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Variation and Inheritance of Juvenile Characters of Eastern Cottonwood

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Commercial cottonwood plantations in the lower Mississippi Valley are commonly established with 20-inch unrooted stem cuttings of Populus deltoides BARTR. (MAISENHELDER, 1960). Competition from weeds drastically retards growth, and plantations require intensive cultivation until crowns shade out competing vegetation. Rapid early growth, therefore, is important in minimizing costs of plantation establishment and is one objective in cottonwood improvement.

Sinee planting stock is propagated asexually, genetically improved material can be obtained by selecting superior genotypes on the basis of performance in a replicated clonal test. Information on genetic variability, measured as heritability in the broad sense, can be used to predict gains from selection in such a test. The purpose of this study was to obtain heritability estimates for growth, form, and phenological characters in 1- and 2-year-old cottonwood.

Methods

Forty-nine seedlings were selected at random in a 2-year-old natural stand near Rosedale, Bolivar County, Mississippi. Six cuttings were made from each selection in February 1963, treated with phorate (MORRIS, 1960) to prevent insect attack during the year of establishment, and planted in a randomized block design with six replications. Single-tree plots were used with a 12-foot (3.66 m.) square spacing. The thickest cutting from each seedling was assigned to the first replication and succeedingly smaller cuttings to the following replications. The purpose of this confounding was to reduce possible effects of cutting size in estimates of clone and error variances.

The plantation was established on a Sharkey clay soil newly cleared of forest and thoroughly disked. Sharkey clay is found in slack-water areas of the Mississippi River flood plain (BRUCE et *al.*, 1958). It is a dark, poorly drained soil with a montmorillonite clay content of 74 to 85 percent and a site index for cottonwood of about 90 feet at 30 years (BROADFOOT, 1960). It represents the poorest of the sites currently being planted to cottonwood commercially.

During the first growing season, the plantation was cultivated to keep it free of weeds.

Total height was measured to the nearest 0.1 foot on May 31, July 2, August 1, August 30, September 20, October 23, 1963, and on October 19, 1964. Diameter was measured 1 foot above the ground to the nearest 0.1 inch on November 8, 1963, and on October 15, 1964. The total number of branches was recorded on September 23, 1963.

In October of 1963 and 1964 the clones were scored for incidence of rust caused by Melampsora medusae THÜM., which infected the trees in late summer. Scores for individual trees were based upon the average infection of four leaves. A leaf was collected from each of 4 cardinal directions at breast height. A score of 1 signified that 0 to 10 percent of the leaf was covered with sori; a score of 5 was maximum, and indicated that 100 percent of the leaf was covered with sori, that leaf edges were necrotic, and that some defoliation had resulted. In 1964 a 0 rating, indicating no rust, was added.

The rating system was on an ordinal scale, and analyses of variance are not strictly applicable. The ordinal data are included here since the ratings were strongly correlated with percent of leaf area covered with sori ($r = .99$), and the system has been effective in predicting clonal performance in subsequent tests.

Date of leaf emergence was recorded in the spring of 1964, as number of days from March 1. Extent of autumnal defoliation was scored on November 26, 1963, on a 1—4 basis. A score of 1 signified 70 to 100 percent of leaves on the tree; a score of 4 indicated less than 5 percent of leaves on the tree.

Thirteen values for missing plots were substituted according to SNEDECOR's (1956) method, and degrees of freedom and treatment sums of squares in the analyses of variance were adjusted accordingly. Data on number of branches were transformed to lag $(x + 1)$ prior to analysis, since the range in branch counts tended to increase with the clone mean.

Results and Discussion

Means and ranges for the characteristics are in Table 1. First-year height increase for the entire experiment was approximately linear from May until mid-September. Growth tapered off rapidly during late September and eeased in early October. Final mean clone height was 12.0

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Table 1. — Means, ranges, estimated genetic and environmental variances, and heritabilities in *Populus deltoides.*

Character	Mean	Range	Genetic variance σ^2_G	Environmental variance σ^2_E	Heritability: Individual-plant basis: $\frac{\sigma^2_G}{\sigma^2_G + \sigma^2_E}$	Heritability: Clone-mean basis: $\frac{\sigma^2_G}{\sigma^2_G + \sigma^2_E/n}$
1963						
Plant height in feet	12.01	9.9—14.0	0.6492	1.8979	0.25	0.66
Stem diameter in inches	1.56	1.13—1.93	.0189	.0778	.20	.58
Number of branches	11.5	6.0—29.0	.0182	.0233	.43	.82
Rust reaction	2.2	1.0—5.0	1.9216	.3757	.84	.97
Defoliation rating	2.8	1.0—4.0	.7158	.2501	.72	.94
1964						
Foliation date[1]	36	26—50	19.9520	.5363	.97	.99
Plant height in feet	16.0	13.4—18.5	.9811	2.1730	.31	.72
Stem diameter in inches	2.38	1.83—2.77	.0353	.1300	.21	.61
Rust reaction	2.1	0.0—4.3	.7645	.2292	.77	.95
1964 height increase	4.0	2.6—5.0	.2989	.3110	.49	.85
1964 diameter increase	.82	.47—1.05	.0097	.0226	.30	.71

[1]) Expressed as number of days from March 1, 1964.

feet (3.66 m.), and stem diameter was 1.56 inches (3.96 cm.). During the second season's growth, mean clone height increased 4 feet (1.22 m.) to a total of 16 feet (4.88 m.), and mean diameter increased 0.82 inch (2.09 cm.) to a total of 2.38 inches (6.05 cm.). The poor second-year growth is normal for the site and probably a better indication of future performance than is first-year growth. The mean rust reaction scores for the 2 years were almost identical: 2.2 and 2.1.

Broad-sense heritabilities *(Table 1)* were computed on an individual-plant basis and on a clone-mean basis according to the method of BURTON and DEVANE (1953). The genetic and environmental variances were calculated from the mean squares in the analysis of variance; σ^2_E = the expected error mean square, $\sigma^2_E + n\sigma^2_G$ = the expected clone mean square, n = the number of replications adjusted for the missing plots, and σ^2_G = the total genetic variance. The environmental variance was reduced to $\frac{\sigma^2_E}{n}$ in computing heritability on a clone-mean basis.

The highest heritabilities were obtained for phenological characters and for reaction to *Melampsora* rust. The lowest were for the growth measurements, i. e., stem diameter and plant height. Number of branches was intermediate at 0.82 (clone-mean basis). Heritabilities computed for the same characters in successive years were almost identical. Values for the 1964 increases in height and diameter were somewhat higher than values for total height and diameter for each year.

Heritabilities calculated on a clone-mean basis were used to compute the predicted response to selection for four of the characters. The formula was $R = ih\sigma_G$ (FALCONER, 1960), where:

R = response to selection in terms of the unit of measurement.

i = intensity of selection in standard deviations.

h = square root of the heritability.

σ_G = genetic standard deviation.

Results are summarized in *Table 2*. In the strictest sense the predicted gains are applicable only to the stand and site conditions sampled. Apparently all four characters are strongly controlled by genotype, and substantial gains can be realized by intensive selection. The greatest percentage gains would be attained by selecting clones with a low score for rust reaction. For similar environmental conditions and the same races of the rust, the best 10 percent of the clones would be expected to average a rust-reaction score no more severe than 1.

Moderate changes in branchiness would be expected from selection. Selection of the top 10% to 0.1% of the clones with fewest branches would reduce mean branch number by 2 to 4.

Mean height of the tallest 10% of the clones would be expected to exceed the mean of the unselected population by 1.2 feet, a gain of 10%.

Expected gains from selection for more than one character at a time will be influenced by correlations among characters. Where correlations are positive, improvement in one character will be accompanied by improvement in the others; where correlations are negative, improvement in one will be accompanied by losses in the others. Phenotypic, genotypic, and environmental correlations, computed

Table 2. — Predicted response (R) of four characters in *Populus deltoides* to three selection intensities, on the assumption that variance components in this material are representative of stand populations.

1963 character	0.1 percent selected		1 percent selected		10 percent selected	
	Units	Percent of mean	Units	Percent of mean	Units	Percent of mean
Plant height in feet	2.16	18	1.75	15	1.15	10
Stem diameter in inches	.35	22	.28	18	.18	12
Number of branches	4.0	35	3.3	29	2.1	18
Rust reaction	4.5	204	2.8	127	2.4	109

Table 3. — Phenotypic, genotypic, and environmental correlations among characters in *Populus deltoides*.

Character	Correlations		
	Phenotypic r_p	Genotypic r_g	Environmental r_e
1963			
Total height with stem diameter	0.60**	0.47	0.83
Number of branches with total height	.09NS	0.00	.36
Number of branches with stem diameter	.39**	.26	.75
Rust reaction with total height	.13NS	.15	.07
Rust reaction with stem diameter	.09NS	.11	.06
Rust reaction with defoliation	.69**	.72	.19
1964			
Total height with stem diameter	.61**	.50	.83
1964 height increase with rust reaction	—.13NS	—.14	—.01
1964 diameter increase with rust reaction	—.29*	—.35	—.01
Foliation date with 1964 height increase	—.52**	—.57	.07
1963—1964			
1963 rust reaction with 1964 rust reaction	.52**	.54	.03
1963 rust reaction with 1964 height increase	—.38**	—.42	.04
1963 rust reaction with 1964 diameter increase	—.45**	—.54	.03
1963 height with 1964 height increase	.02NS	.03	—.02
1963 height with 1964 foliation date	.07NS	.08	.19
1963 diameter with 1964 diameter increase	.28NS	.24	.35
1963 height with 1964 height	.86**	—	—
1963 diameter with 1964 diameter	.88**	—	—

NS nonsignificant at 0.05 probability level.
* significant at 0.05 level.
** significant at 0.01 level.

among characters within and between years, are given in *Table 3*.

The phenotypic correlation represents the observable association between clone characters, $r_p = \frac{\text{Cov XY}}{\sqrt{(\text{Var X})(\text{Var Y})}}$ where Cov XY = the phenotypic covariance of the two characters, X and Y; Var X = the phenotypic variance of X; and Var Y = the phenotypic variance of Y (FALCONER, 1960). The genotypic correlation, r_g, is attributable to the common genetic background of the clones and is calculated from the variances and covariances. The environmental correlation, r_e, represents the extent to which characteristics are influenced by the same environmental conditions and was calculated from environmental variances and covariances.

Phenotypic correlations between clone height and diameter were significant (0.01 level) in both 1963 and 1964. The positive genotypic correlations indicate that selection for either character would result in an increase in the other. The high r_e values suggest that environmental conditions affect the two characteristics similarly. The r_g value of .00 between 1963 height and number of branches shows that selection for height would not produce a concomitant change in number of branches — and vice versa.

Rust infection in 1963 was not related to 1963 growth but was negatively associated with 1964 height and diameter increase. The late summer infection, though not obviously reducing current growth, apparently interfered with accumulation of plant reserves and thus affected growth the following season.

In 1964 the rust infection occurred earlier in the growing season. The low correlation coefficients between 1964 rust and 1964 height increase indicate that height growth was not affected; however, the stronger negative r values suggest that diameter growth was reduced by the rust infection. Rust reaction was also associated with defoliation rating — as would be expected, since defoliation was one of the criteria of the rust ratings.

The significant r_p value and similar r_g value between foliation date and height growth in 1964 indicate that inherently early-flushing clones have some growth advantage over late-flushing ones.

Performance between the 2 years for single characters is illustrated by the correlation coefficients in the lower portion of *Table 3*. The phenotypic correlation for rust reaction between the 2 years was highly significant. This was due primarily to the genetic background of the clones rather than to environmental influences. Total height and diameter were significantly correlated (r_p) from one year to the next, since the major portion of the growth was made during the first season. However, neither height nor diameter increase in 1964 was significantly correlated with 1963 height and diameter.

The nonsignificant correlation between 1963 and 1964 growth appears contradictory to the consistently high heritabilities for total height and diameter and for 1964 growth. This change in the pattern of clonal variation may be due to several factors. The low r_g values for growth between the two years suggest that different genetic systems may be involved. First-year growth may be predominantly a reflection of initial rooting ability or other factors affecting establishment under little or no competition. Second-year growth may reflect clone vigor under stand conditions following establishment — increased competition for moisture, for example. Foliation date is one highly heritable character that influenced height increase the second year but not the first. Clonal effects not under genetic control ("C" effects of LERNER, 1958; LIBBY and JUND, 1962) may have also influenced initial growth, and second-year growth to a lesser extent.

Each year's growth, therefore, may have a high heritability but be uncorrelated with the previous season's increment. This suggests that accurate evaluation of the inherent juvenile growth potential of individual clones may require more than 1 year's performance.

Summary

Forty-nine randomly selected cottonwood clones were studied over a 2-year period in a replicated test to determine inherent variation. Gains from selection were predicted for several growth, phenological, and disease-reaction characters. Expected gains from selecting the best 10 percent of

the clones, expressed as a percent of the population mean, were total height 9.3 percent, stem diameter 11.5 percent, number of branches 19.0 percent, and incidence of *Melampsora* rust 72.7 percent. Phenotypic correlations were obtained among several characters: Stem diameter with total height (0.61), stem diameter with number of branches (0.39), foliation date with height increment (−.52), and incidence of *Melampsora* rust with defoliation (0.69) and with the following season's growth in both height (−.38) and diameter (−.45).

Height increase in the second year was not correlated with first-year height growth, although both characters were highly heritable. Perhaps separate developmental phenomena are involved, or the clones responded differently to the environments encountered during the two growing seasons.

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Reproductive Behavior in Sugar Maple: Self-Compatibility, Cross-Compatibility, Agamospermy, and Agamocarpy

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One of the important requirements of a plant-breeding program is an understanding of the reproductive behavior of the experimental material with which the breeder plans to work. In developing a breeding program in sugar maple *(Acer saccharum* Marsh.) at the Northeastern Forest Experiment Station, the flowering and fruiting habits of the species were explored. Self- and cross-compatibility, agamospermy, and agamocarpy in sugar maple were investigated from 1958 through 1961.

Materials

The trees used in these experiments were mature native specimens, selected for their ability to consistently produce large crops of easily reached flowers. The trees were located near Burlington, Vermont, and at Williamstown, Massachusetts.

In the cross-compatibility study, six tester pollens were applied to three trees used as female parents at Burlington; and four tester pollens were applied to two trees used as female parents at Williamstown. Trees used as females also served as male parents in reciprocal crosses.

Observations on self-compatibility were made on five trees at Burlington and on two trees at Williamstown. Agamocarpy was studied in conjunction with agamospermy on each of four trees at Burlington and two trees at Williamstown. The number of fruits and seeds set in the absence of any pollen source was used in determining the incidence of agamocarpy and agamospermy.

Flowering, Fruiting, and Phenology

Individual sugar maple trees in the Northeastern part of the species' range produce both male and female flowers that are pseudo-hermaphroditic. Although bisexual, only one sex is functional. Extended observations made in New England show that these trees may be divided into two groups based on differences in blooming sequence. One of the groups is characterized by a blooming sequence that is primarily male-female or protandrous; in the other the sequence is primarily female-male, or protogynous.

Between the two groups, the blooming times of flowers of the opposite sexes generally coincide, which results in reciprocating pollination. Thus a heterodichogamous[1]) condition, similar to that described in *A. platanoides* by Stout (1938), is present in *A. saccharum.*

Most trees in the Burlington area bloom within 1 or 2 days of each other. However, a few trees may be found that consistently bloom 3 or 4 days earlier.

Under normal weather conditions, budburst in the Burlington area usually occurs during the first week in May. At Williamstown, some 140 miles to the south, budburst occurs 7 to 10 days earlier.

Under average humidity and temperature conditions, dichogamy is incomplete in sugar maple. The periods of time when male and female flowers on the same tree are mature and functional overlap slightly, thus making self-pollination possible. A more detailed account of dichogamy in sugar maple will be published later.

The compound pistils of sugar maple flowers are composed of two fused carpels and two locules, each locule containing two ovules. The number of ovules that develop into mature seed varies among trees and among flowers on the same tree. Two classes of trees were observed in this respect. In one class, one of the paired carpels is consistently filled with a seed and the other is always empty. In the second class three conditions may be found in the paired carpels on the same tree: (1) one carpel empty and one filled, (2) both carpels empty, and (3) both carpels filled. The first condition is most prevalent.

Normally only one of the ovules in a locule develops into a seed. Instances where both ovules develop have been observed but are extremely rare.

[1]) Terms used with reference to dichogamy are according to Stout (1928).