GEOGRAPHIC PATTERNS OF VARIATION AMONG SWEETGUM POPULATIONS IN THE SOUTHERN UNITED STATES--FOURTEENTH-YEAR RESULTS

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Abstract.--Open-pollinated seeds were collected from 5 trees in 2 stands located in 14 geographic sources across the southern United States. A subsample of trees from 6 of the 14 geographic sources plus a common set of check lots, one from each of the 14 sources, were planted at 7 locations. The patterns of geographic variation among sources, stands, and trees for height and DBH were analyzed using analysis of variance. Differences among families/stands/geographic source were highly significant (.01 level) at 5 of 7 plantings for height and DBH. Variation among stands/geographic source was not significant at any planting. Variation among geographic sources was significant at only 2 plantings. Coastal Plain sources tended to grow better than Piedmont sources at Coastal Plain or bottomland sites. Piedmont sources were generally better on Piedmont sites.

Additional keywords: Liquidambar styraciflua L., provenance variation.

INTRODUCTION

One function of a species provenance study is to determine the geographic patterns of variability of economically important traits. Geographic differences are expected for species that are found over large areas. Previous studies have found significant geographic variation in sweetgum (Liquidambar styraciflua L.) (Webb 1964; Ferguson and Cooper, 1977; Wells et al., 1979). Because the amount of genetic variation in a breeding population affects genetic gain, provenance studies are an appropriate first step in an intensive tree breeding program. Provenance studies can also indicate the best sources for specific locations and guide the movement of seed sources between locations.

MATERIALS AND METHODS

Seed Collection

The Rangewide Sweetgum Provenance Study was initiated in 1964 by the North Carolina State University - Industry Hardwood Research Cooperative.

Seven transects were drawn to cover the range of sweetgum in the southern United States (Figure 1). Transects ranged from North Carolina (1) to Texas (7) and coincided with lands of members of the N. C. State Hardwood Cooperative. Each transect traversed two physiographic regions creating 7 transects by 2 regions or 14 geographic sources. Transects 1 to 4 covered Coastal Plain (designated A) and Piedmont (B) provinces. Transect 5 compares lower Coastal Plain (A) and upper Coastal Plain (B) provinces. Transect 6 compares Mississippi

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riverbottom (A) and Louisiana upland (B) sites. Transect 7 compares Sabine (A) and Neches (B) river stands. The transect number and letter of the physiographic region designates the geographic source. For example, 5A is a Coastal Plain source of transect 5.

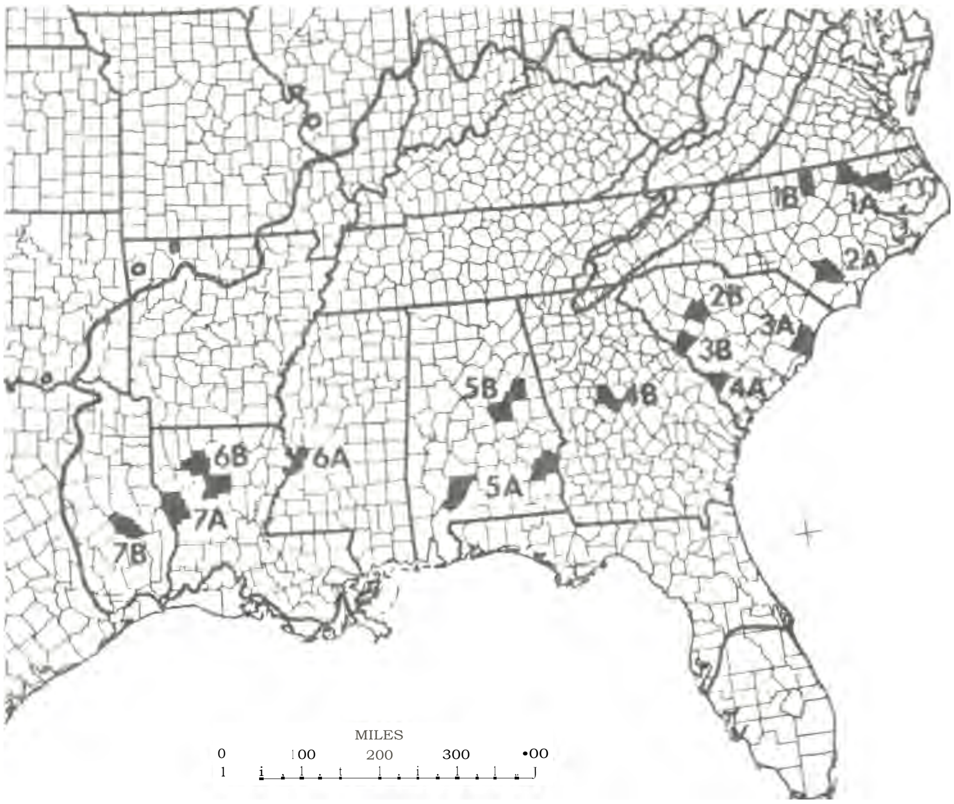

Figure 1.--Location of transects and geographic sources across the natural range of sweetgum.

Two natural sweetgum stands within each of the 14 geographic sources were selected for seed collection. These stands were located on average to good sites.

Open-pollinated seeds were collected from 5 trees in each of the 28 stands. Selection requirements for trees were mild phenotypic superiority, dominance or codominance in their stands, and sufficient quantities of seed for study needs. Selected trees were also separated enough to avoid relatedness through common parentage or similar rootstocks. From the 14 geographic sources X 2 stands/source X 5 families/stand, 140 families were created.

Study Design

Seed collections were made in 1964 and 1965. Seedlings were grown at the North Carolina Forest Service Nursery at Clayton in 1966 at a density of 15 to 20 per square foot. In spring, 1967, seedlings were outplanted onto good sites with one planting located within each area represented by the 14 geographic sources. Each planting of 6 replications was designated by the area representing the geographic sources. For example, planting 3B is located on transect 3 in the Piedmont.

Each of the 14 plantings consists of a check block and a test block. Each check block has 14 check lots, one family representing each of the 14 geographic sources. The same 14 check lots were used at each planting. Check blocks have seedlings from a check lot planted in 3 rows of 12 trees at a 6 X 6 foot spacing.

Each test block consists of 60 families (6 geographic sources X 2 stands/ geographic source X 5 families/stand). The 6 geographic sources planted at a location include sources from the transect the study is planted on plus the 2 adjacent transects (Table 1). A planting on transect 4 includes geographic sources from transects 3, 4, and 5. Studies planted on transect 1 include tran- 1, 2, and 7. The 60 families at each study site are planted in blocks of 5 families common to a single stand from a geographic source. The 5 family blocks are planted in 12-tree row plots at a 6 X 6 foot spacing.

Table 1.--Occurrence of transects planted in the test blocks at each separate planting.

Transect of planting	Transects included in a test block planting 1	2	3	4	5	6	7
1	X	X					
2	X	X	X				
3		X	X	X			
4			X	X	X		
5				X	X	X	
6					X	X	X
7	X					X	X

Seven of the 14 studies established in 1967 were abandoned by age 10. Growth varied widely between plantings. Mean height at age 14 ranged from 21.6 to 50.2 feet. Thinnings were done in most plantings between ages 6 and 9 years.

Analysis of Results

Only 6 of the 14 plantings have sufficient survival and growth for continued evaluation. These 6 trials were measured at age 14. A seventh study using tenth-year measurements was also included in the analysis. The traits measured in the test blocks were total height (ft.) and DBH (in.). Mean height (ft) was also determined for the check blocks of the 6 studies measured at age 14.

Statistical analyses were made using a least squares analysis of variance because data often were unbalanced with occasional missing cells. Not all families had sufficient seedlings for planting needs and were excluded from certain plantings and replications. The PROC GLM option of SAS (Barr et al., 1979) was

[1/] The studies used were located on lands of Champion-International, Continental Forest Industries, Georgia-Pacific, International Paper, Union-Camp, and Westvaco. Their efforts contributed to this study are appreciated.

used for the analysis of variance. Using coefficients estimated by PROC RANDOM of SAS, mean squares were balanced and approximate F-tests constructed (Satterthwaite 1946). The within-plot error was calculated separately and adjusted by the harmonic mean of trees per plot.

All factors were considered to be random, except for transects. The factors (stands, geographic sources, etc.) constitute a subsample of the larger population of sweetgum. Transects were considered fixed, however, because they were chosen to cover lands of members of the North Carolina State University Hardwood Cooperative to facilitate seed collections.

RESULTS

Results of the least squares analysis of variance are listed in Table 2 for height and DBH for each planting. No combined analysis of all plantings was made because of the overlapping of sources only for adjacent transects (Table 1). Means of tree height and DBH for geographic sources and transects are listed in Table 3. Means for physiographic regions/transects are the same as geographic source means.

Variation among Geographic Sources, Transects, and Physiographic Regions

Significant geographic provenance variation was detected mainly at two plantings (3A and 7A) (Table 2). Height differences were significant at 7A and DBH at 3A.

Despite the variable importance of provenance differences at the seven plantings, certain geographic sources appeared better than others when planted over several sites (Table 3). Two sources, 2A (Bladen County, N.C.) and 7A (Sabine Parish, LA.) were among the best geographic sources wherever planted. Also, trees from transects 2 and 7 performed best at all plantings in which they were represented.

Despite the lack of significant differences, mean height at plantings 1A, 2B, 3A, and 3B indicate potential physiographic differences. Transects 1 to 4 were divided into Piedmont and Coastal Plain subsamples. For Coastal Plain plantings (2B, 3B), Piedmont sources were as good as Coastal Plain sources. Plantings 6A and 7A had significant physiographic differences but did not conform to the Piedmont-Coastal Plain breakdown of the other plantings.

Further evidence of provenance variation was observed in the mean height of the 14 check-lot families (Figure 2). Check lots of Southern transects tend to do poorer than those of Northern transects at Northern planting areas (plantings 2B, 3A) and vice versa (5A, 6A). Physiographic region differences are also indicated at all plantings. Coastal Plain check lots (transects 1-4) were as good as or better than Piedmont check-lots when planted at Coastal Plain/bottomland plantings (1A, 3A, 5A, 6A, 7A). Piedmont check lots were better than those of the Coastal Plain at planting 2B. Planting 3B was not included because no check trees were measured at age 10.

Table 2.--Results of the analysis of variance for each planting for height and DBH.

Source of variation	Planting 1A - NC Lower Coastal Plain			Planting 2B - SC Piedmont			Planting 3A - SC Coastal Plain		
	DF	MS Height	MS DBH	DF	MS Height	MS DBH	DF	MS Height	MS DBH
Replications	2			5			5		
Geographic Sources	5	77.46	.805	5	67.41	1.131	4	66.85	1.179**
Transects	2	161.05	.558	2	75.39	.271	2	44.42	1.289**
Physiographic Regions/ Transect	3	23.91	.971	3	68.85	1.596	2	85.84	.978**
Stands/Geographic Source	6	47.61	1.028	5	31.73	.960	5	23.25	.144
Replications X Stands/ Geographic Source	12	22.74*	.435	25	44.37**	.937**	20	13.33**	.223**
Families/Stand/Geographic Source	41	15.65	.433	37	41.64**	1.137**	32	15.63**	.386**
Replications X Families/ Stands/Geographic Source	82	12.31**	.289	185	13.56**	.420**	155	2.33	.078
Within-plot Error	811	6.90	.250	811	8.35	.253	2540	2.24	.072

Source of variation	Planting 3B[a/] - SC Piedmont			Planting 5A - AL Lower Coastal Plain			Planting 6A - MS Riverbottom		
	DF	MS Height	MS DBH	DF	MS Height	MS DBH	DF	MS Height	MS DBH
Replications	5			2			5		
Geographic Sources	5	20.31	.296	5	101.21	1.711	5	91.55	3.411
Transects	2	45.48	.350	2	91.80	2.521	2	70.27	5.832*
Physiographic Regions/ Transect	3	13.16	.429	3	195.55	.803	3	111.49*	2.387
Stands/Geographic Source	5	23.24	.448	5	51.12	.721	5	24.75	.855
Replications X Stands/ Geographic Source	25	38.30**	.739**	12	36.66**	.383*	30	44.74**	.549**
Families/Stand Geographic Source	36	7.40**	.132**	44	8.15	.286	46	12.44*	.391**
Replications X Families/ Stand/Geographic Source	176	2.28*	.058**	83	7.59**	.194**	223	4.41	.157*
Within-Plot Error	2410	1.79	.044	828	3.52	.091	1721	5.12	.132

* - Significant at the .05 level ** - significant at the .01 level

a/ Tenth-year data used for planting 3B.

Table 2. (Continued) -- Results of the analysis of variance.

Source of variation	Planting 7A - LA Branchbottom		
	DF	MS Height	MS DBH
Replications	5		
Geographic Sources	5	122.25**	.649
Transects	2	67.24	.466
Physiographic Regions/ Transect	3	159.43**	.773
Stands/Geographic Source	6	6.69	.418
Replications X Stands/ Geographic Source	30	52.95**	.518**
Families/Stand/Geographic Source	48	17.91**	.413**
Replication X Families/ Stands/Geographic Source	239	9.35*	.170
Within-plot error	1770	7.38	.147

* - Significant at the .05 level ** - Significant at the .01 level

Variation among Stands/Geographic Source

No significant variation among stands was detected at any plantings for stand/geographic *source* variation. Significant stand to stand differences were reported, however, in two earlier papers using data from this study (Johnson and McElwee, 1967; Sprague and Weir, 1973).

Variation among Families/Stand/Geographic Source

The most important source of geographic variation in this study was among families (Table 2). Family differences were significant (.01 level) for height and DBH at plantings 2B, 3A, 3B, 6A, and 7A.

DISCUSSION

The existence of provenance variation across the sampled range of sweetgum is not surprising. The natural range of sweetgum covers a large area (Figure 1) and changes in climate and soils should encourage such variation. Other species with similar ranges (for example, loblolly pine (*Pinus taeda* L.) and sycamore (*Platanus occidentalis* L.)) have similar provenance variation (Wells and Wakeley, 1966; Ferguson et al., 1977).

Patterns of geographic source, transect, and physiographic region variation were not consistent at all plantings for all traits. One problem was that only geographic sources, 3 transects, and 2 regions were compared at each planting. ith low numbers of degrees of freedom, genetic differences are hard to detect. ther studies that have found geographic source variation in the South tested more sources than were used in this study (Wells and Wakeley, 1966; Wells et al., 1979; Land 1981).

Table 3.--Mean height and DBH for each planting by geographic source and transect for fourteenth-year results.

Planting 1A

Geographic Source	Height	DBH
1A	48.9	5.81
1B	48.0	5.63
2A	51.7	5.76
2B	50.3	5.81
7A	52.4	6.20
7B	50.9	5.68

Transect	Height	DBH
1	48.5	5.70
2	51.0	5.80
7	51.7	5.90

Planting 2B

Geographic Source	Height	DBH
1A	47.1	6.04
1B	46.4	5.87
2A	47.9	6.01
2B	48.9	6.17
3A	45.9	5.91
3B	49.2	6.34

Transect	Height	DBH
1	46.8	5.96
2	48.3	6.09
3	47.1	6.07

Planting 3A

Geographic Source	Height	DBH
2A	23.5	2.72
2B	20.3	2.42
3A	21.5	2.48
3B	20.3	2.31
4A	21.6	2.34

Transect	Height	DBH
2	22.6	2.63
3	20.9	2.40
4	21.6	2.34

Planting 3B[a/]

Geographic Source	Height	DBH
2A	17.0	1.61
2B	16.4	1.59
3A	14.7	1.33
3B	16.0	1.61
4A	16.2	1.56
4B	16.9	1.62

Transect	Height	DBH
2	16.7	1.60
3	15.5	1.50
4	16.5	1.58

Planting 5A

Geographic Source	Height	DBH
4A	31.9	4.48
4B	37.9	4.79
5A	35.6	4.47
5B	37.7	4.69
6A	38.2	5.16
6B	37.2	4.85

Transect	Height	DBH
4	34.8	4.63
5	36.6	4.57
6	37.7	5.00

Planting 6A

Geographic Source	Height	DBH
5A	47.2	5.18
5B	45.1	5.04
6A	44.6	5.39
6B	44.8	5.17
7A	48.1	5.77
7B	45.1	5.24

Transect	Height	DBH
5	46.2	5.11
6	44.7	5.28
7	46.5	5.48

Planting 7A

Geographic Source	Height	DBH
1A	43.7	4.91
1B	45.6	5.05
6A	44.3	5.03
6B	47.3	5.17
7A	46.9	5.17
7B	45.1	4.98

Transect	Height	DBH
1	44.6	4.98
6	45.8	5.10
7	46.0	5.07

a/ Planting 3B means are for tenth-year data.

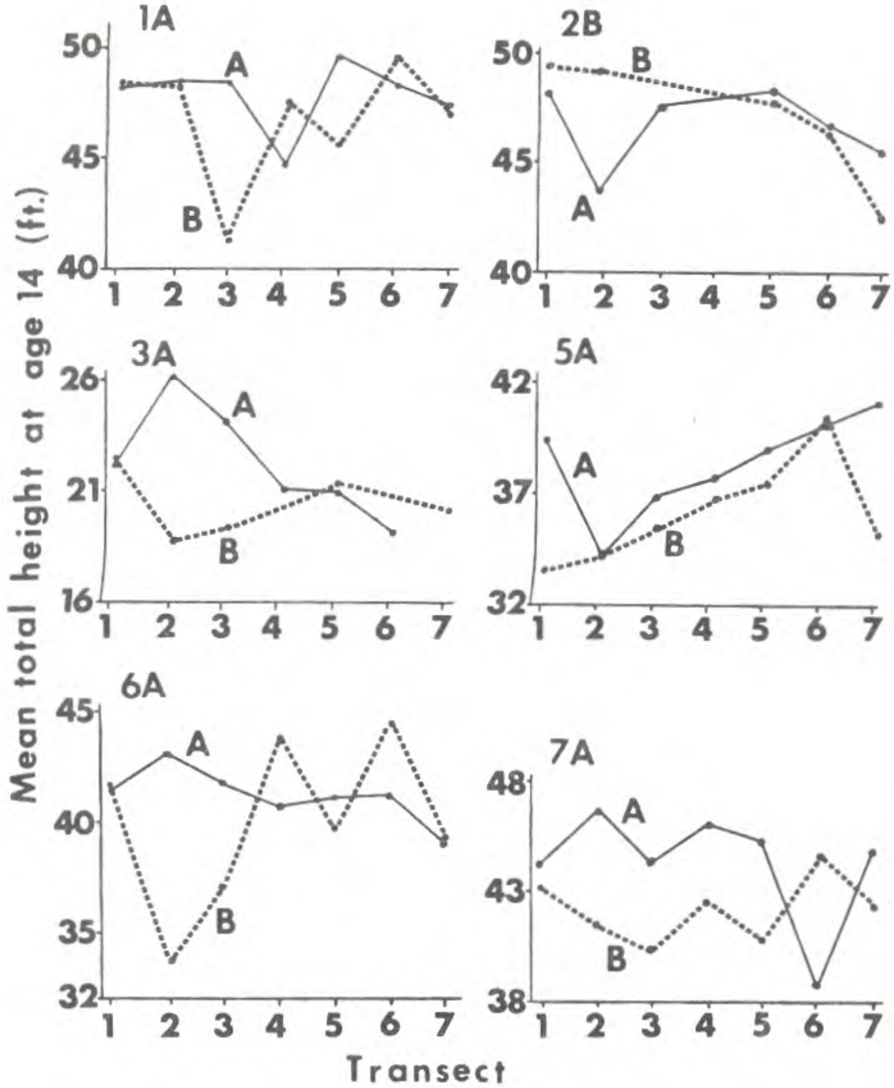

Figure 2.--Height performance of the 14 check lots by transect and physiographic region for the 6 plantings measured at age 14. Transect 1 is the northernmost (North Carolina) and transect 7 is the most southwestern (Louisiana-Texas) (Figure 1.) Plantings 2B and 3A did not include all 14 check lots.

Results do indicate, however, that the choice of geographic seed source can be important in sweetgum. Movement of seed sources long distances can be etrimental, depending upon site and climate. Piedmont sources when planted n Coastal Plain or Bottomland sites did not grow as well as Coastal Plain botomland sources. Planting of Coastal Plain or Southern sources at colder Piedont sites can produce poorer growth than local material. A similar pattern of oastal Plain/Piedmont performance in comparison plantings on respective sites as found for loblolly pine (Wells and Wakeley, 1966).

An exception to the trend of movement of sweetgum sources long distances was planting 1A, located on a fertile North Carolina river flood plain. Southern check lots (Figure 2) and southern geographic sources (Table 3) were taller than local material. Because of the good site and location in the lower Coastal Plain, climatic factors might not have affected growth as they did on the fertile but colder Piedmont site (2B).

Results of two previous studies using data from this study conflict with the fourteenth-year results. Sprague and Weir (1973) found significant stand variation for height at 7 of 10 plantings and significant family height differences at only 3 of 10 plantings for fourth-year results. Johnson and McElwee (1967) repoited significant stand and family variation for several wood characteristics from the parent trees of this study.

The different results at age 4 versus 14 come from different statistical analyses. The analysis of variance at age 4 did not include any replication interactions (i.e., replication X geographic source, etc.). For analyses at age 14, these interactions were separated. The replication X geographic source interactions were not significant. However, replication X stand/geographic source interactions were significant in 13 of 14 F-tests (7 plantings X 2 traits) and replication X family/stand/geographic source interactions were significant in 9 of 14 F-tests. The resulting tests showed no significant stand variation. Family differences were significant at 5 of 7 plantings. However, if all replication interactions were combined into a common error term, then stand differences were significant at the two plantings with no family differences in the previous full analysis (1A, 5A). Three studies still had significant family variation (2B, 3A, and 3B) and two others now had no significant family differences (6A, 7A). Combining the significant replication interactions into the error term decreases the power of F-test to detect family variation.

The large replication X stand/geographic source interactions are a result of the study layout. The five families collected from a particular stand are blocked together within a replication. The genetic variation for families within a stand is estimated more accurately than if the five families had been randomly scattered throughout a replication. The two stands per geographic source are not blocked together, however, and are randomized within a replication. Because environmental heterogeneity should be lower within a family block than across a replication, the experimental error for stands should be greater than for families.

Two plantings (1A and 5A) had results which differed from the other 7. Both had only 3 replications; the other 3 had been abandoned because of poor survival and growth. Planting lA had significant family differences at age 4 and 10 but not at 14. Planting 5A was established on an old field site with no environmental variation across a replication.

STUDY IMPLICATIONS

The large among family variation suggests that mass or family selection should produce good genetic gain. Phenotypic selection in natural hardwood stands is complicated, however, by site variability, relatedness though sprouting, age class variation, and mixture of species. Comparison tree selection for sweetgum is not advisable because neighboring trees are often related by sprouting. Selection of good phenotypes followed by progeny testing is a better method for population improvement of sweetgum.

G eographic origin of seed is important for sweetgum. More sources must be tested to determine the ability to move sources across the South.

Physiographic region differences seem important. Coastal Plain/bottomland sources should be used in their own areas. Piedmont sources should be used in Piedmont plantings.

Cree to tree differences are the most important source of genetic variation in natural 'populations of sweetgum.

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