

JUVENILE GROWTH PERFORMANCE IN A PROVENANCE TEST OF SWEETGUM

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Abstract.--In a provenance test of sweetgum planted at four locations, the tallest trees after four growing seasons in the field were generally of non-local origin. Family-within-provenance variation was significant at two locations, and in every plantation was 23 to 44 percent as large as the provenance component. Sweetgum improvement programs should incorporate both provenance selection and progeny testing of wild parents.

Additional keywords: Liquidambar styraciflua, height, progeny test, natural variation.

Prior genetic evaluations of sweetgum (Liquidambar styraciflua L.) have focused on that part of the species' natural range in which it is planted most frequently, the Piedmont and Coastal Plain (Mohn and Schmitt 1973, Sprague and Weir 1973, Texas Forest Service 1975, Wells et al. 1979). However, sweetgum is also planted commercially in bottomlands of the central interior states, and it is a common street and ornamental tree as far as 200 km north of the natural range.

This study was created to fill the need for a provenance test appropriate to the northern portion of the sweetgum commercial region. Its purpose was primarily to evaluate in northern environments the performance of populations native to the northern two-thirds of the species' range, although two plantations in more southern locations provide a useful opportunity to compare performance. All or portions of the collection have been established in experimental plantations in Georgia, Illinois, Iowa, Michigan, New York, Pennsylvania, South Carolina, Vermont, and West Virginia. Growth performance after one year in three West Virginia plantations was reported by Prowant et al. (1983). We are reporting performance after four growing seasons in plantations in Georgia, Illinois, Pennsylvania, and South Carolina.

METHODS

Seed collections were made fall 1975 from 1 to 4 open-pollinated trees in each of 47 populations of sweetgum distributed broadly, but mostly north of the Coastal Plain (Figure 1). A "population" was arbitrarily defined as occupying an area no larger than 25 km², and parent trees were essentially unselected as to phenotype. The trees in most populations were presumed to

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Putnam County, Georgia (GA). Planted May 1980 with 1-0 stock in 4 randomized blocks of 26 provenances in 4-tree row plots as in PA plantation. Spacing is 2.4 x 2.4 meters between trees. Soil is a Vance sandy loam (upland); site previously clearcut of mixed pine and hardwood and root-raked prior to planting, mowed for three years afterward and fertilized in second year with 560 kg/ha of 10-10-10.

Massac County, Illinois (IL). Planted April 1979 with 1-0 stock in 4 randomized blocks of 83 families in 8-tree row plots, the families representing 31 provenances. Family plots were aggregated by physiographic region, a grouping ignored for the present analysis. Spacing is 3.4 x 3.4 meters between trees. Soil is a Sciotoville silt loam (bottomland terrace); site clearcut in 1977 and the slash burned (ash deposits not planted), disked prior to planting and cultivated for three years afterward.

Each plantation was evaluated for height at the end of its fourth growing season in the field. Height data from the PA, SC, and GA plantations were subjected to analysis of variance for provenance effects. Because of the compact family designs in those plantations, family effects were examined by separate analysis of variance for each provenance. Sums of squares and degrees of freedom for family and error terms were then pooled across provenances to get an overall estimate of the significance of family-within-provenance effects.

For the IL plantation, a separate analysis of variance for provenance and family-within-provenance effects was performed for each physiographic region by which field plots were grouped, and the sums of squares and degrees of freedom were pooled across regions. Sums of squares and degrees of freedom for regional effects, from an analysis of all the data, were combined with those for provenance effects.

Block, provenance, and family were treated as random effects in all analyses. Variance components were calculated for each effect as follows, using mean squares from the pooled analyses:

Provenance	$VAR_{BxF/P} + (b)VAR_{F/P} + (f)VAR_{BxP} + (bf)VAR_P$
Family/Provenance	$VAR_{BxF/P} + (b)VAR_{F/P}$
Block x Provenance	$VAR_{BxF/P} + (f)VAR_{BxP}$
Block x Fam./Prov.	$VAR_{BxF/P}$

Because provenances in the IL plantation were represented by variable numbers of families, component coefficients for that plantation were generated using the VARCOMP procedure of SAS (SAS 1982).

No analysis of variance across all plantations was performed because of the differences in experimental design. Instead, provenance means in each plantation were standardized (by subtracting plantation mean and dividing by standard deviation of provenance means) and provenance contributions to provenance x plantation interaction sum of squares were calculated as follows for each of the six pairs of plantations:

$$SS_i = \sum_{j=1}^2 (x_{ij} - x_{i.})^2,$$

where x_{ij} = mean of provenance "i" in plantation "j" and $x_{i.}$ = mean of provenance "i" across both plantations. This is Wricke's "ecovalence" formula (Sheibourne 1972), but simplified because plantation means using standardized data are 1.0. The use of standardized provenance means eliminates contributions to the interaction that are purely a function of scale as a result of provenances being more variable in some plantations than others. It also enables the comparison of contributions for a given provenance across plantation-plantation combinations.

RESULTS AND DISCUSSION

Mortality after four growing seasons was low in all plantations (SC - 14.6%). Differences among provenances were generally minor, but there were two apparent trends. Provenances native within 300 km of the IL plantation site had slightly lower mortality ($x = 11.1\%$) at that location than those from more distant locations ($x = 17.2\%$). It is obviously not a strong difference, but one which will be worth watching as the plantations develop. In the PA plantation, trees of southern origin have been repeatedly winter-injured, and this is beginning to show up in mortality. Provenances native south of latitude 35° had higher mortality ($x = 15.3\%$) than those of more northern origin ($x = 4.9\%$), and the difference will probably increase with time.

Plantation mean heights varied from 1.4 m in PA to 3.1 m in IL (Table 1). Provenance was a significant source of variation in all plantations (Table 2), and the best provenance in each grew 10 to 20 percent faster than the plantation mean. In general, the best provenances at each plantation were native to locations distant to the plantation site. The tallest 10 percent of the provenances at PA were native to Illinois and Indiana; and at IL the tallest trees were native to North Carolina, Illinois, and Georgia (Table 1). For these two plantations, there was a definite growth advantage in provenances of somewhat more southern origin than the plantation site. In the case of the PA plantation at least, this advantage was associated with no sacrifice in hardiness, since southern Indiana and Illinois trees appear at this time to be as hardy as those from coastal New Jersey and Pennsylvania.

The tallest 10 percent of the provenances at SC were native to Mississippi and Alabama; and at GA, to Mississippi and North Carolina (Table 1). Two of the three provenances involved in each case came from milder, more coastal locations than the respective plantation sites. Mississippi and Alabama sources were consistently superior at GA and SC and showed a 7 or 15 percent average height advantage over Georgia and South Carolina provenances.

Except at GA and SC, there was little positive correspondence between provenance means at different plantations (Table 3). IL means showed only a very weak positive correspondence with those at all three other locations. PA means were significantly and negatively correlated with those at the two southernmost plantations, probably as a result of the interrelationships

TABLE 1.--Relative heights (percentage of plantation mean) of 51 provenances after four growing seasons in four plantations.

Provenance		Plantation			
Number	State	FA	SC	GA	IL
001	GA	--	107.9	106.8	--
006	GA	--	105.8	99.2	--
011	GA	--	109.4	102.7	--
016	MS	--	113.6	120.1	--
033	GA	87.5	101.3	98.8	--
053	NC	91.2	107.4	115.0	--
061	SC	85.3	--	--	--
070	KY	--	--	--	93.2
077	MD	95.6	--	--	--
081	AL	80.2	116.5	109.8	--
085	MS	90.5	102.0	117.7	--
097	IL	114.0	93.7	99.4	--
101	TN	100.8	109.7	97.8	--
105	TN	97.8	--	--	--
109	TN	100.8	--	--	--
117	TN	90.5	97.5	96.2	104.0
121	IN	119.1	92.5	92.0	103.7
125	IN	116.9	--	--	103.4
129	KY	102.2	96.7	101.4	--
133	OH	--	96.3	83.1	100.2
137	MO	--	--	--	94.4
229	MS	89.7	111.6	112.4	--
241	SC	86.0	95.6	95.2	--
245	MO	98.6	--	--	--
257	GA ¹	96.3	104.0	95.7	108.2
261	cv	--	--	--	96.7
281	PA	--	98.2	100.4	--
284	NJ	--	--	--	107.8
285	PA	115.5	77.7	74.3	--
289	TN	--	--	--	106.6
297	NJ	109.6	--	--	93.8
313	NJ	106.6	85.3	95.2	99.5
325	NJ	--	--	--	86.8
329	TN	--	--	--	101.8
333	TN	--	--	--	95.1
377	IL	119.9	--	--	108.2
381	VA	90.5	103.6	85.8	98.3
385	VA	90.5	100.5	107.7	103.7
420	DE	--	--	--	90.6
433	NC	--	--	--	110.4
445	AL	100.8	--	--	96.3
452	KY	--	--	--	100.2
457	AR	86.8	--	--	89.0
461	PA ¹	111.8	--	--	94.8
473	cv	91.2	81.5	83.7	102.1
481	IL	116.9	--	--	100.2
489	MO	114.0	--	--	103.4
545	TN	102.2	91.8	99.4	102.1
549	TN	100.0	103.6	104.6	104.3
553	TN	100.8	102.0	98.3	104.3
557	TN	--	--	--	97.3
Plantation mean:		1.36 m	2.63 m	1.91 m	3.13 m

¹Cultivated origin.

TABLE 2.--Variance components for age 4 height at four plantations.

Source	Component (% of total less "block") for:			
	PA	SC	GA	IL
Provenance	11.1***	10.4***	8.2*	12.3**
Family/Provenance	4.0**	3.5*	1.9	5.4
Error ¹	84.9	86.0	89.8	82.3

¹Pooled over "block x provenance" and "block x family-within-provenance".

*, **, *** Effect statistically significant at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively.

between growth potential, cold tolerance, and latitude of origin. For age 1 performance of the same material in plantations in West Virginia and Maryland, Prowant et al. (1983) documented a negative relationship between latitude of origin and annual growth increment, but a positive relationship between latitude and height as a result of winter dieback on southern trees in the nursery.

Provenance x plantation interactions for the six plantation-plantation combinations are shown more clearly in Table 4. Provenances that contributed most to interactions involving PA and the two most southern plantations were of either extreme northern or extreme southern origin, an obvious consequence of the slow growth of the former in GA and SC and winter injury to the latter in PA. To a degree the same situation occurred in the PA and IL comparison.

TABLE 3.--Coefficients of correlation between provenance mean heights at four plantations.

	SC	GA	IL
PA	-0.57**	-0.44*	+0.20
SC	--	+0.68**	+0.38
GA	--	--	+0.50

*, **Statistically significant at $P < 0.05$ and $P < 0.01$, respectively.

TABLE 4.--Provenance contributions to provenance x plantation interaction sum-of-squares in six plantation/plantation comparisons.

Provenance		Contributions to sum-of-squares ¹ for plantation combinations:					
No.	State	PA + SC	PA + GA	PA + IL	SC + GA	SC + IL	GA + IL
033	GA	(-)0.709	(-)0.416	--	(+)0.029	--	--
053	NC	(-)1.067	(-)2.184	--	(-)0.221	--	--
081	AL	(-)5.930	(-)3.508	--	(+)0.295	--	--
085	MS	(-)0.488	(-)2.896	--	(-)1.063	--	--
097	IL	(+)2.225	(+)1.222	--	(-)0.173	--	--
101	TN	(-)0.306	(+)0.101	--	(+)0.721	--	--
117	TN	(-)0.137	(-)0.074	(-)1.549	(+)0.005	(-)0.043	(-)0.035
121	IN	(+)3.690	(+)3.766	(+)0.379	0.000	(-)0.336	(-)0.224
125	IN	--	--	(+)0.272	--	--	--
129	KY	(+)0.229	(+)0.030	--	(-)0.112	--	--
133	OH	--	--	--	(+)0.740	(+)0.454	(-)0.123
229	MS	(-)2.056	(-)1.967	--	0.000	--	--
241	SC	(-)0.281	(-)0.250	--	0.000	--	--
257	GA	(-)0.193	(+)0.025	(-)2.121	(+)0.330	(-)0.461	(-)1.693
281	PA	--	--	--	(-)0.024	--	--
285	PA	(+)7.522	(+)8.284	--	(+)0.010	--	--
297	NJ	--	--	(+)1.972	--	--	--
313	NJ	(+)2.557	(+)0.789	(+)0.167	(-)0.555	(-)0.031	(+)0.758
377	IL	--	--	(+)0.001	--	--	--
381	VA	(-)0.653	(+)0.181	(-)0.189	(+)1.465	(+)3.355	(+)0.138
385	VA	(-)0.347	(-)1.080	(-)1.439	(-)0.228	(+)0.024	(+)0.820
445	AL	--	--	(+)0.236	--	--	--
457	AR	--	--	(+)0.404	--	--	--
461	PA	--	--	(+)1.986	--	--	--
473	cv	(+)0.692	(+)0.377	(-)0.862	(-)0.064	(-)1.402	(-)0.636
481	IL	--	--	(+)0.942	--	--	--
489	MO	--	--	(+)0.112	--	--	--
545	TN	(+)0.698	(+)0.097	(-)0.053	(-)0.307	(-)0.057	(+)0.338
549	TN	(-)0.027	(-)0.034	(-)0.468	(-)0.002	(+)0.074	(+)0.217
553	TN	0.000	(+)0.080	(-)0.407	(+)0.068	(+)0.017	(-)0.007

¹A "+" indicates provenances that grew relatively better in the first plantation listed, a "-" provenances that grew better in the second.

However, interactions involving the IL plantation were also distinguished by the almost consistently superior performance in IL of provenances from the Cumberland Plateau and associated highlands near southeastern Tennessee, and one collection (473) of cultivated origin. Interactions between SC and GA were small.

Family-within-provenance was a significant source of variation in two of the four plantations (Table 2). Depending upon plantation, family variance components were 23 to 44 percent as large as provenance components, with an

average of 34 percent. This compares closely with an analogous figure of 27 percent that can be calculated from Sprague and Weir's (1973) ANOVAs for age four height in ten plantations containing overlapping sets of 10 to 12 stand collections each represented by five open-pollinated families. Wells et al. (1979) also found significant within-stand variation in growth rate of progenies from 138 stands predominantly in Mississippi.

To determine whether some provenances were consistently more variable than others, we performed separate ANOVAs for family effects in each provenance at each plantation (Table 5). No provenance exhibited significant family variation at more than one location, and in fact there was hardly any consistency across plantations in the relative size of the family mean squares for each provenance. In other words, the expression of within-population variation was too inconsistent from site to site to permit generalization, and family x plantation interactions would probably have been large if we had analyzed for them. Of course, this has little practical import because provenance selection would preclude most opportunities for the selection of identical families for two or more of these plantation locations, except perhaps GA and SC.

CONCLUSIONS

After four years in field plantings, best growth was generally obtained on provenances native fairly **large** distances from the plantation site. For the respective plantations, the fastest growing trees originated as follows:

PA -- southern Illinois and Indiana

IL -- Cumberland Plateau and associated highlands in Georgia, North Carolina, and Tennessee, and one provenance each in New Jersey and Illinois.

SC -- Mississippi, Alabama, and Tennessee

GA -- Mississippi, Alabama, and North Carolina

Whether these patterns will persist, and whether such provenance transfers would entail some risk in adaptation, will require further study to determine. The results must be regarded with caution because vigorous height growth is just beginning to occur in the plantations.

There was little consistency in provenance performance except between SC and GA. The only interpretable interactions were those attributable to winter injury to southern provenances in contrasts between PA and the two most southern plantations.

Although family-within-provenance was a significant source of variation in only two plantations, it consistently accounted for at least 23 percent as much height variation as provenance. This is especially remarkable considering the fact that provenance representation was nearly range-wide. Cooper (cited in Wells 1979) has shown no advantage to plus-tree selection in this species. Consequently, sweetgum improvement programs should incorporate both provenance selection and progeny testing of wild parents.

TABLE 5.--Mean squares for family-within-provenance effects, by provenance and plantation.

Provenance		Plantation			
Number	State	PA	SC	GA	IL
33	GA	0.3980	0.0175	0.0563	--
53	NC	0.7975	0.8886**	0.1383	--
61	SC	0.6144*	--	--	--
77	MD	0.2510	--	--	--
81	AL	0.4161	0.3164	0.1441	--
85	MS	0.2412	0.3220	0.3886	--
97	IL	0.2739	0.2099	0.2597	--
101	TN	0.4043	0.0853	0.0675	--
105	TN	0.7411	--	--	--
109	TN	0.5197	--	--	--
117	TN	0.7160*	0.1641	0.0020	0.1185
121	IN	0.2859	0.0531	0.0653	0.0508
125	IN	0.2505	--	--	0.0692
129	KY	1.0624**	0.1262	0.1285	--
133	OH	--	0.1278	0.1557*	0.0000
229	MS	0.1052	0.2764*	0.1978	--
241	SC	0.3670	0.4867	0.1193	--
245	MO	0.2634	--	--	--
257	GA	1.0633*	0.5233	0.0290	--
261	cv	--	--	--	0.0005
281	PA	--	0.0195	0.0903	--
285	PA	0.1680	0.0313	0.0518	--
297	NJ	0.3408	--	--	0.1329
313	NJ	0.0279	0.3697	0.1623	0.0048
333	TN	--	--	--	0.0140
377	IL	0.2336	--	--	0.1625
381	VA	0.5248	0.2140	0.1449	0.1051
385	VA	0.4521	0.2938	0.2827	0.0840
445	AL	0.8113	--	--	0.4608
457	AR	0.7143	--	--	0.0009
461	PA	0.3220	--	--	0.1826***
473	cv	0.4605	0.0247	0.1872*	0.2174
481	IL	0.5267	--	--	0.1097
489	MO	0.2564	--	--	0.2270
545	TN	0.1074	0.2765	0.0639	0.0918
549	TN	0.0469	0.2175	0.0475	0.1537
553	TN	0.0587	0.0561	0.1338	0.1617

*, **, *** Statistically significant at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively.

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