GENETIC VARIANCE AMONG SELECTED COTTONWOOD CLONES: SEVEN-YEAR-RESULTS

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ABSTRACT. --Fifty-one previously tested cottonwood clones from throughout the lower Mississippi River Valley were tested on Island No. 3 in Carlisle County, Kentucky. The clonal component of variation was highly significant for all traits and on the average accounted for 31 percent of the total variation. Inter-tree competition and the age-three thinning seem to have played a major role in stand development and estimates of genetic parameters. The genetic and phenotypic correlations and correlated responses indicate that clonal selection based on height at ages one and three would be very ineffective for volume at age seven. Selections at age five for either diameter or volume will yield nearly as much gain as direct selection for volume at age seven.

Additional Keywords: *Populus deltoides*, broad-sense heritabilities, genetic correlations, correlated response, genetic gain.

INTRODUCTION

The USDA Forest Service Southern Hardwoods Laboratory, at Stoneville, Mississippi conducted the early genetic work on eastern cottonwood (*Populus deltoides* Batr.) in the lower Mississippi River Valley during the sixties and seventies. However, since that time the majority of the work has shifted to the industrial sector due to abandonment of the cottonwood genetics project by the U.S. Forest Service.

Clones presently in commercial use were largely obtained from early nursery selections of open-pollinated seedlings of selected phenotypes. However, some clonal material was also obtained from selections of juvenile stock in natural stands. Collectively these clones formed the major test population in the lower Mississippi River Valley from which selections were made primarily on growth rates and disease resistance (Mohn et. al. 1970, Land 1974).

These clonal selections are well adapted to alluvial sites between Memphis, Tennessee (35°07'N latitude) and Baton Rouge, Louisiana (30° 28'N latitude). However, cottonwood sites within Westvaco's Central Woodlands region are 100-175 miles north of this area. Paducah, Kentucky (37° 05'N latitude) is roughly in the center of this region. Although the soil type changes very little in the alluvial flood-plain along the Mississippi River, there is evidence of clone by site interactions among eastern cottonwood clones (Mohn and Randall 1973, Randall and Cooper 1973). Because of this interaction, clones have to be adequately tested in the region where they will be used to maximize genetic gain. To further complicate the matter, eastern cottonwood has exhibited poor juvenile-mature correlations increasing the difficulty of effective early selections (Cooper and Ferguson

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1979). A better understanding of age-age correlations, as well as growth and wood property correlations will aid in development of selection strategies and selection indices for eastern cottonwood.

OBJECTIVES

The objectives of this study were: (1) to determine the preferred clones for use in western Kentucky and southern Illinois; and (2) to estimate genetic variability among these clones in order to provide an increased understanding of clonal variation.

METHODS

The clones represented in the 1980 USFS Advanced Cottonwood Clone Test were divided into three test groups; A, B, and C depending on both the amount of information supporting their superiority from clone tests throughout the lower Mississippi River Valley and the number of cuttings available at the time of establishment. This report deals with test group A for which the selection of clones was based on a much older and larger data base than the selections for test groups B and C. The clonal material for test group A was selected, propagated, and provided by the USDA Forest Service, Southern Forest Experiment Station, Genetics Group at Stoneville, Mississippi.

Test group A is composed of 51 clones. Ten of these clones are check clones, commonly referred to as Stoneville selects (ST-66, ST-70, ST-72, ST-124, ST-148, ST-163, ST-240, ST-244, ST-261, and ST-273), which were released in 1982 by the USFS Genetics Group for commercial production. The test design is a randomized complete block located on Island No. 3 in Carlisle County, Kentucky. The test site is an extremely fertile alluvial site, which is characterized by silt loam soils and periodic flooding by the Mississippi River. The plot size was originally a four-tree row plot planted at a spacing of 11.5 x 11.5 feet. Two 20-inch cuttings were placed at each planting spot in order to insure high survival. During the first growing season each spot was thinned to a single individual. Herbaceous competition was controlled by periodic disking and mowing.

Following the third growing season, a diagonal row thinning was employed over the entire test, reducing plot size to two trees. Trees removed during the thinning were used in various wood property studies (Olsen et. al. 1985). Total tree heights at ages one, three, five, and seven (1HT, 3HT, 5HT, and 7HT) , and dbh and volume at ages three, five, and seven (3D, SD, 7D, 3V, 5V, and 7V) were analyzed for this study. Total cubic foot tree volumes were calculated using the equation $V = .08 + .002274 [(D^2 , HT]$ developed by Krinard[1] (personal communication) for plantation grown cottonwood. The analysis of variance was done on a plot mean basis for all traits. Genetic parameters such as variance components, broad-sense heritabilities, genotypic and phenotypic correlations, correlated responses, and expected genetic gains were also estimated. Clonal selection and heritabilities are used out of their normal breeding context, in that no matings are planned, but select clones will be vegetatively propagated.

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RESULTS AND DISCUSSION

Growth has been quite rapid through age seven reflecting high site quality and adequate growing space. Total height, dbh, and individual tree volume of all 51 clones averaged 64 feet, 9.0 inches, and 12.4 cubic feet, respectively (Table 1). This is very similar to growth rates reported by Foster (1986), Krinard (1985) and Krinard and Johnson (1984) for cottonwood clones grown on alluvial sites. The ten Stoneville select clones averaged 67 feet, 9.4 inches, and 14.0 cubic feet, at age seven, for total height, dbh, and volume respectively.

Table 1. Overall means and ranges of data for 51 eastern cottonwood clones growing in test plantations located in western Kentucky and southern Illinois.

Trait	Mean	Range
Age 1 Height (ft)	8.0	6.1 - 9.4
Age 3 Height (ft)	34.0	30.0 - 38.0
Age 5 Height (ft)	49.0	43.0 - 54.0
Age 7 Height (ft)	64.0	57.0 - 71.0
Age 3 DBH (in)	4.6	3.8 - 5.5
Age 5 DBH (in)	7.1	6.1 - 8.3
Age 7 DBH (in)	9.0	7.6 - 10.6
Age 3 Volume (ft^3)	1.8	1.3 - 2.5
Age 5 Volume (ft^3)	5.8	4.0 - 8.3
Age 7 Volume (ft^3)	12.4	8.0 - 17.5

The clonal component of variation was highly significant for all traits and on the average accounted for approximately 31 percent of the total variation with a range of 19 to 37 percent (Table 2). The clonal component for height increased from 19 percent at age one to 32 percent at age three and remained constant until age seven where it dropped to 22 percent. Although the changes in percentage of variation accounted for by the clonal component for volume between ages three and seven are not as large as those for height, the same trend is evident. On the other hand, the variation accounted for by the clonal component of stem diameter remained fairly constant through age seven.

Factors influencing these variance components change as the stand matures. Prior to the third growing season these trees were growing in a competitive free state where the size of cutting, rooting ability, and microsite variation influenced the estimates of variance. Inter-tree competition did not become a factor until the third growing season. Interestingly, the clonal component of variation reached its highest level for dbh, height, and volume at age three. The thinning which followed the age three measurements apparently reduced inter-tree competition resulting in fairly constant clonal components through age five. Stem diameter which has been shown to be much more sensitive than height to spacing or competitive effects exhibited only a slight decline in the amount of variation accounted for by the clonal component. Foster (1986) showed an increasing clonal component with advancing stand development in a young cottonwood clonal test. In contrast, Franklin (1979) showed that the additive genetic variance increased rapidly in the juvenile stage then decreased with the onset of competition in loblolly pine (Pinus taeda L.).

This decline in clonal components for height may be explained by examining more closely the competitive state of the entire stand. The rapid juvenile growth of cottonwood brought the stand into a highly competitive state during the third growing season both in terms of crown and root competition. By this time, the faster growing clones were occupying the area needed to sustain their growth advantage, thus maintaining a state of free growth, while the slower growing clones, under increasing competition, were unable to capture, their microsite. This competition resulted in increased clonal variation at age three and was reflected in the clonal components reaching their highest levels at this time. The development of the stand was then interrupted by the thinning which provided equal growing space to each residual tree independent of its size. Because the faster growing clones were already growing in a fairly competitive free environment, thinning probably had little effect on their growth rates. However, it did provide a more competitive free environment for the slower growing clones allowing them to capture their microsites and develop at a faster rate. Thus the development of the slower growing clones, following the thinning, has resulted in a more uniform stand as reflected in the lower variance seen in height at age seven. The increasing significance of the clonal component through age seven shown by Foster (1986), reflects the intense competition of a young cottonwood stand. Although suppression at this time has not lead to mortality it has given rise to a heterogeneous stand thus resulting in an increasing clonal component through age seven.

Broad-sense heritabilities were large for all traits yet not uncommon with those cited in the literature, Foster (1985, 1986), and Bridgwater (1972), (Table 2). Heritability for height increased between ages one and three but remained fairly constant for the remaining ages. Heritability for both diameter and volume also remained fairly stable between ages three and seven.

Table 2. Variance components, percent of total variation (in parentheses), and broad-sense heritabilities with their respective standard errors for 51 eastern cottonwood clones growing in test plantations in western Kentucky and southern Illinois.

	Variance Due To				
Trait	Block	Clone	Error	$\hat{H}^2$	$SE(\hat{H}^2)$
Age 1 Height	.1237 (10)	.2422** (19)	.9173 (71)	.56	.18
Age 3 Height	.1110 (2)	2.4285** (32)	4.9469 (66)	.71	.19
Age 5 Height	1.8217 (11)	5.2420** (31)	9.9152 (58)	.73	.19
Age 7 Height	15.4057 (32)	7.5161** (22)	15.4057 (46)	.71	.20
Age 3 DBH	.0075 (3)	.0998** (35)	.1780 (62)	.74	.19
Age 5 DBH	.0224 (3)	.2283** (33)	.4389 (64)	.72	.19
Age 7 DBH	.1668 (12)	.4269** (32)	.7458 (56)	.74	.20
Age 3 Volume	.0067 (4)	.0694** (37)	.1124 (59)	.76	.19
Age 5 Volume	.0221 (1)	.9163** (37)	1.5428 (62)	.75	.19
Age 7 Volume	2.4378 (18)	4.3647** (31)	7.2223 (51)	.75	.20

**Statistically significant at the 1 percent level.

Both genotypic and phenotypic correlations were positive for all traits (Table 3). Genotypic correlations were usually larger than phenotypic correlations. Traits at early ages one and three were usually poorly correlated with traits at ages five and seven. For example, genotypic correlations between age-one height and later heights at ages five and seven were .57 and .33, respectively while genetic correlations between ages 5 and 7 was .95. Diameter at breast height was a better indicator of volume then height and improved as age increased (Table 3). Phenotypic correlations of age five dbh and height with age-seven volume were .95 and .65, respectively. Similar results were reported by Ying and Bagley (1976) for phenotypic correlations in a seven-year-old cottonwood study.

Eastern cottonwood has been noted by several authors to demonstrate poor age-age or juvenile-mature correlations, thus hindering the ability to reduce clonal testing time and increase genetic gains per unit of time. Cooper and Ferguson (1979) showed that selection of the top 25 percent of a clonal test population at age one was little better than random selection at age fourteen. They also showed that genotypic correlations between ages one and fourteen were negligible. Foster (1986) showed very high genotypic and phenotypic correlations between diameter and volume at age four with volume at age seven. These high correlations were also reflected in substantial yields through indirect selection by these traits for volume gains at age seven.

Table 3. Genotypic (above diagonal) and phenotypic (below diagonal) correlations for 51 eastern cottonwood clones growing in test plantations in western Kentucky and southern Illinois.

1HT		.59	.57	.33	.56	.37	.25	.62	.45	.31
3HT	.59		.80	.66		.24	.14		.42	.29
5HT	.45	.69	.95				.49			.64
7HT	.30	.57	.89							
3D	.58					.92	.82		.89	.85
5D	.34	.28			.83		.96			.96
3V	.62								.90	.82
5V	.25	.41			.81			.84		.97
7V	.27	.30	.65		.76	.96		.75	.96	

The rapid growth of cottonwood on alluvial sites permits normal pulpwood rotations of ten years. Therefore early age selection is mandatory to maximize genetic gains and shorten the testing cycle. If the desired characteristic is age-seven volume, diameter at younger ages is a much better indicator than height and the gains increase with selection nearer to age seven (Table 4). Clonal selection based on diameter or volume at ages three and five resulted in substantial gains in volume at age seven. These results were similar to those of Foster (1986) in that indirect selection of clones on the basis of age five-dbh and volume yielded a very high percentage, 96 and 98 percent respectively, of the gain expected from direct selection on age-seven volume. Only 27 and 28 percent of the gain from direct selection of age-seven volume could be expected through selection of height at ages one and three, respectively. However, selection for volume at age seven based on age-three diameter would result in 85 percent of the gain expected for direct selection on volume at age seven. These results indicate the efficiency of clonal selection using the correct trait and the proper age (Panetsos 1980).

Table 4. Correlated response[1] for individual tree volume at age 7 for 51 eastern cottonwood clones growing in test plantations in western Kentucky and southern Illinois.

Selected Trait	Correlated Response ft^3	Correlated Response Percent of Mean	Percent of Direct Selection of 7V
1HT	.84	6.8	27
3HT	.88	7.1	28
5HT	1.97	15.9	63
3D	2.65	21.4	85
5D	3.02	24.4	96
3V	2.59	20.9	83
5V	3.06	24.7	98

[1]Correlated response is equal to the indirect effect that selection at early ages and different traits will have on age 7 volume.

Selection intensity was 5/51 clones.

The ability to make effective selections based on these early age traits can also be seen in clonal rankings and their effect on later age traits. Selection of the top 10 percent of the test population for 3D, 3V, 5D, or 5V was compared with clones selected for 7V. As expected from both genetic and phenotypic correlations as well as correlated responses, 5D and 5V were much better indicators of 7V than 3D or 3V. Volume losses at 7V were 12 percent for selections at 3D and 5 percent for selections at 3V. In addition, two clones dropped dramatically in rankings between ages three and seven. Clone ST-275 dropped from third for age-three diameter to 35th for age-seven volume, while ST-268 fell from third at age-three volume to 27th for age-seven volume. If selections had been delayed until age five, only negligible changes in clonal rankings and loss in volume at age seven would have occurred.

Estimated genetic gains from selection of the top 10 percent of the test population resulted in gains ranging from 6.7 to 26 percent (Table 5). Volume gains were the largest at 22.4, 25.1, and 26.0 percent for selecting on the basis of 3V, 5V, and 7V respectively. These gains refer to the test population mean and not the Stoneville selects which are commercially planted in the lower Mississippi River. If age-seven volume were the desired trait, selection of the top 10 percent of the test population would still yield a 19 percent gain over the Stoneville selects.

Table 5. Estimated genetic gains for the test population of 51 eastern cottonwood clones compared to Stoneville select clones when grown in plantations located in western Kentucky and southern Illinois.

Trait	Units[a]	Gain Percent	
Age 1 Height	.64	8.0[b]	7.7[c]
Age 3 Height	2.30	6.7	6.6
Age 5 Height	3.43	7.1	6.7
Age 7 Height	4.05	6.3	6.0
Age 3 DBH	.48	10.5	10.0
Age 5 DBH	.71	10.0	9.6
Age 7 DBH	.98	11.0	10.4
Age 3 Volume	.40	22.4	19.1
Age 5 Volume	1.45	25.1	22.3
Age 7 Volume	3.16	26.0	18.9

(a) Selection intensity was 5/51 clones
(b) Percentage of gain in comparison to the test population
(c) Percentage of gain in comparison to the Stoneville Select clones

However, two of the Stoneville selects, ST-70 and ST-244, performed well ranking in the top 10 percent from age three to age seven. This increase in gain over the check material refers only to alluvial sites of southern Illinois, western Kentucky and western Tennessee.

CONCLUSION

Advanced clonal testing allows increased gains to be extracted through clonal refinement for a specific environment or geographic area. Selection of clones on the basis of height at ages one and three was ineffective, resulting in very little gain in volume at age seven. Both genotypic and phenotypic correlations of 3D, SD, 3V, and SV with 7V were very high indicating effective early clonal selections. For short pulpwood rotations of ten years, it would be advisable to make selection at age five.

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