

FAMILY DIFFERENCES IN EARLY GROWTH AND WOOD SPECIFIC GRAVITY  
OF AMERICAN SYCAMORE (*Platanus occidentalis* L.)

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Abstract. --As part of a selection project to create strains for use under intensive culture, 64 wind-pollinated families were planted in an 8x8 triple lattice twice design using 4-tree square plots at a spacing of 4x4 feet. The plantation was clear-cut at the end of the fourth growing season to reveal family differences in sprout regrowth.

Growth for the first four years was good: plantation total height averaged 24 feet. Total dry weight of wood and bark approximated 10.6 tons per acre, or 2.60 tons per acre per year. Families exhibited significant differences in: dry weight per unit area, dry weight per tree, height, diameter at 1 foot, wood specific gravity, and seedling root collar diameter. The two best families were 50 to 60 percent greater than average for dry weight per tree and dry weight per unit area; the two poorest families were 30 to 35 percent poorer than average for the same traits.

Narrow-sense heritabilities were: seedling root collar diameter, 0.44; fourth year height, 0.27; fourth year diameter at 1 foot, 0.29; fourth year dry weight per tree, 0.31; and fourth year specific gravity, 0.78. These fractions should be corrected downward (multiply each by 0.56) to account for failures of the half-sib assumptions and for planting in only one environment. Genetic correlations between root collar diameter and traits measured at four years were: height, 0.31; diameter at 1 foot, 0.56; dry weight per tree, 0.47; and wood specific gravity, -0.15. Phenotypic correlations between specific gravity, and height, diameter, and dry weight per tree were approximately 0.3; genetic correlations between specific gravity and the same traits ranged between -0.12 and -0.25.

Estimated gains per unit of time from indirect selection on root collar diameter were slightly less than gains from direct selection on dry weight per tree at four years. If seedling densities in the nursery are kept uniform, indirect selection on seedling root collar diameter can be used to shorten the breeding cycle and to supplement direct selection at a later age.

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If hardwoods are to be grown under intensive culture at short rotations (4 to 15 years) with mechanical harvesting and coppice regeneration, specially adapted strains will play an important role in the success of the concept. Phenotypic selection in natural stands probably will not be successful in this case. Instead, selection will be most effective in pedigreed test plantations that receive fertilization, weed control, and periodic harvesting to expose genetic differences in sprout regrowth characteristics. This report covers the quantitative genetic interpretation of the growth of one pedigreed test plantation from the nursery to the time of the first harvest, at the end of the fourth growing season.

#### METHODS

In January 1967, wind-pollinated seed were collected from 64 randomly-chosen sycamore trees growing in the Piedmont of Georgia in Clarke and Greene Counties. Seedlings were produced in an experimental nursery near Athens, Georgia, during the 1967 growing season. The nursery design was a randomized complete block design with four replications.

Soon after germination before intensive competition set in, each progeny was thinned back to 12 seedlings per square foot. As the season progressed, however, densities dropped slightly with increasing competition.

Before lifting, seedling tops were cut off at 4.5 inches above the root collar. Each seedling was identified with a tag of masking tape, and root collar diameter was recorded on each to the nearest 0.01 inch. In this way a nursery measurement was known for each tree in the field.

In March 1968, the seedlings were planted on a well-drained overflow river-bottom site in Greene County, Georgia. The site had been clear-cut and intensively site prepared two years before. An 8x8 triple lattice twice design (Cochran and Cox, 1957, plan 10,5) was used with 4-tree square plots and a spacing of 4x4 feet. Nursery replications were generally kept intact in establishing the field planting: nursery reps 1 and 2 went to field reps 1 and 2, However, nursery reps 3 and 4 were divided longitudinally; one-half of nursery rep. 3 went to field rep. 3, the other half to field rep. 4; one-half of nursery rep. 4 went to field rep. 5, the other half to field rep. 6.

The plantation received 1000 pounds per acre of 12-12-12 fertilizer in May of the first growing season, and 600 pounds per acre of ammonium nitrate in April at the start of the fourth growing season. During the first and second growing seasons, weeds were controlled by mowing.

A triple lattice twice design was used because selection was the objective; individual tree performance and family means were the quantities of primary interest. Early analyses indicated the lattice design gave little improvement in efficiency over a randomized block analysis. Therefore, a randomized block analysis of variance and covariance was used with expectations of mean squares and interpretations of variance components shown in Table 1. In a sense, the estimates of variance components are incidental, and must be qualified because

"...lattices...confound genetic and environmental differences among means..." (Dudley and Moll, 1969) and lattice designs are not the best for estimating variance components.

Table 1.--The form of the analyses of variance and construction of heritabilities and genetic correlations

Source	df	E(ms)
Replication	5	$\frac{\sigma_w^2}{k} + \sigma_{rf}^2 + f\sigma_r^2$
Family	63	$\frac{\sigma_w^2}{k} + \sigma_{rf}^2 + r\sigma_f^2$
RxF	<u>315</u>	$\frac{\sigma_w^2}{k} + \sigma_{rf}^2$
Total	383	
Within plot	993	$\frac{\sigma_w^2}{k}$

k = harmonic mean number of trees per plot = 3.4569

Assumption: half-sib family component  $\sigma_f^2 \hat{=} 1/4 \sigma_A^2$

Narrow sense heritability:

$$h^2 = \frac{4\sigma_f^2}{\sigma_w^2 + \sigma_{rf}^2 + \sigma_f^2}$$

Genetic correlation among two traits, x & y

$$r_G = \frac{\sigma_{fxy}}{\sqrt{(\sigma_{fx}^2)(\sigma_{fy}^2)}}$$

The assumptions underlying the analyses are routine and adequately outlined by Becker (1967) and Stonecypher et al. (1964). Wind-pollinated seed from a single parent tree are assumed to be half-sibs, and this has been subjected to some question (Namkoong, 1960). Furthermore, because the study samples only one planting environment, the estimates of additive variance admittedly carry an additive x environmental component (Namkoong, et al., 1966). Despite these qualifications, the variances deserve consideration.

Primary analyses of variance were calculated on the basis of plot averages because of variable numbers of trees surviving per plot. There were no missing plots; the harmonic mean number of trees per plot was 3.4569. Estimates of within-plot variance were obtained by a between-within analysis of all plots in the experiment. Standard errors of variance components, heritabilities, and genetic correlations were calculated according to Becker (1967).

At the end of the fourth growing season, the plantation was measured and clear-cut to a 3-inch stump. Each tree was weighed immediately to determine green weight to the nearest half-pound. Dry weight per tree was calculated two ways: (1) by converting green weight per tree to dry weight per tree using an assumed moisture content of 145 percent 4/:

$$\text{Dry weight} \hat{=} \frac{\text{Green weight}}{2.45}$$

(2) by the regression equation<sup>5/</sup>:  $\hat{y} = -18.59650 + 28.72726 (D^2H)$

when  $y$  = dry weight stem + branches + bark, without leaves

$D$  = stump diameter at 6 inches

$H$  = total height of tree.

Hence, the two methods of calculating dry weight per tree will be referred to as: "by percent" or "by regression."

Wood samples were collected at breast height when the plantation was harvested. Bark was removed, and disks were cut roughly 1-1/4 inches thick in the longitudinal direction. Green volume was determined by water displacement, and specific gravity expressed as oven dry weight/green volume.

## RESULTS

Growth of the plantation over the first four years was good; total height averaged 24.3 feet- The total dry weight of the 0.56 acre plantation (wood and bark, but without leaves) approximated 10.6 tons per acre, or 2.6 tons per acre per year. Growth was slightly suppressed in parts of replications 2 and 3, due to an unforeseen and still unexplained environmental effect. However, the effects were not too serious.

F-tests of family effects showed significant differences for all traits, with the exception of first year diameter at 1 foot (Table 2). For the very important trait, total dry weight per plot, families exhibited a range of variation of considerable importance in an applied breeding program (Figure 1). The two best families produced 60 percent more dry matter than the plantation average; the two poorest families, 35 percent less than average.

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Table 2.--Summary of plantation means, family f-tests, heritabilities, and standard errors of heritability for each trait

Trait	Study mean		Family F-test	Heritability	Standard error of heritability <sup>a/</sup>
	English	Metric			
Root collar diameter	0.27 in.	6.96 mm	3.06**	0.44	0.12
First year					
Height	6.2 ft.	1.87 m	1.57**	0.17	0.02
Diameter at 1'	0.7 in.	1.80 cm	1.22 N.S.	0.07	0.07
Second year					
Height	13.1 ft.	3.98 m	1.49**	0.19	0.11
Diameter at 1'	1.4 in.	3.63 cm	1.57**	0.16	0.08
Height growth	6.9 ft.	2.10 m	1.57**	0.24	0.12
Third year					
Height	20.2 ft.	6.15 m	1.71**	0.25	0.11
Diameter at 1'	1.9 in.	4.78 cm	2.20**	0.26	0.09
Height growth	7.1 ft.	2.17 m	1.45*	0.15	0.09
Fourth year					
Height	24.3 ft.	7.42 m	2.11**	0.27	0.09
Diameter at 1'	2.2 in.	5.59 cm	2.60**	0.29	0.08
Height growth	4.2 ft.	1.27 m	2.45**	0.29	0.09
Specific gravity	0.412	0.412	5.68**	0.78	0.17
Dry weight/tree by regn	8.3 lb.	3.78 kg	2.66**	0.30	0.09
Dry weight/tree by percent	8.0 lb.	3.63 kg	2.86**	0.32	0.09
Total dry weight/plot	31.1 lb.	14.10 kg	2.39**	- <u>b/</u>	- <u>b/</u>

<sup>a/</sup> From Becker, 1967

$$S.E.(h^2) = \frac{4 \sqrt{\text{Var. } \sigma_f^2}}{\sigma_w^2 + \sigma_{\text{rxf}}^2 + \sigma_f^2}$$

<sup>b/</sup> No heritability calculated; no estimate of  $\sigma_w^2$  possible.

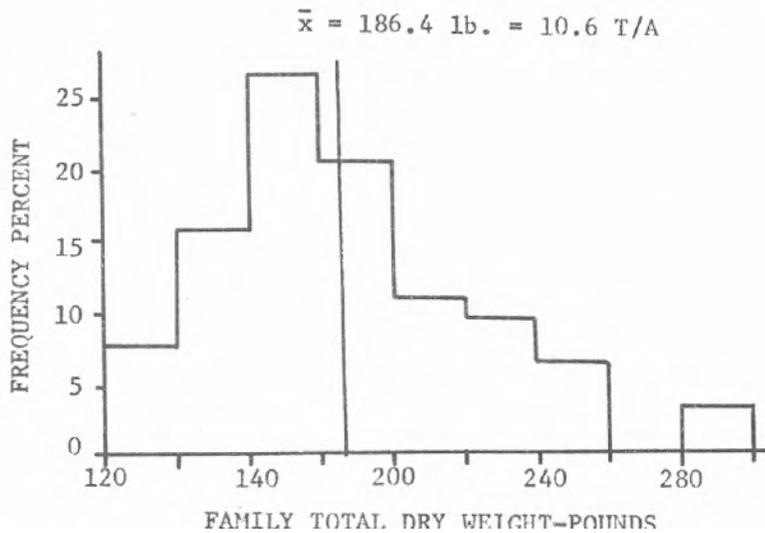


Figure 1.--Frequency distribution of family total dry weight (by regression) produced over all six replications in the plantation.

For specific gravity, individual trees varied between 0.34 and 0.48 (Figure 2). Family means for specific gravity ranged from 0.385 to 0.438. Heritability was high, 0.78, with a standard error of 0.17.

Heritabilities of height and diameter increased as the plantation grew older with the highest values occurring during the fourth growing season. Standard errors of heritabilities were considerably smaller than the heritabilities, and in only one case (first year diameter at 1 foot) did the standard error equal the heritability (Table 2).

Estimates of variance components for the most important traits are shown in Table 3.<sup>6/</sup> Coefficients of variation of  $\sigma^2$  are reasonably small because of the numbers of families and replications in the plantation. Variance components for the two measures of dry weight per tree are essentially the same, with the exception of the family x rep. component: positive for dry weight by regression and negative for dry weight by percent. This may be an artifact created in estimating dry weight per tree by applying a single moisture content over the entire plantation.

For each trait, the phenotypic correlations with root collar diameter remained essentially constant  $u^p$  through four years (Table 4). However, the genetic correlations with root collar diameter started off high and decreased with increasing age. The genetic correlation for diameter at 1 foot may have stabilized around  $0.56 \pm .09$  by three or four years of age, but may drop further for total height. Of particular interest for early selection is the genetic correlation of  $0.47 \pm .08$  between root collar diameter and dry weight per tree.

<sup>6/</sup> Complete sets of components of variance and covariance can be obtained at the Forestry Sciences Laboratory, Athens, Ga. 30602, from the Physiology and Culture of Piedmont Hardwoods Project.

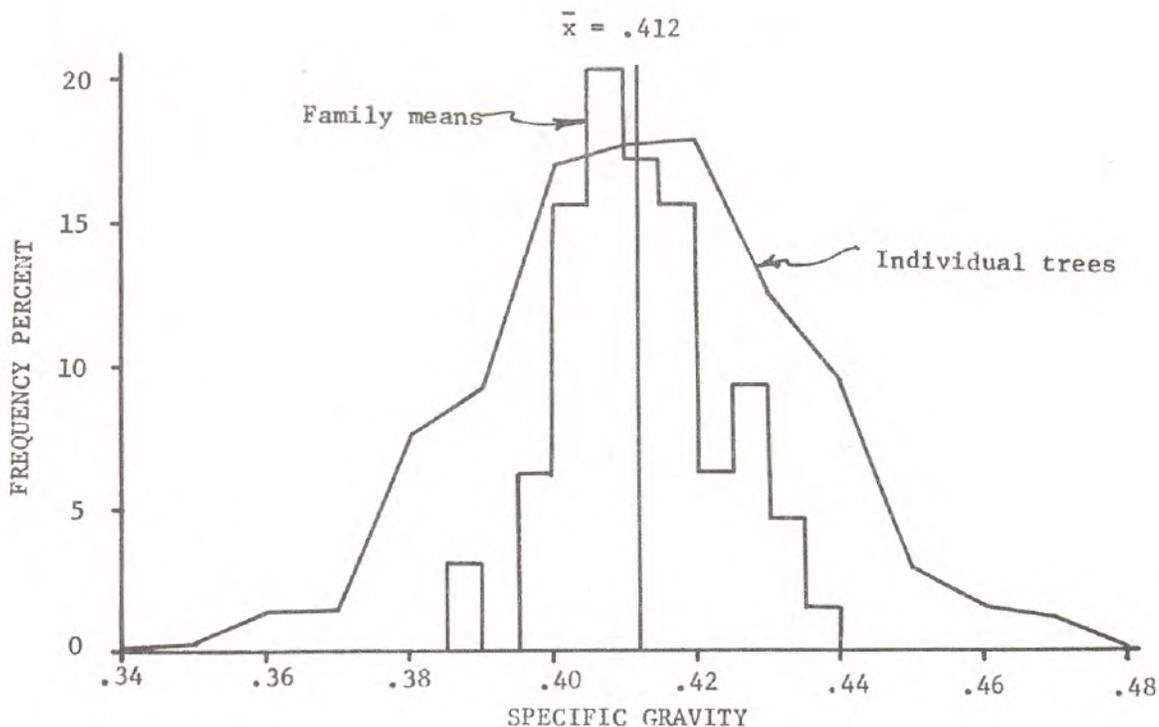


Figure 2.--Frequency distributions of wood specific gravities of individual trees and of family means.

The genotypic and phenotypic correlation among fourth year traits are summarized in Table 5. The phenotypic correlations between growth measurements and specific gravity were positive and approximately 0.3. However, genetic correlations between growth measurements and specific gravity were negative, ranging between -0.12 to -0.25.

The genotypic and phenotypic correlations among height growth during each growing season vary considerably by both sign and magnitude and do not show any clear patterns (Table 6).

#### DISCUSSION

The heritability fractions reported here (Table 2) probably should be considered as estimates of the upper limits of the fractions that could be realized in an applied breeding and planting program. Were the true sib-relationships known for each family, instead of the half-sib assumption that  $\sigma_f^2 \hat{=} 1/4\sigma_A^2$ , a mixed-sib assumption of  $\sigma_f^2 \hat{=} 1/3\sigma_A^2$  might be more appropriate, according to recent calculations by Squillace<sup>7/</sup>. To account for this qualification, the

<sup>7/</sup> Personal communication with Dr. A. E. Squillace, Chief Plant Geneticist, USDA Forest Service, Southeastern Forest Experiment Station, Olustee, Florida.

Table 3.--Estimates of variance components of seedling root collar diameter and traits measured at 4 years of age

Trait	Replication $\sigma_r^2$	Family $\sigma_f^2$	Fam. x Rep. $\sigma_{fr}^2$	Within plot $\sigma_w^2$	CV $\sigma_f^2$
----- Nursery -----					Percent
Root collar diameter	0.000553	0.000575	0.000451	0.004210	26.3
----- End of fourth growing season -----					
Height	1.161161	0.803238	1.705860	9.116149	34.1
Diameter at 1'	0.007029	0.021311	0.001264	0.271865	28.9
Dry weight per tree-regn.	0.858775	1.751527	0.288256	20.939570	28.5
Dry weight per tree-%	0.854042	1.645532	-0.229068	19.159383	27.3
Specific gravity	-0.00000680	0.00009378	0.00001219	0.00037371	21.4

Table 4.--Genotypic and phenotypic correlations between root collar diameter in the nursery and traits measured later in the field

Trait		Genotypic correlation	Phenotypic correlation
First year	Height	0.61	0.36
	Diameter at 1'	0.98	0.32
Second year	<b>Height</b>	<b>0.45</b>	<b>0.32</b>
	Diameter at 1'	0.63	0.36
	Height growth	0.16	0.18
Third year	Height	0.38	0.32
	Diameter at 1'	0.55	0.38
	Height growth	0.26	0.21
Fourth year	Height	0.31	0.35
	Diameter at 1'	0.56	0.38
	Height growth	0.08	0.19
	Dry weight/tree-regn.	0.46	0.38
	Dry weight/tree-%	0.47	0.43
	Specific gravity	-0.15	0.08

Table 5.--Genotypic and phenotypic correlations among traits determined at end of fourth growing season

Trait	Diameter at 1'	Dry weight <u>per tree</u>		Specific gravity
		by regn.	by %	
Height	0.83	0.87	0.91	-0.12
	<u>0.8411 /</u>	0.83	0.83	0.30
Diameter at 1'		1.00	0.97	-0.25
		0.97	0.93	0.30
Dry weight per tree-by regn.				-0.20
				<u>0.28</u>
Dry weight <u>per tree-by %</u>				-0.21
				<u>0.28</u>

a/ Phenotypic correlation underlined.

Table 6.--Genotypic and phenotypic correlations among height growth during each growing season

Trait	Second year Height growth	Third year Height growth	Fourth year Height growth
First year height <sup>a/</sup>	0.32 <sub>b/</sub>	0.93	0.18
	<u>0.38<sup>b/</sup></u>	<u>0.31</u>	<u>0.24</u>
Second year height growth		0.88	0.01
		<u>0.50</u>	<u>-0.06</u>
Third year height growth			0.31
			<u>0.07</u>

2/

Since seedlings were topped 4.5 inches above the root collar before planting, first year height was in essence height growth during the first growing season.

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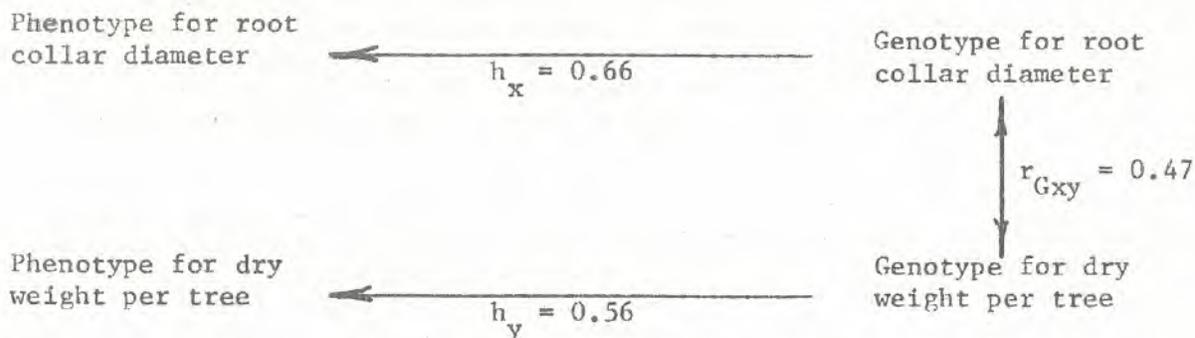
Phenotypic correlation underlined.

heritabilities listed in Table 2 should be reduced by 25 percent (i.e., multiply by .75). Furthermore, because only one planting environment was sampled, the  $\sigma^2_A$  components of the heritability fractions include an additive x environmental component,  $\sigma^2_{AE}$  (Namkoong, et al., 1966). Therefore, the corrected heritabilities should again be corrected downward, possibly by another 25 percent (again multiply by .75). Accounting for both corrections, heritability of height would be reduced to 0.15, diameter to 0.16, dry weight per tree to 0.17, and specific gravity to 0.44. These qualifications must be borne in mind in the discussions to follow. While they affect the size of the heritabilities, they have little effect on the general conclusions that are attempted.

While the absolute size of the heritabilities may be subject to some question, the increases in relative size for height and diameter with age are in a reasonable direction (Table 2). The family components for both total height and diameter increased with age probably as a response to the intensive competition that developed at a spacing of 4x4 feet. In such a case, "the big get bigger and the small get smaller."

Of particular interest in this study are the genetic correlations between seedling root collar diameter in the nursery and later growth in the field (Table 4). Juvenile-mature correlations have received considerable interest in forest genetics, but few definitive results are available. These data represent the first stages of a developing juvenile-mature correlation.

By careful documentation during planting, it has been possible to show that a sufficiently strong genetic correlation exists to reward indirect selection on root collar diameter to increase dry weight per tree. Using path coefficient methods of Sewall Wright, recently outlined by Franklin et al. (1970), the following paths can be established:



where:  $h_x$  = square root of heritability of root collar diameter  
 $h_y$  = square root of heritability of dry weight per tree  
 $r_{Gxy}$  = genetic correlation between root collar diameter and dry weight per tree at age four years.

The gains in dry weight per tree from indirect selection on root collar diameter are approximated by:

$$\Delta_{G_{ind}} \hat{=} (h_x r_G h_y) \sigma_y i \hat{=} 1.648 \text{ lb.}$$

where:  $\sigma_y$  = 4.6 lb. = phenotypic standard deviation of dry weight per tree  
 $i$  = 2.063 = selection intensity for upper 5 percent

The gains from direct selection on dry weight per tree in the test plantation are approximated by:

$$\Delta_{G_{ind}} \hat{=} h_y^2 \sigma_y i \hat{=} 2.942 \text{ lb.}$$

where:  $h_y^2$  = heritability of dry weight per tree  
 $\sigma_y$ ,  $i$  defined above.

To compare gains from each method, they must be expressed as gain per unit time. In this case, gains should be divided by the number of years required to complete a breeding cycle, i.e., to go from mature seed through selection and recombination to mature seed. Here it will be assumed that a total of eight years will be required to propagate a selection, bring a ramet to sexual maturity, control pollinate, and mature seed. For indirect selection in the nursery, the cycle length is: 1 year, nursery + 8 years to seed = 9 years. For direct selection, the cycle length is: 1 year, nursery + 4 years, test plantation + 8 years to seed = 13 years. Gains per unit time for each selection method are:

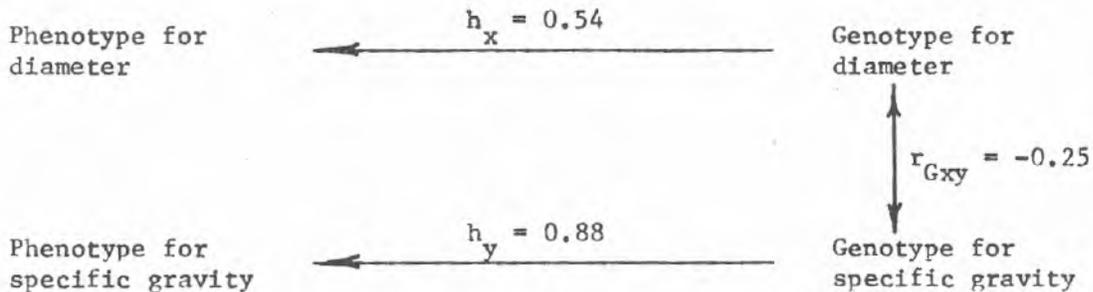
$$\text{indirect} = 1.648/9 = 0.1832 \text{ lb./year}$$

$$\text{direct} = 2.942/13 = 0.2263 \text{ lb./year}$$

If eight years are required to propagate and recombine, direct selection is clearly superior to indirect selection. If the propagation and recombination phases could be shortened to four years by growth hormones and other cultural measures, gains would be divided by four and seven years for indirect and direct selection respectively, and the gains per unit time would become almost equal.

There is a practical limit to how much the existing data can be manipulated. However, it is safe to conclude that, if the genetic correlation of 0.47 between root collar diameter and dry weight per tree does not decrease too much with increasing age, indirect selection on root collar diameter can be used to supplement, but not replace, direct selection at a later age in an effort to shorten the length of the breeding cycle.

The method of path coefficients can be used also to examine the impact of direct selection for growth on wood specific gravity. This path defines the impact of selecting for diameter:



where:  $h_x$  = square root of heritability of diameter  
 $h_y$  = square root of heritability of specific gravity  
 $r_{Gxy}$  = genetic correlation between diameter and specific gravity.

Change in specific gravity is calculated:

$$\Delta_{SG} \hat{=} (h_x r_G h_y) \sigma_y i$$

where  $\sigma_y = .021902$  = phenotypic standard deviation of specific gravity  
 $i$  = selection intensity.

The correlated decrease in specific gravity, summarized in Table 8 for three intensities of selection, does not appear to be severe through one cycle of selection. These data suggest that the correlated negative response in specific gravity will probably be negligible in comparison to the increases in dry matter yield achieved by selection on height and diameter.

Table 8.--The correlated response in specific gravity caused by selection for diameter

Selection intensity Percent		Correlated response S.G.	New population average = $0.412 + A$ S.G.
1	2.665	-0.008	.404
5	2.063	-0.006	.406
10	1.755	-0.005	.407

For two-year-old wind-pollinated progeny of cottonwood, Farmer (1970) found small genetic and phenotypic correlations for diameter x specific gravity, but with signs opposite from those reported here for sycamore. Farmer (1970) dismissed these correlations as being too low to have practical significance. Stonecypher et al. (1964) found negative genetic correlations for diameter x specific gravity in two- and three-year-old loblolly pines. However, Stonecypher et al. (1973) will report 10-year analyses of this same loblolly population showed the genetic correlations had turned strongly positive for specific gravity x volume:  $r_g = +.36$ ,  $r_p = +.28$ . It is possible that in sycamore the genetic correlation between growth and specific gravity may become positive with increasing age. However, in programs breeding for short rotations, the effects should be closely monitored, and selection should favor both high specific gravity and rapid growth rate to achieve the maximum increase in wood substance production.

While this plantation samples only one planting environment, growth during each year samples a different "micro environment." Intensity of competition is changing; roots are exploring an increasing volume of soil; rainfall patterns vary from year to year; the effects of early fertilization are wearing off, and new fertilization was applied at the start of the fourth growing season. For these reasons, it is little wonder that the genetic and phenotypic correlations among height growth during each season are erratic in magnitude and sign (Table 6). First year results of this plantation and a companion plantation in a different environment suggested the existence of a genotype x environment interaction. These erratic correlations for height growth are probably also due to genotype x environment interactions. All this points to the necessity of establishing pedigreed test plantations in different environments to account for the genotype x environment interaction in the selection process.

What of importance to an applied breeding program can be inferred from the results and experiences gained from this single plantation, of a single population sample, of "half-sib families," once the qualifications of Namkoong (1966), Namkoong et al. (1966), and Dudley and Moll (1969) are accepted?

1. There is a sufficient supply of additive genetic variability in growth, dry matter yield, and wood specific gravity to reward a breeding program in sycamore. By using proper nursery techniques and field plantings designed to enhance combined individual plus family selection in a recurrent selection and breeding program, gains in dry weight per tree of 5 to 15 percent should be achieved each generation, at least for a few generations.
2. To be most effective, selection should be practiced in pedigreed test plantations established in at least two, preferably more, planting locations. Test designs should be chosen to facilitate selection on highly variable sites. If operational procedures are expected to call for fertilization, weed control, and coppicing, test plantations should be treated accordingly.
3. A base population can be developed by collecting wind-pollinated seed of better than average phenotypes (i.e. mild selection) from local populations as well as populations to the north and south of the intended planting environment.
4. Maintain the family identity of as many wind-pollinated families as possible. Fewer than 50 families would be considered too small a base population for a recurrent breeding program.
5. In the progeny test nursery, religiously maintain a uniform density from one progeny to the next. Failure to do so will confound early growth comparisons for a number of years. Seedlings should enter the intense competitive stage at densities of 6 to 8 seedlings per square foot.
6. If more families are available at the end of the nursery season than can be planted in the field, reject those families having the smallest root collar diameters.
7. Because sycamore seedlings usually **die** back from the top to varying degrees after field planting, genetic differences in early growth will be revealed better if tops of the seedlings are cut off in the nursery bed or at time of lifting, 4 to 8 inches above the root collar.
8. Indirect selection on root collar diameter can be used to supplement direct selection at a later age, provided seedling densities have been maintained uniformly enough in the nursery. Combined individual and family selection can be applied at the end of the nursery season to select potential breeding candidates. Propagation and sexual aging of these candidates can begin immediately by rooting the tops of the seedlings as dormant cuttings (Schmitt and Webb, 1971). Once rooted, these can be set out in a clone bank for future breeding work--probably sooner than breeding can begin on trees chosen by direct selection.

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