GENETIC VARIATION, HERITABILITIES, AND SELECTION STRATEGIES FOR EARLY GROWTH OF SYCAMORE IN THE GULF SOUTH

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Abstract.--Open pollinated progenies from 160 trees representing 16 geographic seed sources in the Gulf South were planted in each of two years at each of four sites in Mississippi. Three years after outplanting, progenies from sources near the Mississippi River in southwestern Mississippi and southeastern Louisiana had the greatest stem volume. There were source—by—site interactions, but sources from south of the planting site and near the Mississippi River were usually better than sources from north of the site. Source—by—planting—year interactions were still present for root collar diameter and height after three years in the field, but had disappeared for stem volume by that time. Early screening trials of seed source variation should be repeated over both sites and planting years to avoid errors caused by these interactions. There was no variation among local stands within sources, but variation among families from trees within a stand was significant for all traits. Narrow—sense heritabilities on an individual—tree basis were low (.03 to .17). On a family—mean basis these heritabilities were ten times larger (.29 to .74). Heavy emphasis should be placed on progeny testing in a clonal seed orchard program. Gains from seedling orchards will not exceed those from clonal orchards, except when family selection intensity is low and mass selection intensity within families is high. Genetic correlations between traits measured at different ages were positive and increased as the difference between the ages decreased. However, the added number of trees that must be tested to get comparable gains from early selection as from direct selection may make the savings in time unjustifiable.

Additional keywords: Genetic correlations, genetic gains, Platanus *occidentalis*.

The rapid juvenile growth and relative ease of artificial regeneration of American sycamore (Platanus occidentalis L.) make it a prime candidate among southern hardwoods for short rotation energy and pulpwood plantations. Genetic improvement for early growth rate would increase productivity and returns from investments in these plantations. Information is presented here on genetic variation, heritabilities, genetic and phenotypic correlations, and selection strategies for stem size and volume at ages one, two, and four years from seed for trees from the Gulf South region of the United States.

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MATERIALS AND METHODS

Open—pollinated progenies of five trees within each of two stands at each of 16 geographic seed source locations in Mississippi, western Alabama, eastern Louisiana, and eastern Arkansas were planted in each of two years (1975 and 1976) at each of four sites in Mississippi (Figure 1). The seed sources were chosen to represent four latitudinal transects (30°45'N, 32°00'N, 33°15'N, and 34°30'N). There were four sources per transect, with one of the four coming from the banks of the Mississippi River and one from the Tombigbee River (along the Mississippi—Alabama border). Planting site #1 is located on an agricultural field site in the Upper Southern Coastal Plain (Soil Conservation Service et al. 1971) in Tishomingo County, Mississippi. The second site is found on an agricultural field site in the Interior Flatwoods section of the Southern Coastal Plain in Oktibbeha County. Site #3 in Jasper County is located in the Lower Southern Coastal Plain, and it was a forested upland pine site that was cleared and site prepared for planting. The fourth site is in the alluvial plain of the Mississippi River in Issaquena County, and it was a forested bottomland hardwood site that was cleared and site prepared.

Figure 1.--Locations of seed sources and planting: sites used for a provenance-progeny test of sycamore in the Gulf South

Seedlings of the 160 progeny families were grown for one year in a randomized complete block design with three replications at a state nursery in central Mississippi. Nursery bed density was controlled at approximately six seedlings per square foot by thinning. The same nursery procedures were used for each of the two years in which the study was repeated.

The 1-0 nursery seedlings were outplanted at the four sites in a series of split—plot experiments containing six replications and repeated in both space and time. Three—seedling family plots were used, and all families of a seed source were arranged together into compact family blocks within a replication. The three nursery replications were split, so that nursery replication one provided seedlings for field replications one and two at each site, nursery replication two provided field replications three and four, etc.

Root collar diameters and tree heights were measured at the time of lifting the seedlings from the nursery (tree age one), one year after outplanting at the four sites (tree age two), and three years after outplanting (tree age four). Stem volume at age four was determined from root collar diameter, DBH, and height by treating the bottom 4.5 feet of the stem as the frustrum of a cone and the remaining top of the stem as a cone.

Analyses of variance and covariance had the form given in Table 1. Variance and covariance components were calculated by equating estimated with expected mean squares. The composition of the genetic and phenotypic variances (or covariances) from the variance and covariance components is shown at the bottom of the table. Estimates of narrow-sense heritabilities and genetic and phenotypic correlations were calculated from these genetic and phenotypic variances and covariances (Namkoong et al. 1966, Becker 1975). Standard deviations of estimates were derived by procedures outlined in Gordon et al. (1972) and Becker (1975).

RESULTS AND DISCUSSION

Survival after three growing seasons in the field was 98 percent over all sites and planting years. Trees at this age averaged 2.7 inches in root collar diameter, 15.2 feet in height, and 0.225 cubic feet in stem volume. At the time of lifting from the nursery these trees had a mean height of 3.1 feet and a mean root-collar code of 2.25 (code 1 = less than 1/4 inch diameter, code 2 = 1/4 to 1/2 inch, code 3 = 1/2 to 3/4 inch, and code 4 = greater than 3/4 inch diameter). The average root collar diameter and height at one year after outplanting was 0.8 inches and 4.0 feet, respectively.

Effects of Planting Years and Sites

Seedlings for the 1976 planting year were 20 percent larger than those for 1975. These size differences persisted through one growing season at the field sites, but disappeared after three growing seasons. Since the nursery site and nursery bed density were the same in both years, the year differences in seeding size were probably related to weather conditions during the nursery growing season.

At outplanting, seedlings from a family plot in the nursery were sorted to give the same initial average size for that family at all planting sites. Site differences in tree size increased with time following outplanting. After three field growing seasons, trees at site #4 near the Mississippi River were nearly four times larger in stem volume than the average for the other three sites. Obviously, the first step in an improvement program for short rotation sycamore plantations is site selection. Here, production was best on somewhat poorly drained to moderately well drained silt loam soils in an alluvial floodplain, which is characteristic of most major rivers in the Gulf South.

Effects of Seed Sources and Source x Environment Interactions

Trees from sources near the Mississippi River in southwestern Mississippi and southeastern Louisiana contained 24 percent more stem volume at age four

Table 1.--Composition of expected mean squares, genetic variance, and phenotypic variance for a sycamore provenance-progeny test repeated over planting sites and years

Source of Variation	EMS #	Expected Mean Square [a/] (EMS)
Sites		
Years		
Sites x Years		
Reps within Sites x Years		
Seed Sources	#15	#10 + $10\sigma^2_A + 60\sigma^2_{LYP} + 240\sigma^2_{YP} + 120\sigma^2_{LP} + 480\sigma^2_P$
Sites x Sources	#14	#8 + $10\sigma^2_A + 60\sigma^2_{LYP} + 120\sigma^2_{LP}$
Years x Sources	#13	#6 + $10\sigma^2_A + 60\sigma^2_{LYP} + 240\sigma^2_{YP}$
Sites x Years x Sources	#12	#4 + $10\sigma^2_A + 60\sigma^2_{LYP}$
Error (a)	#11	#2 + $10\sigma^2_A$
Stands within Sources	#10	#6 + $12\sigma^2_{LF(SP)} + 60\sigma^2_{LS(P)} + 48\sigma^2_{F(SP)} + 240\sigma^2_{S(P)}$
Families/Stands/Sources	#9	#5 + $12\sigma^2_{LF(SP)} + 48\sigma^2_{F(SP)}$
Sites x Stands/Sources	#8	#4 + $12\sigma^2_{LF(SP)} + 60\sigma^2_{LS(P)}$
Sites x Fam./Stands/So.	#7	#3 + $12\sigma^2_{LF(SP)}$
Years x Stands/Sources	#6	#4 + $24\sigma^2_{YF(SP)} + 120\sigma^2_{YS(P)}$
Years x Fam./Stands/So.	#5	#3 + $24\sigma^2_{YF(SP)}$
Sites x Years x St./So.	#4	#3 + $30\sigma^2_{LYS(P)}$
Sites x Years x F./St./So.	#3	#2 + $6\sigma^2_{LYF(SP)}$
Pooled Error (b)	#2	$(\sigma^2_W/h) + \sigma^2_B$
Within Plot	#1	σ^2_W

Additive Genetic Variance = GV = $4\{\sigma^2_{F(SP)}\}$

Phenotypic Variance:

Individual-tree basis = PVI = $\sigma^2_W + \sigma^2_B + \sigma^2_{LYF(SP)} + \sigma^2_{YF(SP)} + \sigma^2_{LF(SP)} + \sigma^2_{F(SP)}$

Family-mean basis = PVF = $[\sigma^2_W/48h] + [\sigma^2_B/48] + [\sigma^2_{LYF(SP)}/8] + [\sigma^2_{YF(SP)}/2] + [\sigma^2_{LF(SP)}/4] + \sigma^2_{F(SP)}$

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a/ h = harmonic mean no. of trees per plot

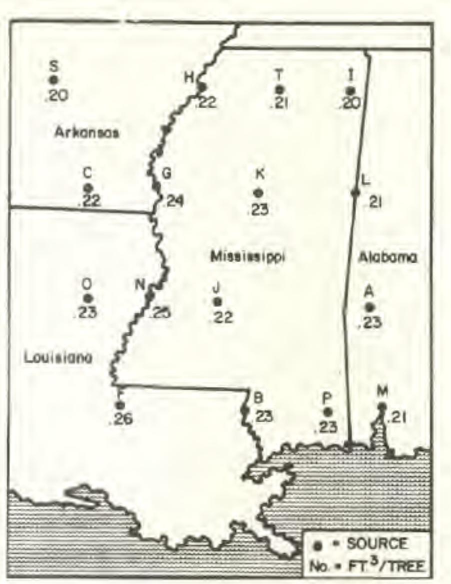

Figure 2.--Map with seed source means for stem volume of four-year-old trees in sycamore provenance-progeny tests in Mississippi

than trees from northeast Mississippi or central Arkansas (Figure 2). This was the only trait for which seed source variation was detected, and the significance test fell between the 0.1 and 0.05 probability levels (Table 2). Differences among sources increased as tree age increased, however, so that seed source variation may reach higher levels of significance at older ages.

Source-by-site interactions were not present after one growing season in the field, but had reached significance following three field growing seasons (Table 2). The interactions resulted from changes in ranks of sources within latitudinal transects, rather than from changes in ranks of latitude means for sources. Mean stem volume per tree was greater at all planting sites for latitudes south of the site than for latitudes north of the site. Even at site #1 in northeast Mississippi the trees from the southernmost latitudinal transect were equally as good as trees from the other transects. Although sources within transects changed in ranks from site to site, the source on the Mississippi River in each transect was always among the top two sources from that transect at every site. Therefore, even though source-by-site interactions occur, trees from sources near the Mississippi River in southwestern Mississippi and southeastern Louisiana should provide above average growth in stem volume at all sites in the Gulf South. There is no need to use specific sources for particular sites.

Interactions between seed source and year of planting were found for root collar diameter and tree height after one and three growing seasons in the field, but not for stem volume (Table 2). There was no pattern to the changes in source rankings from year to year. The interactions contribute to the inability to detect source variation in root collar diameter or height at these early ages. They provide a warning against the use of juvenile traits to interpret geographic patterns of seed source variation in sycamore, especially when results are based on only a single year's planting.

Table 2.--Significance and relative sizes of variance components for seed sources, stands, families, and their GxE interactions with sites and planting years

Variance Component	Root Collar Diameter			Tree Height			Stem Vol.
	1-Year (nursery)	2-Year (1 yr.field)	4-Year (3 yr.field)	1-Year (nursery)	2-Year (1 yr.field)	4-Year (3 yr.field)	4-Year (3 yr.field)
	- - - - - - - - - Variance Components Expressed as % of Total - - - - - - - - -						
Seed Sources (=S0)	5.0	0.0	1.7	3.6	4.3	10.1	12.4
Sites x SO	0.9	4.4	14.8*	0.0	0.0	21.7*	33.3** b/
Years x SO	5.4	18.2*	13.3*	2.7	23.2*	15.7*	4.4
Sites x Years x SO	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Stands in SO (=ST/S0)	0.0	0.0	1.2	0.0	4.9	4.1	0.6
Sites x ST/S0	0.0	3.2	4.8	0.0	2.3	0.0	0.0
Years x ST/S0	4.8	0.0	0.8	2.4	0.6	0.0	0.0
Sites x Years x ST/S0	0.6	10.1	0.2	0.4	2.0	4.0	2.8
Fams.in ST/S0 (=F/ST/S0)	17.1*	34.2**	44.2**	21.7**	22.9**	29.0**	19.9**
Sites x F/ST/SO	0.0	2.8	0.0	0.0	1.3	0.0	22.2**
Years x F/ST/SO	66.2**	20.8**	0.7	69.2**	35.8**	1.9	0.9
Sites x Years x F/ST/SO	0.0	6.3	18.3	0.0	2.7	13.5	3.5
Total of Components	.01127	.00145	.01910	.07544	.04966	.37080	.000989

a/ Significance falls between the 0.1 and 0.05 probability levels.
b/ * = Significant at the 0.05 probability level; ** = significant at the 0.01 probability level.

Variation Amon Local Stands Within Sources

There was no evidence of variation among stands within seed source locations for any of the traits studied (Table 2). Stands within a source were separated by one—half mile to 30 miles. This lack of variation among local stands provides indirect evidence for the absence of highly inbred, isolated stands in the natural population, since high inbreeding would be expected to result in large stand—to—stand genetic differences. No additional genetic gain in juvenile growth rate over that obtained from seed source selection can be expected from selection of phenotypically superior stands within sources to serve as seed production areas.

Variation Among Trees Within Stands, and GxE Interactions

Variation among families from trees within stands within sources was significant for all traits at all ages (Table 2). In every case this family component of variance was the largest of the three components: (i) sources, (ii) stands within sources, and (iii) families within stands within sources. The presence of such large variation indicates that the greatest genetic gains in juvenile growth rate will come from selection among individual trees within stands. This gain can be added to the gain from seed source selection by selecting the fastest growing families from the fastest growing seed sources.

Interactions between sites and families within stands were obtained only for stem volume after three growing seasons in the field (Table 2). However, the six highest families for volume were very stable in performance over all sites, as they never ranked lower than second out of the five families from their respective stands when planted at any site. Selection of specific genotypes for specific site types in the Gulf South should not be necessary.

Family—by—planting—year interactions were highly significant for root collar diameter and seedling height in the nursery and after one growing season in the field (Table 2). These interactions decreased with time, however, and were absent after three field growing seasons. Mohn and Randall (1973) reported no interactions between cottonwood clones and planting years for diameter or height of three—year—old trees, but they did not mention results for younger trees. The early interactions found here indicate that family selection for sycamore should not be conducted on very young material in either the nursery or field, unless the tests are repeated over more than one year.

Heritabilities and Expected Genetic Gains

Narrow—sense heritabilities on an individual—tree basis were very low for all traits, ranging from .03 to .17 (Table 3). When calculated on a family—mean basis, however, the heritabilities were as much as ten times larger (.29 to .74) than those for individual trees. Both types of heritability estimates increased with increasing age of the trees. Similar results were reported by Webb et al. (1973) for a sycamore progeny test on one site in Georgia, after adjustment of their estimates for genotype—by—site interactions. As pointed out by Webb et al., the heritabilities presented here may be slightly overestimated, because some individuals within the open—pollinated families may be more closely related than half sibs (Namkoong 1966). In the following discussion of genetic gains the conclusions will not be affected by

Table 3.--Estimates of additive genetic variances, phenotypic variances, and heritabilities for stem dimensions of one-, two-, and four-year-old sycamore trees in progeny tests in Mississippi

Trait and Age of Tree from Seed	Additive Genetic Variance	Phenotypic Variance		Narrow-Sense Heritability a/	
		Individual Trees	Family Means	Individual Trees	Family Means
	GV (±std.dev.)	PVI (±std.dev.)	PVF (±std.dev.)	h^2_I (±std.dev.)	h^2_F (±std.dev.)
Root Collar Diameter					
1-year-old	.0070 (±.0040)	.2361 (±.0029)	.0066 (±.0015)	.03 (±.017)	.29 (±.095)
2-years-old	.0020 (±.0005)	.0343 (±.0004)	.0010 (±.0002)	.06 (±.015)	.52 (±.055)
4-years-old	.0338 (±.0060)	.3029 (±.0037)	.0115 (±.0018)	.11 (±.019)	.74 (±.035)
Tree Height					
1-year-old	.0653 (±.0255)	.3778 (±.0119)	.0435 (±.0086)	.17 (±.063)	.38 (±.080)
2-years-old	.0488 (±.0158)	.7833 (±.0104)	.0272 (±.0054)	.06 (±.020)	.42 (±.071)
4-years-old	.4302 (±.0815)	3.8604 (±.0499)	.1535 (±.0248)	.11 (±.020)	.70 (±.037)
Stem Volume					
4-years-old	.00079(±.00020)	.01217(±.00015)	.00036(±.00006)	.07 (±.016)	.54 (±.053)

a/ h^2_I = GV/PVI ; h^2_F = (¼GV)/PVF

See Table 1 for composition of GV, PVI, and PVF.

this bias, but the actual estimates of gains should be considered as maximum values.

Expected genetic gains from various combinations of mass selection and progeny test selection for clonal seed orchards can be calculated from equations given by Namkoong et al. (1966) [equations (1) and (2) in Table 4]. Gains will increase when greater selection emphasis is placed upon family performance of a tree's progenies, rather than upon the tree's own phenotype [compare cases (a), (b), (c), and (d) in Table 4]. However, progeny tests are more expensive than mass selection, and there is a limit to how many families can be effectively tested in a field progeny test. Even though case (d) would give the greatest gain of the four cases, one would need to progeny test 2000 families to get a 20—clone rogued orchard. Case (a) would be the least expensive, requiring only the phenotypic measurement of 2000 trees to get a 20—clone orchard, but the gain would be only one—half of that for case (b). A combination of mass selection and progeny testing will usually prove most desirable. A goal must be set determining what amount of genetic gain is needed to justify a tree improvement program. Then, by substituting that gain into equation (1) of Table 4, one can determine what practical combination of intensities for mass selection and family selection will accomplish the goal.

Clonal and seedling seed orchards can he compared for expected genetic gains by holding selection intensities the same in both for mass selection of parent trees and for family selection in progeny tests (Table 4). Gains from seedling orchards will not exceed those from clonal orchards, except when family selection intensity is low and mass selection intensity within progeny families is high. This is attributable to the high heritabilities on a family—mean basis and very low heritabilities for mass selection. Using parents of tested genetic worth for seed production makes a great difference in genetic gain under such conditions.

Genetic Correlations and Correlated Gains

Genetic and phenotypic correlations between measurements on the four-year—old trees and earlier measurements were positive and increased as the time between the two measurements decreased (Table 5). Tree height at an earlier age was not as good an indicator of four—year stem volume as was root collar diameter. Correlations between root collar diameter and height at age four were positive and high.

These estimates of "juvenile—mature" correlations can be used to compare expected gains in a four—year—old trait from (i) selecting for a trait at an earlier age versus (ii) selecting directly for the four—year—old trait. Consider gains from a clonal orchard, where both mass selection and progeny test selection are utilized. When the younger trait is "X" and the four—year trait is "Y", the equation for the correlated gain in "Y" from selection for "X" is (Falconer 1960):

$$(3)\quad CR_y = i_1\sqrt{h^2_{Ix}}\ \sqrt{h^2_{Iy}}\ Rg_{xy}\sqrt{PVI_y} + 2i_2\sqrt{h^2_{Fx}}\sqrt{h^2_{Fy}}\ Rg_{xy}\sqrt{PVF_y}.$$

As an illustration, one can ask what effort would he needed to get as much genetic gain in four—year stem volume from selecting for two—year root collar diameter as from directly selecting for four—year volume. Placing the appropriate values from Tables 3 and 5 into equation (3), one gets:

Table 4.--Expected genetic gains in stem volume of sycamore trees at age four from using various selection strategies for clonal seed orchards and seedling seed orchards

GAIN EQUATIONS (Namkoong et al. 1966):

(1) Clonal Orchard: Gain = (Mass Sel. Gain) + (Family Sel. Gain from Progeny Test)

$$= i_1 h_I^2 \sqrt{PVI} + 2 i_2 h_F^2 \sqrt{PVF}$$

$$= .00717\ i_1 + .02053\ i_2$$

(2) Seedling Orchard: Gain = (Mass Sel. Gain) + (Family Sel. Gain) + (Mass Sel. Gain w/i Families)

$$= i_1 h_I^2 \sqrt{PVI} + i_2 h_F^2 \sqrt{PVF} + i_3 h_W^2 \sqrt{PVW}$$

$$= .00717\ i_1 + .01032\ i_2 + .00721\ i_3$$

where: $PVW = PVI - (\tfrac{1}{4}GV)$ and $h_W^2 = (3/4)GV/PVW$

EXPECTED GAINS FOR VARIOUS SELECTION STRATEGIES: (proportion sel. held constant at 1/100 for mass+fam.sel.)

	Mass Selection		Family Selection		w/i Fam.Selection		% Gain from S.O.	
(Case)	Proportion		Proportion	i_2	Proportion	i_3	Clonal	Seedling
(a)	1/100	2.66	1/1	0.00	1/1	0.00	8.5	8.5
(b)	1/50	2.42	1/2	0.80	1/1	0.00	15.0	11.4
					1/2	0.80	15.0	13.9
					1/4	1.27	15.0	15.4
					1/10	1.75	15.0	17.0
(c)	1/25	2.15	1/4	1.27	1/1	0.00	18.5	12.7
					1/4	1.27	18.5	16.7
					1/10	1.75	18.5	18.3
(d)	1/1	0.00	1/100	2.66	1/1	0.00	24.4	12.2
					1/10	1.75	24.4	17.8
					1/500	3.16	24.4	22.4

Table 5.--Estimates of genetic and phenotypic correlations for "juvenile-mature" relationships between stem dimensions at age four and stem dimensions at earlier ages in sycamore progeny tests in Mississippi

Trait 1	x	Trait 2	Additive Genetic Correlation Rg (±std.dev.)	Phenotypic Correlations Individual Trees Rpi (±std.dev.)	 Family Means Rpf (±std.dev.)
4-Year Stem Volume	x	1-Year Root Collar Class	+.42 (±.251)	+.10 (±.008)	+.21 (±.086)
	x	1-Year Seedling Height	+.30 (±.221)	+.09 (±.009)	+.12 (±.089)
	x	2-Year Root Collar Dia.	+.92 (±.093)	+.61 (±.005)	+.69 (±.048)
"	x	2-Year Tree Height	+.75 (±.144)	+.56 (±.006)	+.53 (±.064)
4-Yr.Root Collar Dia.	x	1-Year Root Collar Class	+.55 (±.218)	+.14 (±.008)	+.29 (±.083)
"	x	1-Year Seedling Height	+.19 (±.190)	+.10 (±.010)	+.05 (±.090)
"	x	2-Year Root Collar Dia.	+.91 (±.070)	+.64 (±.005)	+.75 (±.040)
"	x	2-Year Tree Height	+.52 (±.144)	+.54 (±.007)	+.41 (±.075)
4-Year Tree Height	x	1-Year Root Collar Class	+.02 (±.223)	+.12 (±.008)	+.10 (±.090)
	x	1-Year Seedling Height	+.15 (±.193)	+.14 (±.010)	+.07 (±.090)
"	x	2-Year Root Collar Dia.	+.52 (±.123)	+.53 (±.007)	+.47 (±.070)
"	x	2-Year Tree Height	+.71 (±.124)	+.55 (±.006)	+.56 (±.062)
4-Yr.Root Collar Dia.	x	4-Year Tree Height	+.57 (±.083)	+.76 (±.004)	+.62 (±.054)

(4) $CR = .00619i_1 + .01859i_2$.

By comparing equation (4) with equation (1) in Table 4, it is seen that an increase of 16 percent in i_1 and 11 percent in i_2 is needed for selection on root collar diameter at age two to achieve the same gain in four-year volume as obtained from direct selection for that trait. This means that for case (c) in Table 4 one would need to select one tree out of 60, rather than one out of 25, in mass selection and one clone out of five in the progeny test, rather than one out of four. Three hundred trees in total, rather than 100, must he examined for every one that ends up in the rogued orchard, and these calculations are for two traits with a very high genetic correlation (.92). The added number of trees that must be tested to get comparable gains from early selection and direct selection may make the savings in time unjustifiable.

RECOMMENDATIONS

(i) Repeat progeny tests over more than one year of planting when studying genetic variation in traits of trees that are less than four years old.

(ii) Use seed from sources near the Mississippi River in southwestern Mississippi and southeastern Louisiana for planting throughout Mississippi, western Alabama, eastern Louisiana, and eastern Arkansas.

(iii) Use a clonal seed orchard for the production of genetically improved sycamore seed. Select clones from the above-stated optimal seed source zone using a combination of mass selection of trees in the natural stands and progeny tests of the selections. Place heaviest emphasis on progeny test results for selection of these clones.

(iv) Be very cautious of proposals to save two or three years by selection in the nursery or selection after one year in the field to get correlated genetic gains in volume after three field growing seasons. The greatly increased number of trees that must be measured and progeny tested to get gains comparable with those from direct selection may make the savings in time unjustifiable.

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