INHERITANCE AND CORRELATION OF GROWTH CHARACTERS IN HYBRID POPLAR CLONES

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INTRODUCTION

Replicated clonal tests of hybrid poplar designed for selecting superior genotypes are by nature long-term. The most accurate evaluation of growth potential for selection purposes must be based on tests that encompass the entire length of a commercial rotation.

However, replicated clonal tests can be expensive if they involve several hundred clones from many different families and are to be planted in many locations and in different years.

Selection at the earliest possible age, the age at which the genetic potential of a tree or clone can be effectively determined, would be desirable to minimize costs in time, space, and labor.

Shortening a test rotation by early selection of clones that will be of superior height and diameter at the end of a full rotation implies a strong relationship between size at maturity and earlier ages. This is a report on phenotypic and genetic correlations between height and diameter measurements made over time for hybrid poplars grown in a replicated clonal test for 15 growing seasons.

MATERIALS AND METHODS

All data are from hybrid poplars in a 15-year clonal test on the former Lawrence Hopkins Memorial Experimental Forest in Williamstown, Massachusetts.

The tests, on two sites, included 250 clones in sapling tests and 100 of the apparently best clones in crop-tree tests (Schreiner 1972). The sapling tests, from which the data for this study were obtained, were established at 4- x 4-foot spacing in four randomized blocks (16-tree plots, 4 rows of 4 trees) two on an upland terrace site and two on a slope 100 to 300 feet higher in elevation. Fifty clones were established in sapling tests each year from 1949 to 1953.

Genetic and phenotypic correlations, estimates of genetic variance, and broad-sense heritability were calculated separately for each planting year, for the terrace and slope sites, and for both sites combined. (Broad-sense heritability in this trial is more properly regarded as clonal repeatability due to the non-randomness of the sample imposed by top damage and mortality.) Mortality and top damage to trees by the end of 15 growing seasons restricted the analyses to 40, 39, 35, 32, and 23 clones for the 1949 through 1953 plantations, respectively. All calculations were made on an individual-tree basis; the number of living undamaged trees in each replicate ranged from one to eight. The following variables were examined:

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1. Height after 1, 4, 9 or 10, and 15 growing seasons.

2. Diameter breast height after 4, 9 or 10, and 15 growing seasons. Four-year diameters were not measured in the 1951 and 1952 plantations.

One-, 4-, and 9- or 10-year heights were measured to the nearest 0.1 foot. Fifteen-year heights were measured to the nearest 0.5 foot, and all 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 and ratios of genetic to phenotypic variance (broad-sense heritability) and their confidence limits were calculated (Becker 1967). Genetic and phenotypic correlations were estimated from cross-product analysis for the most recent growth measurements (15-year height and diameter) and earlier measurements (Falconer 1960).

RESULTS AND DISCUSSION

Clonal variation accounted for 15 to 80 percent of the phenotypic variation in total height and 15 to 65 percent of the variation in diameter, depending on age and planting year (tables 1 and 2). Values for broad-sense heritability indicate that clonal variance components were large enough to permit effective selection for height or diameter growth for final rotations of 1, 4, 9, or 15 years.

Selection after nine growing seasons would result in the greatest gains inasmuch as heritabilities for height and diameter growth increase as age increases. Heritabilities were highest for 9-year total growth, but the estimates were not significantly different from the estimates at 15 years (see confidence limits in tables 1 and 2). Conversely, the least effective selection would be for 1-year height in all five plantations and 4-year heights and diameters in the 1949 plantation.

Mohn and Randall (1971) also reported a general increase in heritabilities with age increases from 1 to 5 years for height and from 1 to 6 years for diameter in eastern cottonwood _(Populus deltoides)._

Heritability estimates are useful only for a particular population under a specific environmental regime. This point was clearly illustrated by the estimates for the five separate plantations (populations) considered here. Heritability estimates for height and diameter were quite variable; the highest values were for clones in the 1950 planting, and the lowest were for clones in the 1949 planting despite the similarity in the ranges of clone means for growth characters in both plantings (tables 1 and 2).

Differences in heritability estimates between the terrace and slope sites within each planting year were just as striking (table 3). Whereas heritability for height exhibited no consistent pattern between the two sites, heritabilities for diameter were consistently greater on the slope site.

Table 1.--Range of clone means, variance components, and broad-sense heritabilities for height

Planting year	Character Total height (feet)	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
1949-------	1st year	2.67 - 4.75	0.158	0.784	0.168	0.085 - 0.296
	4th year	10.38 - 16.92	1.623	8.210	0.165	0.083 - 0.293
	9th year	18.00 - 41.16	12.530	27.923	0.310	0.205 - 0.454
	15th year	26.50 - 64.16	37.740	47.187	0.444	0.331 - 0.586
1950-------	1st year	2.08 - 5.85	0.742	0.596	0.555	0.441 - 0.646
	4th year	9.71 - 21.56	7.804	4.521	0.633	0.564 - 0.748
	9th year	20.30 - 44.22	40.005	11.458	0.777	0.696 - 0.855
	15th year	25.14 - 60.21	65.481	28.141	0.699	0.602 - 0.799
1951-------	1st year	1.60 - 4.07	0.318	0.918	0.257	0.144 - 0.419
	4th year	6.35 - 13.02	2.078	4.977	0.295	0.177 - 0.458
	10th year	20.38 - 44.87	32.868	19.182	0.631	0.515 - 0.755
	15th year	23.75 - 53.00	33.186	41.556	0.444	0.317 - 0.601
1952-------	1st year	1.92 - 4.20	0.255	0.481	0.346	0.230 - 0.508
	4th year	5.28 - 13.15	4.007	3.088	0.565	0.441 - 0.705
	10th year	17.72 - 42.23	34.595	23.187	0.599	0.478 - 0.733
	15th year	27.66 - 56.00	40.203	33.163	0.548	0.424 - 0.692
1953-------	1st year	2.48 - 4.68	0.508	0.616	0.452	0.312 - 0.636
	4th year	10.68 - 19.08	3.674	7.556	0.327	0.200 - 0.517
	10th year	28.00 - 45.38	14.820	15.175	0.494	0.352 - 0.672
	15th year	34.00 - 57.63	30.165	38.198	0.441	0.301 - 0.627

Table 2.--Range of clone means, variance components, and broad-sense heritabilities for diameter

Planting year	Character Total diameter (inches)[1]	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
1949--------	4th year	0.60 - 1.62	0.029	0.140	0.172	0.090 - 0.304
	9th year	1.75 - 4.65	0.292	0.744	0.282	0.181 - 0.425
	15th year	2.55 - 8.69	1.372	1.914	0.418	0.305 - 0.561
1950--------	4th year	0.64 - 1.80	0.082	0.075	0.522	0.409 - 0.656
	9th year	1.48 - 4.69	0.687	0.406	0.629	0.521 - 0.744
	15th year	2.08 - 7.90	1.938	1.255	0.607	0.498 - 0.727
1953--------	4th year	0.78 - 1.48	0.020	0.102	0.164	0.070 - 0.326
	10th year	2.70 - 5.58	0.490	0.758	0.393	0.257 - 0.582
	15th year	3.90 - 8.57	1.250	1.646	0.432	0.292 - 0.618

[1] Diameters measured at 4.5 feet above the ground.

Table 3.--Heritability estimates for height at four ages on the terrace and slope sites

Planting year	Age: 1 year T	1 year S	4 years T	4 years S	9 or 10 years T	9 or 10 years S	15 years T	15 years S
1949	0.290	0.190	0.213	0.307	0.513	0.371	0.434	0.476
1950	0.541	0.647	0.633	0.719	0.808	0.863	0.587	0.811
1951	0.568	0.272	0.707	0.341	0.807	0.743	0.798	0.530
1952	0.575	0.493	0.682	0.477	0.706	0.699	0.569	0.653
1953	0.522	0.490	0.417	0.668	0.458	0.739	0.495	0.683

If increased volume growth is the objective of the selection program, then emphasis on improvement of diameter is preferable to height improvement. Heritability estimates for height growth were only slightly higher than those for diameter; the mean differences for all plantings were 0.089, 0.092, and 0.042 for 4-year, 9-year, and 15-year estimates, respectively. Heritabilities were also higher for heights than they were for diameters in eastern cottonwood (Mohn and Randall 1971).

Genotypic correlations between heights and diameter were high (table 4). Selection for either characteristic would result in appreciable gains in the other. Moreover, genotypic correlations between heights and diameters were uniformly high for 4-, 9-, and 15-year measurements whereas environmental and phenotypic correlations decreased progressively with increasing age.

Heritability estimates are valuable for predicting gain and for providing guidelines for the most efficient direct selection of traits for improvement. But what about early selection for mature characteristics? With only one exception, 15-year heights and diameters were positively correlated, both genotypically and phenotypically, with earlier measurements (tables 5 and 6). Phenotypic and genotypic correlations tended strongly to increase with increases in the ages at which the heights or diameters serving as the independent variables were measured. Except for the correlations between 1-year and 15-year heights, the genotypic correlations were stronger than the phenotypic correlations.

Genetic differences in the growth patterns of the various clones in each planting probably account for the wide differences in genetic correlations between early height growth and 15-year heights (fig. 1). Genetic correlation between 1- and 15-year heights, in particular, were quite variable from one plantation to another. Wakely (1971) found that height regressions up toe 5 with 30-year measurements varied greatly between four species of southern pine. The weakest regressions were for early measurements and 30-year height in loblolly pine, a characteristically late starter.

Table 4.--Phenotypic, genotypic, and environmental correlation coefficients between heights and diameters

Planting year	Characters	Phenotypic correlations r	Genotypic correlations r	Environmental correlations r
1949-----	4th year	0.921	0.806	0.944
	9th year	0.857	0.800	0.881
	15th year	0.805	0.858	0.764
1950-----	4th year	0.963	0.944	0.998
	9th year	0.910	0.901	0.979
	15th year	0.892	0.925	0.843
1953-----	4th year	0.873	0.860	0.900
	10th year	0.720	0.854	0.653
	15th year	0.653	0.741	0.585

Table 5.--Phenotypic and genotypic correlation coefficients between early measurements and 15-year heights

Planting year	Characters	Phenotypic correlations		Genotypic correlations	
		r	95-percent confidence limits	r	Standard error
	15th year with:				
1949--------	1st year	0.30	0.19-0.40	-0.087	0.057
	4th year	0.55	0.47-0.62	0.697	0.030
	9th year	0.80	0.75-0.84	0.867	0.012
1950--------	1st year	0.54	0.46-0.61	0.678	0.012
	4th year	0.73	0.67-0.78	0.875	0.005
	9th year	0.89	0.86-0.91	0.964	0.001
1951--------	1st year	0.26	0.13-0.38	0.234	0.061
	4th year	0.59	0.49-0.67	0.632	0.036
	10th year	0.86	0.82-0.89	0.952	0.004
1952--------	1st year	0.47	0.37-0.56	0.452	0.032
	4th year	0.65	0.57-0.72	0.819	0.010
	10th year	0.82	0.77-0.86	0.923	0.004
1953--------	1st year	0.28	0.16-0.39	0.290	0.039
	4th year	0.52	0.42-0.61	0.620	0.030
	10th year	0.70	0.63-0.76	0.902	0.008

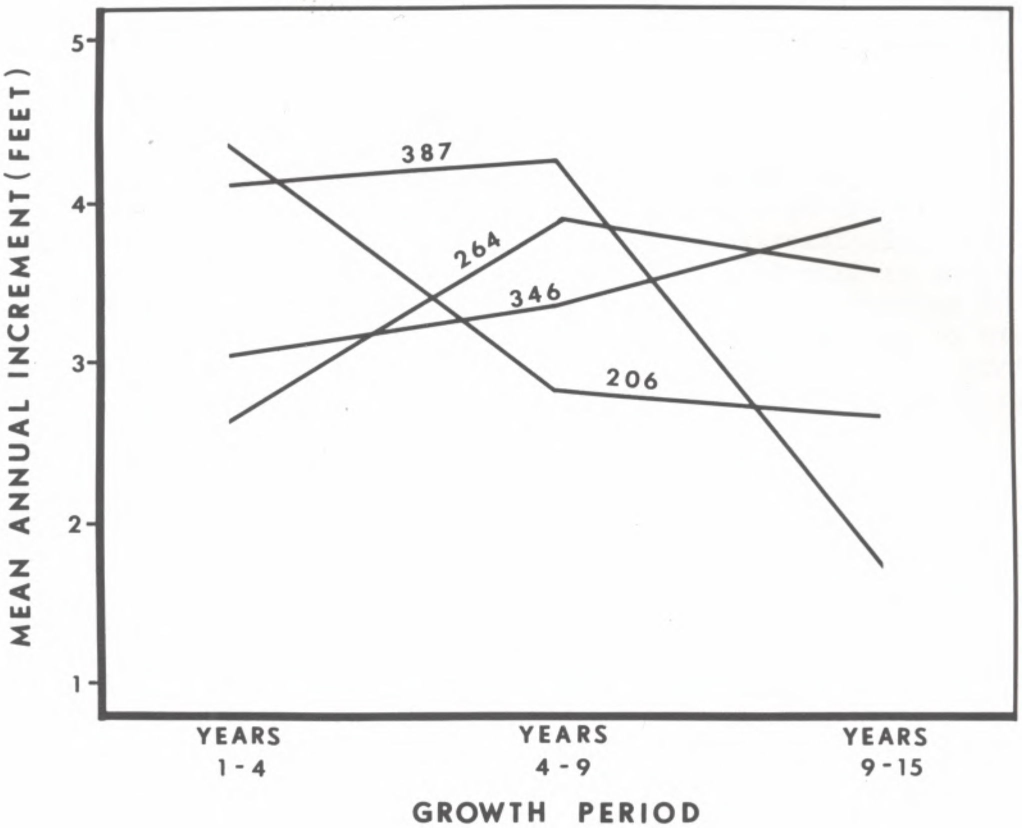

Figure 1.--Height-growth patterns of four hybrid poplar clones selected for superior performance after 15 growing seasons.

Table 6.--Phenotypic and genotypic correlation coefficients between early measurements and 15-year diameters

Planting year	Characters	Phenotypic correlations		Genotypic correlations	
		r	95-percent confidence limits	r	Standard error
	15th year with:				
1949------	4th year	0.62	0.55-0.69	0.402	0.049
	9th year	0.92	0.90-0.94	0.949	0.005
1950------	4th year	0.70	0.64-0.75	0.872	0.007
	9th year	0.94	0.92-0.95	0.982	0.001
1953------	4th year	0.57	0.48-0.65	0.627	0.037
	10th year	0.94	0.92-0.95	1.00	0.000

The negative genetic correlation (table 5) for 1- and 15-year heights in the 1949 planting can also be explained by genetic differences in growth pattern of clones of different species and parental origin. Unlike the case of loblolly pine, the 1949 plantation had a large proportion of early-starting Populus maximowiczii hybrids.

Nine-year and 15-year correlations for both height and diameter were high in all five plantations. The amounts of genetic variation in heights or diameters at age 15 that were accounted for or predicted by heights or diameters at 9 years were as much as 92 percent and not less than 76 percent. Therefore, selections for a 15-year rotation made at 9 years of age would be highly reliable. The chances of selecting genotypes of only average performance and, more important, eliminating superior genotypes would be low.

Genetic correlations between 15-year measurements and measurements made after four and specifically after one growing season were mostly positive but relatively low (table 5). These relatively low correlations, coupled with lower heritabilities at early ages, would render selection at these ages less effective, especially if early selection is used as a simple substitute for long-term tests. However, even these low correlations might be important in tree-improvement programs in which multi-stage selection is used.

Schreiner (1970) predicted that by 1980 the present long-rotation forestry in the Northeast will begin to give way to intensive short-rotation management. He suggested the term "mini-rotation forestry" to include production of fiber on rotations of 2 to 4 or 5 years. Can 1-year performance of hybrid poplar clones be used to predict performance at 4-years for fiber-oriented mini-rotation?

Genotypic correlations between 1-year and 4-year heights were higher 441
than those between 1-year and 15-year heights (table 7).

Table 7.--Phenotypic and genotypic correlation coefficients between 1-year and 4-year heights

Planting year	Phenotypic correlations		Genotypic correlations	
	r	95 percent confidence limits	r	Standard error
1949	0.70	0.64-0.75	0.356	0.073
1950	0.60	0.52-0.67	0.712	0.013
1951	0.71	0.64-0.77	0.630	0.049
1952	0.71	0.64-0.76	0.729	0.018
1953	0.61	0.52-0.69	0.644	0.028

The highest correlation was obtained in the 1952 planting, but even in that planting only 53 percent of the genetic variation at 4 years was accounted for by 1-year height variation. In the 1949 planting the same value was less than 15 percent.

These results support the conclusion of Mohn and Randall (1971) that early selection could be profitable, especially if it is based on data collected after more than 1 year of growth. Their conclusion was based on genetic correlations of 0.307 between 1-year heights and 5-year heights and 0.890 between 3-year and 5-year heights in eastern cottonwood.

SUMMARY

Clonal variance components were large enough to permit effective selection for final rotations of 1, 4, 9, or 15 years. The amount of realized genetic gain would depend on selection age, clonal component of the test, and site. Selection for height or diameter after nine growing seasons would result in the greatest gains, whereas selection for 1-year height would be the least effective. Selection for either height or diameter would result in appreciable gains in the other at any age.

Genetic correlations between 15-year heights and diameters and measurements made before nine growing seasons were generally positive but relatively low and quite variable from one plantation to another. Genetic differences in growth patterns of hybrid poplar clones probably account for the low correlations between 1-year measurements and later measurements.

Whether or not these correlations are sufficient to justify early selection would depend to a great extent on the structure of an improvement program and on technical limitations faced by the breeder.

Although these early measurements of height at 1 and 4 years and diameter at 4 years were found to be of limited value in predicting future performance of hybrid poplar, Santamour (1961) found that root bark percentage in 1-year old hybrid poplar was inversely highly correlated (r = -0.8) with height, diameter, and volume at 9 years. He concluded that it would be possible to select inherently fast growers after 1 and 2 years of testing. There may be other anatomical, chemical, or metabolic criteria that would be more suitable for predicting future growth potential of hybrid poplars, than early growth in height and diameter.

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