ESTIMATION OF GAIN IN FORM, QUALITY AND VOLUMETRIC TRAITS OF AMERICAN SYCAMORE IN RESPONSE TO THE SELECTION FOR TREE DRY WEIGHT

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Abstract.--The genetic relationship of tree dry weight to form, quality and volumetric traits of American sycamore (*Platanus occidentalis* L.) was obtained from 1080 open-pollinated eight-year-old trees measured for DBH, height, straightness and crown score and from 233 trees measured for tree dry weight, specific gravity and moisture content. Tree dry weight is positively correlated with taller (r_G = 0.94), larger (r_G = 0.99), straighter trees and with better crown configuration, lower moisture content and higher specific gravity. Selection for tree dry weight is estimated to improve tree dry weight 23.9 percent from roguing first generation seed orchards and 42.9 percent from establishing second generation seed orchards. Selection pressure should be placed on total height to achieve optimum amounts of gain for tree dry weight in combination with other desirable traits.

Additional keywords: *Platanus occidentalis* L., heritability, genetic correlation, expected gain, correlated response.

INTRODUCTION

Selection criteria for tree improvement need to be flexible to the multiple uses of a species. American sycamore (*Platanus occidentalis* L.) has rapid juvenile growth, is amendable to plantation cultural practices (Steinbeck et al. 1972) and tree improvement programs, and is suitable for a variety of products: veneer, sawtimber, energy and pulpwood (Merz 1958, McElwee et al. 1970, Panshin and deZeeuw 1980, Steinbeck et al. 1972). Whole tree chips are utilized for energy and pulp uses, whereas only the stemwood is suited for timber purposes. If the ratio of stem-to-total tree dry weight is essentially the same for all trees, then a selection criterion for improvement common to each of these uses is increased dry weight of the tree. Other characteristics important for the particular uses are: stem straightness and taper for veneer; straightness, high density and low fibril angle for sawtimber; dry weight per unit volume for energy (Goldstein 1979); and high cellulose content, long fibers and fiber flexibility for pulp yield, tear strength and burst and tensile strength (Amidon 1981). Specific gravity, an easily measured trait, is positively correlated with the proportion of fibrous and ray tissues and with thick walled fibers (r = 0.78) and negatively correlated with vessel volume (Taylor 1969). A measure of specific gravity will indicate the density of the wood (important for energy and sawtimber) but not the particular microscopic traits that determine the quality of the pulp for different **uses**.

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This paper addresses the following objectives through the examination(an open-pollinated progeny test: (1) evaluate the correlated response in volumetric, form and wood morphological traits resulting from direct selection for tree dry weight and (2) assess trait(s) on which selection should be placed to achieve an increase in tree dry weight in a practical breeding situation

MATERIALS AND METHODOLOGY

An eight-year-old open-pollinated American sycamore progeny test, belonging to the North Carolina Forest Service, was the data base for this study. The 30 parent trees were selected in natural stands in western North and South Carolina (Figure 1) according to the North Carolina State University Hardwood Cooperative selection criteria of crown configuration, straightnes pruning, branch angle and epicormic sprouting (Purnell and Kellison 1983). These trees were grafted into a first generation seed orchard located in Morganton, North Carolina. Open-pollinated seed of the parent trees, collected from ortets, was the source of a progeny test established adjacent to the Catawba River in McDowell County, North Carolina.

The progeny test was established in 1973 with 1-0 bare root seedlings on soils of alluvial deposition. Seven replications of ten tree row-plots were randomly planted by family at 3m between rows and 2.4m within rows. Three replications were excluded from the analysis because of inferior tree growth caused by their location on an excessively well drained sand ridge. Survival of the remaining four replications exceeded 90 percent.

After eight years of plantation growth, the North Carolina Forest Service measured all trees in the study for diameter at breast height (DBH), total height, crown configuration score (1 = best to 6 = worst) and straightness score (1 = best to 6 = worse). Following measurement, thinning to five trees per row-plot was prescribed to maintain growth in the closed crown plantation. The marking system was based upon removing inferior trees while maintaining balanced spacing. Two of the trees marked for thinning were used for destructive biomass sampling. Since the thinning was not random, the trees to be destructively sampled were chosen to be as representative as possible in terms of the mean and variance of the row-plot. Some of the ramifications of using this system are dealt with later in this paper; a more detailed account is given by McCutchan (1982).

Field procedures

Two trees per family row-plot per replication (233 trees) were felled at ground level and bucked into quarter lengths to obtain green weight, specific gravity and moisture content for each stem and limb component. Diameter at breast height, total height and live crown length were also recorded. Green weight of each stem quarter section was measured to the nearest 0.05 kg on a portable scale. A 5-cm thick disk sample (wood and bark) was removed at breast, quarter, half and three-quarters heights for estimation of unextracted specific gravity and moisture content (Figure 2). To estimate these traits for the limb wood and bark, a representative limb in each of the low-, middle- and high-crown areas was selected for removal of a 10-cm long disk sample near the middle of the limb. All limbs greater than 0.6cm in diameter were cut off

Figure 1.--Distribution of American sycamore parent trees in North Carolina and South Carolina and the progeny test location (indicated by dot).

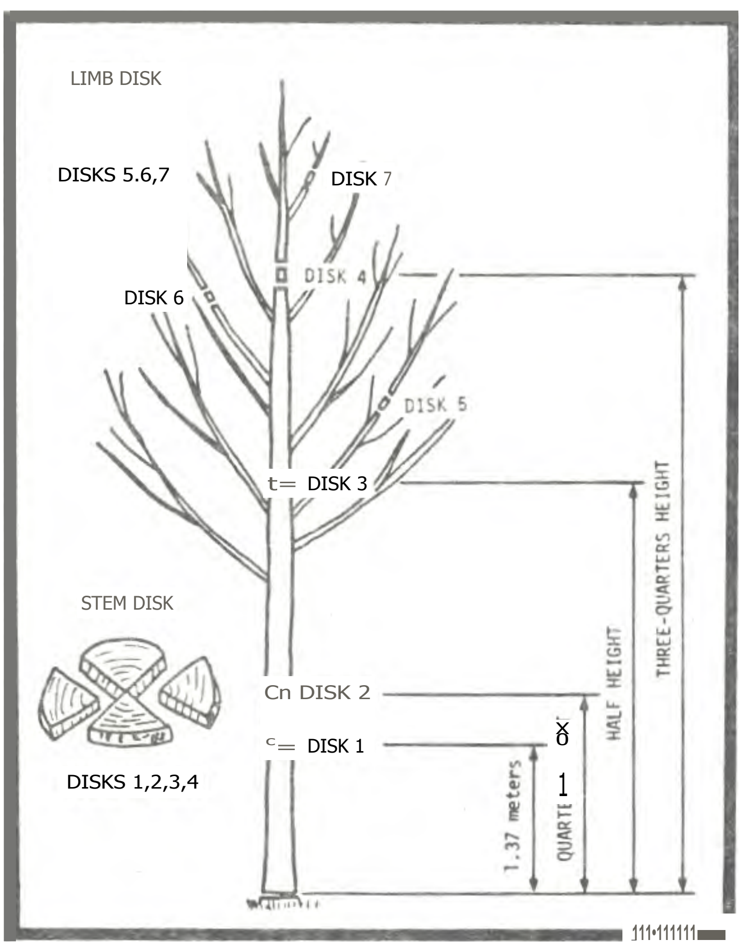

Figure 2.--Diagrammatic sketch of stem and limb sampling positions.

at the junction with the stem and then weighed. The calculation of whole stem specific gravity and moisture content values was based upon an average of sample values weighted by stem volume (Messina et al. 1982); limb values are an average of limb sample values weighted by limb sample radius. Limb and stem dry weights were estimated by applying the estimates of limb and stem moisture content percent to the respective green weights.

Data anlysis

The height, DBH, straightness score and crown score data (1080 observations), and crown length, specific gravity, moisture content and dry weight data (233 observations) were analyzed as a randomized complete block design, examining the random effects of replication, family, replication by family and within plot. Variance components (σ^2_R, σ^2_F, σ^2_{RF} and σ^2, respectively) were estimated for each trait and covariance components were estimated for each trait with tree dry weight, DBH and height. Estimates were obtained using Henderson's Method III for unbalanced data (SAS Varcomp Procedure) (Goodnight 1982). The open-pollinated families were assumed to represent half-sib families; additive genetic variance (σ^2_A) was estimated as four times the family variance component (σ^2_F). Family heritabilities ($h^2_F = \frac{1}{4}\ \sigma^2_A/\sigma^2_{\overline{P}}$, where $\sigma^2_{\overline{P}}$ is the phenotypic variance among open-pollinated family means) and individual-within-family heritabilities ($h^2_W = \frac{3}{4}\ \sigma^2_A/\sigma^2_W$, where $\sigma^2_W = \sigma^2_{RF} + \sigma^2$) were estimated for each trait, as well as the genetic correlation (r_{Gxy}) of each trait "y" with tree dry weight, DBH and height ("x"). Expected genetic gain from direct selection on tree dry weight and the correlated response expected in other traits were estimated for the roguing of the first generation seed orchard (G1[1/]) and for the establishment of a second generation seed orchard (G2 + G3[1/]). Roguing the clonal seed orchard involves only family selection based on progeny test results, whereas the establishment of a second generation seed orchard involves combined selection on family (G2) and individual-within-family (G3) (Namkoong et al. 1966). The calculated expected genetic gain or correlated response in either case does not include the gain from mass selection of parent trees in natural stands.

[1/] where $$G1 = \left[\sqrt{h^2_{Fx}}\ \sqrt{h^2_{Fy}}\ \ \sigma_{\overline{P}y}\ \ r_{Gxy}\ \frac{100\%}{\overline{y}}\ \ 2\right] i_1$$

$$G2 = \left[\sqrt{h^2_{Fx}}\ \sqrt{h^2_{Fy}}\ \ \sigma_{\overline{P}y}\ \ r_{Gxy}\ \frac{100\%}{\overline{y}}\right] i_2$$

$$G3 = \left[\sqrt{h^2_{Wx}}\ \sqrt{h^2_{Wy}}\ \ \sigma_{Wy}\ \ r_{Gxy}\ \frac{100\%}{\overline{y}}\right] i_3$$

"x" refers to the trait on which direct selection is applied, "y" refers to the trait in which correlated response is expected and i_1, i_2 and i_3 are selection intensities (Becker 1975). When "x" is the same trait as "y", then the gain calculated is expected genetic gain; when "x" differs from "y" then the gain calculated is the correlated response.

RESULTS AND DISCUSSION

The effects of nonrandom sampling were evaluated by comparing the ratio of each gain (G2 and C3) from the trees which had been destructively sampled to the respective gains estimated using all 1080 trees for each DBH and height. Gain due to family selection (G2) for DBH was 39 percent over that estimated using all trees and individual-within-family (G3) was 186 percent higher; for height, G2 was 10 percent higher and G3 was 79 percent higher. To compensate for the overestimated pain, in particular with tree dry weight, tree dry weight was regressed upon DBH x height using an intercept $_2$ The predictive equation (tree dry weight in kg/tree = 2.4427 + 0.0189 x DBH x height), with R was applied to each tree to estimate its tree dry weight. Variance components and heritabllities were estimated for predicted tree dry weight. The genetic correlations and gain estimates of tree dry weight with other traits is based upon predicted tree dry weight data, where the genetic correlation between predicted tree dry weight and the observed tree dry weight is 0.98. The correlations of predicted tree dry weight with DBH and height includes a correlation of error terms since predicted tree dry weight is a function of DBH squared times height. However, the genetic correlations of DBH and height with predicted tree dry weight in contrast to those with the actual tree dry weight values are the same or less: 0.99 versus 0.99 for DBH and 0.94 versus 1.02 for height

The mean descriptive statistics for the 30 open-pollinated families are given in Table 1. Mean DBH and height of these eight-year-old trees are similar to the plantation average of five-year-old trees in Mississippi, 9.32 cm and 9.43m, respectively (Tuskan 1980). The mean stem specific gravity, 0.412, was lower than the value 0.43 reported by Tuskan (1980), and lower than the 0.463 value obtained by Lee (1972) for older trees. The stem moisture content of 138.0 percent is slightly higher than that which Tuskan (1980) found, 136.9 percent, and also higher than the value (125 percent) reported by Lee (1972). Eighty-three percent of the mean tree dry weight was in the stem; the comparable ratio of 78 percent was found for Tuskan's five-year-old trees (1980). The amount of variation due to families for the stem-to-tree dry weight ratio and for limb moisture content was nonsignificant at the 5 percent level. All other traits had significant family effects, which indicates that sufficient genetic variation exists to select upon, and were included in subsequent analyses.

Family and individual-within-family heritabilities are listed in Table 2. Family heritabilities for DBH and height agree closely with those found for seven-year-old sycamore of 0.75 and 0.72, respectively (Nebgen and Lowe 1982). Individual-within-family heritabilities for the destructively sampled trees ere much higher than for the 1080 trees for both height and DBH, implying that h for other destructively sampled traits are higher than if sampling had been random. In addition to sampling problems, additive genetic variance and hence family and individual-within-family heritabilities may be inflated if some of the open-pollinated progeny are full sibs. Inflation may also result from genotype by environment (G x E) variance being confounded with family variance, since the progeny test was established at only one planting site. However, the G x E influence on DBH, height, specific gravity and moisture content may be nonsignificant, inferring from the results of other studies (Land et al. 1983 , Nebgen and Lowe 1982).

Table 1.--Descriptive statistics for mean traits of 30 parents (weighted by the number of progeny)

Trait	Mean	Standard Deviation
Diameter at breast height (cm)	9.72	1.01
Height - total (m)	10.59	0.73
Crown length (m)	6.88	0.90
Live crown ratio	0.65	0.05
Crown score (1 = best, 6 = worst)	3.8	0.5
Straightness score (1 = best, 6 = worst)	3.5	0.5
Limb specific gravity	0.406	0.011
Stem specific gravity	0.412	0.010
Limb moisture content (%)	144.1	6.2
Stem moisture content (%)	138.0	7.4
Limb dry weight (kg/tree)	3.78	1.49
Stem dry weight (kg/tree)	17.57	5.50
Tree dry weight (kg/tree)	21.36	6.87
Predicted tree dry weight (kg/tree)	25.75	5.25
Stem to total tree dry weight (%)	83	2.5

Table 2.--Estimation of family and individual-within-family heritabilities for eight-year-old American sycamore

Traits	Heritabilities	
	Family	Individual-within-family
DBH[a/]	0.74	0.26
Height[a/]	0.69	0.27
Crown length	0.66	0.85
Live crown ratio	0.46	0.35
Crown score[a/]	0.64	0.23
Straightness score[a/]	0.68	0.30
Limb specific gravity	0.41	0.30
Stem specific gravity	0.55	0.50
Stem moisture content	0.64	0.89
Limb dry weight	0.45	0.40
Stem dry weight	0.56	0.59
Tree dry weight	0.54	0.56
Predicted tree dry weight[a/]	0.74	0.27

[a/] Results based on data from all 1080 trees

Genetic correlation estimates (Table 3) of tree dry weight, DBH and height with other traits show that tree dry weight is positively correlated with other desirable traits. The negative correlations of tree dry weight with crown and straightness score indicate that a better crown and straighter tree is associated with higher tree dry weight. The genetic correlations of height with DBH, height with specific gravity, and DBH with specific gravity confirm Nebgen's (1980) results using seven-year-old sycamore, 0.94, 0.30 and 0.28, respectively. Tree dry weight is most strongly correlated with DBH, height and crown length, the latter being a function of height.

Table 3.--Genetic correlation estimates of eight-year-old plantation grown American sycamore[a]

Trait	Predicted tree dry weight	DBH	Height
DBH	0.99	1.00	0.91
Height	0.94	0.91	1.00
Crown length	0.87	0.89	0.96
Live crown ratio	0.43	0.55	0.64
Crown score	-0.08	-0.18	-0.43
Straightness score	-0.22	-0.29	-0.53
Limb specific gravity	0.49	0.52	0.64
Stem specific gravity	0.28	0.31	0.28
Stem moisture content	-0.08	-0.14	0.11

[a] Genetic correlations whose absolute values are greater than 0.36 are significantly different from 0.00 at the 5 percent level.

The major objective of this research was to determine the correlated response associated with direct selection for tree dry weight. Those results for roguing the first generation seed orchard (G1) and establishing a second generation seed orchard (G2 + G3) are shown in Table 4. The correlated responses in DBH and height associated with direct selection on dry weight are comparable to expected genetic gains from direct selection on DBH and on height. Better crowns, straighter stems, increased specific gravity and decreased moisture content are expected to be associated with increased tree dry weight.

Practical applications

The proposal for the first generation seed orchard is to rogue the orchard from 30 to 15 parents. For the establishment of a second generation seed orchard the proposal is to select 15 of the 30 parents and to select 2 of the 36 progeny in each of the 15 families. The resulting gains expected in tree dry weight per tree are listed in Table 5. The goal to improve tree dry weight, which is a destructively sampled trait, behooves us to select easily measured traits to use as selection criteria for tree dry weight gain. Diameter at breast height and height are particular traits of interest because of high genetic correlations with tree dry weight, and the ease and common occurrence of DBH and height measurements. The correlated response in tree dry weight for

Table 4.--Coefficient of gain resulting from direct selection on each predicted tree dry weight, DBH and height

Genetic response trait		Direct selection traits		
		Predicted tree dry weight	DBH	Height
Predicted tree dry weight	G1[ad]	30.74i	30.44i	28.01i
	G2	15.371	15.22i2	14.01i
	G3	16.191	15.64i	15.11i
DBH	G1	15.581	15.7711	13.891
	G2	7.79i	7.8911	6.941;
	G3	8.211	8.111	7.491.4,
Height	G1	9.351	9.05i	9.55i
	G2	4.671	4.531	4.781,
	G3	4.92i	4.65i	5.151.
Crown length	G1	16.231	16.611	17.39i.
	G2	8.121	8.301	8.701;
	G3	8.551	8.53i	9.381',
Live crown ratio	G1	3.85i	4.93i	5.46i.
	G2	1.931	2.46i1	2.731,
	G3	2.03i	2.52i	2.94i'
Crown score	G1	-1.321	-2.93i	-6.83i
	G2	-0.6611	-1.47	-3.42i
	G3	-0.701	-1.511	-3.68i
Straightness score	G1	-4.27i	-5.59i	-9.83i
	G2	-2.13i	-2.80i	-4.92i
	G3	-2.25	-2.87i	-5.30i
Limb specific gravity	G1	1.53i1	1.62i1	1.93i
	G2	0.76i2	0.811	0.96i
	G3	0.801	0.8313	1.04i
Stem specific gravity	G1	0.91i	1.0111	0.87i
	G2	0.4511	0.511	0.44i
	G3	0.481	0.521	0.47i
Stem moisture content	G1	-0.621	-1.06i	0.811
	G2	-0.311	-0.5311	0.41i
	G3	-0.32i	-0.54	0.44i

ai G1 refers to the percent expected gain from roguing first generatic seed orchards; G2 and G3 refer to the expected gain from family and individual-within-family gains, respectively, for establishing sect generation seed orchards.

selection on DBH or height are comparable, given the variation that is associated with these estimates. Comparison of these figures can be made in columns two and three of Table 4. Selection for height is expected to result in larger desired gains in crown length, live crown ratio, crown configuration and straightness for both family and within-family selection than if DBH were selected at the same intensities. Less gain in stem specific gravity would be associated with selection for height than with selection for DBH. This situation could be desirable depending upon the type of pulp being made, as Land et al. (1983) pcints out. Also associated with selection for height would be an increase in moisture content, which is undesirable for any manufacturing process. Moisture content can be manipulated to a greater extent by season of harvest and harvesting technique than can other traits (Land et al. 1983), reducing the seriousness of the positive (nonsignificant) correlation of height and moisture content.

Table 5.-- Expected genetic gain and correlated responses in tree dry weight when selecting on tree dry weight, DBE and height

Metic response trait	Direct selection traits: Predicted tree dry weight (%)		DBH (%)		Height (%)	
Predicted tree dry weight	G1=23.88 G2=11.94 1 G3=30.95/	42.89	G1=23.65 G2=11.82 G3=29.89	41.71	G1=21.77 G2=10.88 G3=28.88/	39.76

Another factor which has bearing in choosing between height and DBH is whether or not the half-sib assumption is valid. If there were full-sibs in the open-pollinated families, then there would be some dominance variance in the family variance component; gain estimates would be inflated. No information on the amount of dominance variance in DBH or height is available for sycamore, but for loblolly pine, there is a larger proportion of dominance variance in the full-sib family variance component for basal area than there is for height (Stonecypher et al., 1973). If there is a larger proportion of dominance variance in DBH for sycamore compared to height, then selection for roguing the first generation seed orchard and for establishing the second generation seed orchard should be on height. If the half-sib assumption is valid, then we can select upon either DBH or height to improve tree dry weight. Given the possible failure of the half-sib assumption and the higher correlated response generally associated with selection for height, selection in both the roguing of the first generation seed orchard and for establishment of the second seed orchard should be for height.

CONCLUSIONS

The evaluation of 1080 trees for DBH, height, straightness and crown score and a subset of 233 trees for tree dry weight, specific gravity and moisture content has elucidated the relationships of tree dry weight with the other aforementioned traits. Tree dry weight is positively correlated with taller, larger, straighter trees with better crown configuration, lower moisture content and higher specific gravity. Selection for tree dry weight is estimated to result in 23.9 percent improvement in tree dry weight from roguing first generation seed orchards and 42.9 percent improvement from establishing second generation seed orchards. Selection pressure should be placed on total height to achieve optimum amounts of gain for tree dry weight in combination with other desirable traits.

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