RESULTS OF THE SOUTHWIDE PINE SEED SOURCE STUDY THROUGH 1968-69

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The Southwide Pine Seed Source Study 2/ was undertaken in 1951 to determine the degree to which inherent geographic variation in longleaf pine (*Pinus palustris* Mill.), slash pine (*P. elliottii* Engelm. var. *elliottii*), loblolly pine (*P. taeda* L.), and shortleaf pine (*P. echinata* Mill.) is associated with geographic variation in climate and physiography. The information was intended for use in delimiting practical seed-collecting zones for these species.

The main features of the study are a randomized block design with four Hocks in each planting, large plots, and relatively few seed sources but at least one planting in the vicinity of each seed source. The longleaf and shortleaf tests include a replication by year, since seed was collected in both 1951 and 1955 and plantings were established in 1952 and 1956. All of the loblolly and slash plantings were established in 1952-53 from seed collected in 1951.

The seed sources and plantings of longleaf, shortleaf, and loblolly are divided into series. The division was necessitated by the practical difficulty of planting trees from all seed sources of a species in all the areas judged necessary for an efficient test. Sources and plantings in each series were selected to test specific hypotheses. Thus, shortleaf Series 4 samples the north-south extremities of the species' range to test whether climatic effects associated with latitude are important determinants of geographic variation. Similarly, shortleaf Series 6 holds latitude nearly constant to determine the effect of

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Messrs. Henry and Zobel have served on the subcommittee since the planning stages of the study, as did Mr. Bercaw. The original chairman and principal organizer of the study, P. C. Wakeley, retired from the Southern Forest Experiment Station in 1964.

Establishment, maintenance, and measurement of the plantings are by Federal, State, educational, and industrial cooperators who generously contribute their time and effort.

longitude. Within any one series all seed sources are represented in all plantings. One or two sources are represented in more than one series, and make possible some comparison between plantings of different series. This design kept the individual plantings small (3.2 acres maximum) and, because each series tested a specific effect, probably yielded most of the information that could have been obtained from much larger plantings.

This paper summarizes measurements taken through the 10th year in the longleaf and shortleaf plantations, and through the 15th year in the loblolly and slash plantations. Detailed analyses of all four species have been published elsewhere or are in press (Wells and Wakeley 1966, 1970a, 1970b; Snyder et al. 1967).

While the maxim, "local seed is best," has been a useful guide to southern tree planters for many years, the Southwide Study indicates that in some areas sizable genetic gain over local seed probably can be attained by moving seed considerable distances. In other situations, particularly near the northern limits of the species' ranges, no improvement over the local source appears possible.

The study was begun with the object of providing information to guide seed collection in natural stands. If tree improvement programs continue to develop at their present rate, it will be only a decade or so before most seed in the southern pine region is harvested from orchards rather than from natural stands. Results of this and similar research can then be used to guide the distribution of progenies from the orchards.

LOBLOLLY PINE

The loblolly pine phase of the study consists of 15 seed sources and 18 plantings distributed over the major portion of the loblolly range. The seed sources and plantings are divided into two series. Series-1 sources represent the major part of the range. Series 2, with the exception of the southeastern Louisiana seed source, is restricted to an east-west transect from North Carolina to Arkansas. The latest measurements were made during the winter of 1967-68, when the plantings were 15 years old.

Well-developed patterns of variation in survival, rust infection, and height growth are evident in both loblolly series.

On an average for all plantings, about 10 percent more trees from the two areas west of the Mississippi River (east Texas and southwestern Arkansas) survived than did trees from other sources. As drought is most common and most intense in the western part **of** the loblolly range, this variation seems the result of natural selection.

Trees from Maryland, southeastern Louisiana, and the two sources west of the Mississippi River are only lightly infected by the southern fusiform rust. Trees from the other sources, all east of the Mississippi River, are much more heavily diseased. In the 15 plantings where rust infections occurred, 11.6 percent of the trees from the four resistant sources were infected, as compared to 41.2 percent of the trees from the other sources.

In survival and rust infection, the interaction between seed sources and planting location was small and conformed to no discernible pattern. In height growth, the interaction was considerable and had a definite geographic pattern. In the majority of the plantings, trees from seed collected in areas with high summer rainfall and mild winters were tallest, but in the two coldest planting locations, Maryland and Tennessee, trees from such areas were outperformed by those from areas with low summer rainfall and cold winters. The general relationship between 15-year height and summer rainfall at seed source in Series 1 is illustrated in figure 1.

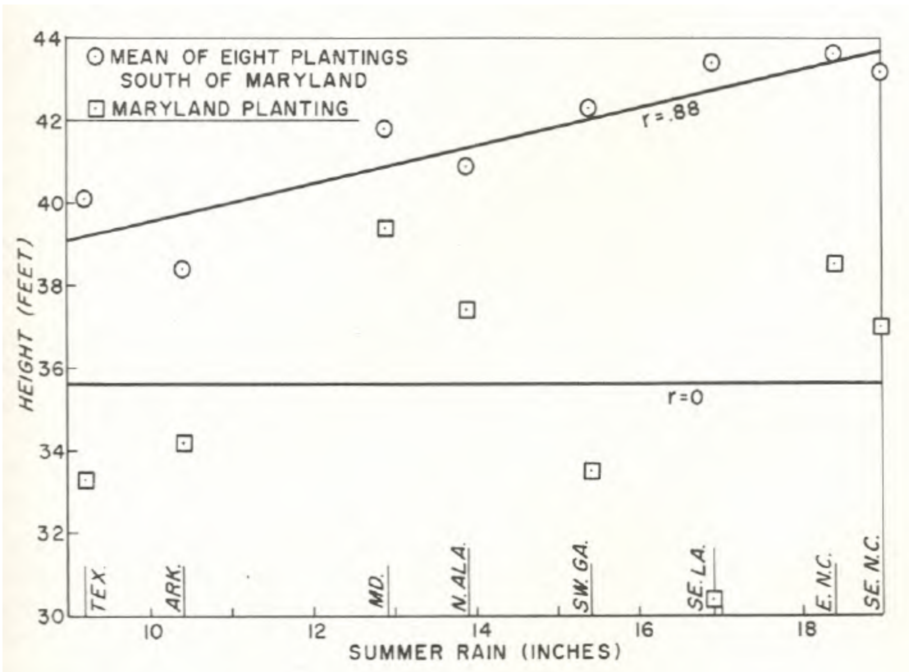

Figure 1.--Interaction of seed source x planting location in loblolly Series 1 at age 15 years.

There is little or no correlation among the three traits that vary geographically in loblolly--that is, trees with genetic potential for high survival, fast growth, and rust resistance do not occur in the same area. The trees from southeastern Louisiana do, however, combine fast growth and considerable rust resistance even though their survival has been only average. Therefore, use of seed from southeastern Louisiana is indicated in the area designated zone 2 in figure 2. More specifically, seed from southeastern Louisiana had best be collected from Livingston Parish (crosshatched area in zone 2). This was the source for the present study, and differences in rust susceptibility among loblolly pines from different parishes in southeastern Louisiana have been reported (Crow 1964). The northern limit of zone 2 was determined by good performance of the southeastern Louisiana trees in central Mississippi, central Alabama, and Georgia. The northeastern limit of zone 2 was set at the Georgia border because the Livingston Parish trees survived and grew less well in South Carolina and North Carolina than they did farther west. The western limit is set at the Mississippi River, as beyond that the frequency and intensity of droughts place a premium on survival.

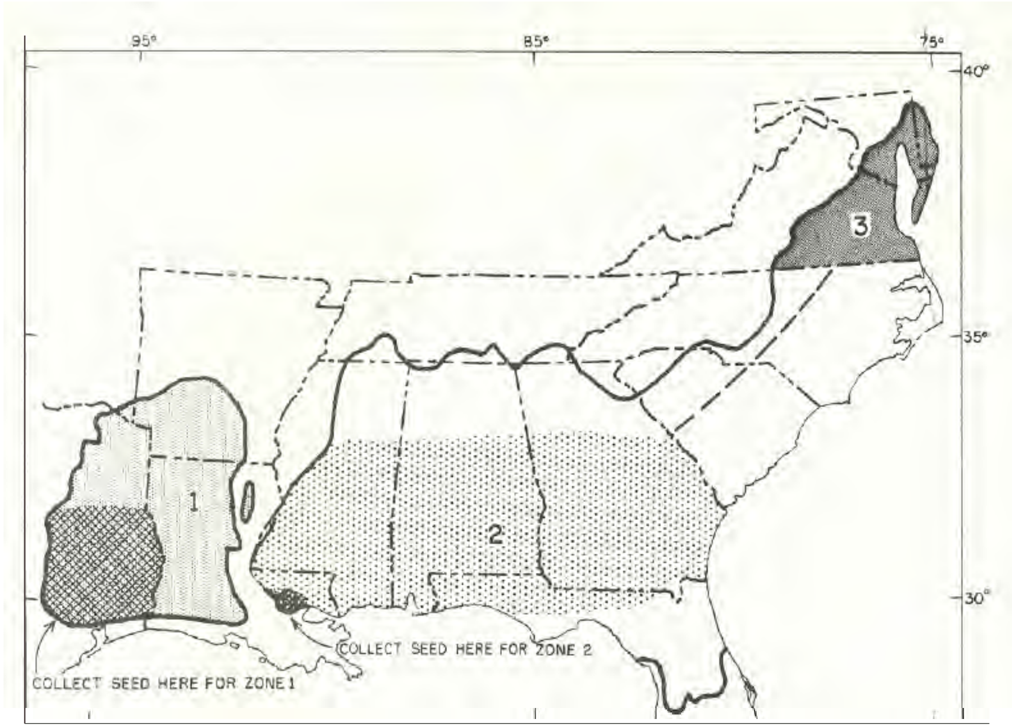

Figure 2.--Suggested seed collection and planting zones for loblolly pine. Natural range outlined by solid black line.

West of the Mississippi River the effect of latitude should be taken into consideration, as well as the likelihood of drought. There is a high probability of genetic variation in growth rate between the southern and northern populations. The Texas trees were taller than the Arkansas trees in the present study, even though they did not represent the southern extremity of the range in Texas. When the variation patterns for both survival and height are considered, it seems that loblolly seed for zone 1 should be collected south and west of the Sabine River (crosshatched area in zone 1). For plantings north of this zone, seed from north of the Sabine River would probably be better.

The network of plantings and seed sources is not as strong in North and South Carolina as it is in the Midsouth, but there is enough information from this and other work to show that Coastal Plain seed should be used only in the Coastal Plain and Piedmont seed only in the Piedmont. With this restriction, seed can probably be moved parallel to the coast anywhere within North and South Carolina; the dashed line in figure 2 divides the Coastal Plain from the Piedmont in this area.

In Virginia and northward the distance seed can be moved freely, without danger of growth loss, is much less than farther south; results in the Maryland planting clearly show this. "Collect seed in zone 3 for planting in zone 3" is probably a sound rule.

For planting north of zone 2 a TVA seed source study (Zarger 1961) clearly shows that inland sources (northern Mississippi, northern Alabama, northern Georgia, or the Piedmont of North and South Carolina) are best adapted.

SHORTLEAF PINE

The shortleaf pine phase of the study is considerably larger than the loblolly phase. It consists of 23 seed sources and 40 plantings distributed throughout the shortleaf range. The test is divided into six series of seed sources and plantings.

Plantations of the first three series were established during the winter of 1952-53, but losses from drought were so heavy that three more series were established in 1956-57. Though there are many exceptions, the last three series generally sample the same area as the first three, but the 10 surviving plantations from the first series constitute valuable replications by year. Thus, Series 1 and 4 sample the shortleaf pine range from near its southern extremity to near its northern extremity. Sources and plantings in Series 2 and 5 are in three distinct geographic areas: west of the Mississippi River, the southern Appalachian Mountains in Georgia and Tennessee, and the Allegheny Mountains in Pennsylvania. Series 3 and 6 test differences associated with longitude along a transect from southeastern Oklahoma to South Carolina.

The most important genetic variation has been in height and volume growth. Trees from the warmest parts of the range have excelled all others in Coastal Plain plantings up to 250 miles north of their point of origin. In the loblolly test more western than eastern trees survived, but in shortleaf the differences in survival have been small in all but the most northern plantings, where the superiority of the northern trees is striking.

The relationship between growth rate and temperature at seed source and the interaction between seed source and planting location are the dominant effects in the shortleaf test. Results in Series 4 are illustrative (fig. 3).

The two southernmost seed sources (southeastern Louisiana and southwestern Georgia) show a potential for fast growth that is well expressed in the southern plantings but not in the northern ones. In southern Mississippi, southeastern Louisiana, and southwestern Georgia (southern plantings in figure 3), trees from the two most southern sources in Series 4 average about 4 feet taller than the other trees.

In northern Mississippi, Tennessee, and North and South Carolina (middle-latitude plantings in figure 3) trees from southeastern Louisiana and southwestern Georgia still grow satisfactorily but are not as clearly superior to trees from other seed sources as they are in the most southern plantings. Still farther north, in Missouri and New Jersey, trees from southern sources grow considerably slower than more northern trees.

The strong relationship with temperature at seed source and the same interaction with planting location is also evident in Series 1, 2, and 5. For example, in all nine of the Series-5 plantings south of Pennsylvania trees from southern sources are taller than those from northern sources (fig. 4). In the

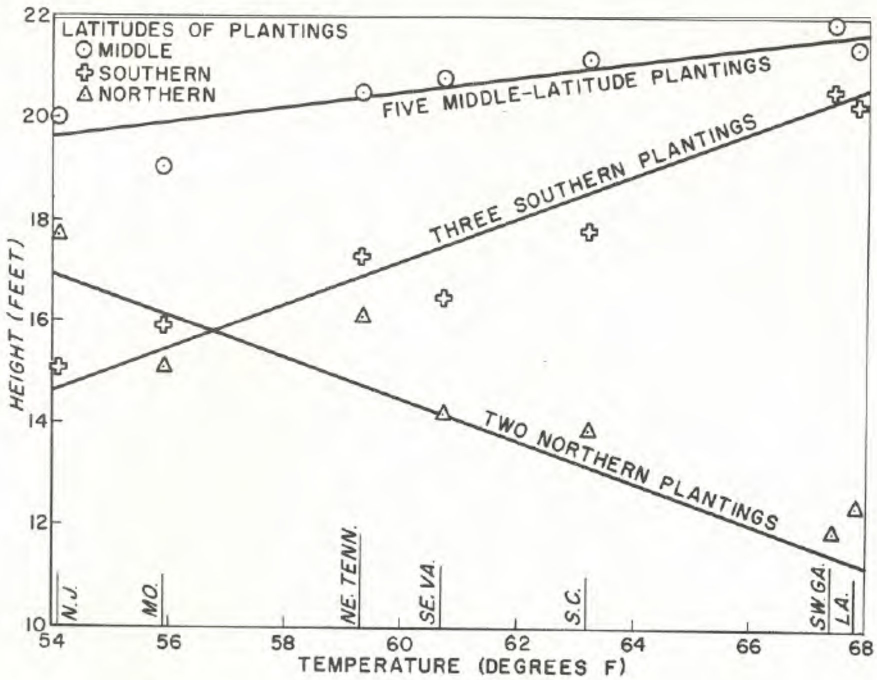

Figure 3.--Relationship between 10-year height and mean annual temperature at seed source in southern, northern, and middle-latitude plantings of shortleaf Series 4.

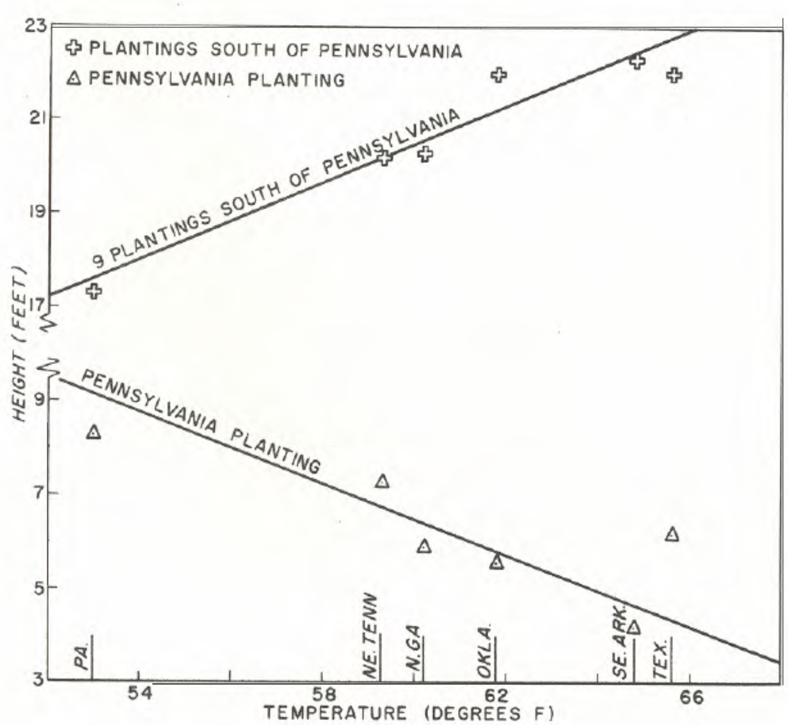

Figure 4.--Relationship between 10-year height and mean annual temperature at seed source in a Pennsylvania planting and in nine plantings to the southward. Shortleaf Series 5.

Pennsylvania planting the pattern is completely different. Survival and growth have been poor throughout this planting but the superiority of the northern, particularly the Pennsylvania trees, is obvious.

Figure 4 also illustrates another, more subtle, effect. In the nine plantings south of Pennsylvania, when trees from all six seed sources from Pennsylvania to Texas are considered, the relationship between height and climate at seed source is clearcut. This relationship is not evident, however, when only the trees from the three most western sources are considered; they are all about the same height in spite of a difference of 3.8° in mean annual temperature at seed source.

Shortleaf Series 3 and 6, 12 plantings in all, have revealed that very little genetic variation is associated with longitude along an east-west transect from southeastern Oklahoma to South Carolina.

Two results from the shortleaf phase of the study lend themselves to forestry practice: (1) the tendency for trees from the two southernmost seed sources east of the Mississippi River to grow faster than those from northern sources in southern plantings and in plantings as far north as northern Mississippi, and (2) the superiority, in terms of both growth and survival, of trees from the most northern sources in the plantings near the northern extremities of the species' range. In the middle of the range, on both sides of the Mississippi River, the relationship between growth in the test plantings and temperature at seed source does not seem strong enough to be of practical value.

Tentative seed-collection and planting zones are mapped in figure 5. If

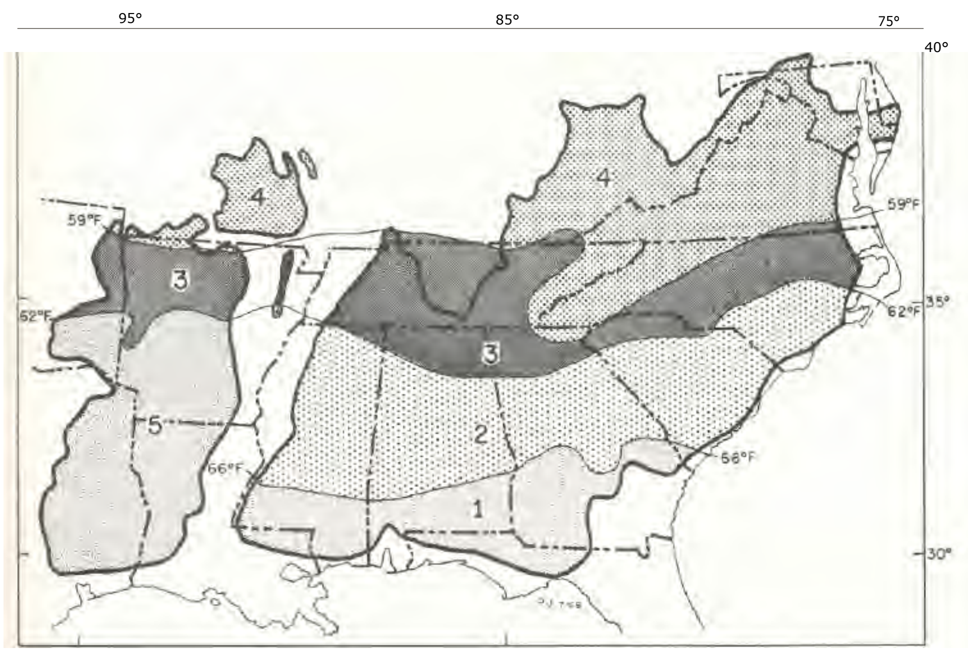

Figure 5.--Suggested seed-collection and planting zones for shortleaf pine, with isotherms of average annual temperature. Natural range is outlined by heavy black line.

shortleaf pine plantings are to be made in zones 1 or 2, seed should be collected in zone 1. In six plantations in zone 2, trees from zone 1 sources had about 17 percent more volume than trees originating in zone 2. Seed from zone 5 would very likely also be a good choice for planting in zone 2. For planting in zone 3, seed can be collected in either zones 2 or 3 or in the northern half of zone 5. Seed for planting in zone 4 and beyond should be collected only in zone 4. In the three zone-4 plantings in this study, trees from zones 3, 2, and 1 had 27, 48, and 76 percent less volume, respectively, at age 10 than trees from zone 4.

LONGLEAF PINE

The longleaf phase of the Southwide Study is similar in design to the shortleaf phase in that there are six series of seed sources and plantings; the plantations were established in 1952-53 and 1956-57. Series 1 and 4 sample the longitudinal range of the species from central Georgia to eastern Texas. Series 2 and 5 test two major influences that could be expected to cause genetic variation: one is the difference in climate between the Carolinas and the central Gulf Coast; the second is soil type--sandhill soils or Coastal Plain soils. Series 3 and 6 sample the northern, western, and southeastern extremities of the range and three intermediate points; they were designed to test the influence of climatic extremes within longleaf's range. In all, there are 15 seed sources and 35 surviving plantations.

After 10 years, geographic patterns of variation were evident in survival, initiation of height growth, total height, volume, and infection by brown spot.

Survival of the 32,900 seedlings originally planted in 1956-57 averaged 71 percent after 3 years, 69 after 5 years, and 57 at age 10. Trees from the two most westerly sources, central Louisiana and eastern Texas, survived well for 3 years but suffered proportionately more mortality between the fifth and 10th year than did trees from other sources. The western sources were also more heavily infected by brown spot than those from the central part of the range. These findings suggest a cause-and-effect relationship between brown spot susceptibility and survival.

As judged by height growth and volume at age 10, trees from southern Florida performed poorly in all plantings. Gulf Coast trees from southern Mississippi, southern Alabama, and western Florida grew faster than other trees in plantings 150 miles north and 250 and 300 miles east and west of the point of origin. Farther north and west, trees of more local origin performed as well as or better than those from the central Gulf Coast.

Height growth and volume per acre of the southern Alabama trees, for example, were outstanding in most of the Series-1 and -4 planting locations (fig. 6). Growth rate of trees from southern Alabama was well above average as far west as central Louisiana (Rapides Parish) and in central Alabama up to about 150 miles north of the Gulf Coast (Perry and Autauga Counties). Ninety miles still farther north in Alabama, however, growth rate of southern Alabama trees was below average. The northernmost Alabama planting is on the Piedmont Plateau, where average annual temperature is 62.3° F. and the elevation is about 1,400 feet. The central Alabama plantings are in the Prairie Belt at an elevation of less than 500 feet; average annual temperature is 64.0°. The southern Alabama seed source is on the Coastal Plain near sea level, and average annual temperature is 67.3°. Thus it has proved advantageous to move southern Alabama seed northward about 3° of average annual temperature but not 5°.

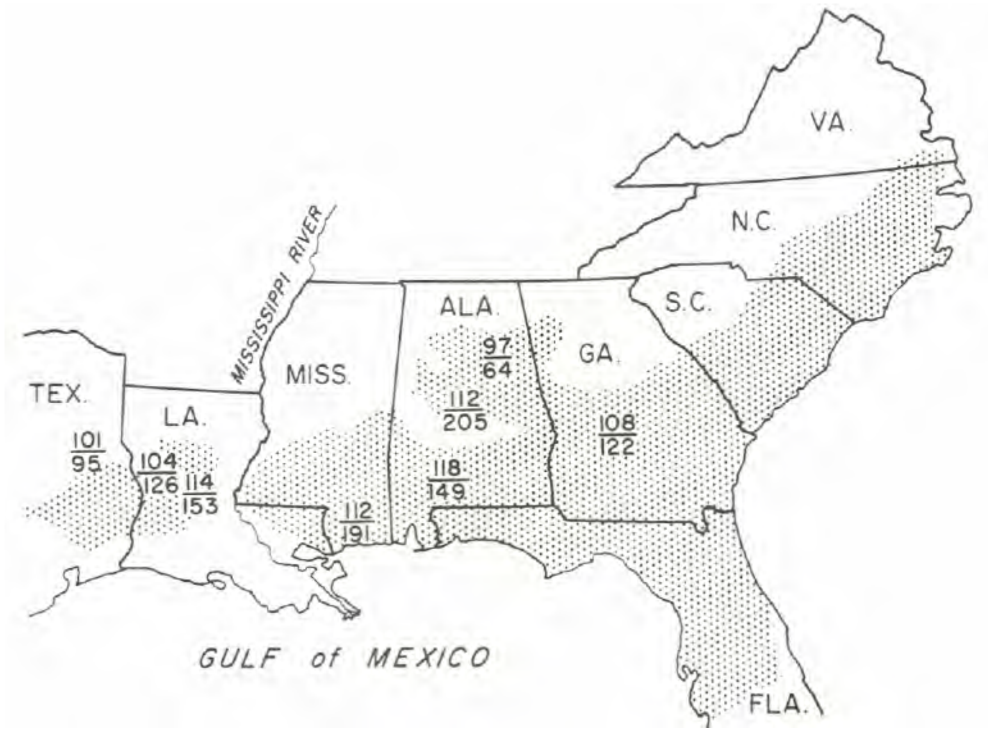

Figure 6.--Tenth-year height (numerator) and volume per acre (denominator) of longleaf pines from southern Alabama seed, expressed as percent of mean of trees from all seed sources represented in planting. Position on map indicates planting location, and the stippled area represents the natural range. Series 1 and 4 combined.

The southern Alabama trees are only performing slightly better than average in central Georgia, but in the more northern plantings of Series 2 and 5, near the North Carolina-South Carolina border, they are outgrowing local stock.

Trees from southeastern and central Louisiana ranked low in 10th-year height and volume in all plantings.

Taking results from all series into consideration, it is possible to map the zone within which trees from Gulf Coast seed sources have performed better than trees from other sources. If plantings are to be made in the area signified by the stippling in figure 7, collecting the seed from the hatched area (central Gulf Coast) seems advisable.

West of the stippled area in figure 7, seed from west of the Mississippi River is indicated. From present data the Texas counties of Polk, Tyler, and Hardin appear a better source than central Louisiana. The data do not define any "best" seed source for areas north or west of the stippled area. They do, however, show that there is no advantage in moving longleaf seed north more than 4° of average annual temperature. Reference to the isotherms of mean annual temperature in figure 7 will aid in making decisions along these lines.

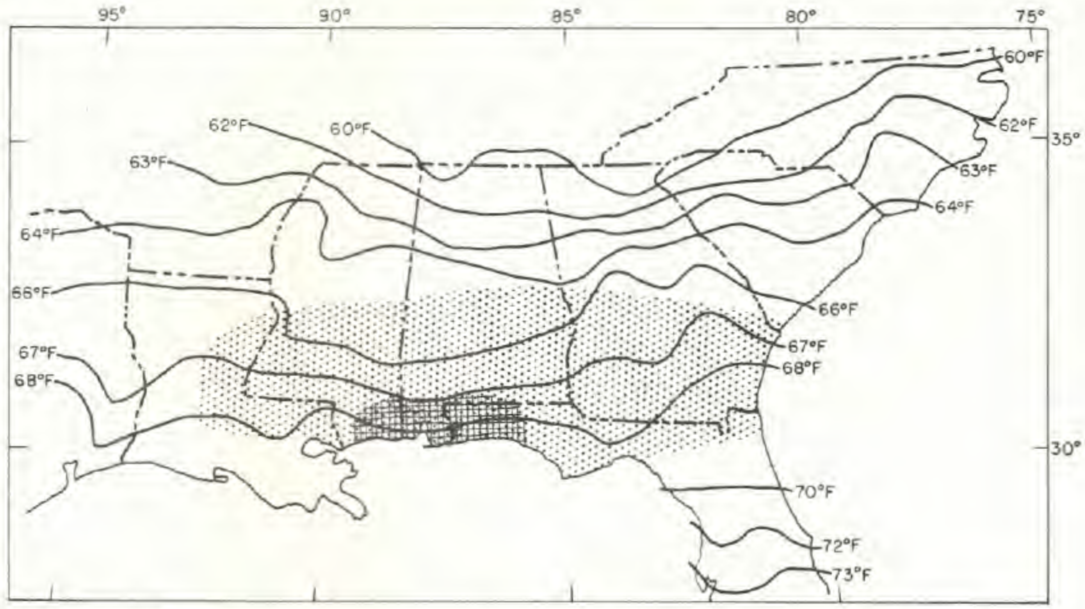

Figure 7.--Optimum longleaf seed-collection area (hatched) for plantings to be made within stippled area. Isotherms of average annual temperature are shown.

Moving longleaf seed from southern Florida into northern Florida or beyond is inadvisable. Present indications are that such a shift would result in almost complete failure.

The longleaf test also indicates some other combinations of seed sources and plantings that should be avoided if at all possible, as they are likely to occasion a growth loss of perhaps 10 or 20 percent. Thus, seed collected west of the Mississippi River should not be used east of the river. Seed from southeastern Louisiana seems a poor choice for use anywhere, unless further research shows that the two collections made for the present study are not representative. Seed from near the extremity of the range in northern Alabama should not be moved south or east more than about 150 miles, and it should particularly not be used near the central Gulf Coast. Similarly, seed from near the northern extremity of the range in Virginia or northeastern North Carolina should probably be avoided. Sources nearer the North Carolina-South Carolina border would be a better choice for plantings anywhere in the northeastern part of the natural range.

The slash pine phase of the study consists of trees from six seed sources planted in eight areas. Seed was collected in 1951 and plantings established in 1952-53.

By far the largest genetic variation was the poor survival and growth of trees from the southern Florida source (Polk County) in all plantings. The differences among the other sources, which are distributed in an east-west transect across the species' range, were generally small, but some differences between the northeastern Florida source and the other sources are of biological and probably economic significance. Most important, the northeastern Florida stock did not survive as well in some plantings as did stock from sources farther to the west or northeast. A good illustration occurred in Sabine Parish, Louisiana, where an adverse site, combined with drought during 1953, lowered overall 10th-year survival to 35 percent. Under such severe conditions the superiority of sources other than northeastern Florida was particularly well expressed (fig. 8). A similar result had been demonstrated previously in six other seed-source plantings established between 1937 and 1948 (Snyder et al. 1967). All of the earlier plantings, like the one in Sabine Parish, were well outside the natural range of slash pine. Within the range survival differences are smaller.

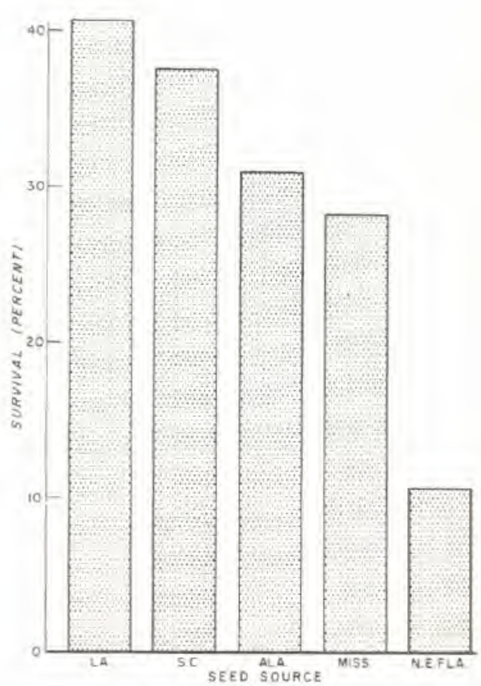

Figure 8.--Tenth-year survival, in a western Louisiana planting, of slash pine from five seed sources.

Two other Southwide Study plantings provided additional evidence of genetic differences between northeastern Florida slash pine and sources farther west and north. In Georgetown County, South Carolina, an ice storm in March 1962 damaged almost twice as many northeast Florida (Baker County) trees as it did trees of any other source. Also, when hogs rooted in the Baker County, Florida, planting in 1959, the local stock was significantly less damaged than that from Polk County, but significantly more damaged than the South Carolina, Louisiana, and Alabama trees, which were scarcely touched.

These variations all indicate that the northeastern Florida source is more like the southern Florida source than are the Louisiana, Mississippi, or South Carolina populations. The survival and ice-damage data indicate that trees from north or west of northeastern Florida would be more suited for planting north or west of the species' range or on droughty sites anywhere that use of the species is contemplated.

The performance of the northeastern Florida trees is of particular value for judging the suitability of seed collected from planted stands of unknown seed source, because almost all of the slash pine plantings established before

1940 and many established even later were from seed collected in northeastern Florida and south Georgia. On the basis of the present results, trees from seed collected in these old plantings would be less suitable for planting north or west of the natural range than trees of more western or northern provenance.

The only height differences evident in the Southwide slash pine plantings are attributable to the southern Florida seed source, which by virtue of its low survival was poorly represented in most of the plantings. Except locally, where their performance was average, trees from the southern Florida source grew relatively slowly in all plantings where enough of them survived to make a comparison possible.

Tests currently in progress at the Southeastern Forest Experiment Station sample the slash pine range much more thoroughly than did the Southwide Study and have shown genetic differences in height growth. The geographic pattern of this variation is complex, but the poor performance of the southern Florida trees when they are moved north is a strong feature of it (Squillace and Kraus 1959; Squillace 1966). The east-west component of the variation in height is much smaller than the north-south component in both the Southwide and the Southeastern Station study.

RELIABILITY OF RESULTS

In conclusion, it is evident that the 10-year data on disease resistance and survival for all species are as reliable and useful as anything that is likely to be obtained from future reexaminations. In height and volume growth some changes from present patterns may occur, but the plantings have grown through a third to a half of a pulpwood rotation with no drastic reversals in ranking of individual sources. The basic patterns of variation that first appeared are still present and, most important, there have been no instances of outright cold-induced injury when southern sources have been moved northward within the limits suggested in this paper. Such injury has occurred only in the Missouri, Pennsylvania, and New Jersey plantings, which are the most northern in the study. In other plantings trees moved too far north have responded only by growing slowly.

The plantings also have withstood some severe weather. Three events in particular put them to a harsh test:

> The drought west of the Mississippi River during 1950-56, which was one of the worst on record in the area.
>
> An extremely destructive freeze late in March 1955, after an extended warm period. All plantings established in 1952-53 were exposed.
>
> The cold winter of 1962-63, which brought alltime record or near-record low temperatures to all plantings in the study.

The ability of trees from areas of relatively mild climate to withstand these events seems strong evidence in favor of the present proposals for seed movement.

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