SELECTION OF SWEETGUM AND SYCAMORE FROM PROVENANCE-PROGENY TESTS

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Abstract. In support of the N.C. State Cooperative Hardwood Research Program plan to establish seed orchards of improved Southern hardwoods, scions were collected from selected trees in a 13-year-old sweetgum provenance-progeny test and a 10-year-old sycamore provenance-progeny test, both established in the Georgia Piedmont. The primary basis for tree selection was expected breeding value for volume. Expected breeding values were determined for each test tree from indices incorporating provenance, family within provenance, plot within family or provenance, and tree within plot values. A spline regression model was used to describe and eliminate environmental variation in the tests, markedly improving heritabilities. Indices were constructed using log transformed data to minimize effects of site quality on selection. Provenance means had the greatest influence on breeding values. Family within provenance and tree within plot were next in importance and of equal influence. Plot within family or provenance had a negligible influence. In making final selections, consideration was given to maximizing family diversity and stem straightness.

Keywords: *Liquidambar styraciftua.* Platanus *occiclentalis,* selection indices, progeny tests, advanced generation selection.

INTRODUCTION

This year, the North Carolina State Cooperative Hardwood Research Program assembled selections from progeny tests of several Southern hardwood species for later incorporation in seed orchards. We, at The University of Georgia, contributed sweetgum *(Liquidambar styraciflua)* and sycamore *(Platanus occidentalis)* selections to that collection. In this paper, we describe what selections were made, and how they were chosen.

For both sweetgum and sycamore, selections were made from provenance- progeny tests established more than 10 years ago. The primary criterion for selection was predicted breeding value for current age volume, but consideration was also given to form characteristics and to maintaining genetic diversity.

In constructing the indices for breeding value determination, three practices were employed which may not be considered standard. First, environmental trends within the progeny test were modelled with spline regression and then eliminated. Second, the within family term in the selection indices was divided into plot within family and within plot components. Third, the indices were build with log-transformed data.

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PROGENY TEST DESCRIPTIONS

Sweetgum

Sweetgum selections were taken from a single provenance-progeny test established in February, 1980 with 1+0 stock grown in a nursery at The University of Georgia. Seeds for that test were provided by K. C. Steiner of The Pennsylvania State University and by the senior author. Fifth-year results of this and related tests were reported in an earlier SFTIC Proceedings (Steiner *et* aL 1985).

The test contains trees from four (or rarely three) open-pollinated families from each of 27 provenances located throughout the natural range of sweetgum east of the Mississippi River. The test design is split-plot with four single-tree family subplots within each provenance main plot, replicated in four complete blocks. Tree spacing was 2.6 x 2.6 m. Survival was 95% leaving 410 test trees for consideration.

The test site is located about ten miles north of Eatonton, Georgia, in Putnam County, in the lower Piedmont. The soil at the site is an eroded Cecil, typical of Piedmont uplands. Average tree height after thirteen field seasons was approximately 6 m.

Sycamore

Sycamore selections were also taken from a single provenance-progeny test This test was established in March, 1982 with 1+0 stock grown at The University of Georgia. The test contains trees from three (occasionally two) open-pollinated families from each of 80 provenances located throughout the native range in Georgia and adjacent parts of South Carolina, Alabama and Florida.

The test design is a randomized complete block with two-tree family plots established in each of four replications. Tree spacing was 3 x 3 m. Altogether, 1724 trees from 221 families were planted. The survival was 91%, leaving 1563 trees for consideration.

This test is located about one mile from the above-mentioned sweetgum test, but on a bottomland site (bordering the Little River). The soil at this location was typed as a mix of Chewacla and Starr series soils. Average height of dominant and co-dominant trees after ten field seasons was approximately 14 m, with the largest trees over 20 m.

PREDICTING BREEDING VALUES

Subtracting Environmental Variance

If one can reduce environmental variation in a progeny test, the effectiveness of selection can be improved by increasing the heritability. One practice that has been productive for this purpose is subtracting the block effect from individual phenotypes before analysis (Cotterill 1987). The intent of this procedure is to remove variation associated with environmental trends within the progeny test.

An elaboration of this technique is to use spline regression, rather than blocks, to describe environmental trends (Bongarten and Dowd 1987). The spline regression method allows for modelling of complex trends, and may, in many circumstances, account for more environmental variation than blocks.

To describe environmental trends with spline regression, the genetic values of the data must be spatially randomly distributed. Therefore, when the test design includes contiguous-tree plots, it may only be applied to plot means. In the case of the sweetgum test, a spline regression was fit to the provenance plot means. For the sycamore test, it was fit to family plot means.

The effectiveness of spline regressions in reducing environmental variation and increasing heritability may be seen in Figure 1. There, heritability for relative volume (D^2H) after subtraction of block effects is compared with heritability for relative volume after subtraction of environmental effects determined by spline regression. For sycamore, individual tree heritability increased from 0.27 to 0.37 when spline regression was used in place of block adjustment. A similar comparison could not be made for sweetgum because individual tree heritability was calculated from within provenance plot deviations which were not affected by either adjustment technique. However, provenance mean heritability increased from 0.85 to 0.95 when spline regression was used. As a consequence of these results, the selection indices described below were constructed using deviations from the values predicted by spline regression as data.

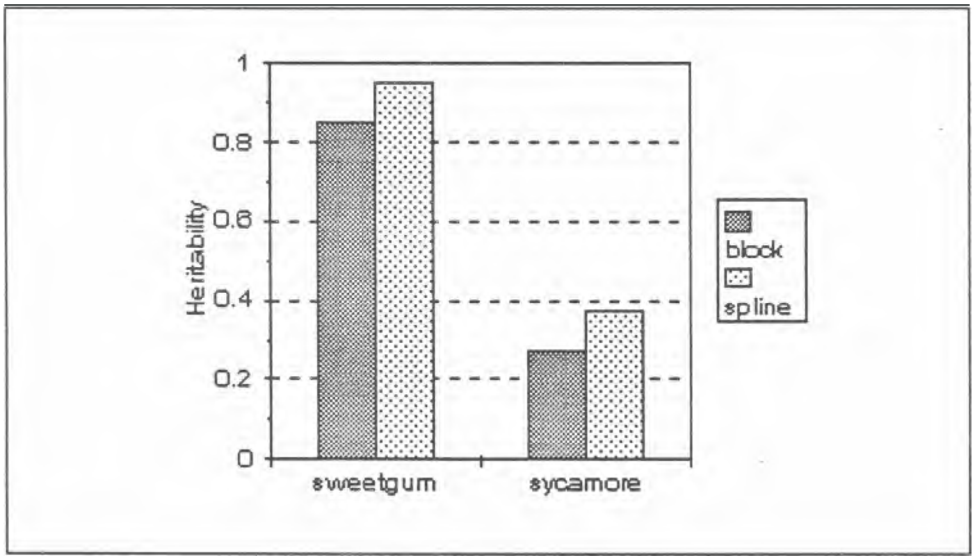

Figure 1. Provenance mean heritability in the sweetgum progeny test and individual tree within provenance heritability in the sycamore progeny test following substraction of environmental effects determined by block means and spline regression.

Development of Selection Indices

The purpose of selection indices in the present case is to determine expected breeding values of progeny test individuals for current-age volume. The indices incorporate information from each observational effect contributing to the individual's phenotype following Land *et al.'s* (1987) approach. The observational effects are also called "sources of variation" in an ANOVA table (see Table 1).

Provided that each of the observational effects is independent of the others, the breeding value (A_1) of an individual may be estimated as the sum of the additive genetic effects contributed by each effect (Falconer 1991):

$$A_i = \Sigma A_{xi} \text{ over all x's} \qquad (1$$

where x's are the observational effects and = the additive genetic effect of observational component x on individual i. Each A, may be estimated by:

$$A_{xi} = sd_{xi} \cdot h_{xi}^2 \qquad (2)$$

where sd_{xi} = the value of observational effect x for individual i, and h, $_1^2$ is the portion of the variation in observational effect x which is additive genetic; i.e., each observational effect represents a selection differential, which may be multiplied by an appropriate heritability to yield the portion which is additive genetic.

In developing the heritabilities for the observational effects, it was assumed that all genetic variation among provenances was additive. That is, crosses between provenances would yield progeny that were exactly intermediate between the parents. It was also assumed that the coefficient of genetic relatedness (r) for trees within a provenance was 0.30. In all cases, family effects were treated as family within provenance effects.

Sweetgum: For sweetgum, individual phenotypes (P,) may be considered to be the sum of the following observational effects, expressed as deviations from the test mean: provenance (Pr), plot within provenance (P1), family within plot within provenance (F) and within family between plots (W) (Table 1). Therefore, for each individual, 1,

$$P_i = Pr_i + Pl_i + F_i + W_i \qquad (3$$

Note, the total within family variation is divided between two components -- and among plot component, Pl, and a within plot component, W. The among plot component is due to the fact that, by chance alone, a plot may be composed of trees with above (or below) average breeding values.

Sycamore: For sycamore, the observational effects that make up an individual's phenotypic effect are somewhat different because of the different experimental design (Table 1). However, the within family variation is still divided between an among plot component and a within plot component.

Scaling Data

In progeny tests, the phenotypic variance of growth traits typically varies with tree size and site quality. Generally, variance increases as tree size or site quality increases, at least during the site-capture years. As a result, if site quality varies within the test, most of the selections will come from the high quality sites when absolute measures of tree size serve as selection criteria.

The problem may be solved by scaling growth measures to units whose variance is not related to tree size. Log-transformation is often applied in such cases. When applied to the sweetgum and sycamore progeny tests under consideration, it had little influence on family ranking, but it did alter breeding values within families so that they were more randomly distributed throughout the test. Therefore, we based selections on estimates of breeding values of log-transformed data.

IMPORTANCE OF PROVENANCE, FAMILY AND WITHIN FAMILY VARIATION

The mean of the expected breeding values of the selected trees is the expected gain made from selection. And, the mean of the breeding values may be viewed as the sum of the gains contributed by each component in the selection index (equation 1). Because the gain from each component may be calculated as the selection differential times the heritability (equation 2), and the intensity of selection is approximately equal for each component, the relative gain from each component may be determined as the product of the phenotypic standard deviation of the component and the heritability of the component.

Table 1. Relative gain contributed by provenance, family and within family variation as determined by the product of the phenotypic standard deviation and the heritability of each source of variation.

SWEETGUM		SYCAMORE	
Source of Variation	Relative Gain (%)	Source of Variation	Relative Gain (%)
Provenance	55	Provenance	60
Family w/in Prov.	17	Family w/in Prov.	20
Plot w/in Prov.	6	Plot w/in Family	0
w/in Family w/in Plot	22	Tree w/in Plot	20

For both sweetgum and sycamore, the largest share of the gain (about 60%) comes from provenance selection (Table 1). This is to be expected in sweetgum where the provenances cover a large geographic range, and there is a strong tendency for trees from north of 35° N latitude to be smaller than those from farther south (Figure 2). For sycamore, the great gains from provenance selection may result because trees within a provenance have common parentage; gene flow for species distributed linearly, as along rivers, is expected to be less than for species whose coverage is wider (Wright 1978).

Forty percent of the gain, in both species, comes from selection within provenances. This is distributed approximately equally between gains from family and within family selection (gains from within family selection may be calculated as the sum of among and within plot terms). Although family (within provenance) heritability was greater than within family heritabilities, over two-thirds of the additive genetic variation within a provenance lies within a single open-pollinated family.

If one divides total gain into family and within family components, then the family component, comprised of the provenance and family within provenance sources, accounts for approximately three-quarters of the total gain; the within family component makes up the remaining one-quarter.

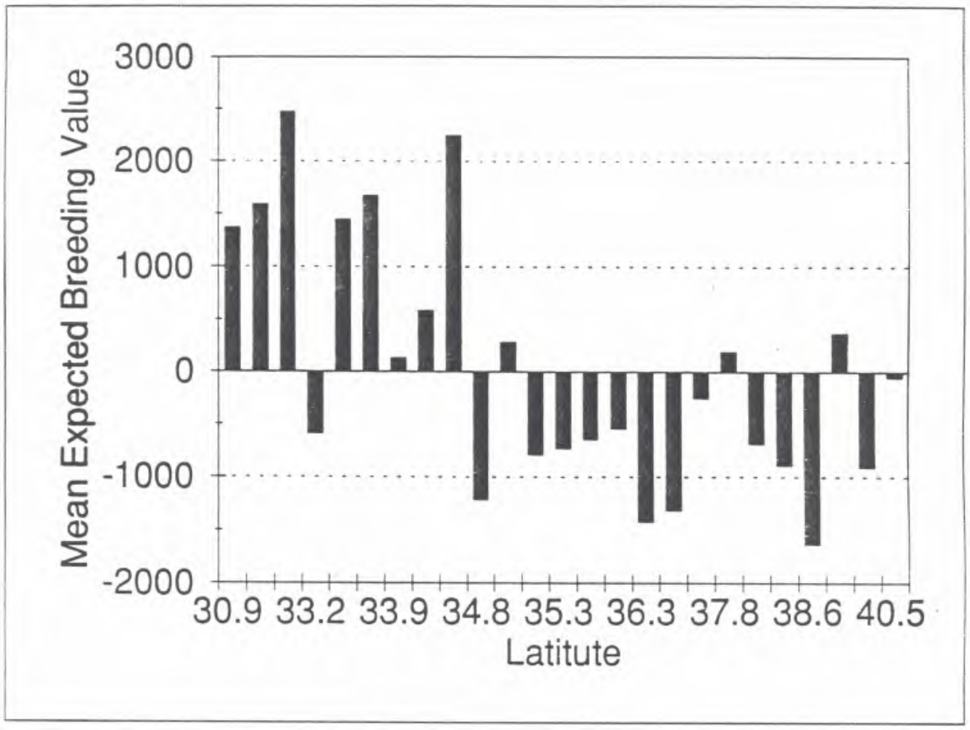

Figure 2. Mean expected breeding values for sweetgum provenances arranged by latitude of origin.

CONCORDANCE OF SELECTION FOR HEIGHT, DIAMETER OR VOLUME

In addition to estimating breeding values for volume, we also estimated breeding values for height and diameter. The same procedures used to estimate volume breeding values were employed to estimate height and diameter breeding values. Although many trees having high expected breeding values for volume also had high expected breeding values for height and diameter, this was not always the case. Table 2 shows the ten sycamore families with the highest mean breeding values for volume. Of these, seven were also among the top ten for height, and six were among the top ten for diameter. Only four families were in the top ten for height and diameter. Therefore, selection based on height or diameter would produce a different population than selection based on volume, even though height and diameter are strongly correlated with volume. Furthermore, these results provide evidence for genetic differences in height:diameter ratio -- differences which are visually evident in walking through provenance tests of either species.

SELECTION CRITERIA

As previously mentioned, in assembling the selected population, the principle selection criterion was volume breeding value, estimated by the selection index. However, several other criteria were also used to some extent in the final selection. (1) **Genetic diversity:** Because of the large family component to gain, the best families had several members with high expected breeding values. In most cases we decided to include no more than one tree per family in the selected population to maintain genetic diversity, allowing users of the material flexibility to design seed orchards for varying needs. (2) **Form:** Most sweetgums and sycamores have very straight stems. However, some fast-growing trees exhibit sinuosity. Trees with sinuous stems were not selected. (3) **Sufficiency of collectable material:** In a few cases we were not able to collect ten usable scions from a tree selected on the basis of volume breeding value. In such cases, the tree was not utilized.

Table 2. The top ten sycamore families for volume breeding value (ranked in descending order) and their presence (✓) or absence (—) in the group of ten families having the highest height or diameter breeding values.

Trait		
Volume	Height	Diam.
332	✓	✓
122	✓	✓
120	✓	—
182	✓	✓
167	✓	✓
151	—	—
145	✓	—
179	✓	—
134	—	✓
567	—	✓

DESCRIPTION OF THE SELECTED POPULATIONS

Of the 410 sweetgums available for consideration, 14 were selected. Scions 01 these were forwarded to North Carolina State University for inclusion in a clone bank. Of the 1563 sycamores available for consideration, 11 were selected. Scions of these were forwarded to Union Camp Corporation for inclusion in a clone bank. Family numbers and origins of the selected trees are shown in Table 3. Most selections are from trees originating in the Coastal Plain; only sweetgum families 11, 13, 14 and 66 and sycamore family 565, all from the Piedmont, are not.

While collecting scions from the selected trees, in early March, 1993, we observed considerable variation in traits which were not used as selection criteria including, height:diameter ratio, crown width, branch thickness, frequency of branches along the bole, branch angle, presence of lammas growth, autumn frost damage and time of spring bud swell. These traits appeared to be relatively consistent within a family, suggesting a genetic component to their expression. Our impression is that much of the variation we observed in these traits is included within the population of selected trees. This should help to provide breeders the flexibility to develop custom varieties to meet varying needs in the future.

Table 3. Family and geographic origin of the selected sweetgums and sycamores.

SWEETGUM		SYCAMORE	
UGA Family No.	County, State of Origin	UGA Family No.	County, State of Origin
1	Burke, GA	120	Burke, GA
2'		121	
11	Greene, GA	122	
13		134	Jackson, FL
14		145	Dougherty, GA
16	George, MS	146	
27	Jones, NC	167	Treutlen, GA
28		182	Upson, GA
29		332	Laurens. GA
33	Covington, AL	565	Taliaferro, GA
34		567	Jefferson, GA
66	Greenwood, SC		
90	Lancaster, VA		

'Two selections were chosen from this family. In all other cases only one tree per family was chosen.

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