Heritability Estimates for Height Growth of Tennessee Yellow-poplar[1])

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Summary

Full-sib, open-pollinated, and “selfed” progeny from 47 Tennessee Valley parent clones of yellow-poplar were tested for 5 years in five replicated plantings in eastern Tennessee and western North Carolina. Observations of variation and heritability indicate that about 15 to 28 percent genetic gain in 5-year height can be obtained by selecting the top 10 percent of full-sib families. Comparison of heritabilities computed from data on full-sib and open-pollinated families suggests that open-pollinated families are not made up to half-siblings, due to a restricted pollen mix.

Key words: Progeny tests, genetic gain, full-siblings, selfing, geographic variation.

Zusammenfassung

In fünffach wiederholten Pflanzungen in Ost-Tennessee und im westlichen North Carolina wurden Vollgeschwister, frei abgeblühte und geselbstete Nachkommenschaften von 47 Eltern-Klonen von *Liriodendron tulipifera* L. aus Tennessee Valley fünf Jahre lang geprüft. An Hand der Variation und Heritabilität konnte beobachtet werden, daß durch Selektion von 10% der wüchsigsten Vollgeschwister-Familien bei der Höhenentwicklung etwa 15 bis 28% an genetischem Gewinn erzielt werden können.

Der Vergleich der Heritabilitäten auf Grund der errechneten Daten von Vollgeschwistern und frei abgeblühten Familien legt den Schluß nahe, daß frei abgeblühte Familien nicht aus Halbgeschwistern bestehen, da das Pollengemisch eingeschränkt ist.

Introduction

While phenotypic variation in yellow-poplar *(Liriodendron tulipifera* L.) has been reported for several characteristics and some limited provenance tests have been conducted (Thor 1975, Wilcox and Taft 1969), no data have been published on variation and genetic control of growth under plantation conditions. However, observations of reproductive characteristics by Boyce and Kaeiser (1961) suggest that production of full-sib families from parents with high specific combining ability should be a genetic improvement goal. With these objectives in mind we have evaluated open-pollinated and full-sib yellow-poplar families from parents in the Tennessee Valley.

Methods

The 47 parents used in this study were clones in breeding arboreta of The University of Tennessee and the Tennessee Valley Authority. They were propagated (by grafting) from ortets selected throughout the Tennessee Valley. In 1971 and 1972 a large number of cross and self-pollinations were made using techniques described by Taft (1966). Resulting cones were collected in September and October and were dried out of doors in the shade until sufficiently dry to permit separation of samaras. Seed were stored dry in polyethylene bags at 4° C until sown in nursery beds in the fall of 1972. Seedlings were grown during the 1973 season in unreplicated family blocks.

In spring 1974, material from 216 families (full-sibs, selfs, open-pollinated) were assigned to five plantings, all of which had a randomized complete block design with either 2- or 4-tree family plots *(Table 1).* Because of highly variable numbers of available seedlings from individual families, many families were represented in a given test by only one to three replications. These families were not included in statistical analyses.

Total height was measured at establishment during the spring of 1974 and after one, two, four (Test IV only), and five growing seasons. Maintenance at the Jones Island planting site (Tests I, II, and V) consisted of annual mowing. Trees in North Carolina tests (III and IV) were spot treated with a mixture of Simazine, Dalapon, and 2, 4-D to control competition.

Variation in height was evaluated using data from trees that were present at all measurements. In the Jones Island test of eastern Tennessee parents (Test II), the mating design was such that the a/b hierarchical design of Cockerham was used in analysis (see Namkoong 1979, pages 235—238). In the other tests such an analysis was not possible due to limited and variable numbers of male parents,

Table 1. — Description of tests and test means for total height and 5-year survival percentage.

Test number and location	Number families	Source of families	Number replications	Trees/ plot	Height, m				Survival percentage
					Year 1	Year 2	Year 4	Year 5	
I. Jones Island	33	W.TN.	6	2	0.8	1.4	-	5.0	90
II. Jones Island	95	E.TN.	6	4	0.9	1.2	-	3.0	86
III. Mill Ridge, NC	156	E.TN. W.TN.	5	4	0.6	0.7	-	1.6	72
IV. Kale Gap, NC	103	E.TN. W.TN.	5	4	0.8	-	1.6	2.0	75
V. Jones Island	30	E.TN W.TN. (selfs)	5	4	0.7	0.8	-	1.4	23

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Table 2. — Analysis of variance for progeny of predominantly west Tennessee parents on Jones Island (Test I).

Source	df	Year 1		Year 2		Year 5		Expected mean square
		Mean square	Variance	Mean square	Variance	Mean square	Variance	
Replications (R)	5	4,165		2,649		94,327		$V_w^2 + 1.84V_{RC}^2 + 34.13V_R^2$
Families (F)	24	3,209	319	3,050*	167	35,263*	2,278	$V_w^2 + 1.82V_{RC}^2 + 8.63V_F^2$
R X F	88	452*	120	1,611	± 0	15,578*	2,676	$V_w^2 + 1.91V_{RC}^2$
Within plot	109	223	223	1,949	1,949	10,467	10,467	V_w^2
Total	226							
h^2			.96		.16		.30	

*Statistically significant at the .05 level of probability.

Table 3. — Analysis of variance of height for progeny of east Tennessee parents on Jones Island (Test II).

Source of variation	df	Year 1		Year 2		Year 5		Expected mean square
		Mean square	Variance	Mean square	Variance	Mean square	Variance	
Replications (R)	5	12,874		6,537		53,018		$V_w^2 + 1.92V_{RF}^2 + 85.77V_R^2$
Families (F)	50	3,223*	268	2,477*	142	23,649*	1,210	$V_w^2 + 1.92V_{RF}^2 + 10.29V_F^2$
R X F	229	464*	150	1,022*	150	11,202*	3,926	$V_w^2 + 1.92V_{RF}^2$
Within plot	241	176	176	733	733	3,664	3,664	V_w^2
h^2			.90		.28		.27	

*Statistically significant at the .05 level of probability.

and analysis of variance was used simply to compare individual crosses. Juvenile-mature correlation analyses of family means at 1, 2, and 5 years were completed using data from Tests I, II, and IV.

Results

Survival at the end of the 5-year observation period and average height for the three measurements are presented for each test in *Table 1.* Trees in Test I, containing mostly western Tennessee parents, were largest, with an average height of 5.0 m at 5 years; selfs were the smallest. Formal comparison of average height in the three tests (I, II, and V) on Jones Island cannot be made since each contains different plant material.

In Test III there were no significant height differences among families at 5 years due to site variation within replications, which was not apparent at the time of establishment. Therefore, data on genetic variation in this test are not presented.

Test I. Predominantly West Tennessee Progenies at Jones Island

Represented in Test I are 30 full-sib and 3 open-pollinated families; 25 were represented in 3 or more of the 6 replications and therefore were included in the analysis of variance *(Table 2).* Mean family height at 5 years ranged from 3.3 to 6.0 m. Family variance ranged from 48 percent of total variance (not including replication variance) in the first year to 8 percent in the second year and 15 percent after 5 years, when narrow-sense heritability for height was .30.

Because families were not replicated in the nursery, genetic variances in early height (years 1 and 2) probably contain a large component of variance associated with environmental preconditioning in the nursery and are not suitable for computing reliable estimates of heritability and gain. The data for 5-year height are more reliable in terms of genetic gain prediction. Selection of the top 10 percent of the families would give a 15-percent gain (FALCONER 1960, page 235).

Test II. East Tennessee Progenies at Jones Island

Of the 95 families represented in this test, 51 full-sib families were represented in 5 or 6 replications and are therefore included in the analysis of variance *(Table 3).* Since 10 females were each crossed with 3 to 9 of 11 males, nested analyses were also used for 5-year height; in one analysis males were nested within females, while in the other females were nested within males *(Table 4).* Mean family height at 5 years ranged from 2.2 to 4.1 m. The ranges of average height were similar for both male (2.4—3.4 m) and female (2.5—3.4 m) parents. However, in both analyses the variance associated with females was much less than with males partly because only three of the male parents were also used as female parents. The coefficient of variation for male parent means (both open-pollinated and average for full-sib) was higher than that for equivalent female means (15 percent vs 8 percent). Therefore, the resulting heritabilities were .09 for females and .44 for males (FALCONER 1960, page 175). Heritability of 5-year height based on a full-sib analysis was .27 using either the randomized complete block *(Table 3)* or Design I nested analyses *(Table 4).* The most practical and effective selection procedure would therefore be selection for specific breeding value, *i.e.*, for the best 10 percent of individual crosses.

Table 4. — Analyses of variance of 5-year height for east Tennessee progenies at Jones Island (Test II).

Source of variation	df	Mean square	Variance component	Expected mean square
Replications (R)	5	47,942		$\sigma^2_w + 1.86\sigma^2_e + 84.93\sigma^2_R$
Females (F)	9	32,204	214	$\sigma^2_w + 1.86\sigma^2_e + 9.84\sigma^2_{M/F} + 50.77\sigma^2_F$
Males/Females (M/F)	42	21,359	1,010	$\sigma^2_w + 1.86\sigma^2_e + 10.01\sigma^2_{M/F}$
R X F (error)	226	11,246	3,844	$\sigma^2_w + 1.86\sigma^2_e$
Within plot	241	4,097	4,097	σ^2_w
Replications (R)	5	32,091		$\sigma^2_w + 1.86\sigma^2_e + 84.93\sigma^2_R$
Males (M)	10	51,474	824	$\sigma^2_w + 1.86\sigma^2_e + 9.93\sigma^2_{F/M} + 45.72\sigma^2_M$
Females/Males (F/M)	41	13,801	186	$\sigma^2_w + 1.86\sigma^2_e + 9.82\sigma^2_{F/M}$
R X F	226	11,965	4,230	$\sigma^2_w + 1.86\sigma^2_e$
Within plot	241	4,097	4,097	σ^2_w

Test IV. Full- and Half-sib Families at Kale Gap

Seventy-two families represented in four or five replications were included in an analysis of variance, which indicated that there were significant family difference in heights at 1, 4, and 5 years. Mean family heights at 5 years ranged from 0.9 to 3.5 m. Eighteen families from western Tennessee maternal parents had an average 5-year height of 1.9 m, a figure not significantly different from the test mean. Since 21 of the 72 families included in the overall analysis were open-pollinated separate analyses of full-sib and open-pollinated families were completed *(Table 5)*. These analyses indicated that family variance accounted for about 20 percent of total variation in 4- and 5-year height and that family variances were similar for both types of parentage. However, narrow-sense heritabilities were estimated to be .74 and .42 for open-pollinated families and full-sibs, respectively. The especially high heritability for first year height is a reflection of environmental preconditioning effects.

If open-pollinated families were true half-sibs, heritability estimates based on open-pollinated family analysis should be the same as estimates based on full-sib analysis. Since they are not, our results strongly suggest that the open-pollinated progenies used in this test are not half-sibs. Therefore, only a full-sib analysis will give reliable estimates of heritability and gain. This gain would be 28 percent for selecting the top 10 percent of families.

Test V. Selfs at Jones Island

Because of generally poor survival, data from this test were not subjected to an analysis of variance. Of the 348 trees planted 63 percent survived the first year of the test; 55 percent, the second year; and 23 percent, by the fifth year. Fifth-year survival ranged among families from 0 to 65 percent. While formal comparison is not possible, survival of selfs was less than one-third and height was less than one-half of that for outcrossed material in other tests on Jones Island. The selfs were, however, planted on a relatively poor site.

Table 6. — Coefficients for correlations of mean family height at various ages.

	Test I	Test II	Test IV
Year 1 vs year 2	.84	.79	-
Year 1 vs year 4	-	-	.64
Year 1 vs year 5	.58	.39	.69
Year 2 vs year 5	.38	.64	-
Year 4 vs year 5	-	-	.97
Number of families used in analysis	25	51	72

Additional Analyses

The major changes in heritability noted above suggest shifts in family rankings from year 1 through year 5. This possibility was examined by correlation analysis of family

Table 5. — Analysis of variance of full- and half-sib families at Kale Gap (Test IV).

Source of Variation		Year 1		Year 4		Year 5		Expected mean square
		Mean square	Variance	Mean square	Variance	Mean souare	Variance	
				Open-pollinated Families				
Replications (R)	4	6,980		15,286		40,664		$\sigma^2_W + 3.11\sigma^2_{RF} + 55.56\sigma^2_R$
Families (F)	20	6,061*	412	14,210*	641	26,168*	1,197	$\sigma^2_W + 3.11\sigma^2_{RF} + 13.76\sigma^2_F$
R X F	67	396*	55	5,393*	1,150	9,692*	2,113	$\sigma^2_W + 3.11\sigma^2_{RF}$
Within plot	201	225	225	1,816	1,816	3,120	3,120	σ^2_W
Percentage family variance			60		18		19	
Narrow-sense heritability			2.38		.71		.74	
				Full-sib Families				
Replications (R)	4	18,485		40,160		59,240		$\sigma^2_W + 3.08\sigma^2_{RF} + 116.21\sigma^2_R$
Families (F)	50	3,190*	206	11,289*	599	19,190	974	$\sigma^2_W + 3.08\sigma^2_{RF} + 12.36\sigma^2_F$
R X F	149	639*	142	3,889	843	7,153*	1,679	$\sigma^2_W + 3.08\sigma^2_{RF}$
Within plot	431	201	201	1,293	1,293	1,983	1,983	σ^2_W
Percentage family variance			38		22		21	
Narrow-sense heritability			.75		.44		.42	

*Statistically significant at the .05 level of probability.

means (*Table 6*). Correlation coefficients for year 1 vs year 2 were 0.8 or greater, and those for year 1 and year 2 vs year 5 were 0.4 to 0.7. Unexpectedly, the year 1 vs year 5 coefficient was higher than the year 2 vs year 5 in Test I, containing predominantly western Tennessee parents. These coefficients thus substantiate the hypothesis of some major changes in family ranking over time.

Fourteen families well represented in both Test II and Test IV were included in an analysis of variance designed to evaluate family × site interaction. In this analysis neither family nor family × site terms were statistically significant.

Discussion

With the exception of the selfs, survival and growth in all the tests have been within expectations for an operational planting. Family variation exhibited to date over several site conditions offers good opportunities for improving early growth rate.

Despite design problems and some effects of environmental preconditioning, the data provide some guides for the use of yellow-poplar breeding material. The narrow-sense heritability for height (averaging about 0.3) and observed phenotypic standard deviation will give genetic gains of around 14 to 28 percent if the top 10 percent of full-sib families are selected. Though there was an apparent stabilization of heritability (i.e., similar estimates in years 4 and 5), environmental preconditioning is still suspect in this test, and gain estimates are tentative.

Comparison of heritabilities estimated from full-sib and open-pollinated families in this study strongly suggests that the assumption of half-sibs for open-pollinated families is not appropriate for yellow-poplar and that, in fact, open-pollinated progeny tests may have no role in yellow-poplar breeding. It is likely that, because of the predominance of insect pollination and restricted movement of insects during feeding, open-pollinated families range between full-sibs and siblings resulting from a restricted pollen mix, i.e., made up of pollen from a few male parents in close proximity to the female (Thor *et al.* 1976). Therefore, breeding should continue to rely on full-sib progeny tests, and mating should be aimed at identifying parental combinations with high specific combining ability or parents with exceptionally good general combining ability. Orchard design may vary from a number of two clone mini-orchards for the purpose of producing single high-value crosses to a relatively larger orchard with small numbers of clones, all with high general combining ability.

The relatively large contribution of male effects to genetic variance in Test II was an unexpected observation and may be an artifact of the experimental design. Therefore, breeding strategy should not be altered in light of this relationship until it is substantiated by further testing, perhaps via diallel crossing designs.

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Genetic Variation in Traits Important for Energy Utilization of Sand and Slash Pines

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Summary

Half-sib families of Choctawhatchee sand pine and slash pine were utilized to estimate genetic variation for a number of biomass traits including stem, branch, and total green weights; percent stem biomass; stem wood dry weight, volume, and energy content; foliage and branch moisture content, specific gravity, and ash content; and basal stem wood and bark moisture content, specific gravity, and heat value. Variation among families was observed for many traits, although significant differences were not detected for several traits due in part to limited sample size. Heritabilities of biomass quantity traits were moderate to high, and estimated genetic gains from parent plus family selection were appreciable. Biomass quality traits generally had low heritabilities which, coupled with less variation, resulted in limited gain potential. Meaningful increases in sand pine and slash pine productivity in "silvicultural energy plantations" appear possible through selection for increased stem biomass, better survival, and higher biomass density.

Key words: *Pinus clausa* var. *immuginata* Ward, *Pinus elliottii* var. *elliottii* Engelm., biomass production, genetic improvement.

Zusammenfassung

Halbgeschwister Familien von *Pinus clausa* var. *clausa* und *P. elliottii* var. *elliottii* wurden zur Schätzung der genetischen Variation von Biomasse-Eigenschaften verwendet: Stamm, Äste Gesamt-Grüngewicht; Prozent Stamm-Biomasse; Trockengewicht des Stammholzes, Volumen und Energiegehalt; Feuchtigkeitsgehalt, spezifisches Gewicht und Aschengehalt der Blätter und Äste; Feuchtigkeitsge-

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