Inheritance of Growth and Crown Characters in American Sycamore[1])

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Introduction

Forest tree improvement programs for American sycamore (Platanus occidentalis L.) are currently underway in the southern United States. Information about genetic variation, heritabilities, potential genetic gains, and genetic and phenotypic correlations between characters is a necessary prerequisite for evaluating breeding strategies.

Both growth rate and crown characters influence the quality and yield of sycarnore grown in short and long rotations for pulpwood and sawtimber. Limb frequency and branch angle influence knotwood and reactionwood volume, which may affect both quality and yield (Dadswell 196.0). Although early height and diameter growth of sycamore are apparently under moderate genetic control (Schmitt and Webb 1971, Webb et al. 1973), little is known about limb frequency and branch angle, which are under moderate genetic control for several conifer species (Faulkner 1969, Ehrenberg 1970). Possible correlations between growth and crown characters have been reported for mature sycamore in natural stands (Schmitt and Wilcox 1969) but not for young trees. This paper reports among- and within-source variation, narrow-sense heritabilities, expected genetic gains, and genetic and phenotypic correlations for height, d.b.h., limb frequency, and branch angle of five-year-old sycamore progeny from parents in natural stands along the southern portion of the Mississippi River.

Materials and Methods

Parents were selected from five stands containing at least 150 trees and assumed to represent a random sample of the study area (Table 1). Open-pollinated seed was collected from 25 randomly selected trees per stand in the fall of 1967, and the seedlings were grown in a nursery in 1968. Because of the poor germination of some seedlots, only a total of 100 families were available for outplanting. In 1969, seedlings were planted at 10 X 10 ft. spacings at Huntington Point, Mississippi, 10 miles northwest of Greenville. The soil was Commerce silt loam, an excellent soil for sycamore. For each family, row plots containing six trees were arranged in a repeated triple lattive design of six replications (Cochran and Cox 1957). Near the end of the fifth season in the field trees that were obviously diseased, suppressed, or vine-damaged were removed. After further thinning of randomly selected normal trees, three trees per plot remained for measurement of branch angle, limb frequency, height, and d.b.h. Branch angle and limb frequency were measured only for the portion of the crown formed during 1971, the third

year in the field. Branch angles were estimated visually by assigning each branch a value from one to five; each number represented an 18^0 interval in the 90^0 arc from vertical to horizontal. Class-5 limbs — the closest to horizontal — were considered the most desirable. A pole-mounted protractor was used frequently to verify the accuracy of the visual estimates. Limb frequency was expressed as the number of limbs counted an a five-foot section of the 1971 crown formation. Height was recorded to the nearest foot, and d.b.h. to the nearest tenth of an inch.

Table 1. — Location of seed sources for 100 open-pollinated families

Seed Source	Number of Families	Location Latitude N	Longitude W
Vidalia, LA	25	31°25'	91°30'
Newellton, LA	25	32°05'	91°05'
Greenville, MS	24	33°20'	91°10'
Catfish Point, MS	16	33°40'	91°10'
New Madrid, MO	10	36°25'	89°35'

Table 2. — Form of anaiysis used to partition variance[e])

Source of Variation	df	Expected Mean Squares[b/]
Replications (R)	5	
Among Sources (S)	4	$\sigma^2 + 3\sigma^2_{RF(S)} + 18\sigma^2_{F(S)} + 52.78\sigma^2_{RS} + 316.68\sigma^2_{S}$[c/]
Among Families Within Source	95	$\sigma^2 + 3\sigma^2_{RF(S)} + 18\sigma^2_{F(S)}$
R X S	20	$\sigma^2 + 3\sigma^2_{RF(S)} + 52.78\sigma^2_{RS}$[c/]
R X F/S	475	$\sigma^2 + 3\sigma^2_{RF(S)}$
Within Plot	1200	σ^2
Total	1799	

[a/] Analogous procedures were used to partition covariance between characters.

[b/] σ^2 = variance among individuals within plotc.
$\sigma^2_{RF(S)}$ = variance attributable to replication by family interaction.
$\sigma^2_{F(S)}$ = variance among familics within a source.
σ^2_{RS} = variance attributable to replication by source interaction.
σ^2_{S} = variance of source effects.

[c/] Coefficients computed using harmonic mean of families in sources.

Components of variance for each character and of covariance between characters were estimated by analyses of variance and covariance (Table 2). In the analyses, the randomization restrictions of the lattice design were ignored, and randomized block analyses were substituted. Genetic variation among seed sources and that among families within seed sources were eomputed, and narrow-sense individual-tree heritabilities pooled over sources were estimated as follows:

$$\text{Heritability} = \frac{4\sigma^2_{F(S)}}{\sigma^2 + \sigma^2_{RF(S)} + \sigma^2_{F(S)}}$$

Within-source expected genetic gains (EGG) were computed for a hypothetical clonal seed orchard comprised of select trees from a single seed source in the plantation. The general expected gain formula (standardized selection dif-

ferential times the phenotypic standard deviation times the appropriate heritability) was modified using the methods of Namkoong et al. (1966). Both selection without regard to family and combined selection of the best individuals within the best families were considered. Standardized selection differentials (i) from Becker (1967) were used with pooled components of variance to estimate the expected genetic gains as follows.

For selection without regard to family, it was assumed that the best individuals would be selected from a 25-family (450 tree) source ($i_m = 2.39$):

$$EGG_m = i_m \left[\frac{4\sigma_{F(S)}}{\sqrt{\sigma^2 + \sigma^2_{RF(S)} + \sigma^2_{F(S)}}} \right]$$

For combined selection of the best individuals within the best families, it was assumed that the one best individual per 18-tree family ($i_{I/F} = 1.82$) would be selected from each of the 10 best families of a 25-family seed source ($i_F = 0.94$):

Among families

$$EGG_F = i_F \left[\frac{\sigma^2_{F(S)}}{\sqrt{\frac{\sigma^2}{18} + \frac{\sigma^2_{RF(S)}}{6} + \sigma^2_{F(S)}}} \right]$$

Within families

$$EGG_{I/F} = i_{I/F} \left[\frac{3\sigma^2_{F(S)}}{\sqrt{\sigma^2 + \sigma^2_{RF(S)}}} \right]$$

Total gain $= EGG_F + EGG_{I/F}$

Genetic and phenotypic correlations between characters were computed from the components of variance and covariance.

Results and Discussion

At age five, among-source variation represented 77 percent of the family differences for d.b.h., 82 percent for height, 38 percent for limb frequency, and 12 percent for branch angle. Means of all families were 36.4 feet for height, 4.65 inches for diameter, 9.4 limbs for a 5-foot stem segment, and 3.1 (approximately 45°) for branch angle. The family means ranged from 31.4 to 38.8 feet for height, 3.84 to 5.28 inches for d.b.h., 7.8 to 11.0 limbs per segment for limb frequency, and 2.6 to 3.7 for branch angle class. The range among families for height and d.b.h. was principally due to differences among sources (Table 3).

Pooled over sources, narrow-sense heritability estimates computed from variance components in Table 4, were 0.26 for d.b.h., 0.26 for height, 0.15 for limb frequency, and 0.16

Table 3. — Mean height, diameter, limb frequency, and branch angle of 5-year-old sycamore progeny

Seed Source	Diameter (breast high)	Height	Limb Frequency	Branch Angle
	in.	ft.	per 5-ft. segment	score
Vidalia, LA	4.9	37.3	9.7	3.0
Newellton, LA	4.8	37.3	9.4	3.1
Greenville, MS	4.6	36.1	9.5	3.1
Catfish Point, MS	4.5	35.6	9.0	3.1
New Madrid, MO	4.2	33.5	8.9	3.0

Table 4. — Variance component estimates

Character	Component Estimated				
	σ^2_S	$\sigma^2_{F(S)}$	$\sigma^2_{RF(S)}$	σ^2	σ^2_{RS}
d.b.h.	.0608	.0181	.0571	.2036	-.0014
Height	1.8251	.4027	2.5629	3.2528	+.0561
Limb Frequency	.0895	.1482	.5188	3.3911	-.0565
Branch Angle	.0022	.0163	.0623	.3294	-.0033

for branch angle. The heritability estimates were probably inflated because of genotype-by-environment interactions and because the members of the open-pollinated families may have been more closely related than half-sibs (Namkoong 1966). The results indicate that growth is under greater genetic control than branch characters. Heritability estimates for d.b.h. and height were consistent with those reported by Webb et al. (1973) for 4-year-old sycamore; similar heritabilities for height, diameter, and limb frequency have been reported for 6-year-old sweetgum (Liquidambar styraciflua L.) (Mohn and Schmitt 1973).

The highest within-source genetic gains would occur with selection without regard to family, but the expected gain from selection of the best individuals within the best families is only slightly less (Table 5) and would offer the advantage of a broader genetic base in the next generation, since 10 families would be represented.

Since variation among sources accounts for most of the genetic variation for the two growth characters, worth-while additional gains in growth rate should be achievable from selection among sources for these characters. The sources used in this study were not considered adequate in number or distribution for estimating gain among sources applicable to other studies.

Table 5. — Expected genetic gains from selection

Selection Scheme	Expected Genetic Gain			
	Diameter (breast high)	Height (feet)	Limb Frequency	Branch Angle
	in.	ft.	per 5-ft. segment	score
Mass selection[a]	0.32	1.50	0.68	0.24
Combined Selection[b]				
Family Selection	0.09	0.38	0.21	0.07
Individual/Family Selection	0.19	0.91	0.41	0.14
Total	0.28	1.29	0.62	0.21

[a] Mass selection based on selecting the top 10 individuals within a 25-family seed source.

[b] Combined selection based on selecting the top individual within each of the top 10 families within a 25-family seed source.

The only appreciable correlations between characters were between height and d.b.h. (0.75 genetic, 0.56 phenotypic) and between limb frequency and branch angle (0.25 genetic, 0.19 phenotypic). Schmitt and Wilcox (1969), studying phenotypic correlations in natural stands, obtained a similar correlation between height and d.b.h. (0.58) and a slightly higher correlation between limb frequency and branch angle (0.31).

The two crown characters showed low heritabilities and should therefore be considered less important in a selection index for sycamore tree improvement than should height and diameter growth. It might be advisable to ignore limb characteristics during the first cycles of improvement and to concentrate on selection for diameter and height growth. However, if the breeder is concerned with improving branch angle and limb frequency, he will need to develop more precise measurement techniques than were used in this study. The low correlation between growth and crown characters would allow selection for growth without sacrificing variability in crown characters, which might then be improved in later generations.

Abstract

At age five, genetic variation was detected both among and within seed sources for d.b.h., height and limb frequency, and within seed sources for branch angle. Pooled narrow-sense heritabilities were 0.26 for d.b.h., 0.26 for height, 0.15 for limb frequency and 0.16 for branch angle. The only appreciable genetic correlation was one of 0.75 between d.b.h. and height.

Key words: Platanus occidentalis L., branch characters, genetic gains, phenotypic and genetic correlation.

Zusammenfassung

Sämlingsnachkommenschaften von je 25 ausgewählten Einzelbäumen von *Platanus occidentalis* L. in 5 Beständen wurden im Wachstum und in ihren Formeigenschaften mit den Elternbäumen verglichen. Im Alter 5 der Sämlinge waren in mehreren Eigenschaften, insbesondere im Höhenwachstum und im erreichten Durchmesser Beziehungen zu den Elternbäumen zu erkennen.

Literature Cited

Becker, W. A.: Manual of procedures in quantitative genetics. Washington State Univ. Press., Pullman, 130 p. (1967). — Cochran, W. G., and Cox, G. M.: Experimental design. John Wiley and Sons, Inc., New York, 454 p. (1957). — Dadswell, H. E.: Part I: Tree growth — wood property inter-relationships. Pages 5—88 *in* Proc. Spec. Field Inst. in For. Biol. Sch. For. N. C. (T. E. Maki, ed.) State Univ. of N.C., Raleigh (1960). — Ehrenberg, C.: Breeding for stem qulaity. Unasylva 24: 23—30 (1970). — Faulkner, R.: Some characters of secondary importance to stem straightness in the breeding of conifers. Pages 273—283 *in* Second World Consultation on For. Tree Breeding. FAO-FO-FTB-69-3/2 (1969). — Mohn, C. A., and Schmitt, D.: Early development of open-pollinated sweetgum progenies. Pages 228—232 *in* 12th South. For. Tree Improv. Conf. Proc. 1973 (1973). — Namkoong, G.: Inbreeding effects on estimation of genetic additive variance. For. Sci. 12: 8—13 (1966). — Namkoong, G., Snyder, E. B., and Stonecypher, R. W.: Heritability and gains concepts for evaluating breeding systems such as seedling orchards. Silvae Genet. 15: 76—84 (1966). — Schmitt, D. M., and Webb, C. D.: Georgia sycamore seed sources in Mississippi plantings: site adaptability a key factor. Pages 113—119 *in* 11th South. For. Tree Improv. Conf. Proc. (1971). — Schmitt, D. M., and Wilcox, J. R.: Sycamore variation in the lower Mississippi Valley. USDA For. Serv. Res. Note SO-91. 6 p. (1969). — Webb, C. D., Belanger, R. P., and McAlpine, R. G.: Family differences in early growth and wood specific gravity of American sycamore (*Platanus occidentalis* L.) Pages 213—227 *in* 12th South For. Tree Improv. Conf. Proc. (1973).

Comparison of Shortleaf, Loblolly, and Putative Hybrid Pines in the Piedmont of South Carolina

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Introduction

Shortleaf pine (*Pinus echinata* Mill.) is the most common pine native to the Piedmont of South Carolina. However, since the 1930's, loblolly pine (*P. taeda* L.) has been the preferred pine for planting in that area. Growth rates of loblolly pine are generally greater than those of shortleaf pine on eroded Piedmont sites, especially on rotations of short or intermediate lengths. Shortleaf pine is also more susceptible to littleleaf disease caused by *Phytophthora cinnamomi* Rands. The fungus can cause severe epidemics on eroded Piedmont sites where it attacks pine root systems.

Shortleaf pine, however, does have some advantages over loblolly pine. The former species, typically, has better stem form and is more resistant to ice damage. In addition, it is less susceptible to fusiform rust (*Cronartium fusiforme*

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Hedgc. and Hunt ex Cumm.), the most serious disease of the southern pines.

For years, forest research and management personnel have observed trees on the Clemson Experimental Forest which exhibited characteristics intermediate between shortleaf and another pine. These trees nearly always occurred in natural stands of shortleaf pine. Loblolly pine, whose natural range barley extends into the upper Piedmont of South Carolina (Schoenike, *et al.*, 1975), but which certainly was planted at scattered locations in the region during the early 1900's and which is known to interbreed with the other southern pines species, appeared in most cases to be the other parent.

These putative hybrid pines often occurred on typical littleleaf sites, i.e., on eroded, compacted, and heavy-textured soils. In fact, the more vigorous appearance of these trees in relation to neighboring shortleaf pines exhibiting typical littleleaf symptoms was the primary reason for categorizing them as putative hybrids. In this study, a com-