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The Efficiency of Early and Indirect Selection In Three Sycamore Genetic Tests[1])

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Abstract

The efficiency of early and indirect selection was examined for 21 open pollinated sycamore families in Texas, Louisiana, and Arkansas from plantings at two locations in Texas and one location in Louisiana. Direct selection (best families + best individual within a family) for seven-year height, DBH, and volume resulted in predicted gains of 20, 27, and 77 percent over their plantation means. Expected gains from direct selection for wood specific gravity and branch angle were 7.4 percent and 6.3 percent.

Indirect selection for seven-year height or DBH would be highly efficient in improving 7-year volume (89 and 91 percent). Selecting for seven-year growth traits would result in slight positive gains in wood specific gravity (0.1 to 0.6 percent gain over the plantation mean) and slight losses in branch angle (0.7 to 3.3 percent under the plantation mean).

Height at three years and height, DBH, and volume at five years all appear to be good predictors of seven-year volume. Early selection for any of these traits would result in 88 to 105 percent as much gain as would direct selection for 7-year volume. Selection for one-year height was 67 percent as effective as direct selection for seven-year volume. Selection based on any of the early growth traits resulted in slight gains in specific gravity and slight losses in branch angle.

Summary

The efficiency of early and indirect selection was examined for 21 seven-year-old open-pollinated families of sycamore from Texas, Louisiana, and Arkansas planted at three locations. Traits measured were: total height, DBH, volume, branch angle, and wood specific gravity.

Results were:

(1) Gains in seven-year height, DBH, or volume from direct selection of the best tree in each of the best 10 families represented a 20, 27, and 77 percent increase over the plantation means, respectively (1.5 m, 2.0 cm, and 14.34 dm^3 increases). Direct selection for wood specific gravity resulted in a 7.4 percent increase over the plantation mean and branch angle could be increased 3.4^0 towards horizontal.

(2) Combined selection for seven-year height or DBH would be highly efficient in improving volume growth (89 and 91 percent). Selection for seven-year growth traits would result in slight positive gains in wood specific gravity (5 to 10 percent as much gain as direct selection) and a slight or negligible loss in branch angle (0.5^0 to 1.8^0).

Key words: *Platanus occidentails* L., genetic gain, direct selection, breeding cycle.

Zusammenfassung

Bei 21 sieben Jahre alten Familien von *Platanus occidentalis* L. (frei abgeblüht), aus Texas, Louisiana und Arkansas, die in drei Versuchsflächen, zwei in Texas und eine in Louisiana, ausgepflanzt worden waren, wurde der Nutzeffekt frühzeitiger und indirekter Selektion geprüft. Es wurden die Merkmale Gesamthöhe, Durchmesser in Brusthöhe, Volumen, Astwinkel und spezifisches Gewicht des Holzes gemessen bzw. festgestellt.

Ergebnisse:

1.) Bei direkter Selektion des besten Baumes in jeder der besten 10 Familien lagen die Gesamthöhe im Alter 7, der Brusthöhendurchmesser und das Volumen 20,27 and 77% bzw. 1,5 m, 2,0 cm und 14,34 m^3 über den Versuchsflächen-Mittelwerten. Bei direkter Selektion ergaben sich für das spezifische Gewicht des Holzes 7,4% mehr und der Astwinkel konnte $3,4^0$ mehr zur Horizontalen hin zunehmen.

2.) Bei der kombinierten Selektion würde bei der Gesamthöhe im Alter 7 oder beim Brusthöhendurchmesser das Volumenwachstum in höchstem Maße verbessert werden (89 und 91%). Aus einer Selektion auf Wachstumsmerkmale im Alter 7 würden nur geringe positive Gewinne resultieren, was das spezifische Gewicht des Holzes betrifft (5—10% der bei der direkten Selektion erzielten Gewinne) und leichte oder unbedeutende Verluste beim Astwinkel ($0,5$—$1,8^0$).

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Introduction

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

Selection plays a major role in sycamore tree improvement programs. Deciding which traits to select for, how intensive to select and in what manner, as well as how early to begin selection, are major descisions that affect the success and continuity of a program.

Correlations between growth traits (height, diameter, volume, and dry weight per tree) have been found to be moderate to high in most sycamore studies. A genetic correlation of .91 between height and diameter at breast height (DBH) at age eight was reported by McCUTCHAN (1983). FERGUSON *et al.*, (1977) found the genetic and phenotypic correlations between five-year height and DBH to be .75 and .56, respectively.

The relationship of branch angle with growth characters and specific gravity is variable. FERGUSON *et al.*, (1977) found no appreciable correlation between branch angle and height or DBH, whereas SCHMITT and WILCOX (1969) found branch angle independent of height and specific gravity, but positively correlated (phenotypic) with DBH (.31). JOURDAIN and OLSON (1983) reported a negative correlation between diameter and branch angle. They concluded that selection for faster diameter growth would result in trees with more acute branch angles.

The relationship between specific gravity and growth has received considerable attention since selection for increased volume could possibly lower wood specific gravity. Positive genetic correlations between height and DBH and specific gravity (.28 and .31, respectively) were reported for eight-year-old sycamore by McCUTCHAN (1983), whereas WEBB *et al.* (1973) found negative genetic correlations between specific gravity and height (−.12), diameter (−.25) and percent dry weight per tree (−.21) for the four-year-old trees of the same species.

Table 1. — Genetic Gain Formulas for Different Selection Methods.

	DIRECT SELECTION (Select Trait x to Improve Trait x)	EARLY OR INDIRECT SELECTION (Select Trait x to Improve Trait y)
FAMILY SELECTION	$i_F * \dfrac{\sigma^2_F}{\sqrt{\dfrac{\sigma^2_e}{rnl} + \dfrac{\sigma^2_{R(L)F}}{rl} + \dfrac{\sigma_{LF}}{l} + \sigma^2_F}}$	$i_{Fx} * \dfrac{\sigma^2_{Fxy}}{\sqrt{\dfrac{\sigma^2_{ex}}{rnl} + \dfrac{\sigma^2_{R(L)Fx}}{rl} + \dfrac{\sigma^2_{LFx}}{l} + \sigma^2_{Fx}}}$
INDIVIDUAL WITHIN FAMILY SELECTION	$i_{I/F} * \dfrac{3\sigma^2_F}{\sqrt{\sigma^2_e + \sigma^2_{F(L)F} + \sigma^2_{LF}}}$	$I/F_x * \dfrac{3\sigma^2_{Fxy}}{\sqrt{\sigma^2_{ex} + \sigma^2_{R(L)Fx} + \sigma^2_{LFx}}}$

where $\sigma^2 e_x$, $\sigma^2 R(L)F_x$, $\sigma^2 LF_x$, $\sigma^2 F_x$, are the variance components due to error, replication (location)* family, location* family and family respectively; σ^2_{Fxv} is the family covariance between traits x and y; i_F and $i_{I/F}$ are selection intensities for family selection and individual within family selection respectively; and r, n, l are the number of replications within a location, average number of trees per plot, and number of locations, respectively.

Genetic correlations between root collar diameter of sycamore in the nursery, and height, diameter at one foot, and percent dry weight per tree of field-planted trees four years later were all moderately positive (.31, .56, and .47, respectively) (WEBB *et al.*, 1973.) Genetic and phenotypic correlation between root collar diameter and specific gravity were negligible (−.15 and .08). LAND (1981) also reported positive genetic correlations between one-and two-year nursery measurements of sycamore with four-year growth data. The size of the correlations with four-year growth data increased between first and second year measurements.

The objectives of this study were to examine the relative efficiencies of early and indirect selection for comparison to seven year data. Family selection and combined selection using the best individual tree from the best families were determined. Gains and selection efficiency for height, DBH, volume, specific gravity and branch angle at age seven were examined.

Materials and Methods

The study populations were seven-year old half-sib geographic variation studies established in 1972 by hardwood members of the Western Gulf Forest Tree Improvement Program. Thirty-one open-pollinated families from East Texas, Louisiana, and South Arkansas were outplanted at Washington Parish, Louisiana, Angelina County, Texas, and Montgomery County, Texas. Twenty-one families were selected for this study. Geographic locations and additional establishment data were reported by NEBGEN and LOWE (1982).

In the winter of 1978—1979, total height, DBH and branch angle were measured. Specific gravity of a 5.15 mm increment core was determined by the maximum moisture content method. Individual tree volumes were calculated by volume (dm^3) = .036288*DBH^2*height. Laboratory and measurement techniques are described in NEBGEN and LOWE (1982).

A least squares regression was performed using the General Linear Models (GLM and Multiple Analysis of Variance (MANOVA) procedures of Statistical Analysis Systems (SAS) as described by BARR *et al.* (1979). A combined location analysis using plot means over all three locations was performed, and between and within plot analysis was used to determine within plot (error) variance components. Coefficients of variance components were determined by the RANDOM option of GLM (BARR *et al.*, 1979).

Previous analyses showed no significant geographic effects in the study area on progeny performance (NEBGEN and LOWE, 1982), so the geographic term was dropped from the models for all results reported here. Locations were considered fixed effects; replications and families were considered random. Except for volume (where missing trees were given a volume of 0 dm^3), missing trees were treated as missing observations.

Expected genetic gains were calculated on a family selection and on a combined selection (family + individual/family) basis for a hypothetical clonal seed orchard (FERGUSON *et al.*, 1977). Selection intensities were determined from graphs published by NAMKOONG and SNYDER (1968). For combined selection, it was assumed that the best tree ($i_{I/F}$ = 1.59) from each of the best 10 families (i_F = .83) would be selected. *Table 1* presents the gain formulas for the different selection methods.

Table 2. — Summary of Seven-Year Sycamore Measurements Taken on the Three Study Areas (Combined).

Trait	Overall Mean	Range of Family Means
Height (m)	7.4	6.0 to 8.3
DBH (cm)	7.5	4.9 to 8.7
Volume (dm^3)	18.52	3.73 to 28.23
Specific Gravity	0.460	0.444 to 0.480
Branch Angle (°)	54	49 to 57

Results and Discussion

A summary of the combined location plantation means and family ranges are given in *Table 2*. Because heritability estimates were erratic between planting locations, only the results from the combined location analysis are presented (Nebgen and Lowe, 1982).

Sufficient variation was present to warrant selection for growth traits. Selecting the best tree in the ten best families for height, DBH, or volume should have yielded gains of 1.5 m, 2.0 cm, and 14.34 dm^3, respectively which represents gains of 20, 27, and 77 percent over the plantation means *(Table 3)*. These estimates may be inflated because members of the open-pollinated families were probably more closely related than half sibs (Namkoong, 1966). Significant family survival differences due to top dieback may have also increased the expected volume gains. Expected gain in wood specific gravity was .034 for direct selection which represents a 7.4 percent increase over the plantation average of .460. Similar selection procedures for a horizontal branch angle resulted in a 6.3 percent (3.4°) gain. Bcause of th low selection intensity for families (10 out of 21 families were selected), selecting the best individuals from the best families often resulted in more than twice the gain of only family selection. In an operational program the amount of family gain should be increased because a larger genetic base would result in a higher selection intensity.

Table 3. — Gain by Direct Selection and the Efficiency of Indirect and Early Selection for Seven-Year Traits in Three Sycamore Populations.

Trait	Estimated Gain for the Improved Trait				
	7-Year Height(m)	7-Year DBH (cm)	7-Year Volume (dm3)	Wood Specific Gravity	Branch Angle (°)
7-Year Height					
Family	0.4(1.00)[1]	0.6(.97)	3.81(.89)	.001(.07)	-0.5(-.42)
Combined	1.5(1.00)	2.0(.98)	13.00(.91)	.002(.06)	-1.8(-.53)
7-Year DBH					
Family	0.4(.93)	0.6(1.00)	3.81(.89)	.001(.10)	-0.4(-.33)
Combined	1.4(.91)	2.0(1.00)	12.74(.89)	.003(.08)	-1.3(-.38)
7-Year Volume					
Family	0.4(.82)	0.5(.84)	4.27(1.00)	.001(.06)	-0.4(-.33)
Combined	1.2(.80)	1.7(.84)	14.34(1.00)	.002(.05)	-1.2(-.35)
Wood Specific Gravity					
Family	0.0(.09)	0.1(.12)	0.35(.08)	.008(1.00)	0.0(.00)
Combined	0.2(.10)	0.3(.14)	1.45(.10)	.034(1.00)	0.1(.03)
Branch Angle					
Family	-0.2(-.39)	-0.2(-.30)	-1.25(-.29)	.000(.02)	1.2(1.00)
Combined	-0.5(-.32)	-0.5(-.25)	-3.53(-.25)	.000(.01)	3.4(1.00)
5-Year Height					
Family	0.4(.93)	0.6(.97)	4.47(1.05)	.001(.08)	-0.8(-.33)
Combined	1.3(.90)	1.9(.95)	14.64(1.02)	.002(.07)	-1.4(-.41)
5-Year DBH					
Family	0.4(.84)	0.6(.97)	4.39(1.03)	.001(.13)	-0.3(-.25)
Combined	1.2(.81)	1.9(.94)	14.40(1.00)	.004(.10)	-1.0(-.29)
5-Year Volume					
Family	0.4(.80)	0.6(.90)	4.14(.97)	.001(.13)	-0.3(-.25)
Combined	1.1(.71)	1.7(.82)	12.65(.88)	.003(.10)	-0.8(-.24)
3-Year Height					
Family	0.4(.86)	0.6(.92)	4.25(1.00)	.001(.11)	-0.5(-.42)
Combined	1.1(.76)	0.7(.81)	12.69(.88)	.003(.08)	-1.4(-.41)
1-Year Height					
Family	0.3(.61)	0.4(.69)	3.70(.87)	.001(.10)	-0.4(-.33)
Combined	0.7(.47)	1.1(.54)	9.67(.67)	.002(.06)	-1.1(-.32)

[1] The efficiency of indirect or early selection (gain by indirect or early selection/gain by direct selection) is given in parenthesis.

Selection based on seven-year height or DBH would be highly efficient in improving volume growth (89 and 91 percent as efficient as direct selection), regardless of the selection method used. Selecting for any seven-year growth trait should also result in slight positive gains in wood specific gravity (from) 5 to 10 percent as much gain as direct selection for specific gravity). Branch angle would be negatively affected by selection for growth traits. It would be reduced from 0.4° to 1.8°, but this affect is of doubtful practical importance. Conversely, direct selection for branch angle would be expected to reduce growth from 23 to 39 percent *(Table 3)*.

Selection based on three-year height, and on five-year height, DBH, and volume all appeared to be excellent predictors of seven-year volume *(Table 3)*. Selecting for any of these traits would result in 84 to 105 percent as much gain as direct selection for seven-year volume. The estimated efficiencies for indirect selection may be inflated because open-pollinated progeny may be more closely related than half sibs. This is especially apparent in the cases where indirect selection for seven-year volume appears to be more efficient than direct selection. Combined selection for three-year height is 88 percent as effective as direct selection for improving seven-year volume while selecting on height after one growing season in the field was only 67 percent as effective.

Selecting for any of the early traits would have a slight positive effect upon wood specific gravity (from 5 to 13 percent as much gain as direct selection), and a negligible effect on branch angle (−0.3° to −1.4°).

Sycamore scions from mature trees tend to flower at a young age when grafted; therefore, control-pollinated seed should be obtainable by age five. Assuming that one year is used to produce bare-root seedlings, the breeding interval would vary from seven to 13 years for progeny test rotations of one to seven years. *Table 4* shows the estimated gain per year in volume production at age seven for the different breeding cycles. Direct selection at age seven for volume results in the greatest volume gain, even though it makes the least gain per year. Selection on the basis of height at either age one or three would result in the greatest gain per year (1.61 dm^3 and 1.59 dm^3, respectively). The reduction in the breeding cycle because of early selection more than compensates for the loss of selection efficiency which results in increased gain per year. It would apparently be feasible to conduct a few cycles of breeding with a short generation interval followed by longer term field tests to improve volume growth with sycamore.

(3) Three-year height and five-year height, DBH, and volume were all excellent predictors of seven-year volume

Table 4. — Estimated Volume Gain per Year for Different Breeding Cycles with Three Sycamore Populations.

	Selection Age (Years)			
	1	3	5	7
Total Breeding Cycle (yrs)	7	9	11	13
Total Vol. Gain(dm^3)	9.67	12.69	12.65	14.34
Vol. Gain/ Year (dm3)	1.61	1.59	1.26	1.20

(88 to 105 percent as effective as direct selection for volume). Combined selection for one-year height was only 67 percent as effective as direct selection for seven-year volume. However, average volume gains per year were greater for one-year selection (1.61 dm^3 vs. 1.20 dm^3 per year), because of the reduced breeding cycle.

(4) Selecting for one, three, or five-year growth traits would have slight positive effects on wood specific gravity (from 5 to 13 percent as much gain as direct selection) and a negligible effect on branch angle (-0.3^0 to -1.4^0).

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Juvenile Selection in Tree Breeding: Some Mathematical Models

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Abstract

Four different juvenile selection models are developed and evaluated. When the heritability is assumed to be constant for all ages and the coefficient of juvenile mature correlation function is set at .308 (Lambeth, 1980), the optimum selection age varied between 1.3 and 21.5 for the rotation age of 25 years.

The large differences in the optimum selection age was due to the differences in the models and the evaluation criteria used. Important findings of the models are as follows. 1) Basic model: When linear functions are used to represent the heritability ratio ($g = h_t/h_T$) and the genetic juvenile mature correlation (r), the intercept of g must be equal or greater than that of r to guarantee that the early selections are always beneficial. When a linear function and a log function were used to represent g and r ($= 1 + B\ln x$), respectively, g did not influence the time of maximum annual genetic gain (x_{max}) significantly up to B values around 0.3. 2) Extended time models: These models delayed the x_{max} of the basic model. 3) Maximum future net worth model: The early selection t_{max} is independent of the rotation age (T), and an economic criterion k was the prime factor which influenced x_{max}. 4) Multiple cycle model: Under many simplifying assumptions this model reduced to the basic model.

It was concluded that extremely early selection time such as earlier than 1/3 of rotation age should be used with caution. Other shortcomings of the models were discussed.

Key words: Accelerated tree breeding, juvenile selection, heritability ratio, juvenile-mature correlation, tree breeding.

Zusammenfassung

Es wurden vier verschiedene Methoden zur Frühselektion entwickelt und ausgewertet. Unter gewissen Voraussetzungen konnte gezeigt werden, daß das optimale Selektionsalter zwischen 1,3 und 21,5 Jahren variiert. Jedoch ist eine Selektion, die vor dem Ende des ersten Drittels der Umtriebszeit erfolgt mit Vorsicht durchzuführen. Andere Unzulänglichkeiten der Selektionsmodelle werden diskutiert.

Introduction

Accelerated tree breeding is receiving a new emphasis with success in early flower induction and potential early selection. The concept is based on the premises that an early return on investment is desirable, and that there is an optimum juvenile selection age at which the early return on investment will overcome the shortcomings of misclassifying good trees because of imperfect juvenile-mature correlation. Therefore, the central question has been: What is the optimum selection age? Recent reports show there is no single answer to the question. For example, Franklin (1979) and Lambeth (1980) addressed this question for several conifers and, although sharing some common data base (from Namkoong and Conkle 1976. Namkoong *et al.* 1972, Squillace and Gansel 1974), suggested different selection ages. Franklin concluded that accurate selections might be made after half the rotation length, while Lambeth suggested that selection much earlier was feasible.

Such discrepancies indicate that either the premises of accelerated breeding are not sufficient to address the issue properly, or that there is more than one answer to the question of optimum selection age, depending on the model and the parameters used. A corollary to this point is that any answer obtained from a model in isolation should not be used for making generalized inferences.