VARIATION AND HERITABILITY OF BRANCHING AND GROWTH CHARACTERISTICS AMONG SYCAMORE PROGENY

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Abstract.--Forty-eight open-pollinated families of American sycamore from 5 seed sources were analyzed at the end of the fifth growing season for variation in height, diameter, live crown, branch angle, and branch frequency. All traits differed significantly among families, while diameter was the only trait which differed among seed sources. All traits were moderately inherited. Mass selection of the best 10 trees without regard to family resulted in genetic gains approximately 3.5 times as great as those from family selection. Direct selection to improve crown form will lead to decreased diameter growth, while selection for diameter will result in trees with larger and more fastigate crowns.

Additional keywords: Platanus occidentalis, live crown, branch angle, branch frequency, open-pollinated families, genetic gain.

American sycamore (Platanus occidentalis L.) plantations are currently being established throughout the southern and central Mississippi River valleys on sites not suitable for eastern cottonwood (Populus deltoides Bartr.). Selection of superior genotypes is needed to maximize the utilization potential of this species. Due to the influence of crown form on growth rate and wood quality (Larson 1962) genetic variation of branching characteristics must be quantified. Variation and inheritance of certain branching traits of sycamore have been examined by Nebgen and Lowe (1982) and Ferguson et al. (1977). These reports conclude that branch angle and branch frequency are weakly to moderately inherited and that only minor genetic gains would result from direct selection for these characteristics because of their limited variation. Further work with mass selection and progeny testing should lead to a more thorough understanding of the potential for genetic improvement of growth rate and crown form in sycamore. The objectives of this study were: (1) to analyze a sycamore progeny test for variation and inheritance of growth rate and branching characteristics, and (2) to estimate expected genetic gains and correlations between traits.

METHODS

Six progeny from each of 48 open-pollinated families representing 5 geographic seed sources were analyzed at the end of the fifth growing season for variation in height and diameter growth rate, percent live crown, branch angle,

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and branch frequency. This progeny test was established by Westvaco Corp. on Island No. 3 in the Mississippi River in Carlisle Co., KY. The test consists of 6 replications of the 48 families planted in 10-tree row plots at a 3.35x 3.35 m spacing.

Branch angle was measured on all branches in the middle one-third of the crown with a diameter greater than 0.5 cm at the point of insertion. Measurements were made using a large Plexiglas protractor which was marked-off in 10 intervals of 9 degrees. Branch frequency was calculated as the number of measured branches per meter of stem. Live crown was calculated as the percent of total tree height occupied by functional branches.

Analysis of variance employed a nested factorial model with families nest within seed sources. Narrow-sense heritability estimates were calculated for individual trees as:

$$h^2_I = \frac{4\ \sigma^2_{F(S)}}{\sigma^2_W + \sigma^2_{RF(S)} + \sigma^2_{F(S)}} \tag{1}$$

and for families as:

$$h^2_F = \frac{\sigma^2_{F(S)}}{\frac{\sigma^2_W}{rn} + \frac{\sigma^2_{RF(S)}}{r} + \sigma^2_{F(S)}} \tag{2}$$

where: $\sigma^2_{F(S)}$ = families within seed source variance

σ^2_W = trees within family variance

$\sigma^2_{RF(S)}$ = replication x family variance

r = number of replications

n = number of trees per plot.

Expected genetic gains and phenotypic and genetic correlations were calculated according to Falconer (1981).

RESULTS AND DISCUSSION

Branch frequency and diameter at breast height were the most variable traits, while total tree height was the least variable (Table 1). Mean values for height and diameter were intermediate to those reported by Nebgen and Lowe (1982) and Ferguson et al. (1977). Branch angle and branch frequency averaged 46 degrees and 6.5 branches per meter, respectively. These values compare favorably with those of Ferguson et al. (1977) for the same traits in 5-year-old sycamore progeny (45 degrees and 6.1 branches per meter, respectively). Nebgen and Lowe (1982) reported a much greater average branch angle (54 degrees) in 7-year-old sycamore.

Table 1.--Means, ranges and coefficients of variation (CV) for growth and crown traits.

Trait	Mean	Individual Tree Range	CV	Family Range	CV
Height (m)	8.08	4.85-10.55	10.76	6.70-9.18	4.70
Diameter (cm)	8.77	3.51-15.60	18.94	6.62-11.19	11.09
Live Crown (%)	75	43-97	13.36	63-86	8.93
Branch Angle (°)	46	30-68	13.35	40-56	7.61
Branch Freq. (br/m)	6.5	2.6-10.8	22.47	4.7-8.3	12.31

All traits differed significantly between families within seed sources (F(S)) (Table 2). Diameter was the only trait which differed significantly between seed sources (S). Significant differences between replications (R) for height, diameter, and live crown and significant interaction effects for height and live crown resulted from microsite variation and possibly non-uniform survival among replications. Mortality among replications ranged from a low of 70 percent to over 91 percent. As a result, sample trees in proximity to one or more non-surviving trees developed under varied degrees of wider spacing. However, this did not influence branch angle or live crown development as a separate analysis indicated that there were no significant differences in live crown or branch angle between trees growing with 0, 1, or 2 non-surviving neighbor trees.

Table 2.--Analysis of variance for growth and crown traits for 5-year-old American sycamore.

Source	d.f.	Mean Square[a]				
		Height	Diameter	Live Crown	Branch Angle	Branch Freq.
S	4	6.84	18.16**	391.42	26.29	2.18
F(S)	43	1.89**	4.83*	265.98*	77.35*	4.43*
R	4	18.89**	21.89**	339.36*	92.69	1.35
R x S	14	2.04*	2.83	112.84	41.37	1.45
R x F(S)	78	.93	2.74	172.48**	42.89	2.68
E	144	.76	2.76	100.37	38.28	2.11

[a] ** significant at $\alpha<0.01$
* significant at $\alpha<0.05$

Variance and covariance components were generated for heritability estimates and correlation coefficients. Expected genetic gains were calculated for two alternative selection strategies. The first was family selection in which the 10 best families out of the total of 48 were selected. The second represented mass selection in which the best 10 trees were selected without regard to family. Selection intensities for these 2 strategies (i=1.38 for family selection and i=2.23 for individual tree selection) were derived from the graphs published by Namkoong and Snyder (1969).

All traits were moderately inherited. Individual tree values were higher than family values (Table 3). The estimates are potentially bia to the single test location analyzed. Nebgen and Lowe (1982) reported al range in heritability estimates between test locations and emphasized the for multiple location testing. However, Webb et al. (1973) suggested that tability estimates may be adjusted for the lack of genotype x environment action by multiplying the estimates by 0.75.

Table 3.--Heritabilities, standard errors, and expected genetic gains for family and individual tree selection.

Trait	$h^2_F \pm SE$	$h^2_I \pm SE$	Family Selection a/	Individual Tree Selection b/
			- - - - percent gain - - - -	
Height	.44 ± .16	.51 ± .14	4.0	13.9
Diameter	.41 ± .10	.41 ± .14	5.6	18.2
Live Crown	.35 ± .17	.41 ± .15	4.2	15.0
Branch Angle	.44 ± .15	.49 ± .12	4.7	16.2
Branch Frequency	.40 ± .16	.45 ± .14	7.2	25.4

a/ selection for the best 10 families

b/ selection for the best 10 trees

As a result of their large ranges of variation, branch frequency and di eter exhibited the largest expected genetic gains for both selection strategi Mass selection of individual trees without regard to family resulted in expec genetic gains which averaged approximately 3.5 times greater than those from family selection. Estimated gains from individual tree selection averaged nearly 18 percent while gains from family selection averaged around 5 percent The expected genetic gain for branch angle resulting from mass selection (16.2 percent) is twice as great as estimates at similar selection intensities from previous studies. Major reasons for this difference include greater variation in the population than that reported by Nebgen and Lowe (1982) and higher heri tability estimates than those of Ferguson et al. (1977). Different methods us to measure branch angle may also have influenced these values.

To analyze the relationship between growth rate and crown form, phenotyp and genetic correlation coefficients were calculated (Table 4). Due to the h standard errors usually associated with genetic correlation coefficients (Gogg 1964), statistical significance levels have been determined solely for the ph typic values.

Statistically significant phenotypic correlation coefficients indicated a negative relationship between live crown and both height and diameter growth rate. However, the respective genetic correlations showed that trees with greater growth rates had larger live crowns, the genetic relationship between live crown and diameter was particularly strong (0.68). The environmental component of the phenotypic correlation coefficients probably confounded that relationship.

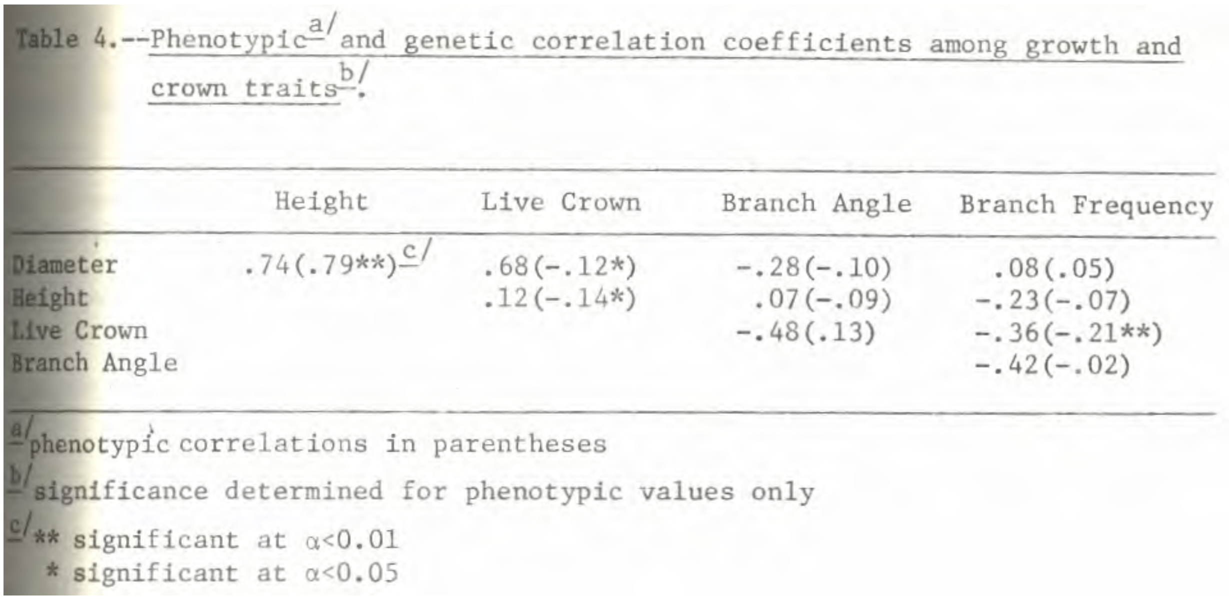

Table 4.--Phenotypic[a] and genetic correlation coefficients among growth and crown traits[b].

	Height	Live Crown	Branch Angle	Branch Frequency
Diameter	.74(.79**)[c]	.68(-.12*)	-.28(-.10)	.08(.05)
Height		.12(-.14*)	.07(-.09)	-.23(-.07)
Live Crown			-.48(.13)	-.36(-.21**)
Branch Angle				-.42(-.02)

[a] phenotypic correlations in parentheses

[b] significance determined for phenotypic values only

[c] ** significant at $\alpha<0.01$
  * significant at $\alpha<0.05$

The negative correlation between live crown and branch frequency suggested that trees with larger live crowns had fewer productive branches per meter of stem than smaller live crowns. Genetic correlations also indicated that direct selection for diameter growth rate would result in trees with larger live crowns and more acute branch angles. These findings are in accordance with those of Nelson et al. (1979), who predicted that the fast-growing cellulose-producing tree of the future would have much larger crowns with a more fastigate form than has been tolerated in the past. Changing objectives from short-rotation fiber production to longer rotation sawlog or veneer log production may require some sacrifice in growth rate as selection is made for flatter branch angles, lower branch frequency and reduced live crown.

CONCLUSIONS

(1) Significant variation existed among families for all growth and crown traits studied to reward a breeding program based upon family selection. Diameter growth rate was the only trait which could be improved through selection from broad geographic seed sources in our study.

(2) All traits were moderately inherited. Average genetic gains approaching 18 percent are possible if mass selection is made for the best10 trees without regard to family. These gains are approximately 3.5 times larger than potential gains resulting from family selection.

(3) Selection for flatter branch angles to potentially improve wood quality may not be advisable due to a correlated reduction in diameter growth rate. Selection for fewer branches would result in increased height growth and flatter branch angles.

(4) If the primary objective is wood fiber production, selection should be made to increase diameter growth rate. The resulting trees will have more fastigate crowns and persistent live branches.

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