A Study of Racial Variation in Loblolly Pine in Georgia--Tenth-Year Results

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The Georgia Loblolly Pine Racial Variation Study was designed to complement the Southwide Pine Seed Source study?! by testing samples of loblolly pine seed, from collections made in all provinces of Georgia, in plantations established throughout the state. It has performed this function in a most admirable fashion. In general, the results do not conflict in any way with those recently reported on the tenth-year results of the loblolly phase of the Southwide Pine Seed Sour ce Study (Wells and Wakeley, 1966). Basically, the data obtained in the Georgia study indicate that the variation in the growth of loblolly pine from different parts of the state is of sufficient magnitude that it will require consideration in seed procurement and planting plans. It is an important factor in the seed orchard program of the Georgia Forestry Commission.

STUDY DESCRIPTION AND HISTORY

In the fall of 1954, cones were collected from between 20 and 26 trees in each of 14 collection areas in Georgia (figure 1). One collection was made from each of six Georgia Forestry Commission forestry districts, and two collections were made from the remaining four forestry districts. In addition to the 14 collections from Georgia, three lots were obtained from north Florida and one from Arkansas table 1).

In the spring of 1955, the seed were sown in the Georgia Forestry Commission's Davisboro Nursery in a randomized block design with two replications. The seedlings were machine lifted in December 1955; bundles made up by plot, block, and plantation; and all necessary stock, including

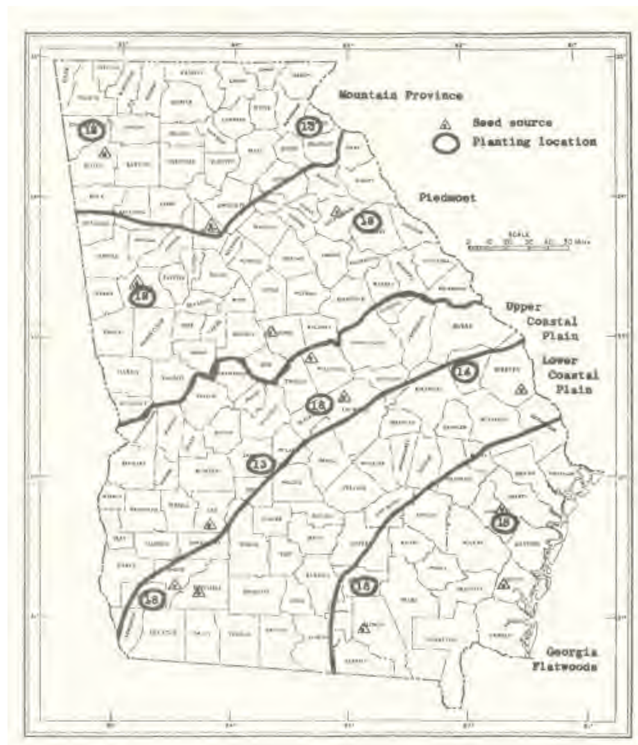

Figure 1. Location of 14 loblolly pine seed sources and 10 planting locations in Georgia. (0 = number of seed sources in plantation)

border-row seedlings, were shipped to the coopera-

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3/ Cooperators in this study are: the Georgia Forestry Commission, Union Camp Corporation, Georgia Kraft Company, International Paper Company, Georgia National Forests, Champion Papers Incorporated, and the Georgia Forest Research Council.

Table 1-- Sources of 18 loblolly pine seed lots used in the Georgia Study

PROVINCE	COUNTY	NEARESTTOWN
Mountain	Floyd	Shannon
	DeKalb	Stone Mountain
Piedmont	Oglethorpe	Lexington
"	Coweta	Newnan
"	Jones	Wayside
Upper Coastal Plain	Wilkinson	Gordon
"	Laurens	Dublin
'	Lee	Leesburg
Lower Coastal Plain	Screven	Halcyondale
"	Baker	Newton
"	Mitchell	Cotton
Flatwoods	Clinch	Homervi lle
"	Long	Walthourville
"	Glynn	Waynesville
Florida	Baker	Taylor
"	St. Johns	Palm Valley
	Walton	DeFuniak Springs
Arkansas	Ashley	Crossett

Plantations were established at 10 locations. They were as uniformly distributed throughout the state as the availability of cooperators made possible (figure 1). All 18 seed sources were used at six of the plantations. Due to shortages in planting stock, two plantations contained only 13 sources while the other two each contained 14 and 15 sources. The three north Florida seed sources were planted in both of the Piedmont plantations but only at one location in each of the other four physiographic provinces,

A randomized complete block design was used with four replications of 36-tree-square plots planted at a spacing of 10 x 10 feet. A two-row border strip of commercial stock was planted around all outside boundaries.

With one exception, all the plantations have been remarkably free of damage by fire or man. The plantation in Long County sustained some cattle damage during the first few years, and two corner plots were damaged by site-preparation equipment. Even in these plots, however, sufficient trees remained to permit measurement of heights and fusiform rust (**Cronartium fusiforme** Hedgc. & Hunt ex Cumm.) infection.

During the winter of 1965-66, when the trees were 11 years old from seed, measurements were taken at all plantations of the 16 trees in the center of each plot. Survival, total height, d.b.h., and the incidence of fusiform rust stem cankers and branch galls were recorded on IBM Mark Sense Cards. These cards were processed in the facilities of the Georgia Forestry Commission, and all analyses have been made on plantation-seed source means.

Cubic-foot volume growth was calculated on an individual tree basis using the formula for a cone having a height equal to the plot mean total height and a basal area equal to that at breast height. This value was also used to estimate volume production on a per acre basis in which survival was also a variable.

ANALYSIS AND RESULTS

The principle analysis used combined the data from all plantations for the 14 Georgia seed sources (table 2). In this analysis the state was divided into five physiographic provinces, each containing two plantations (figure 1). The four southern provinces were sampled by three seed sources, while the mountain province was sampled by two.

For each trait, the average values by seed source province and planting province are summarized in table 3. For example, the entry under the piedmont seed source province for the Georgia flatwoods planting province is the mean of six values (three piedmont seed sources planted in two Georgia flatwoods locations). All tests of statistical significance were at the .01 level because there were no comparisons that differed only at the .05 level.

DIFFERENCES AMONG PLANTING PROVINCES

There were no statistically significant differences among the five provinces for any of the traits examined with respect to the overall performance of the Georgia seed sources. Despite the lack of statistical significance, there were two noticeable tendencies. Rust infection and mortality were lowest in the mountain province, and as a consequence, volume production was highest in that area (table 4). In the piedmont, volume growth excelled that of the other provinces as a result of that province producing trees with the best average heights and diameters (table 4). Whether these tendencies are meaningful can best be judged on the basis of the results which follow.

Table 2.--Analysis of variance and mean squares for tenth-year survival, fusiform rust nfection height, d.b.h., volume growth and volume production

Source of variation		Degrees of freedom	Mean squares: Survival	Rust infection	Height	D.b.h.	Volume growth	Volume production	E (MS)
Planting province	A	4	1,342.64	7,257.31	164.20	6.66	6.21	541,980	$\sigma^2_e + 2\sigma^2_{as(b)} + 14\sigma^2_{1(a)} + 28\ {}^2$
Locations in province	L(A)	5	1,092.22 **	1,908.22 **	51.48 **	3.08 **	2.38 **	150,842**	$\sigma^2_e + {}_{1(a)}\ 14$
Seed source province		4	613.25 **	143.31	48.93 **	1.67 **	1.73 **	9,911	$\theta^{2b}_{b1(a)} + 10\sigma^2_{s(b)}$ 300
Seed sources in province	S(B)	9	107.77 **	263.45 **	1.84	0.21	0.11	11,706	$\sigma^2_e + 1\ {}_{s(b)}$
A x B		16	55.80	25.14	16.00 **	0.41 **	0.46 **	57,266 **	$\sigma^2_e + 2\sigma^2_{as(b)} + 2.8\sigma^2_{1(a)} + 5.6\theta^{2a}\ b$
A x S(B)		36	28.33	30.93	1.90	0.12	0.08	7,029	$\sigma^2_e + 2\sigma^{2}_{as(b)}$
8 x L(A)		20	26.91	53.99	1.71	0.08	0.08	7,849	$\sigma^2_e + 2.8_{b1(a)}$
5(8) x L(A)			25.24	40.74	2.29	0.11	0.07	9,434	σ^2_e

** Significant at the 0.01 level.

DIFFERENCES BETWEEN PLANTING LOCATIONS WITHIN PROVINCES

Within each of the major physiographic provinces, there were plantations at two locations (figure 1). There were highly significant differences between these plantations for all traits, indicating that site, planting procedure, and other local factors were more important than the location of the plantation, Only in the case of rust infection do the data seem to warrant qualification since, despite the lack of statistically significant differences between provinces, rust infection was much lower in both plantations in the mountains, It appears that only the large variation between plantations in the other provinces prevented this difference being significant, The incidence of rust in the most heavily infected of the two mountain locations (Stephens County) was only 12 percent, compared to 42 percent in the next least infected plantation (Dooly County), located in the upper coastal plain.

DIFFERENCES AMONG SEED SOURCE PROVINCES

There were highly significant differences among the five provinces as seed source in survival, height, diameter, and volume growth (table 2). Although the magnitude of these differences was not large for all traits, their trends were rather consistent,

Survival averaged over all plantations was highest for the mountain seed sources (80 percent) and got progressively poorer for each of the southern provinces, averaging 62 percent for the sources from the Georgia flatwoods,

The trend was reversed for height, diameter, and volume growth, The best performance for these traits was attained by trees from the Georgia flatwoods sources and tended to decrease in each succeedingly more northerly province (table 5),

There was a slight tendency for rust infection to be lowest among trees from the mountain seed sources and highest among trees from sources in the Georgia flatwoods, but the differences were neither large enough nor the trend consistent enough to attain statistical significance.

Although it was not included in the analysis of the combined data from the Georgia sources, the performance of the single source from Arkansas was interesting. Trees from this source were unexcelled in survival and resistance to rust infection (table 5), Their exceptional rust resistance throughout the state reinforces previous reports of the low susceptibility to fusiform rust infection of the western sources of loblolly pine (Wakely, 1944, 1961; Bethune and Roth, 1960; Wells, 1966; Wells and Wakeley, 1966), In height, diameter, and volume growth they were intermediate of trees from the piedmont and mountain sources. Due to its high survival and rust resistance, this source produced the highest volumes per acre in all but the mountain and flatwoods provinces (table 3).

The performance of the three north Florida sources is difficult to evaluate since in three of the four provinces in which they were only planted at one location, that location had the poorer average growth for all seed sources. Several correction fac-

Table 3.--Average performance of loblolly pine seed lots grouped by seed source provinces and planting provinces

	Seed Source Province						
Planting Province	Florida 1/	Georgia Flatwoods	Lower Coastal Plain	Upper Coastal Plain	Piedmont	Mountain	Arkansas
			Survival-percent				
Georgia Flatwoods	38.8	59.4	67.3	74.6	72.6	71.5	84.7
Lower Coastal Plain	59.8	60.7	65.3	69.7	66.9	78.1	85.7
Upper Coastal Plain	53.2	66.5	68.0	67.2	75.4	82.5	95.1
Piedmont	46.5	48.1	48.6	59.2	72.5	74.1	77.9
Mountain	79.7	76.5	82.1	87.9	96.2	91.8	98.8
			Fusiform rust infection-percent				
Georgia Flatwoods	90.2	67.6	61.3	63.3	63.6	51.0	14.2
Lower Coastal Plain	92.0	76.5	72.4	73.1	72.5	68.6	21.1
Upper Coastal Plain	89.0	68.0	64.6	62.1	68.2	59.3	9.4
Piedmont	83.1	76.5	59.1	59.6	61.3	62.6	7.8
Mountain	23.3	12.6	9.2	12.6	8.6	8.8	0.1
			Height-feet				
Georgia Flatwoods	26.9	33.3	30.2	29.9	26.8	24.4	28.0
Lower Coastal Plain	31.8	33.3	32.0	31.2	28.2	28.2	29.7
Upper Coastal Plain	26.4	26.0	26.1	26.3	24.9	23.9	25.2
Piedmont	32.8	33.2	32.0	32.9	30.5	30.4	31.2
Mountain	28.4	28.6	29.6	30.7	32.1	30.3	28.6
			D.B.H.-inches				
Georgia Flatwoods	5.6	6.4	5.7	5.7	5.3	4.7	5.4
Lower Coastal Plain	6.4	6.6	6.5	6.2	5.9	5.8	6.1
Upper Coastal Plain	6.1	5.6	5.7	5.7	5.4	5.2	5.2
Piedmont	6.8	7.0	7.0	6.8	6.4	6.4	6.3
Mountain	5.9	6.1	6.2	6.2	6.4	6.3	6.0
			Volume growth-cubic feet				
Georgia Flatwoods	1.74	2.60	1.92	1.82	1.46	1.10	1.52
Lower Coastal Plain	2.42	2.68	2.47	2,22	1.83	1.75	1.99
Upper Coastal Plain	1.78	1.50	1.55	1.61	1.35	1.19	1.26
Piedmont	2.78	2.96	2.96	2.97	2.30	2.26	2.30
Mountain	1.80	1.96	2.10	2.20	2.43	2.17	1.37
			Volume production-cubic feet/acre				
Georgia Flatwoods	307	676	574	584	473	331	532
Lower Coastal Plain	608	678	681	655	515	582	730
Upper Coastal Plain	400	420	420	444	374	395	508
Piedmont	531	566	600	630	690	712	744
Mountain	626	627	739	798	986	817	791

1/ The three Florida sources arerepresentedin both Piedmont plantings but in onlyoneplantationineach of the other provinces.

tors were tried on these data to see if they might better fit the growth trends established by the Georgia sources. Since the corrected values did not change the relative values appreciably, they have been left uncorrected in tables 3 and 5, and in figure 2. In general, trees from the Florida sources grew slightly slower than trees from sources in the Georgia flatwoods and coastal plain, and sustained slightly higher mortality and rust infection.

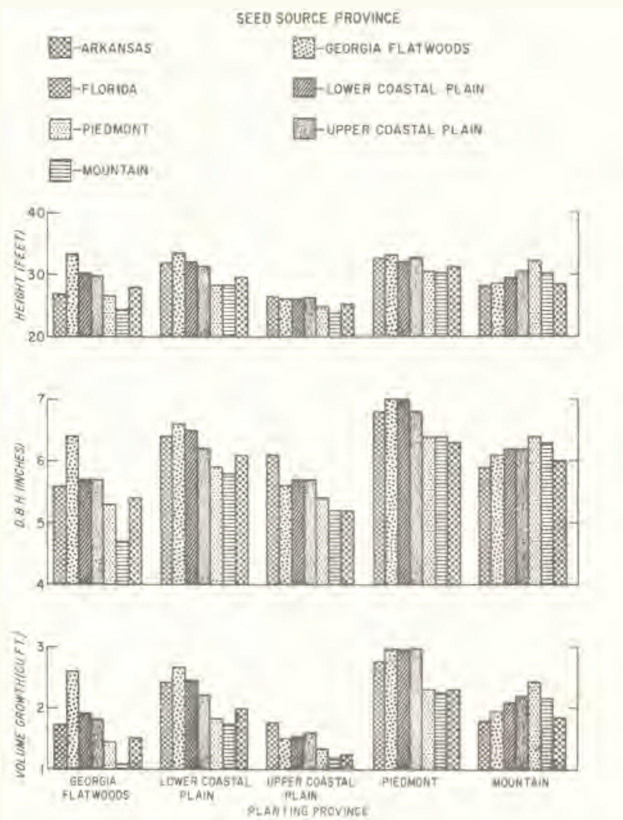

Figure 2-Average height, d.b.h., and volume growth of loblolly pine from seven source provinces planted in five Georgia provinces.

SEED SOURCE DIFFERENCES WITHIN PROVINCES

There were highly significant differences between seed sources within the five major seed collecting provinces in only two traits, survival and rust infection. In the case of survival it is probably best not to place too much weight on these results. Two factors suggesting this interpretation are: (1) the fact that in the Georgia study the seed source with the poorest average survival was not poorest at all locations nor was the best source best at all locations, and (2) too large a portion of the variation in survival may be associated with nursery environment and outplanting procedures.

Differences in rust infection among seed sources were probably less influenced by external factors in this study. The results show that detectable genetic differences exist between specific seed sources in Georgia. These differences are randomly distributed rather than being strongly associated with the major seed source provinces. On the basis of other studies it is entirely possible that a portion of the variation among seed sources is due to the variation between families sampled at each seed source (Barber, 1966),

The least infected seed source in this study consistently had the lowest infection at all planting locations. However, the converse was not true with respect to the most heavily infected source.

THE INTERACTION BETWEEN PLANTING PROVINCE AND SEED SOURCE PROVINCE

The interaction between planting province and seed source province was highly significant for height, diameter, volume growth, and volume production. This interaction is most noticeable in the poor performance of trees from the piedmont and mountain sources when planted in the flatwoods and coastal plain provinces, and the relatively good performance of trees from the flatwoods and coastal plain sources everywhere except in the mountains (table 3, figure 2).

In the Georgia flatwoods the average growth of the local seed sources was noticeably superior to all the non-local sources. When only the Georgia seed sources are considered, trees from the local sources produced the highest volumes per acre in all but the piedmont and mountain provinces (table 3).

GENERAL PERFORMANCE OF THE SEED SOURCES

If the average performance over all locations of the trees from the various sources is plotted on a map at their point of origin, a general trend develops, This trend is shown for height, d. b. h., and volume growth in figure 3, where the average values for the 14 Georgia seed sources are plotted along a transect running from the northwestern corner of Georgia southeast to the Atlantic coast at the southern corner of Camden County. This transect was chosen in preference to a straight north-south line because it comes closer to being at a right angle to a number of biologically important variables, such as physiographic province, altitude, average January temperature, the average number of days without a killing frost, and the average warm season precipitation. The general trend along this transect is definitely clinal, with the values for all growth components increasing from northwest to southeast across the state. There is a slight tendency for this cline to be "stepped" as it crosses the fall line, with generally higher values below the fall line than above it.

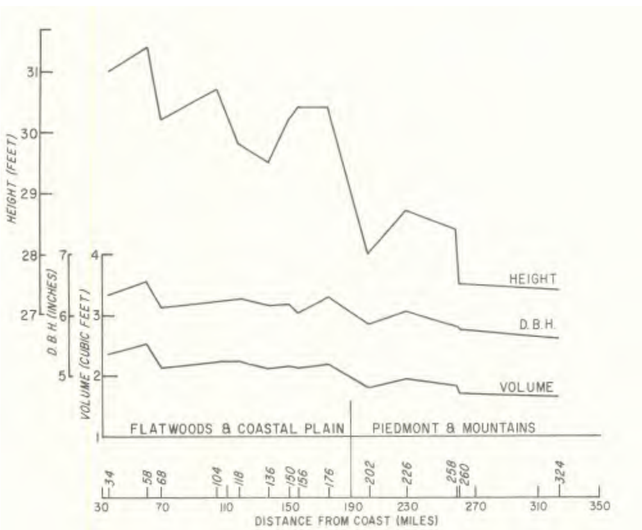

Figure 3- Trend along a SE-NW transect of growth of 14 Georgia seed sources averaged over 10 plantations.

DISCUSSION

To the forest manager, these results may at first present a dilemma; that is, the fast growing trees from the southern sources are generally less adaptable from the standpoint of initial survival and fusiform rust resistance than the slower growing northern sources. Stand density, however, is one of the more easily controlled factors in plantation management, and given a seed source with with good growth characteristics, it would take only a slightly closer initial spacing to assure a productive, well-stocked stand. Conversely, (liven a seed source with known good resistance to fusiform rust, many foresters might wish to give serious consideration to a western source, such as that from Arkansas, at the risk of some loss in individual tree performance. Information on total volume yield in relation to specific gravity of wood may be obtained later.

From the standpoint of height, diameter, and individual tree volume growth, the results of the Georgia study clearly show that as far north as the upper coastal plain either the local source or one from the south would be preferable. In the piedmont, trees from the southern sources also grew best and should out-yield the local sources if adequate initial survival is obtained.

In the mountain province, trees from the local sources were inferior in all traits to those from the piedmont, but were generally superior, or nearly equal, to any source from below the fall line.

In the Southwide Study, growth decreased with

Table 4.— Average performance (in the five physiographic provinces) of the 14 loblolly pine seed sources from Georgia

Planting Province	Survival	Fusiform rust infection	Height	D. B. H.	Volume growth	Volume production per acre
	percent	percent	feet	inches	cu. ft.	cu. ft.
Georgia Flatwoods	69.0	62.1	29.2	5.6	1.83	542
Lower Coastal Plain	67.6	73.0	30.8	6.2	2.22	625
Upper Coastal Plain	71.3	64.8	24.6	5.6	1.46	412
Piedmont	59.7	64.1	31.9	6.7	2.72	634
Mounta ins	87.5	10.4	30.3	6.3	2.17	792

Table 5.-- Average performance of labially pine seed sources from seven geographic areas when planted at 10 locations in Georgia

Seed Source Province	Survival	Fusiform rust infection	Height	D. B.H.	Volume growth	Volume production per acre
	percent	percent	feet	inches	cu. ft.	cu. ft.
Georgia Flatwoods	62.5	59.9	30.9	6.3	2.34	593
Lower Coastal Plain	66.6	52.2	30.0	6.2	2.20	603
Upper Coastal Plain	72.3	53.4	30.2	6.2	2.16	623
Piedmont	78.1	53.6	28.5	5.9	1.87	607
Mountain	80.2	48.7	27.4	5.7	1.69	567
	55.6	75.5	29.3	6.2	2.10	494
Arkansas	88.4	10.5	28.5	5.8	1.79	661

1/ The three Florida sources were only planted at six locations.

increasing distance from the coastand a clinal trend was suggested with a possible, but undetected, discontinuity between the coastal I and inland sources (Wells and Wakeley, 1966). The growth trends shown in the Georgia study are definitely clinal along a northwest-southeast transect. Trees from the two sources closest to the coast showed a noticeable tendency toward faster growth than trees from the other seven Coastal plain sources. However, an even more abrupt transition was shown between the average growth rates of trees from sources above and below the fall line.

Wells and Wakeley (1966) suggested that selection pressure from climatic variables has influenced the development of clinal variation in loblolly pine. The results of the Georgia study tend to confirm their hypothesis. The "step" in the clinal trend at the fall line coincides fairly well with a general decrease in warm season precipitation. Several additional factors, which could also be associated with changes in the cline, are the increased topographical and soil variation above the fall line and the possibility of introgression with shortleaf pine (Pinus echinata Mill.).

It seems quite possible that, with the relatively more abrupt changes in topography and the greater site variation north of the fall line, the loblolly pine in that region have maintained or developed a higher degree of adaptability to the wide range of sites and competitive situations it encounters. This adaptability may be maintained at the expense of fast growth rates.

On large-scale maps, it can be seen that the intensity of shortleaf pine occurrence increases greatly north of the fall line while it is very scarce, near the Georgia coast, in Livingston Parish, Louisiana, and in Onslow County, North Carolina (Mohr, 1897, Roberts and Cruikshank, 1941; Janssen and Weiland, 1960). Shortleaf pine also attains its its heaviest concentration in southwest Arkansas, very close to the origin of the most fusiform rust resistant trees in the Georgia study. Introgression of shortleaf with loblolly pine in that area has already been suggested to account for the similar low rust infection of the Arkansas and Texas sources in the Southwide Study (Wells and Wakeley, 1966). It may also be associated with the clinal variation in loblolly pine growth rates.

SUMMARY

For a smaller but more intensively sampled area, the tenth-year results of the Georgia Loblolly Racial Variation Study largely substantiate those obtained from the Southwide Pine Seed Source Study. The general conclusions which apply are similar:

1. Racial variation in loblolly pine in Georgia is clinal, with growth rate decreasing with increasing distance from the coast.
2. Within Georgia, trees from provinces south of the planting province grew best in all but the Georgia flatwoods.
3. Trees from a western source (Arkansas) had the lowest percentage of rust infection.

Among the Georgia sources, trees from the northern seed sources survived best.

If the trends shown by these tenth-year data continue in the same relative pattern until rotation age, and pulp yields are satisfactory, they will be of great practical and theoretical significance.

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