Inheritance of Growth, Branch Angle, and Specific Gravity in Three American Sycamore Populations[1])

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(Received 23th December 1981)

Abstract

At age seven, family variation was more important than regional differences when 21 open-pollinated families of sycamore from Texas, Arkansas, and Lousiana were planted at three locations. Family variation accounted for between 78.6% to 100% of the total genetic variation for total height, dbh, volume, branch angle and specific gravity. A significant genotype by environment interaction occurred for branch angle and volume. Estimates of heritabilities and genetic gains indicate that good improvement can be made by selection for total height, dbh, and volume (22%, 27%, and 57%, respectively). Moderate gain is indicated for specific gravity (7.4%) and a small amount of gain for branch angle (4.8%).

Key words: Platanus occidentalis, heritabilities, genetic gain, genotype × environment interaction.

Zusammenfassung

Bei 21 siebenjährigen frei abgeblühten Familien von *Platanus occidentalis* aus Texas, Louisiana und Arkansas, die an drei Standorten ausgepflanzt worden waren, wurden die genetische Variation, die Heritabilitäten und die erwarteten genetischen Gewinne untersucht.

Die untersuchten Merkmale waren Gesamthöhe, BHD, Volumen, Astwinkel und Holzdichte. Resultate waren: (1) Die Familienvariation überwog regionale Differenzen, die 78,6—100% der gesamten genetischen Variation betrugen. So scheint es, als ob es nicht nötig wäre, in den untersuchten Zonen für *Platanus* Samenernte-Zonen einzurichten. (2) Höhe, BDH und Volumen wurden mäßig genetisch kontrolliert. (h^2 = 0,48, 0,51 bzw. 0,48). Das spezifische Gewicht war in hohem Maße genetisch bedingt (h^2 = 0,73), während der Astwinkel der geringsten genetischen Kontrolle unterlag. (h^2 = 0,26). (3) Der Bedarf an multiplen Standort-Tests wird durch das unregelmäßige Verhalten der h^2-Schätzwerte zwischen den Standorten bestimmt. (4) Genotyp × Umwelt-Interaktionen waren für Volumen und Astwinkel signifikant. Für Höhe, BHD und spezifisches Gewicht waren die Genotyp × Umwelt-Interaktionen nicht signifikant. (5) Erwartete Gewinne bei Höhe, Durchmesser in Brusthöhe und Volumen durch Selektion der besten Bäume der 10 besten Familien betrugen 22, 27 bzw. 57% gegenüber dem Versuchsflächenmittel. Der erwartete Gewinn beim spezifischen Gewicht betrug 7,4%, während der als gering angenommene Gewinn im Astwinkel (4,8%) für die Durchführung von Züchtungsprogrammen von zweifelhafter Bedeutung ist.

Introduction

Timber companies and other public and private agencies have initiated tree improvement programs for American sycamore (*Platanus occidentalis* L.) in the Southeastern United States. The rapid growth, abundant seeding, relative shade intolerance and ease of propagation of sycamore make it an excellent choice for plantation management and tree improvement work (Briscoe 1969).

The success of tree improvement efforts depends upon many factors including genetic variation between regions, stands, and individual trees, heritability of desired traits and potential gains derived.

Regional variation has been found to be three to four times greater than family variation for total height and diameter at breast height (dbh) (Schmitt and Webb 1971, Ferguson *et al.* 1977) in two studies with broad ranges in seed sources.

Land and Lee (1981) found that 80% of the phenotypic variation in wood specific gravity of 24 natural populations of sycamore in the South was due to differences among trees; stand differences accounted for 16% of the variation. Thus, variation between stands and individual trees overshadowed geographic differences.

Height and diameter growth of sycamore appear to be under moderate genetic control (h^2 range = .26 to .29) (Webb *et al.* 1973 and Ferguson *et al.* 1977). However, most heritability studies have been based on data from only one planting location and family by location interactions for growth could not be determined. Branch angle is reported to be weakly inherited (h^2 = .16) (Ferguson *et al.* 1977), but the authors suggested that more precise measurement techniques were necessary to quantify the trait. Specific gravity was found to be under strong genetic control (h^2 = .78) in a four year old half-sib progeny test (Webb et al. 1973).

The objectives of this study were to examine regional and family variation, planting location* family interactions, narrow sense heritabilities, and potential genetic gains in three seven-year old sycamore plantations. Height, dbh, volume, branch angle, and wood specific gravity were examined.

Materials and Methods

The Study Populations

The study populations were seven-year old, half-sib geographic variation studies established and maintained by members of the Western Gulf Forest Tree Improvement Program-Hardwood. In 1971 open-pollinated seed from 31 parent trees were sown by family in the Texas Forest Service Nursery at Alto, Texas. In January 1972, the seedlings were lifted, top pruned to 5 inches and root pruned to 8 inches, then outplanted at three locations: (1) Washington Parish, Louisiana, (2) Angelina County, Texas, and (3) Montgomery County, Texas. Twenty-one families common to the three plantings comprised this study; their breakdown into regions and counties or parishes are shown in *Figure 1.* The experimental design was a randomized complete block with six replications per location and four-tree row plots (24 trees per family at each location).

[1]) This report is partially based upon the senior author's M. S. Thesis submitted to the graduate school at Texas A & M University. The study was supported by the Texas Agriculture Experiment Station (MS-6227) and the Texas Forest Service.

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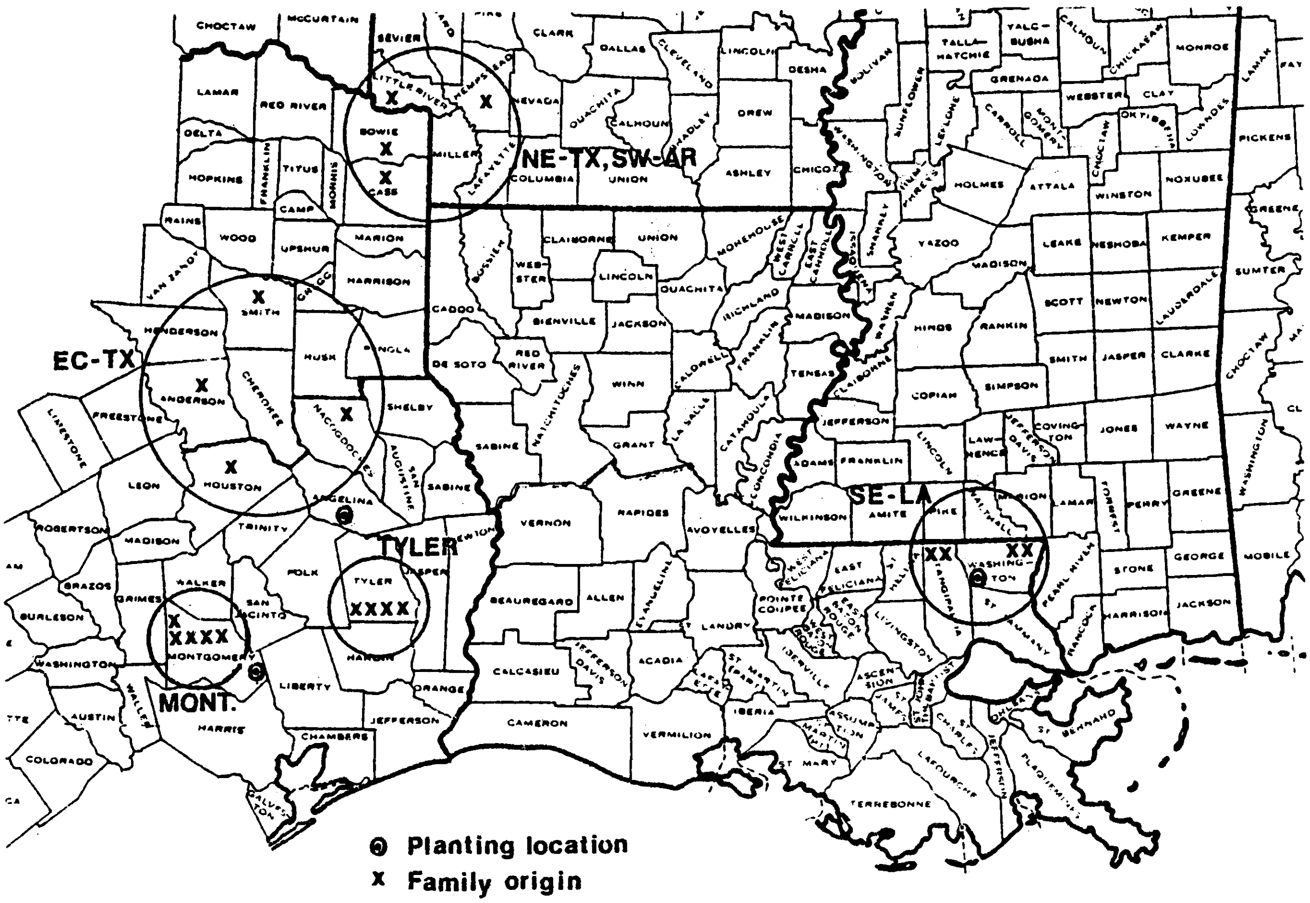

Figure 1. — Origin of the 21 parent trees and locations of the 3 plantings comprising the study.

Field Measurements and Statistical Analysis

In the winter of 1978—1979, total height, dbh, volume, and branch angle were measured or determined. Total height and dbh were measured to the nearest .5 m and .1 cm, respectively. Total stem volume was calculated for individual trees by the constrained regression developed by Belanger (1972) for plantation grown sycamore:

$$\text{Total stem volume (dm}^3) = .036288\ d^2h$$
$$\text{Where } d = \text{dbh in cm and } h = \text{total height in m}$$

Branch angle data were obtained for each tree by measuring six consecutive major branches down the bole starting at the second major whorl from the top and continuing down to the bottom one-third of the tree. The angles were measured to the nearest five degrees with a protractor and averaged; this average was used for the individual tree.

For specific gravity determination, an increment core was extracted from bark to bark through the pith at 1.2 m above average ground level along the east-west axis of each tree with a 5.15 mm increment borer. The core was cut in half at the pith and specific gravity was determined for each half and averaged for the individual tree. Specific gravity was calculated by the maximum moisture content method described by Smith (1954).

To examine regional and family variation and obtain heritability estimates, a least squares regression was performed using the General Linear Models (GLM) procedure of Statistical Analysis Systems (SAS) as described by Barr *et al.* (1979). Separate GLM analyses were performed for each of the three locations on an individual tree basis. This evaluation was followed by a combined analysis using plot means of all three locations. A between and within plot analysis was used to determine within plot variances. All coefficients of variance components were determined by the RANDOM option of GLM.

Locations and regions were considered fixed effects; replications and families were considered random. If there was no valid test for a term, a Satterthwaite-F (pseudo-F) test (Hicks 1973) was performed to generate the appropriate error degrees of freedom and mean squares. Missing or dead trees were assigned a volume of 0 dm^3 to account for survival differences. For height, dbh, branch angle, and specific gravity, missing trees were treated as missing observations.

Expected genetic gains were calculated on a mass selection and on a combined selection (family + individual/family) basis for a hypothetical clonal seed orchard (Ferguson *et al.* 1977). Selection intensities were determined from graphs published by Namkoong and Synder (1968). For mass selection, it was assumed that the ten best trees would be selected from the combined analysis, without regard to family. This resulted in a selection intensity (I_m) equal to 2.56. The gain formula is:

$$\text{Gain}_m = i_m^* \frac{4\sigma^2_F}{\sqrt{\sigma^2_e + \sigma^2_{R(L)F} + \sigma^2_{LF} + \sigma^2_F}}$$

For combined selection, it was assumed that the best tree (i I/F = 1.59) from each of the best 10 families (i F = .83) would be selected. Here,

$$\text{Gain}_F = i_F^* \frac{\sigma^2_F}{\sqrt{\frac{\sigma^2_e}{rnl} + \frac{\sigma^2_{R(L)F}}{rl} + \frac{\sigma^2_{LF}}{l} + \sigma^2_F}}$$

and

Table 1. — Summary of measurements taken on the three study areas (7-year data)

Trait	Montgomery Co.			Washington Parish			Angelina County			Combined		
	Mean	S.D. [1]	Range of Family Means	Mean	S.D. [1]	Range of Family Means	Mean	S.D. [1]	Range of Family Means	Mean	S.D. [1]	Range of Family Means
Height(m)	4.7	0.8	3.4 to 6.0	9.2	1.2	5.6 to 11.4	8.4	1.2	7.4 to 9.5	7.4	1.3	6.0 to 8.3
dbh(cm)	5.7	1.3	3.1 to 8.2	8.8	1.8	4.3 to 10.7	8.2	2.3	6.1 to 10.3	7.5	1.6	4.9 to 8.7
Volume(dm^3)	5.16	6.18	.27 to 13.03	27.64	17.36	2.17 to 47.86	22.76	15.18	8.20 to 38.92	18.52	11.29	3.73 to 28.23
Branch Angle(°)	52	6	48 to 56	57	6	51 to 66	53	5	48 to 57	54	4	49 to 57
Specific Gravity	.464	019	.447 to .488	.451	.020	.428 to .469	.464	.019	.444 to .484	.460	.012	.444 to .480
Survival (%)	63.7	0.3	20.8 to 91.7	85.3	0.2	37.5 to 100.0	89.7	0.2	68.8 to 100.0	79.6	21.3	47.2 to 79.6

(1) Standard deviation

$$\text{Gain}_{I/F} = i_{I/F} * \frac{3\sigma^2_F}{\sqrt{\sigma^2_e + \sigma^2_{R(L)F} + \sigma^2_{LF}}}$$

where σ^2_e, $\sigma^2_{R(L)F}$, σ^2_{LF}, and σ^2_F are the variance components for the error, replication (location)*family, location*family, and family terms, respectively; r, n, l, are the number of replications, trees per plot, and locations, respectively.

Results and Discussion

The plantation mean, standard deviation and range of family means for height, dbh, volume, branch angle, wood specific gravity and survival are shown in *Table 1* for single and combined locations. The Montgomery County site had the poorest survival and slowest tree growth, whereas the Washington Parish Plantation had the best tree growth. Specific gravity and branch angle indicated smaller amounts of variation among the three locations than did the growth traits.

Table 2. — Heritability estimates and standard errors for the Montgomery Co. (Mont. Co.), Washington Parish (Wash. Par.) and Angelina Co. (Ang. Co.) study areas, and the Combined Location Analysis

Character Location	Heritability Estimates			
	Ind. h^2	SE h^2	Family h^2	SE Fam. h^2
7 Year Height				
Mont. Co.	.52	.38	.54	.39
Wash. Par.	.44	.31	.52	.36
Ang. Co.	.18	.19	.35	.36
Combined	.48	.21	.72	.31
7 Year dbh				
Mont. Co.	.91	.47	.71	.37
Wash. Par.	.35	.25	.51	.36
Ang. Co.	.38	.21	.62	.35
Combined	.51	.20	.75	.30
7 Year Volume				
Mont. Co.	.27	.20	.48	.36
Wash. Co.	.59	.31	.67	.35
Ang. Co.	.55	.27	.71	.34
Combined	.48	.19	.69	.27
Specific Gravity				
Mont. Co.	.56	.29	.70	.37
Wash. Par.	.66	.31	.74	.35
Ang. Co.	.98	.39	.85	.34
Combined	.73	.26	.87	.32
Branch Angle				
Mont. Co.	.21	.20	.42	.41
Wash. Par.	.57	.27	.74	.35
Ang. Co.	.45	.21	.72	.34
Combined	.26	.11	.53	.24

None of the region or location by region effects were significant for any of the traits. This means that establishing seed collection zones in this study range would not be effective. This result is in contrast to that of Fogg (1966), Ferguson *et al.* (1977), and Schmitt and Webb (1971). For height and dbh, they found regional differences to be significant and 3 to 4 times greater than family differences. This study sampled a relatively limited geographic range when compared to the other studies which could explain the lack of regional differences.

Family effects were significant for all traits at all locations except for height at Angelina County and branch angle at Montgomery County. Planting location × family interactions were significant for branch angle and volume only. Some tree mortality was caused by top dieback infection in the Washington Parish and Montgomery County plantings and families differed significantly in their resistance to it. These family differences in survival contributed to the significant interaction for volume because the location × family interaction was not significant for volume when dead trees were treated as missing observations.

Sufficient variation was present to warrant selection for volume traits. The best family (combined analysis) was 12, 16, and 52 percent above the combined analysis mean for height, dbh and volume, respectively. Selection of the best family for specific gravity would result in a 4 percent increase as compared to the plantation mean. Although branch angle from the best family was 6 percent better than the overall mean, the restricted range in family means, raises doubts about the practical significance of the difference.

Heritability estimates tended to be erratic between planting locations *(Table 2)*. The heritability estimate obtained from the combined analysis for seven year height was .48 which was larger than the estimate of .27 for four year height reported by Webb *et al.* (1973). It was also larger than the heritability estimate for five year height (.26) reported by Ferguson *et al.* (1977). Similarly, our heritability estimate for dbh (.48) at age seven was larger than the five year estimate (.26) reported by Ferguson *et al.* (1977). Our generally larger heritability estimates may be accounted for by the different age of material among studies. The combined location heritability for specific gravity was similar to the estimate reported by Webb *et al.* (1973) for four-year old trees (.73 versus .78). A significant family by plantation location interaction contributed to the reduction in he combined heritability estimate for branch angle. However, that estimate was larger (.26 versus .16) than that reported by Ferguson *et al.* (1977).

Heritability estimates we obtained were probably inflated because members of the open-pollinated families were

Table 3. — Region and family components of variance expressed as a percentage of the total family variation.

Trait	Region Component	Family Component
	Percent of Total Family Variation	
Height	14.5	85.5
dbh	4.5	95.5
Volume	0.0	100.0
Specific Gravity	21.4	78.6
Branch Angle	2.5	97.5

probably more closely related than half-sibs (NAMKOONG 1966). The erratic behavior of the individual location heritability estimates emphasizes the need for multiple location testing.

The lack of regional differences is illustrated by examining the relative magnitude of regional versus family components of variance (expressed as a percentage of total family variation from the combined analysis) (*Table 3*). The family component accounts for 78.6% to 100% of the total variation and overshadowed any regional differences.

Because none of the region effects were significant in the analysis, it would be impractical to establish seed collection zones. Thus, another analysis predicting expected genetic gains was made ignoring the region term and selecting only the best individual or families from the three planting locations combined (*Table 4*). Predicted genetic gains would be highest from mass selection whereby the best individuals from the one or two best families would be selected. However, combined selection would assure a broader genetic base for future breeding and volume production. The gains expected for height, dbh, and volume (1.6 m, 2.0 cm, 10.56 dm^3, respectively) look promising as they represent a 22%, 27%, and a 57% gain over the plantation means. Calculated gain for specific-gravity was 0.034 which represents a 7.4% increase. For branch angle, expected gain is low (2.6°), representing only a 4.8% increase in the population mean. It is doubtful that this small increase in branch angle would have any significance in an operational tree improvement program.

Table 4. — Expected genetic gains from selection (combined analysis).

Selection Method	Height (m)	dbh (cm)	Volume (dm^3)	Specific Gravity	Branch Angle(°)
Mass selection [1]	2.1	2.9	20.44	.050	4.5
Combined selection [2]					
Family selection	0.6	0.6	4.23	.008	1.2
Individual/family Selection	1.0	1.4	6.33	.026	1.4
Total	1.6	2.0	10.56	.034	2.6

[1] Mass selection of the top 10 individuals (from the combined analysis)

[2] Combined selection based on selecting the single best individual from each of the top 10 families (from the combined analysis)

Summary

Genetic variation, heritabilities, and expected genetic gains were examined for 21 seven-year-old open pollinated families of sycamore from Texas, Louisiana, and Arkansas planted at 3 locations. Traits measured were total height, dbh, volume, branch angle, and wood specific gravity. Results were:

(1) Family variation overshadowed regional differences, accounting for 78.6% to 100% of the total genetic variation. Thus, there appears to be no need to establish seed collection zones for sycamore in the regions examined.

(2) Height, dbh, and volume were under moderate genetic control (h^2 = .48, .51, and .48, respectively). Specific gravity was highly inherited (h^2 = .73), while branch angle was under the least genetic control (h^2 = .26).

(3) The need for multiple location testing is emphasized by the erratic behavior of the h^2 estimates between locations.

(4) Genotype × environment (GXE) interactions were significant for volume and branch angle. For height, dbh, and specific gravity, GXE interactions were not significant.

(5) Expected gains in height, dbh, and volume from selection of the best tree in the best 10 families represent a 22%, 27% and 57% gain over the plantation means. Expected gains in specific gravity represent a 7.4% increase, while the small expected gain in branch angle (4.8) is of doubtful importance in an operational tree improvement program.

Acknowledgements

We thank the personnel of Crown Zellerbach Corporation, Champion International, and the Texas Forest Service for permitting us to use their plantations and for their assistance in data collection.

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