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Inheritance and Correlation of Growth Characters in Populus deltoides

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Introduction

Since unrooted cuttings rather than seedlings of eastern cottonwood (Populus deltoides BARTR.) are usually planted for timber production in the Lower Mississippi Valley (MCKNIGHT, 1970), replicated clonal tests are ideally suited for selecting superior genotypes for planting there. These tests cannot be adequately designed without phenotypic and genetic correlations between measurements made over time and estimates of total genetic variance and covariance. The few data published to date have been based on first- and second-year measurements (WILCOX and FARMER, 1967; FARMER and WILCOX, 1968). We report here figures gathered over six growing seasons in a replicated clonal test.

Materials and Methods

Clones were taken randomly from a natural stand of 2-year-old seedlings near Rosedale, Mississippi (Bolivar County). For the test, unrooted cuttings from these clones were planted at 9- by 9-foot spacing on a recently cleared site near Stoneville, Mississippi. The soil was a Sharkey clay, which BROADFOOT (1960) described as marginally suitable for cottonwood in the Mississippi alluvial plain. Details related to establishment were given by WILCOX and FARMER (1967).

The test design was a randomized complete block with six replications, 49 clones, and single-tree plots. Data collected after 1 and 2 years were analyzed on the basis of this design and reported by WILCOX and FARMER (1967). Mortality and damage to trees by the end of six growing seasons led to the restriction of current analyses to 38 clones in five replications with no missing plots. The following variables were examined:

1—4. Total height after one, two, three, and five growing seasons.

5—6. Height growth in the second and third growing seasons.

7—11. Diameter at 1 foot after one and two growing seasons and at 4½ feet after three, five, and six growing seasons.

12—13. Diameter increment in the second and sixth growing seasons.

All heights were measured to the nearest 0.1 foot with the aid of a pole, and diameters were measured to the nearest 0.1 inch.

Following analysis of variance, the clone and error variance components were estimated from the mean square for all variables. Ratios of genetic to phenotypic variance (broad-sense heritability) and their confidence limits were calculated from two formulas:

$$H^2 = \frac{\sigma^2{}_c}{\sigma^2{}_c + \sigma^2{}_e} \qquad (1)$$

$$P\,[1\text{-}K_{\alpha/2} \leqq H^2 \leqq 1\text{-}K_{1-\alpha/2}] = 0.95 \qquad \text{(BECKER, 1967)} \quad (2)$$

$$\text{where } K_x = \frac{r\ MS_2F_x}{MS_1 + MS,\ (r\text{-}1)\ F,}$$

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Table 1. — Means, range of clone means, variance components and broad-sense heritabilities.

Character	Test mean	Range of clone means	Clone variance	Error variance	H^2 $(\sigma^2_c/\sigma^2_c + \sigma^2_e)$	95 percent confidence limits for H^2
Total height (feet)						
1st year	11.93	9.66—13.90	.639	1.368	.318	.178—.493
2d year	16.02	14.20—18.44	.859	1.433	.375	.230—.547
3d year	18.83	15.88—21.88	1.421	1.672	.459	.313—.622
5th year	23.82	19.90—27.06	2.252	3.632	.383	.238—.545
Height increment (feet)						
2d year	4.09	2.70— 5.04	.284	0.272	.510	.362—.662
3d year	2.81	1.30— 4.00	.324	0.333	.493	.347—.651
Total diameter (inches)[1]						
1st year	1.58	1.06— 1.88	0.020	0.067	.230	.098—.402
2d year	2.42	1.96— 2.68	0.028	0.102	.215	.090—.391
3d year	2.23	1.76— 2.64	0.029	0.079	.268	.139—.450
5th year	2.89	2.52— 3.36	0.051	0.129	.283	.147—.460
6th year	3.41	2.68— 4.26	0.096	0.177	.352	.208—.535
Diameter increment (inches)						
2d year	0.84	0.60— 1.08	0.005	0.020	.199	.046—.357
6th year	0.52	0.26— 0.90	0.009	0.032	.219	.088—.389

[1] First- and second-year diameters measured at 1 foot above the ground, all others measured at 4.5 feet.

r = the number of replications
c = the number of clones
MS_1 = the mean square for clones: $\sigma^2_e + r\sigma^2_c$
MS_2 = the mean square for error: σ^2_e
F_x = the tabular values for "F" distribution with c-1 and (c-1) (r-1) degrees of freedom
$\alpha = .05$

Correlations between the most recent growth measurements (5-year height and 6-year diameter) and earlier measurements of the same characters were examined by cross-product analysis. Sums of crossproducts, rather than sums of squares, were partitioned and components of covariance were estimated. Genetic and phenotypic correlations were estimated from these values (Falconer, 1960).

Confidence limits for phenotypic correlations were obtained by Fisher's method (Steel and Torrie, 1960). Standard errors for genetic correlations were calculated with the formula:

$$\sigma_r = \frac{1-r^2}{\sqrt{2}} \sqrt{\frac{\sigma_{H_x^2} \cdot \sigma_{H_y^2}}{H_x^2 \cdot H_y^2}} \qquad \text{(Falconer, 1960)}$$

when σ_{H^2} was estimated by:

$$\sqrt{\frac{2\,(N-1)\,(1-H^2)^2\,[1+(r-1)H^2]^2}{r^2\,(N-c)\,(N-1)} \cdot \frac{N-1}{N}} \qquad \text{(Becker, 1967)}$$

where N = number of observations
r = the number of replications
c = the number of clones
H^2 = the broad-sense heritability (interclass correlation).

The same analysis was used to examine the correlations between 5-year height and 5-year diameter.

Results

Growth has been slow when compared to that usually observed for this species in plantations. This is, no doubt, a reflection of the low site quality and close (9 by 9 feet) spacing.

Estimates of broad-sense heritability remained relatively constant from year 1 to year 6 (*Table 1*). Clonal variation accounted for between 30 and 50 percent of the phenotypic variation in total height and from 20 to 35 percent of the variation in total diameter. Heritabilities may have increased with age but estimates are not accurate enough to conclusively demonstrate this trend (see confidence limits in *Table 1*).

Without exception, fifth-year heights and sixth-year diameters were positively correlated with earlier measurements (*Table 2*). Phenotypic correlations increased with age from 0.41 to 0.81 for height and from 0.53 to 0.81 for diameter. The same trend was noted for genotypic correlations which were generally higher. Between years 1 and 3 they increased from 0.30 to 0.89 for height and from 0.35 to 0.89 for diameter.

Since measurements of total diameter or height are the summation of annual effects, these correlations would be expected to increase with age. There were, however, high genetic correlations (above 0.6) for single year increments after the first year (i. e., second- and third-year height increment and second- and sixth-year diameter increment in *Table 2*). These correlations are higher than expected for the contribution of a single season's growth to total

Table 2. — Phenotypic and genotypic correlation coefficients between early measurements and 5-year heights and 6-year diameters.

Characters	Phenotypic correlations[1]		Genotypic correlations	
	r	95 percent confidence limits	r	Standard error
5th year with:		*Heights*		
1st year	.48	.36—.58	.307	.202
2d year	.62	.52—.70	.661	.121
3d year	.81	.75—.86	.890	.043
2d year increment	.31	.17—.43	.690	.107
3d year increment	.51	.39—.61	.784	.079
6th year with:		*Diameters*		
1st year	.53	.42—.63	.351	.216
2d year	.67	.58—.73	.572	.167
3d year	.81	.75—.86	.885	.051
2d year increment	.46	.34—.56	.725	.098
6th year increment	.60	.50—.68	.972	.014

[1] All phenotypic correlation coefficients significant at 0.05 level.

growth, and indicate consistency in a clone's relative growth from year to year.

Height and diameter were apparently strongly correlated. Wilcox and Farmer (1967) and Farmer and Wilcox (1968) found positive correlations between these two characters when using first- and second-year measurements. In this test considerably higher correlations were found in fifth-year heights and diameters. The phenotypic correlation was 0.85 (95 percent confidence interval: 0.80—0.89), and the genetic correlation coefficient was estimated as 0.84 ± 0.047. These high correlations indicated that selection for one characteristic would effect meaningful gains in the other.

Discussion and Conclusions

Analyses of first- and second-year growth data based on the original 49 clones and six replications were previously published by Wilcox and Farmer (1967). Their heritability values for early growth were very close to those given in *Table 1*. There is no reason to suspect bias as a result of mortality or damage and the restriction of the analysis to a balanced set of data.

The estimates given in *Tables 1 and 2* can serve as a rough guide for selection despite the relatively large associated errors. Since they refer to a particular population under particular circumstances, the estimates will be most useful for populations and environments similar to those tested.

Values for broad-sense heritability indicate that the clonal components of variance were large enough at all ages to permit effective selection for height or diameter growth in adequately designed tests. Emphasis on improvement in diameter is preferable if increased volume growth is the objective of a selection program. Diameter, obviously, has a much greater impact on volume than height and it is more easily measured with accuracy.

The data confirm the potential value of short-term screening tests suggested for eastern cottonwood improvement by Farmer and Wilcox (1968); and Mohn and Randall (1969). Wilcox and Farmer (1967) did not find significant correlations between first- and second-year increments in either height or diameter. In contrast, Mohn and Randall (1969) found apparent gains in third-year mean height and fourth-year diameter for a population of clones tested after screening on the basis of first-year growth. The present study's positive correlations between measurements made over time support the conclusion that early selection or culling can be profitable, particularly if it is performed on the basis of data collected after more than 1 year of growth.

Summary

In a test of 38 eastern cottonwood clones to age 6 years, genetic variation accounted for 30 to 50 percent of the total variation in height and 20 to 35 percent of the variation in diameter. Height and diameter were strongly correlated both genetically and phenotypically. Phenotypic and genotypic correlations between measurements made in the first 3 years and in the sixth year were high, suggesting that culling after two growing seasons is feasible.

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Einige Fragen zur Resistenzforschung bei der durch Fomes annosus (Fr.) Cooke verursachten Rotfäule der Fichte

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I. Einleitung

Der Pilz *Fomes annosus* („*F. a.*“) verursacht in vielen Gebieten der Welt vor allem in den Nadelholzbeständen große wirtschaftliche sowie waldbauliche Schäden. In Kontinentaleuropa und den skandinavischen Ländern werden in erster Linie die Fichte und in Ost-England die Kiefer geschädigt. In Nordamerika werden auch mehrere Arten der Gattungen *Picea* und *Pinus* von diesem Parasiten befallen.

Die große Verbreitung des Pilzes und die von ihm verursachten beträchtlichen wirtschaftlichen Einbußen waren entscheidend dafür, daß man sich seit nahezu einem Jahrhundert mit ihm beschäftigt. Die Zahl der in der internationalen Literatur veröffentlichten Arbeiten ist kaum mehr zu übersehen. Interessanterweise wurden aber die bisherigen Arbeiten ausschließlich aus der Richtung der Pathologie, des Waldbaues oder der Bodenkunde bearbeitet. Man hat mit anderen Worten das Vorkommen und die Verbreitung des Pilzes sowie die Rolle der Umweltbedingungen (z. B. Einfluß des Bodens, der Exposition, der Höhenlage, des Vorbestandes u. a. m.) studiert (Rohmeder, 1937; Zycha u. Kató, 1967). Die genetische Komponente im komplexen Zusammenwirken der Erkrankung, wie z. B. die erblich bedingte Variabilität der Wirtspflanzen und der Erreger, wurde weitgehend vernachlässigt. Der Züchter kann andererseits die genetische Resistenz der Wirtspflanzen nicht untersuchen, somit widerstandsfähige Herkünfte, Rassen oder Individuen nicht selektieren, vermehren oder miteinander kreuzen, bevor er gesicherte Kenntnisse über die Entstehung und über den Verlauf der Erkrankung hat. Im folgenden sollen deshalb einige der bei der Resistenzzüchtung gegenüber der Rotfäule wichtigen Gesichtspunkte beschrieben werden.