population 1. The trial included 17 families with an average of 6.2 cloned individuals per family (range of 1 to 17; 105 clones total).

Experimental Design

The experimental design consisted of five replications of two-tree plots planted at a 12x12 ft. spacing. The design employed a compact family block configuration in which families were arranged as randomized complete blocks with cloned individuals randomized within their respective families.

Two unrooted, 20 inch cuttings were planted at each planting spot. During the second growing season, survival was recorded; and if more than one tree survived per spot, then the second one was cut.

The test -Received standard cultural maintenance with several diskings during the first growing season (personal communication, Pat *Weber, Fitler* Managed Forest, Crown Zellerbach Corp.).

Analyses

Three traits were measured in each test including: second-year survival of the two cuttings planted at each planting spot, total height (ft) at age four, and d.b.h. (inch) at age four. Merchantable tree volume (to a three inch top) was calculated using equation 4 from Mohn and Krinard (1971).

The analysis of variance (Table 1) utilized plot mean data and employed a least-squares procedure due to imbalance of clones-in-families. Variance components were calculated by equating mean squares with expected mean squares, and coefficients of variance components were adjusted for the data imbalance (Searle 1971).

The calculation of narrow-sense and broad-sense heritabilities

utilized standard formulas (Sorensen and Campbell 1980, Foster et al. 1984). Estimates of additive and dominance variance were derived by equating variance components to their genetic expectations (Bohren et al. 1965). Nonadditive variance was assumed to be due solely to dominance variance. The ratio of dominance variance to phenotypic variance provided a measure of its relative importance.

Table 1.--Form of the analysis of variance for growth and survival traits for two populations of eastern cottonwood

Source	D.F.	Expected mean squares[a/]
Families(F)	(f-1)	$\sigma^2 + r\sigma^2_{C/F} + c\sigma^2_{FR} + rc\sigma^2_{F}$[b/]
Replications(R)	(r-1)	$\sigma^2 + c\sigma^2_{FR} + cf\sigma^2_{R}$
FxR	(f-1)(r-1)	$\sigma^2 + c\sigma^2_{FR}$
Clones(C)/F	(c-1)f	$\sigma^2 + r\sigma^2_{C/F}$
Error	remainder	σ^2
Total	frc - 1	

[a/] Population 1: r = 2.9; c = 9.3; f = 14.0
Population 2: r = 3.9; c = 5.7, (5.9 for survival); f = 9.0
[b/] Synthetic F test (Cochran 1951)

Uniformity of family-mean performance between replications was estimated by calculating appropriate correlation coefficients.

RESULTS

Population 1

Tree growth in this study was considered good for the test site conditions for the first three replications, but replications four and five were inadvertently located on very wet areas and suffered from low survival. For this reason, further analyses refer only to the first three replications. Total height, d.b.h., survival and volume averaged 41.3 ft., 5.4 inch, 78.1 percent, and 2.0 cu. ft., respectively.

Analysis of variance results were similar among the four traits. No significant variation occurred among families for any of the traits (Table 2), with family variation accounting for a very small proportion (0.0 to 1.0 percent) of the total variation (Table 3). Replication effects were significant for all traits (p = 0.10) (Table 2) and accounted for 2.5 to 12.9 percent of the total variation (Table 3). The replication x family interaction was surprisingly large and significant for all traits (Table 2), representing an average of seven percent of the total variation (Table 3). For survival, d.b.h., and volume, this interaction equaled or exceeded the replication effect in importance. Considering height, d.b.h., and volume, the most important effect, except error, in the analysis arose from clones-in-families (Table 2)

representing 27 percent of the total variation (Table 3). No differences occurred among clones-in-families for survival.

Table 2.--Mean squares and F tests for the analysis of variance for Population 1 of eastern cottonwood

Source	D.F.	Mean Squares			
		Height	D.B.H.	Survival	Volume
Families(F)	14	40.98^{NS}	1.74^{NS}	899.27^{NS}	1.35^{NS}
Replications(R)	2	331.55^{**}	3.49^{1}	4789.03^{**}	4.57^{**}
FxR	28	24.78^{**}	1.11^{**}	836.63^{*}	0.76^{*}
Clones(C)/F	132	21.61^{**}	1.12^{**}	501.89^{NS}	1.14^{**}
Error	251	10.37	0.48	489.85	0.45

^{1} Significant at p = 0.10
* Significant at p = 0.05
** Significant at p = 0.01
^{NS} Nonsignificant at p = 0.10

The large replication x family interaction manifested itself in the family-mean correlations between replications. While the correlation between replications one and two was significant (p = 0.05) and positive (0.65), the correlations between replications one and three (-0.32) and two and three (-0.25) were nonsignificant.

Given nonsignificant family effects and highly significant clones-in-family effects (except for survival), estimates of additive variance were small and nonsignificant (Table 3); estimates of dominance variance were significant and apparently accounted for all the genetic variance (Table 3).

Heritability estimates reflect the importance of genetic variance to phenotypic variance; therefore the trends for heritabilities followed previous results for variance components. Narrow-sense heritability for height was 0.05, for survival was 0.01, and 0.00 for the other two traits (Table 3). Broad-sense heritability ranged from 0.25 to 0.33 for height, d.b.h., and volume and equaled 0.01 for survival (Table 3). Broad-sense heritability based on clone-means ranged from 0.51 to 0.60 for height, d.b.h., and volume (Table 3).

Dominance variance as a proportion of phenotypic variance equaled broad--sense heritability for d.b.h. and volume and was only slightly lower in the case of height (Table 3).

Population 2

Although tree growth in Population 2 did not equal that of Population 1, it was still acceptable for the site. Average fourth-year height, d.b.h., survival, and volume reached 38.1 ft., 5.1 inch, 77.2 percent, and 1.5 cu. ft., respectively. Correlations of family-means

Table 3.--Variance components and genetic parameter estimates for Population 1 of eastern cottonwood

Parameter	Estimate							
	Height		D.B.H.		Survival		Volume	
σ^2_F	0.18	(1.0)[d]	0.00	(0.0)	1.88	(0.3)	0.00	(0.0)
σ^2_R	2.36	(12.9)	0.02	(2.5)	30.36	(5.4)	0.03	(4.0)
σ^2_{FR}	1.55	(8.5)	0.07	(8.9)	37.29	(6.6)	0.03	(4.0)
$\sigma^2_{C/F}$	3.88	(21.2)	0.22	(27.9)	4.15	(0.7)	0.24	(32.0)
σ^2	10.37	(56.4)	0.48	(60.7)	489.85	(87.0)	0.45	(60.0)
V_A[a]	0.72		0.00		7.52		0.00	
V_D[b]	3.34		0.22		0.00		0.24	
h^2	0.05		0.00		0.01		0.00	
H^2	0.25		0.29		0.01		0.33	
H^2_x[c]	0.51		0.55		0.03		0.60	
V_D	0.21		0.29		0.00		0.33	
phen. variance								

[a] V_A = additive genetic variance = 4 (σ^2_F)
[b] V_D = dominance genetic variance = $\sigma^2_{C/F}-(3)(\sigma^2_F)$

[c] H^2_x = broad-sense heritability of clone means

[d] Variance components as a percent of total variation

between replications (although nonsignificant in most cases) were positive except with replication two (Table 4). The importance of this result will be discussed fully later, but it was used as rationale to delete replication two from further analyses.

Table 4.--Correlation coefficients between replications based on family means of eastern cottonwood

Replications	Replications			
	2	3	4	5
1	-0.03^{NS}	0.35^{NS}	0.15^{NS}	0.67^{**}
2		-0.40^{NS}	-0.13^{NS}	-0.17^{NS}
3			0.32^{NS}	0.41^{NS}
4				0.17^{NS}

^{NS} Nonsignificant at p = 0.10
** Significant at p = 0.01

The analyses of variance for Population 2 followed a somewhat different pattern than for Population 1. Differences among families achieved significance (p = 0.10) for height (Table 5) and accounted for

Table 5.--Mean squares and F tests for the analysis of variance for Population 2 of eastern cottonwood

Source	D.F.	Mean Squares			
		Height	D.B.H.	Survival	Volume
Families(F)	16	49.50^{1}	1.68^{NS}	1397.18^{NS}	1.73^{NS}
Replications(R)	3	63.90^{**}	0.40^{NS}	3006.03^{*}	0.99^{1}
FxR	48	11.30^{*}	0.42^{1}	903.57^{**}	0.41^{*}
Clones(C)/F	88	24.40^{**}	1.33^{**}	963.94^{**}	1.17^{**}
Error	251[a/]	7.20	0.31	488.07	0.29

1 Significant at p = 0.10
* Significant at p = 0.05
** Significant at p = 0.01
NS Nonsignificant at p = 0.10
a/ D.F. for survival = 264

six percent of the total variation (Table 6). The family source of variation for the other three traits was nonsignificant (Table 5) and accounted for little of the total variation (0.1 to 3.5 percent of the variation) (Table 6). Replication effects were significant for height and survival (p = 0.05) as well as volume (p = 0.10) but not for d.b.h. (Table 5). Variation represented by replication effects ranged from 0.0 to 7.0 percent (Table 6). Family x replication interaction was again significant for all traits (Table 5) and accounted for an average of 5.4 percent of the total variation (Table 6), a smaller percentage than in Population 1. Clones-within-families clearly exceeded all other sources of variation in importance. It was highly significant (Table 5) and contributed an average of 32.8 percent of the variation (Table 6).

The family x replication interaction appears to be largely due to the unusual family rankings in replication two (Table 4). Replications one, three, four, and five are positively correlated (though only replications one and five were significantly correlated), while replication two was clearly an outlier. With replication two in the analyses, the family x replication interaction represented an average of 9.7 percent of the variation.

Though still nonsignificant for three of the four traits, additive genetic variance estimates were all positive (Table 6). Dominance variance clearly represented the major proportion of the total genetic variation for d.b.h., survival, and volume; while additive variance for height was double the dominance variance.

With one exception, narrow-sense heritabilities were still quite small, and broad-sense heritabilities considerably exceeded the

Table 6.--Variance components and genetic parameter estimates for Population 2 of eastern cottonwood

Parameter[a/]	Estimate							
	Height		D.B.H.		Survival		Volume	
σ^2_F	0.90	(6.0)	0.01	(1.7)	0.75	(0.1)	0.02	(3.5)
σ^2_R	1.00	(7.0)	0.00	(0.0)	39.59	(5.5)	0.01	(1.8)
σ^2_{FR}	0.70	(5.0)	0.02	(3.3)	70.42	(9.8)	0.02	(3.5)
$\sigma^2_{C/F}$	4.40	(31.0)	0.26	(43.3)	118.97	(16.6)	0.23	(40.3)
σ^2	7.20	(51.0)	0.31	(51.7)	488.07	(68.0)	0.29	(50.9)
V_A	3.60		0.04		3.00		0.08	
V_D	1.70		0.23		116.72		0.17	
h^2	0.27		0.07		0.004		0.14	
H^2	0.40		0.45		0.18		0.45	
H^2_x	0.73		0.77		0.45		0.76	
V_D / phen. variance	0.13		0.43		0.17		0.30	

[a/] Parameter symbols explained in Tables 1 and 4.

narrow-sense. Narrow-sense heritability for height equaled 0.27; it ranged from 0.004 to 0.14 (Table 6) for the other three traits. Broad-sense heritabilities averaged 0.37 with a range of 0.18 to 0.45 (Table 6). Clone-mean heritabilities ranged from 0.45 to 0.77 (Table 6).

The ratio of dominance variance to phenotypic variance exceeded the ratio of additive genetic variance to phenotypic variance (narrow-sense heritability) for all traits but height (Table 6).

DISCUSSION

Family differences achieved significance only for height in Population 2, with nonsignificant variation for the other traits in both populations. The low amount of family variability led to either no additive genetic variation or a small amount, at best, for the traits. These results were unexpected based on the significant findings of Farmer and Wilcox (1966), Farmer (1970), and Ying and Bagley (1976).

Clones-within-families comprised the major portion of the genetic variation in these two studies. Ying and Bagley's (1976) results also concurred that, for growth traits, clones-within-families comprised a larger proportion of the total variation than families. In the present study, the clonal variation derived mainly from dominance genetic effects rather than additive genetic effects for all traits except survival in Population 1 and height in Population 2. Cooper and Randall (1973) found that additive genetic variance accounted for three times the level of dominance variance for first-year height and one-fifth the level of dominance variance for first-year survival.

Three possibilities exist for the results of this study compared to earlier studies. The findings may be real but unique (compared to earlier studies) for the two sampled populations. Intra-locus genetic interactions (dominance) may actually be the major cause of genetic variation in these populations. Selection pressure in these populations may favor survival of heterozygous individuals with very similar genotypes. The earlier studies cited above sampled many more populations and therefore had a greater chance of sampling ones with significantly different gene frequencies.

The second possibility is that these results are an artifact of analyzing data only for fourth-year growth traits and second year survival. Only one of the cited studies in the literature examined data for a range of ages (Ying and Bagley 1976) while the others examined data only for first and second-year traits. Ying and Bagley's fourth--year analysis agreed that a larger proportion of variation was due to clones-within-families compared to families; but families were still a significant source of genetic variability.

The last explanation relates to the large microsite variability in this flood-prone test site and the experimental design. The area is situated behind a levee and is not subjected to major river flooding but still receives regular backwater flooding from the Mississippi River. Undoubtably though, the soil profile originally resulted from alluvial deposits from the river and is characterized by ribbons of fairly different soil types (Wynn et al. 1961). The topography is slightly undulating and water pools up in the low spots following rains or flooding. The interaction of these site factors yields a large amount of microsite variability. Block sizes of 0.7 to 1.0 acre were probably too large and included too much within-block variability. Incomplete block designs (i.e., as described by Schutz (1966) and Libby and Cockerham (1980) hold promise for reducing block size thereby increasing efficiency of test results. In addition as Lambeth et al. (1983) demonstrated, contiguous family plot configurations (as compared to noncontiguous plots) cause larger block-by-family interactions and larger coefficients of variation for family means. A compact family plot design was used in this study as well as (contiguous) row plots for clones-within-families which probably contributed to the high family x replication interaction and nonsignificant differences among families. The efficiency of future tests of this type could be increased by using smaller blocks and a noncontiguous configuration of both clones-within-families and ramets-within-clones.

Results from this study as well as others (Ying and Bagley 1976) demonstrate the larger importance of clone-within-family variability compared to family variability. A tree improvement program should be designed which, while taking advantage of additive genetic variation through family selection, lends major emphasis to clone--within-family selection thereby tapping the large amount of dominance variance. One alternative includes a main line program emphasizing family and within-family selection for gains from additive genetic variation while in each generation utilizing a production population derived mainly from pure clonal selection.

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