CHAPTER 6

RACIAL VARIATION—TREES PLANTED

This chapter is devoted to a discussion of traits and *genotypic* variation in trees grown in study plots at a few geographic locations. The seed for these studies was collected at different locations within the range of each species. It is in contrast to the preceding chapter discussing *phenotypic* variation in trees growing at various locations generally within the natural range.

RACIAL VARIATION IN LOBLOLLY PINE

Loblolly pine has a more extensive natural range than either slash or longleaf pines but not as extensive as shortleaf pine; wood volume is unevenly distributed as shown by maps in chapters 1 and 5. In central Florida, the southern limit of typical slash pine and loblolly pine is approximately the same, at latitude 28° N. Along the Atlantic Coast, however, slash pine extends northward only to latitude 30° N., while longleaf goes to 37°, and loblolly and shortleaf to 40° and 41°, respectively.

Climatographs shown in chapter 1 (Wahlenberg and Ostrom 1956) indicate quite strong differences in climate throughout the range of loblolly pine. In central Florida, yearly range in temperature is relatively small. Low winter temperatures are accompanied by low rainfall, and summer temperatures by high rainfall. At Dover, Delaware, however, rainfall is fairly uniform from a period of low temperatures in winter to midsummer, when there is a slight increase in rainfall occurring with maximum temperatures. At Booneville, Mississippi, at the northern extension of the range of loblolly pine near the Tennessee State line, low winter temperatures are accompanied by high rainfall, and rainfall decreases as temperatures increase during spring and summer. In Texas, rainfall is uniform from midwinter to early summer but then decreases during the months of highest temperature. The wide range in temperature, length of growing season, and variation in the pattern of seasonal rainfall may exert quite strong influences in the development of racial strains over the entire range of loblolly pine. Elevation occupied by loblolly pine within its natural range is greater than that of slash and longleaf pines but not so great as that of shortleaf pine.

Many studies of racial variation in loblolly pine have been attempted since 1928. These vary in size and geographic locations. Because of the large geographic range of loblolly pine, few, if any, studies could adequately sample all of the possible conditions. For the purposes of summarization, studies in racial variation of loblolly pine have been divided into three groups. These are: studies within the range of loblolly pine, studies outside the range of loblolly pine in the United States, and racial variation studies outside the United States. Groups of studies under these subject matter headings will be discussed in this order.

Studies Within the Natural Range

Louisiana

The oldest racial variation study in the South, established with 1–0 stock during December 27–30, 1926, was with loblolly pine. Thus, it formed something of a base on which research programs were started for other parts of the South and other species. The most recent publication on the results of the Bogalusa, Louisiana, racial variation study was based on 35-year results (Wakeley and Bercaw 1965) and earlier reports were by Wakeley (1944, 1950) and Bercaw (1955). In addition to local stock for Louisiana, the study contained seedlings of Texas, Georgia, and Arkansas origin. Although the number of seedlots was small, they sampled quite different areas within the natural range of loblolly pine. The Georgia stock came from the north-central part of the State, and the Arkansas seedlot from the northern part of the natural range, where the growing season is shorter and temperatures are lower than at the site of the test plantation in southeast Louisiana. The Texas seedlot was obtained in an area where low summer rainfall combined with high temperature occurs, a condition resulting in considerable drought resistance as expressed by increased survival in subsequent tests. The four loblolly stocks were planted in single-row plots, replicated six times. Rows are 8 feet apart and contain 33 trees apiece, spaced 6 feet apart, to get totals of 200 trees of each stock and a grand total of 800 trees. The authors have pointed out that although the design provided an error term for testing the significance of any difference observed among stocks, it was marred by the arrangement of the four stocks in the same order—Louisiana, Texas, Georgia, and Arkansas—in each of the six sets of replications or "blocks." To offset the effect of border rows, analysis of variance was applied to the four stocks in each of the four interior blocks. Although the close spacing and row plots had a limiting effect on accurate comparison of growth, particularly in volume per acre, the study provides a large amount of information over a long period of time. The row plots permitted photographic pres-

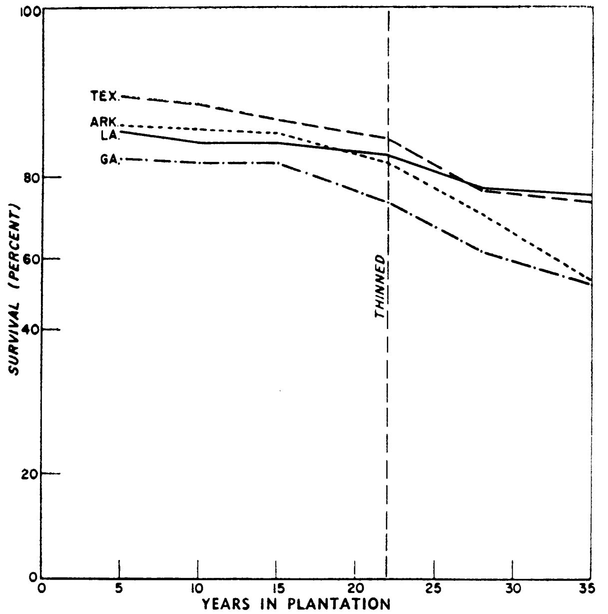

Figure 60.—Survival percent of four loblolly pine racial selections decreased slightly with time, but there was no important change in ranking. Survival was based on trees originally planted and unmodified by thinning at age 22. (Wakeley and Bercaw 1965)

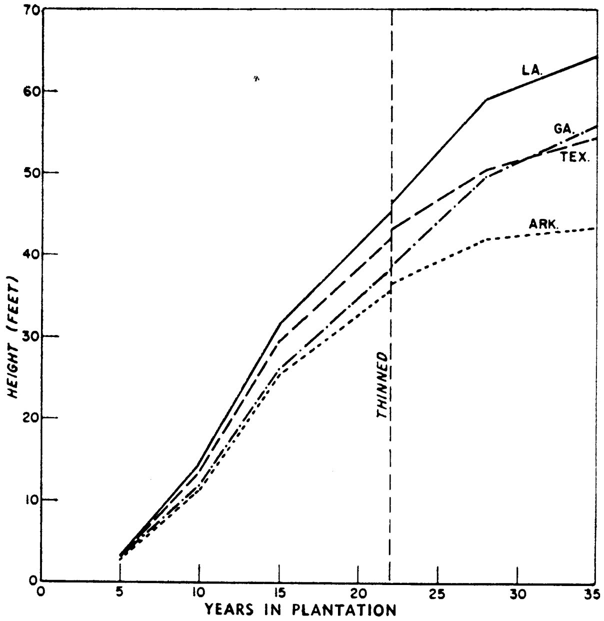

Figure 61.—Ranking of loblolly pine races by heights of living trees when measured did not change appreciably with time. Only for number of trees did the mean of trees lost in thinning differ significantly from the mean before thinning. Selection of the more vigorous group from which to obtain seed early in the period of study would have been as reliable as at age 35, and the superiority of the local trees is demonstrated. (Wakeley and Bercaw 1965)

entation of results that may have been more effective than volume growth figures.

Differences were significant at the 1-percent level for height, diameter, individual tree volume, and volume per acre, and at the 5-percent level in survival and in percentage of living trunks infected with fusiform rust (figures 60 to 62). In all traits the Louisiana or local stock performed better than that from any other area.

Although the 1926 study had limitations in design, it did focus attention on extreme differences that might result in volume production through use of stocks from different geographic locations. This is emphasized by the fact that local stock produced 78.03 rough cords per acre, that from Texas 32.49, Georgia 34.45, and Arkansas 13.38 cords. Thus, local Louisiana seed stock produced 5.8 times as much wood as that from Arkansas. The result of the early reports on this small study alerted silviculturists to the importance of seed source and also stimulated more consideration in seed collection and further research into the subject. The authors are concerned about the accuracy of results at various stages throughout the 35-year life of the study, but it is evident from the figures for volume growth and the curves of various traits over age that had silviculturists acted on the evidence of the study in its early years, they would have proceeded safely in view of the results available at age 35.

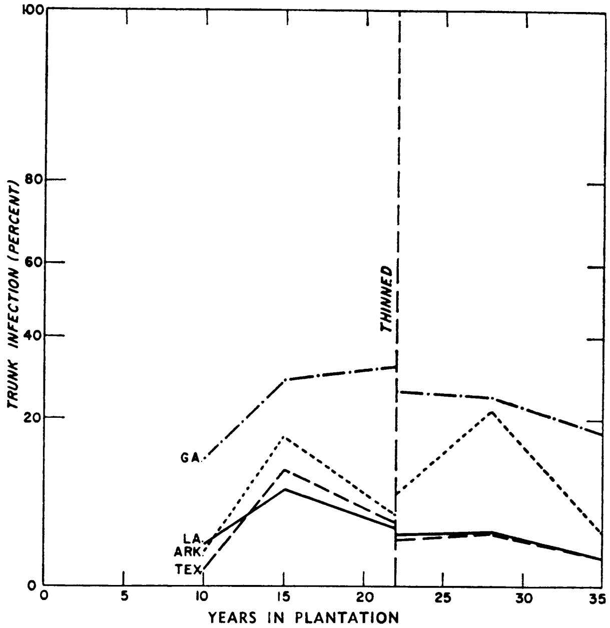

Figure 62.—Ranking of loblolly pine races by percentage of trees infected with fusiform rust remained relatively constant during the 35-year study period. Trees of the Georgia race were the most susceptible to rust. (Wakeley and Bercaw 1965)

Another study of racial variation in loblolly pine was started in Louisiana in 1953 (Crow 1964). Results have been reported through the tenth growing season, with differences small and nonsignificant among the sources in survival, total height, d.b.h., and relative volume, but different growth trends seem to be established. Although the differences among stock from various locations are not statistically significant, height is increasing at different rates among the four seed stocks. At age 2 all seedlots were 2.4 feet tall; at age 10 the shorter race was 24.7 feet and the taller race 29.5 feet, or 19 percent taller. A randomized block design was used with four replications of each seed source. Spacing was 6 by 6 feet, with 1,210 trees per acre. Seed was obtained from two locations not far apart in southeast Louisiana, namely Washington and Livingston Parishes; and also from Rapides Parish in central Louisiana and from Ashley County in Arkansas. The latter is near the Louisiana State line in the eastern part of the State. In this study as well as in the study previously reported at Bogalusa, Louisiana, Arkansas stock has consistently grown at a slower rate than trees from Louisiana. However, the growth rate is somewhat different between seedlots collected a short distance apart in southeast Louisiana, such as Washington and Livingston Parishes. Survival has been good throughout the period of the study, varying from 66 to 74 percent. Survival of Ashley, Arkansas, stock was 74 percent, while that from Louisiana ranged only from 64 to 67 percent. Although survival was practically the same for stock from Livingston and from Washington, Louisiana, the stock from Livingston Parish, Louisiana, had produced 140 cubic feet per plot, or 17 percent more than the 119 cubic feet for the stock from Washington Parish, Louisiana, a short distance away. When compared with trees from Ashley, Arkansas, the Livingston, Louisiana, trees were 19 percent taller and at age 10 had produced 140 cubic feet per plot, or 27 percent more than the 110 cubic feet for the Ashley, Arkansas, stock. The ranking of stock by volume growth has not changed over the 10-year period. Interaction between survival and height and diameter growth is emphasized by these results. Where survival is constant, the small increase in height growth, such as 19 percent between Livingston Parish and Ashley County stock, and also the 9-percent increase in diameter, resulted in a 27-percent superiority in cubic-foot volume of wood per plot. Although differences are not statistically significant, they are approaching the magnitude of considerable economic importance, particularly cubic-foot volume growth. The results of this study lend emphasis to the importance of fairly sensitive statistical designs, particularly if results are to be interpreted correctly at an early age. Early results of this racial variation study were reported by Crow (1958a, 1958b, 1961).

An additional study of loblolly pine racial variation in Louisiana has been described by Merrifield *et al.* (1965). This study involved loblolly pine seed collected from a number of trees at 12 different locations in Louisiana and outplanted at 1 location in north Louisiana at Homer. The study is of a randomized block design with plots replicated four times. The seedlings were planted at a spacing of 6 by 6 feet in 11 rows of 11 trees each, or 121 trees per plot; a border strip of 2 rows surrounds the 49 trees in each plot. Established in 1959, study results only through the first 5 years are available. At neither 1 or 5 years were there any differences attributable to seed source. Between sources no differences in susceptibility to insects or diseases were observed. Fusiform rust infection was less than 1 percent over all plots. Survival of seedlings was very high, ranging from 94 to 99 percent at the end of the fifth year. It may be of some significance that local stock, which in this case is that from north Louisiana near the Arkansas State line, is growing as fast as loblolly from southern parts of the State, more than 200 miles away. This is in contrast to the slow growth of Arkansas stock when compared to other stocks in southern Louisiana in the studies reported by Crow (1964) and Wakeley and Bercaw (1965). The study, as yet, does not show the same clinal variation as the Georgia-Florida study described by Kraus (1967b). However, the Louisiana study compares seed collected over a range from 66° F to 68° F, while the Georgia-Florida study contains seed collected over a range from about 62° F to nearly 71° F, or a range of 2° versus 9°.

Arkansas

Plantings of seed from 36 geographic locations throughout the loblolly pine range were evaluated at 10 years. Height and diameter were greatest for trees from southeastern Atlantic Coast areas, drought resistance was highest for trees from drier sites and western locations, and rust resistance was greatest for northern and western trees. Trees from South Carolina produced 30 percent more volume and had 9 percentage points more fusiform rust than local trees.

There were north-south and east-west patterns in susceptibility to rust (fig. 63). Volume growth was directly correlated with summer rainfall and average January temperature at the seed source, and inversely correlated with distance of the seed source from the coast.

Texas

Loblolly pine from different locations within the State and from other states varied in drought re-

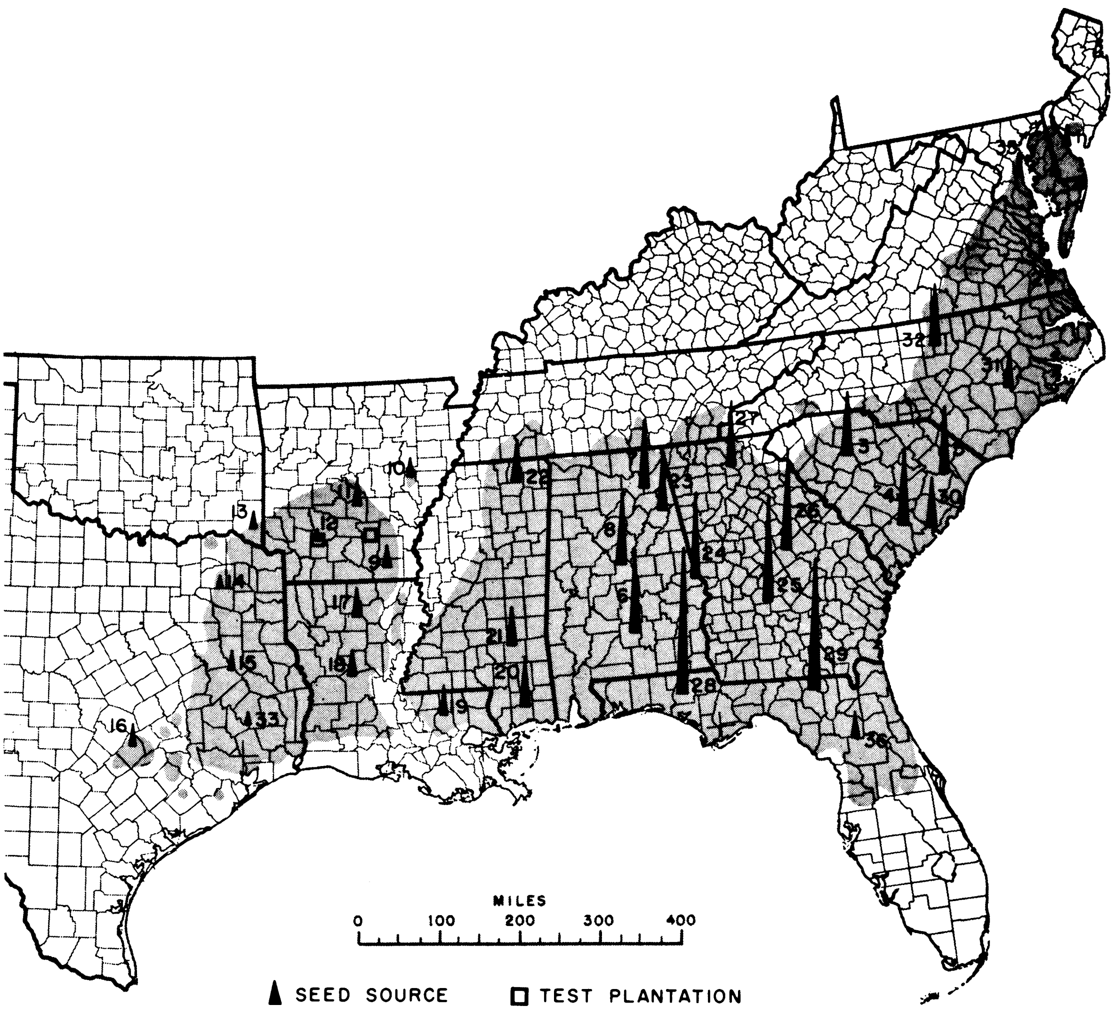

Figure 63.—Trees from seed sources throughout the range of loblolly pine (shaded) were planted in southern Arkansas. Height of cones indicates relative susceptibility to fusiform rust. (Grigsby 1973)

sistance and several other traits (Zobel and Goddard 1955). Seed was obtained from stands in isolated areas known as the "Lost Pines," which lie west of the limits of the natural range of loblolly pine, and from different areas within the range of loblolly pine in Texas and from other states including Louisiana, North Carolina, and Florida. Outplantings were made at several places in Texas, in Louisiana, and in Mississippi. Because the year of 1954 was extremely dry, conditions for testing drought resistance were ideal. After 2 years, seed from the Lost Pines area were consistently better in survival than those from more eastern areas. Survival of trees from the drier sites on the western edge of the pine region was also good, while that for the Coastal Plain trees was poor. Trees from one location in Louisiana, Evangeline Parish, survived as well in the southern test areas as trees from western areas but did poorly in the northern area. Survival differences were considerable. In the Robertson County test area in 1954, the best lot of seed, that from Bastrop County, had 95-percent survival, while lowest survival was 8 percent for the loblolly pine from Florida. Within Texas, average survival for collections in the four different locations varied from 44 percent to 60 percent. Survival from areas farther east in the natural range of loblolly pine was lower—that from Louisiana 46 percent, North Carolina 31 percent, and Florida 10 percent. It was thought that survival of the Florida trees was unusually low because seed of Florida origin planted in other years survived somewhat better. On the basis of overall performance, summarizing results at seven plantations, the Fayette County stock was best, followed by Bastrop County, then seed from the western edge of the natural range of loblolly pine, Texas Coastal Plain, Louisiana, North Carolina, with Florida last (Cech and Goddard 1957). After 5 years in the field there were no apparent differences in bole form and quality between seedlings of Lost Pines origin and other more eastern sources of seed (Goddard and Brown 1959). Survival patterns remained unchanged from the 3-year performance data. The results indicated significant differences in height and d.b.h. among seedlings from different locations within Texas and Louisiana. The differences were relatively small, however, and when height growth was averaged for all sites, maximum growth was only about 12 percent taller than the shortest lot of seedlings. On the other hand, pronounced differences occurred among groups of trees in growth on different planting sites. In Texas, average growth on three sites ranged from 2.48 meters to 3.51 meters, although there was little indication of interaction between site and source of seed in growth rate. The more drought-resistant seedlings have more efficient transpirational apparatus than the less drought-resistant loblolly pine seedlings (Gilmore 1957). The more drought-resistant seedlings can absorb water almost as fast as they lose water, even at high soil moisture stress. Also, total carbohydrate content and calcium content of the roots appear to be associated with drought resistance. These observations were based on tests with seedlings supplied by the Texas Forest Service which came from mother trees at different geographic sources. They were divided into groups of more drought-resistant and less drought-resistant seedlings based on progeny performance in the field. From a study of germination responses of seeds and growth responses of seedlings, it was concluded also that some edaphic differentiation occurs primarily in seedling growth response to moisture (Youngman 1967). Seedlings from the drier disjunct populations in Texas generally have faster growth rates than seedlings from eastern Texas. Local ecotypic differentiation within areas was shown also by the root-growth responses of seedlings of lowland and upland origin. In further tests of variation in drought resistance, it was observed that progenies of individual parents selected from sites subjected to drought exceeded average differences among seedlots from different geographic locations (van Buijtenen 1966b). Survival ranged from 7 to 85 percent among progenies of individual parent trees and from 27 to 55 percent among lots of seedlings collected at different geographic locations. It was concluded that survival could be increased by about 10 percent of the average by selection, and increased still further by controlled breeding.

Seedlings from the seedlots used in tests described by Zobel and Goddard (1955) in studies of drought resistance in Texas were planted in southern Mississippi (Wells 1966). At 10 years of age the range in height among nine seedlots from different locations in Texas was very small, and height ranged from 18.8 feet to 22.2 feet, or about 18 percent. However, loblolly pine seedlings from Texas had only 5.8 to 16.6 percent rust infection, and Louisiana stock 9.5 percent, while seedlings from Spalding County, Georgia, averaged 32.1 percent. Differences in height growth were not statistically significant, but there were significant differences in rust infection among the loblolly pine trees from different locations within the State of Texas. Loblolly pine seedlings of Georgia origin were slower growing than those from Texas or Louisiana, and averaged only 18.1 feet.

Mississippi

Observations of erosion control plantings showed large differences in amount of litter deposited by different species of southern pine from different geographic areas (Thames 1962). In 4-year-old plantings, height in feet and litter production in grams per square meter of ground area for loblolly pine from different areas were as follows: Caldwell County, Texas (Lost Pines), 5.8 feet, 221 grams; Cherokee County, Texas, 4.8 feet, 206 grams; northwest Georgia, 4.7 feet, 190 grams; and Ashley County, Arkansas, 3.9 feet, 112 grams. Loblolly pine from one of the locations in Texas was 49 percent taller and produced nearly twice as much litter as the Ashley County, Arkansas, loblolly pine. The other southern pines tested, which were shortleaf, Virginia, and sand pines, grew much slower in height than loblolly pine and produced relatively small amounts of litter.

In south Mississippi, loblolly pine from 11 locations varied slightly in height growth and widely in southern fusiform rust infection at 10 years of age (Wells 1966). Seedlings from middle Georgia were the shortest, averaging 18.1 feet, and the most susceptible to rust, with 32.1 percent infected. Trees from southeastern Louisiana were 20.8 feet tall and only 9.5 percent infected. The other nine lots of trees were all from east Texas locations and ranged from 18.8 to 22.2 feet in height and from 5.8 to 16.6 percent infection by rust. The fastest growing race of trees from Texas was about 23 percent taller than that from Georgia.

Studies of needles from trees of different geographic origin grown in northern Mississippi (Thames 1963) showed significant differences in many characteristics. Trees from Lost Pines (Caldwell County, Texas), northwest Georgia, Crossett, Arkansas, and Cherokee County, Texas, were available for study. Both locations in Texas from which seed was obtained were in belts of low rainfall, while the areas in Arkansas and Georgia had more rain. Cross-sectional area and perimeter of needles varied significantly by source of seed. Both measurements were highest for the Lost Pines trees, intermediate for Cherokee County and for north Georgia, and lowest for trees from Crossett, Arkansas. Ratios of perimeter to area were 1 to 0.104, 0.095, 0.099, 0.084 for the seed of different origin. Since needle lengths were not significantly different, these ratios reflect relations of needle surface to volume. Number of rows of stomata did not vary significantly by source of seed, but the numbers of stomata per unit length of row differed significantly at the 1-percent level, the Lost Pines plants having the fewest and those from north Georgia the most. The Lost Pines trees thus had the fewest stomata per unit of surface area and needle volume; those from Cherokee County, north Georgia, and Crossett, Arkansas, had progressively more. Results of microscopic examination also showed differences significant at the 1-percent level among seed sources in thickness of the epidermal cell layer and in numbers of hypodermal cells. Hypodermal cells of the Lost Pines seedlings averaged 7.2μ in thickness, and those from Crossett, Arkansas, 9.4μ, with trees from other locations intermediate. Similarly, the Lost Pines seedlings had the most hypodermal cells per needle cross section and the Crossett plants the fewest. There were no consistent differences among seedlings from different geographic locations in thickness and number of endodermal cells, or in the area occupied by conduction or mesophyll tissue. All the anatomical differences observed in the needles of Texas loblolly pine, particularly those from the Lost Pines seedlings, tend to reduce the opportunities for moisture loss from needles, and these may be inherited adaptations to a more xeric climate. Thames (1962) felt that the resultant improvement in their water economy was probably responsible for the superior growth of these trees on droughty sites in Mississippi, in which needle production was much higher for Lost Pines or Texas seedlings than for those from Georgia or Arkansas.

Loblolly pine stands nearest the Gulf Coast in Mississippi and Alabama were least resistant to fusiform rust, and resistance increased gradually to the north and west in a clinal pattern in a large study by Wells and Switzer (1971). Resistance was estimated on 4-year-old trees in wind-pollinated families of 5 trees in 115 stands in Mississippi and adjoining areas in Alabama and Louisiana. Stands with a high degree of resistance were located in the Florida Parishes of Louisiana and adjacent areas in southwestern Mississippi. Information about the variation among stands and trees within stands in resistance to rust is given in the chapter on stand variation.

Florida

Results of a large study with loblolly pine showed a distinct response to a "natural photoperiod treatment" by plants of northern origin, and little or no response by plants of southern origin. The response was primarily one of prolonged seasonal growth (Perry *et al.* 1966). Thirty-one lots of loblolly pine seed from different geographic areas over the South, sampling north to south and east to west, were used in the study. Half the trees were grown under the normal photoperiod of Gainesville, Florida, and half were subjected to an extended photoperiod regime equivalent to that of Worchester County, Maryland. Under natural photoperiods, more than a twofold variation in height growth occurred between different loblolly pine lots and seedlings from different locations (fig. 64). Plants from a local area near Ocala, Florida, grew nearly 18 feet during the experiment. The trees from the northernmost latitude in Maryland grew barely 7 feet. The effect of floodlights was to increase the growth of the trees of northern origin considerably (fig. 65). However, even under prolonged photoperiods, northern trees did not grow as well in the Florida environment as the local trees. This indicates other factors than a shortened photoperiod are limiting growth of northern trees when they are grown in Florida. The height growth of the local trees under floodlights was only ½ foot greater than in the normal Florida day-length plot. The loblolly pine from northern locations produced only 2 whorls of branches per growing season, while local and other southern trees produced 6 to 10 whorls. Another effect of the floodlights was to prolong the duration of seasonal growth. Height growth was significantly correlated with daily rate of growth, duration of seasonal growth, initial height, frost-free season, and latitude of origin. Regression analyses showed that differences in daily rate of growth could account for about 60 percent of the variation in height growth, and differences in duration of seasonal growth could account for about 30 percent. The two variables account for about 85 percent of the variation in total growth when combined in a multiple regression analysis.

Georgia

Highly significant differences in several traits were found among loblolly pine from different geographic locations in a study covering an area from north Florida to north Georgia (Kraus 1967b; Barber 1966). The results at 10 years of age were based on a study that started in 1954 in an area not included in other studies. Cones collected from 20 to 26 trees in each of 14 locations in Georgia and 3 in north Florida were outplanted at 10 locations. One

Figure 64.—In the normal photoperiod of Florida, 3-year growth of loblolly pine decreased as latitude of seed origin increased. Trees from different geographic locations are (left to right) Florida, Georgia, North Carolina, and Maryland. Intervals on the measuring pole = 1 foot. (Perry *et al.* 1966)

seedlot from southeast Arkansas was included in the study. Highly significant differences among the broad areas within the State were found for survival, height, diameter, and volume growth. Magnitude of these differences was not large for all traits, although the trends were consistent. Survival averaged over all plantations was highest for the mountain seed source (80 percent) and declined for each of the southern provenances, 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 flatwood areas and tended to decrease in each successively more northern province. There was a slight tendency for rust infection to be lowest among trees among the northern seedlots and highest among trees from areas in the Georgia flatwoods, but the differences were neither large enough nor the trend consistent enough to attain statistical significance. Although not included in the analysis of the combined data for the State of Georgia, performance of the single lot of seed from Arkansas was important. Trees from this area were unexcelled in survival and resistance to rust infection. Their exceptional rust resistance throughout the State supported previous reports on the low susceptibility of fusiform rust infection in the western races of loblolly pine. In height, diameter, and volume growth, they were intermediate between trees from the Piedmont and mountain areas. Due to their high survival and rust resistance, Arkansas trees produced the highest volumes per acre in all but the mountain and flatwoods planting provinces. The relationship between source of seed and growth in each planting province as expressed by height, diameter, and volume is shown in figure 66. In general, trees from the Florida areas grew slightly slower than trees from areas in the Georgia flatwoods and Coastal Plain, and sustained slightly higher mortality and rust infection. There were highly significant differences between loblolly pine seed from different locations within the five major seed-collection provinces in only two traits: survival

Figure 65.—In Florida at 3 years of age, loblolly pine from southern locations grew faster than northern trees, although the day length was adjusted to the normal for northern trees. However, northern trees grew faster under their normal day length than under the Florida day length. Trees from different locations (left to right) are Florida, Georgia, North Carolina, and Maryland. Intervals on the measuring pole = 1 foot. (Perry *et al.* 1966)

and rust infection. 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 areas when they were 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. In the Georgia flatwoods, the average growth of the local seed sources was noticeably superior to all the nonlocal seed. When solely Georgia seed sources are considered, trees from local sources produced the highest volumes per acre in all but the Piedmont and mountain provinces. This trend is shown for height, d.b.h., and volume growth (fig. 67), where the average values for the 14 Georgia seedlots 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, 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. From the standpoint of guiding seed collections and seed orchard clones, it was concluded, based on the first 10 years of results, that within Georgia, trees from areas south of the planting province grew best in all but the Georgia flatwoods.

A small study with plus-tree progeny reported by Sluder (1973) gave evidence of tree-to-tree and racial variation in loblolly pine similar to those of

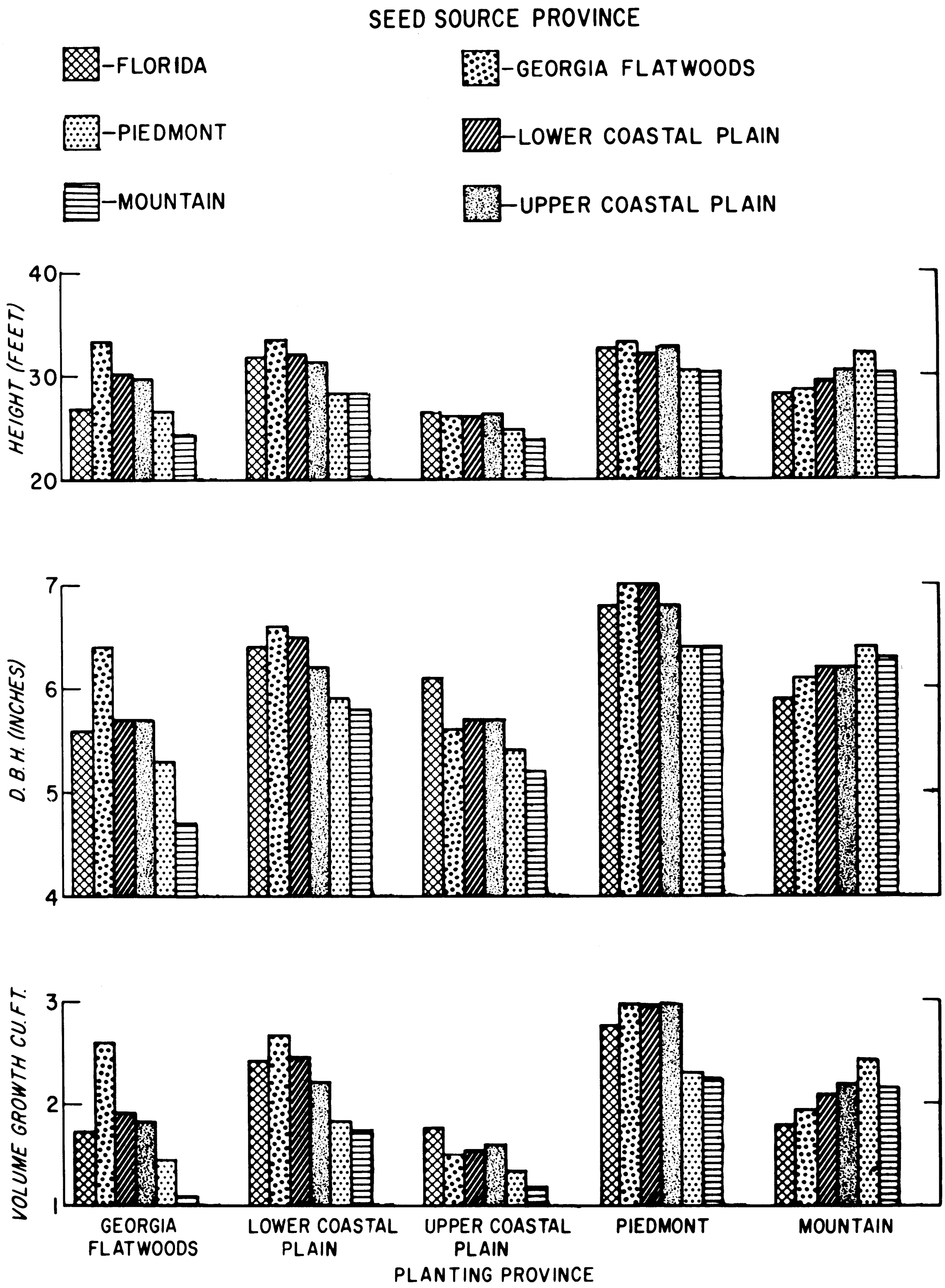

Figure 66.—Loblolly seed from the flatwoods is best for the flatwood province and the lower Coastal Plain. Local seed seems best to use for the upper Coastal Plain and the Piedmont, but Piedmont seed is clearly better for planting in the mountain area. (Kraus 1967b)

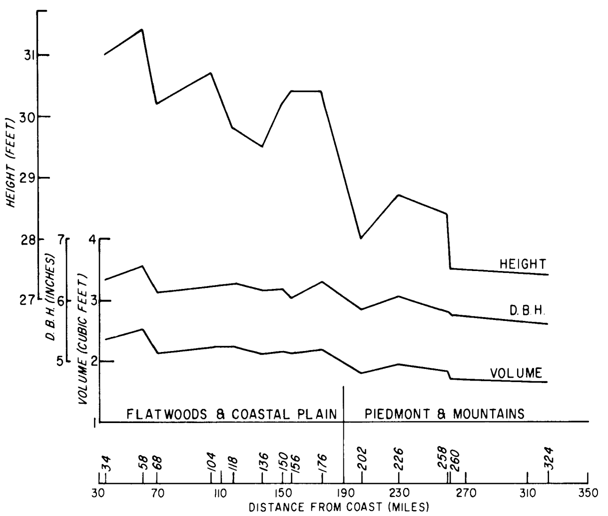

Figure 67.—Trends in height, d.b.h., and volume growth along a SE-NW transect in Georgia in 14 local races averaged over 10 plantations show decreasing vigor as distance from the Atlantic Coast increases. (Kraus 1967b)

the large Georgia study reported by Kraus (1967b). Two plus-tree progenies from Crossett, Arkansas, produced 9.81 and 12.39 cubic feet per plot compared with three Georgia progenies that produced only 4.23, 4.26, and 4.60 cubic feet per plot. The progenies of Arkansas trees had 38.5 and 100.0 rust-free stems and more than 91.0 percent survival in contrast to Georgia progenies that had only 5.7 to 14.6 rust-free stems and 32.9 to 67.1 percent survival. Thus, there were wide differences in performance between loblolly pine races and between progenies of plus trees within races.

A phase of the Georgia-Florida study described by Kraus (1967b) included a comparison among offspring of 11 mother trees of each of three widely separated locations outplanted in the center of the State, and this adjunct plantation showed essentially the same pattern of racial variation (Barber 1966). However, the differences among progeny of individual trees in height, survival, and fusiform rust infection were much greater than between geographic locations. Variation among progeny of individual trees was summarized in detail in the chapter on tree-to-tree variation in loblolly pine but, briefly, at 5 years, the slowest growing family of the slowest race averaged 8.4 ft, while the fastest growing family of the fastest growing race was 12.0 ft, a superiority of nearly 43 percent.

In Georgia, near the northern extension of the range of loblolly pine, specific gravity and length of tracheids varied with latitude and longitude of loblolly pine from different geographic locations (Jackson and Strickland 1962). There was a highly significant linear relationship between latitude of seed origin and specific gravity, with trees from Florida, Georgia, and South Carolina showing lower specific gravity than those from Maryland and Virginia. This trend is the reverse of that in geographic variation studies. However, the differences were not great (0.51 to 0.55). Wood specific gravity increased in the westward direction through the seven Coastal and Gulf States from South Carolina (0.51) to Texas (0.54). Specific gravity was not significantly correlated with mean annual rainfall, tracheid length, total tree height, tree diameter, bark width, or crown area. Tracheid length in the Texas and South Carolina trees was significantly longer than in those of Georgia, Mississippi, Louisiana, and certain individual trees from Maryland, Virginia, and Florida. Tracheid length was not significantly correlated with specific gravity, total tree height, bark depth, crown area, or d.b.h. Stem growth on the basis of width of the four outer rings was significantly greater for seedlings from Maryland and North Carolina than for those from Alabama, Mississippi, and Texas.

Alabama

Results after 7 years of a racial variation study in Alabama were roughly parallel to those for loblolly pine in Georgia (Goggans *et al.* 1972). Seed from eight geographic locations representing a range in latitude were used for planting at each location, thus sampling the north to south loblolly range in Alabama as did the study for Georgia described by Kraus (1967a). In Alabama, loblolly pine growth rate decreased from south to north, survival did not vary significantly, and resistance to fusiform rust appeared to be higher in trees from northern locations. On the basis of preliminary results it was recommended that local seed be used for planting in the southern part of the State, and southern seed in the central and northern areas. No estimate of possible gains in volume growth was made. The early height growth estimates, however, indicated that substantial losses in wood volume might occur if northern seed is planted in southern areas.

North Carolina

The early performance of loblolly and shortleaf pines in plantations of the local seed source and several other locations indicated that on both good and poor sites individual shortleaf trees attained heights as great as the best loblolly pines (Lane 1961). Seedlings that were taller after 1 year's growth continued to be significantly taller 5 to 7 years after planting. An attempt was made to relate growth to nutrient content of loblolly pine needles by Steinhof (1961). Of special interest was a very large tree-to-tree variation in nutrient content of needles as well as dry matter in trees from different locations, although all were growing under similar conditions. A later analysis of two separate studies (Lantz and Hofmann 1969) showed that, in general, the trees from Coastal Plain locations had greater heights and volumes than those from Sandhills and Piedmont locations. The average yield of wood per acre based on tree size and specific gravity for all plantations was about 101 pounds more for trees from coastal locations than those from the Piedmont and about 198 pounds more than those from the Sandhills.

In studies of the effect of photoperiod on growth, photosynthesis, and respiration of loblolly pine seedlings from two geographic sources, Georgia seedlings carried on photosynthesis at a significantly higher rate than did Florida seedlings, but the difference in rates per seedling were caused by differences in amount of foliage, or total photosynthetic surface (McGregor *et al.* 1961). Long-day (15 hours) treatment stimulated height growth significantly more in Florida than in Georgia seedlings. In another study loblolly pine seedlings from St. Johns County, Florida, made more height growth under long or short days than seedlings from farther north in Glynn, Laurens, or Floyd Counties, Georgia (Allen and McGregor 1962). Shortleaf pine seedlings exhibited the same clinal change as found with loblolly seedlings in that the seedlings from more northerly areas tended to grow less than the southern seedlings. In longleaf pine there was no difference in performance attributable to geographic origin in the seedlings, but the short test period, the species' dwarf growth habit, and perhaps the lack of latitudinal distribution contributed to nonsignificant response. The relationship between height growth of loblolly pine seedlings and day length and effect on height of changing day length are shown in figure 68. Under short days, seedlings from three locations broke dormancy and made height growth, but those from Floyd County did not. The authors conclude that at least two processes control dormancy and extension growth, one being photoperiodic control and the other a rhythm effect that produces a spring growth flush.

Tests with loblolly pine seedlings from the Lost Pines area of Texas and from eastern Tennessee showed that they differed in the day temperatures required for optimum growth (Perry 1962). Data indicated that the Texas trees were adapted to grow at a higher day temperature than the Tennessee trees. Also, the trend in growth with increasing temperature conditions indicated that the temperature required for optimum growth is considerably higher for Texas trees than for those from Tennessee. No distinct optimum night temperature for growth was demonstrated by either group of loblolly pines.

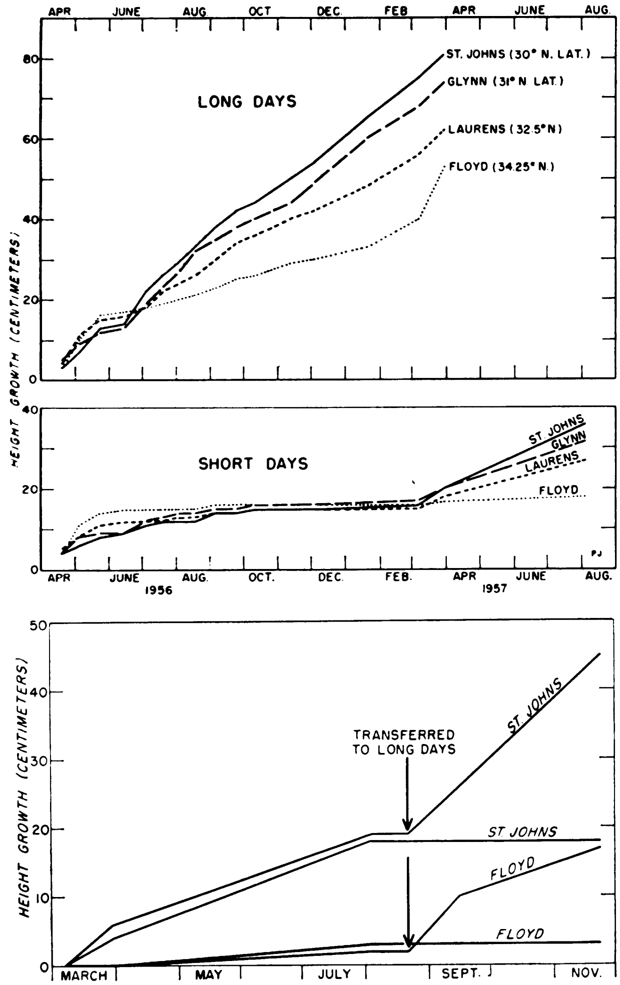

Figure 68.—Top and middle graphs: Height growth of loblolly pine seedlings from different latitudes in north Florida and southern Georgia varied widely under 15-hour days but very little under 9.5-hour or short days, until in February of the second year, when those from three counties broke dormancy and grew but those from Floyd County, the northernmost location, did not. Bottom graph: Moving loblolly pine seedlings of a Florida (St. Johns County) and Georgia race that differed in growth rate from a 9.5-hour day to a 15-hour day in August resulted in increased height growth in both. (Allen and McGregor 1962)

Southwide Study

The southwide pine seed source study was undertaken in 1951 to determine the degree to which inherent geographic variation in longleaf pine, slash pine, loblolly pine, and shortleaf pine is associated with geographic variation in climate and physiography. The first 10 years of results of the loblolly phase of the study are reported by Wells and Wakeley (1966). The study was initiated by the Committee on Southern Forest Tree Improvement through its subcommittee on geographic source of

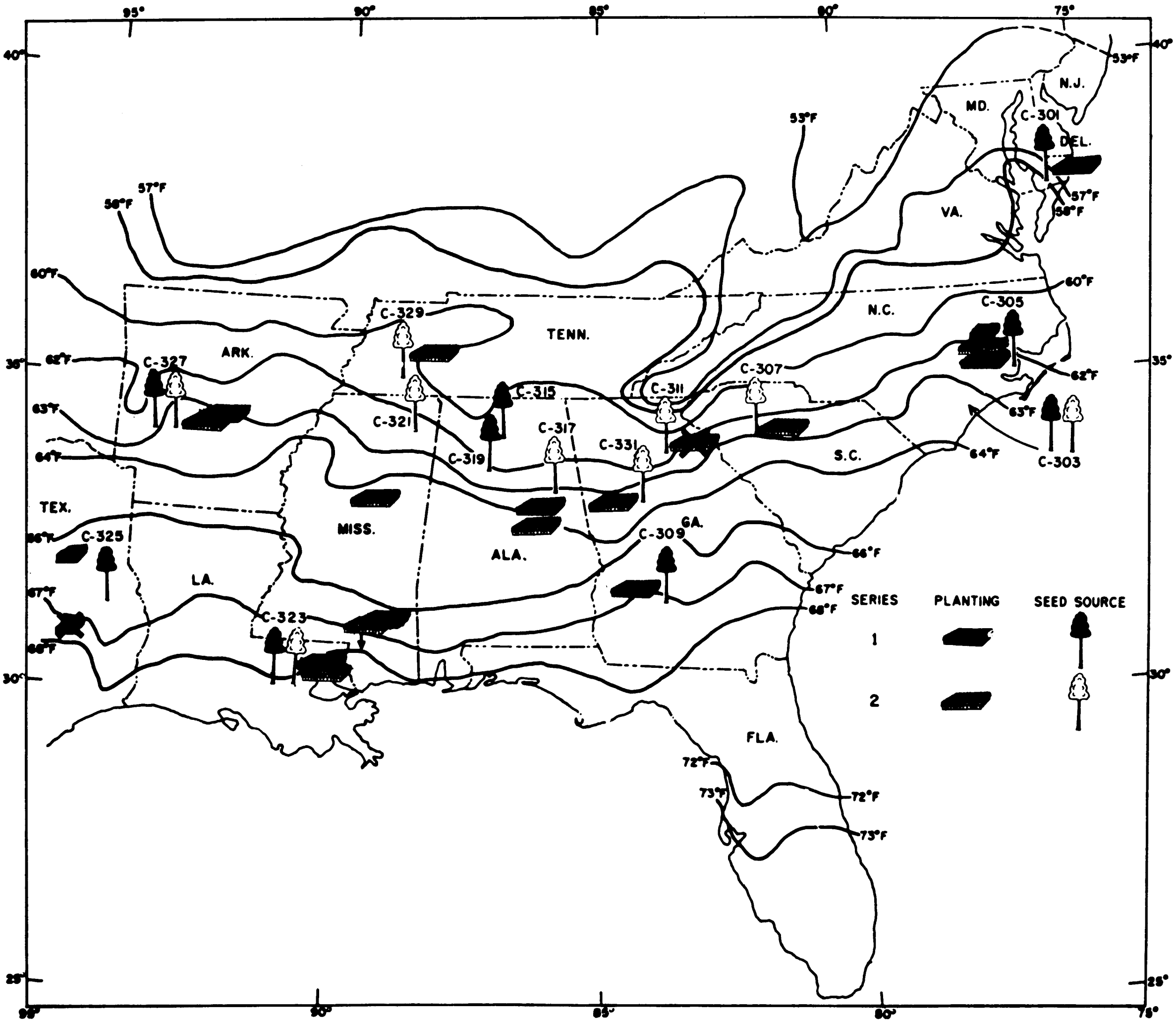

Figure 69.—The seed collection and outplanting locations in the southwide loblolly pine racial variation study sample most of the range with the exception of the lower Atlantic Coastal Plain from South Carolina to Florida. All population centers could not be sampled. The lines represent isotherms of average annual temperature. (X = abandoned plantations). (Wells and Wakeley 1966)

seed. The Southern Forest Experiment Station coordinated seed collections in 1951, nursery stock production in 1952, and the establishment of test plantations in the winter of 1952-53. It has also coordinated periodic plantation measurements and analyzed the results. The study has been made possible through the excellent cooperation of 17 agencies such as industrial corporations, schools of forestry, State organizations, and Federal agencies that either collected seed, produced nursery stock, or established, maintained, and periodically remeasured plantations. Several agencies contributed in all three ways. The entire study has been described and the results summarized through the third and fifth years in the field by Wakeley (1953a, 1959, 1961), the tenth year by Wells and Wakeley (1966), and the fifteenth year by Wells (1969). In addition, Henry (1959), Henry and Coyne (1955), and Henry and Hepting (1957) have reported insect and disease attacks during the same period.

Geographic locations included in the loblolly pine study are shown in figure 69.

In summarizing general results Wells and Wakeley (1966) indicate that genetic variation is becoming increasingly evident with passage of time. After 10 years, trees from the various geographic locations differed more in survival, and especially in height in the western section, than they did after 5 years. Estimates of volume growth are based on the data given for survival and height growth. The most recent remeasurements of the loblolly pine plantings showed strong correlations between the 10- and 15-year results (Wells 1969). Well-developed patterns of variation in survival, rust infection, and height growth were 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 survived than did trees from other locations. As drought is most common and most intense in the western part of the loblolly range, the variation in survival seems the result of natural selection. Height growth was fastest in trees of seed originating in areas with high summer rainfall and mild winters, except that in the northernmost plantations trees from northern locations grew just as fast (fig. 70). Trees from Maryland, southeastern Louisiana, and two locations west of the Mississippi were only lightly infected by fusiform rust, in comparison with trees from other locations (fig. 71).

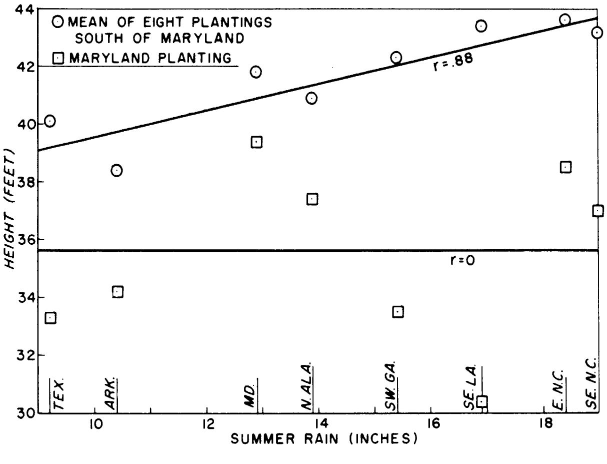

Figure 70.—Height growth was directly correlated with rainfall at the source of seed in plantations south of Maryland, but there was no correlation in the Maryland plantations. (Wells 1969)

For certain installations of the southwide pine seed source, various authors have published short reports on performance in the local area and its importance in seed selection.

Significant differences in percent summerwood, specific gravity, and tree dry weight occurred among seed from different geographic locations (Saucier and Taras 1967). This study is the only one so far made of wood quality yields from parts of the southwide pine seed source study. Determinations of wood characteristics were based on disks cut from trees in two replicates in the planting in central Alabama that were to be destroyed by mining operations. The planting was located in Talladega County, Alabama, and survival, height, and volume figures were given by Wells and Wakeley (1966). Trees from the northernmost area (Maryland) had the highest average specific gravity—0.435, while the Georgia trees were lowest with 0.393. This genetic pattern was the reverse of that obtained from geographic variation studies. Excluding these high and low values, there is only a difference of 0.02 unit in specific gravity separating the remaining seven groups of trees from different locations. Analysis of variance for specific gravity indicated a highly significant difference among seed sources, but a Duncan's multiple range test showed that the significant seed source difference was confined to the extreme values. That is, the Maryland trees had significantly heavier wood than Georgia trees at the 5-percent level. The percent summerwood varied essentially in the same manner as specific gravity. The Maryland trees had the greater proportion of summerwood, with 32 percent, and the Georgia trees the lowest, with 22 percent. All other seed sources varied between 31 and 28 percent. The analysis of variance for percent summerwood indicated a significant difference among seedlot sources at the 10-percent confidence level only. The experimental error for both specific gravity and percent summerwood was highly significant, indicating large individual differences among trees within plots. Since gross wood yield is of primary importance for many uses, dry-weight yields of trees from different geographic locations were compared. The Maryland trees, which ranked first in specific gravity, ranked seventh in tree volume, while Georgia, which ranked last in specific gravity, ranked first in tree volume. There was an overall tendency for seed sources which ranked high in specific gravity to rank lower in tree volume and vice versa. The rank of seed sources by tree dry weight changed slightly from that of tree volume. The east North Carolina trees ranked fifth in specific gravity, second in volume, and first in dry weight. Trees from other geographic locations changed rank order as they reflect the compositive effect of specific gravity and tree volume. Correlations for tree and wood characteristics and several physiographic and climatic factors were determined for the point of origin of various groups of trees. Specific gravity and percent summerwood were found to be significantly correlated at the 5-percent confidence level, as were tree volume and tree dry weight with June-August rainfall. The relationships between specific gravity and latitude, tree volume and longitude, and tree dry weight and longitude were not significant. In addition, specific gravity was negatively associated, but not significantly, with average annual temperature and January minimum temperature. In tree volume, Wilcox and Crisp Counties, Georgia, trees averaged 1.86 cubic feet and tree dry weight was 47.36 pounds. Trees from Somerset County, Maryland, had a volume of 1.60 cubic feet and weighed 43.43 pounds. Trees of local origin, Jefferson County, Alabama, had a volume of 1.40 cubic feet and weighed 35.99 pounds. Thus, the range in volume

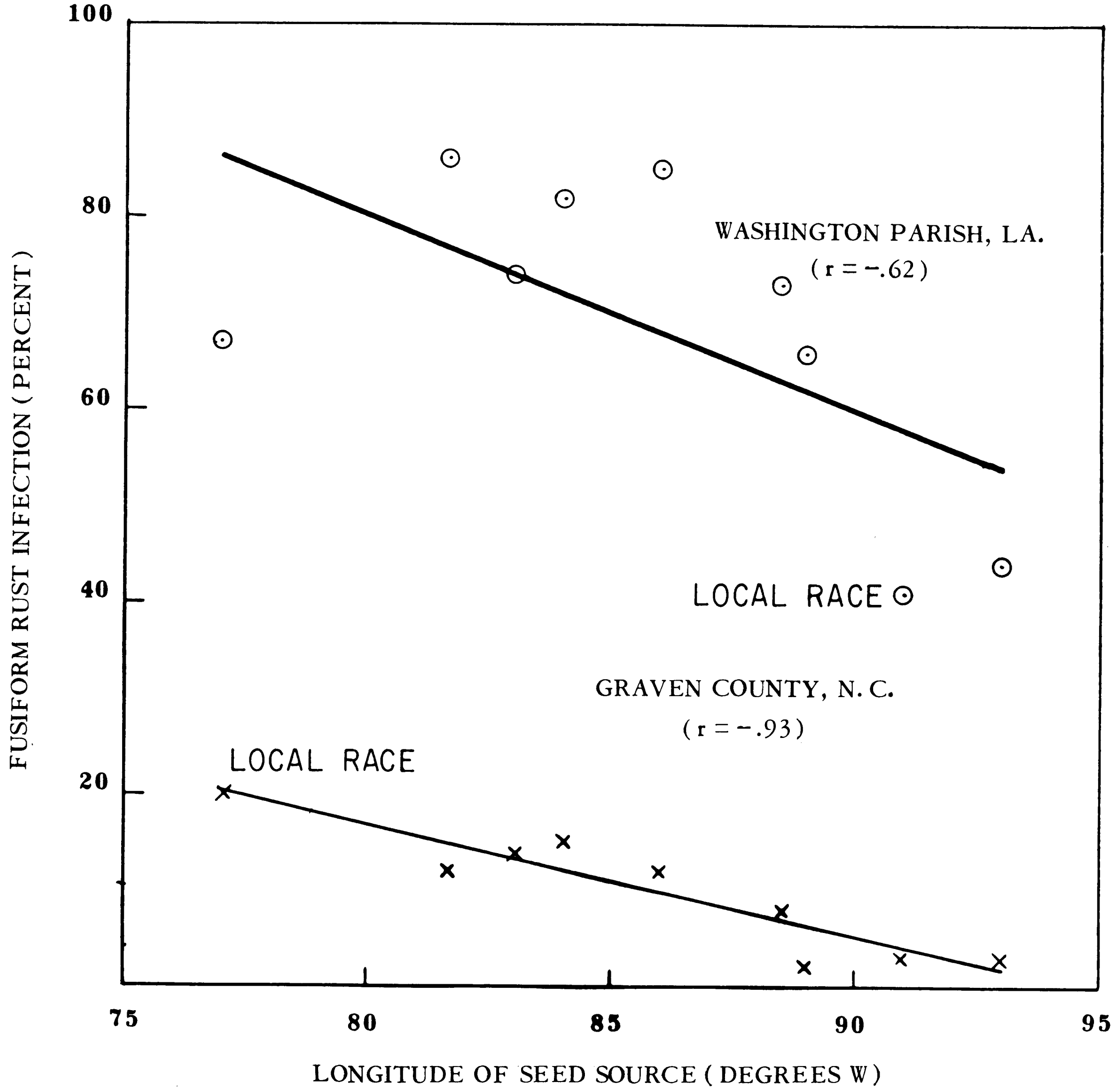

Figure 71.—Fusiform rust infection of loblolly racial selections at 5 years, over longitude of seed source, in western and eastern plantations in the southside study. There was no interaction of rust resistance with location, and western trees had low infection whether planted in Louisiana or North Carolina. (Wakeley 1961)

growth plus differences in specific gravity made a difference in weight between local Alabama trees and Georgia trees of nearly 10 pounds. There was a volume-dry weight superiority of 27 percent for the Georgia trees over Alabama trees. Trees with the lowest dry weight were from Angelina County, Texas, with an average of 31.33 pounds. Trees with the greatest dry weight were from Pamlico County, North Carolina, with a weight of 47.36 pounds, or 51 percent more dry weight.

For the Dooly County, Georgia, outplanting, Collins (1964b) determined that the regression of height on latitude and longitude shows that height growth increases as seed origin becomes more southerly. The trend seemed to be strengthening with time, on a basis of measurements after the third, fifth, and tenth years in the field. In height growth, trees of different geographic origin did not change in rank to any great extent during the first 10 years. Rust infection not only varied widely among seedlings from different geographic locations, but there were significantly many more infected trees at 10 years of age than at 5. In Maryland, trees from different geographic locations suffered from damage by wet snow (Little and Tepper 1959; Little and Somes 1964). By mid-July damage from heavy, wet snow was 30 to 35 percent for seedlings from Jefferson County, Alabama, and from Pamlico County, North Carolina, and 11 percent to 15 percent for seedlings from Texas, Arkansas, and Maryland. Seedlings originating in Maryland and from Pamlico County, North Carolina, were of equal height, yet damage to Maryland seedlings was only 12 percent while 35 percent of the North Carolina seedlings were damaged.

In the Ozark Mountains, Shoulders (1952) reported that after a cold spell in November 1951, trees from Maryland were unharmed but others suffered appreciable dieback. More than 10 percent of the trees from Tennessee and Virginia were damaged, and those from more southerly areas fared worse, except that only 8 percent of the trees from north Alabama seed were affected. The total number of seedlings in the test was 306, and 68 of these —22 percent—were damaged. They had been in the field for 2 years when they were examined for frost damage.

Switzer and Wells (1964) reviewed 10-year results from the study in Winston County and concluded that they support results from other studies in Mississippi. They suggest that loblolly seed for planting in the part of Mississippi in which the seed source study was located should come from south or west of the planting site because trees from those areas seemed to have the best combination of characteristics for volume growth and rust resistance.

It was found, on the basis of loblolly pine needles grown in Mississippi and Louisiana, that no differences in the dry-matter content were caused by geographic location or climatic conditions at the origin of the various races under test (McLemore *et al.* 1961).

Studies Outside the Natural Range But In the United States

Racial variation studies to guide seed collection for planting outside the natural range of the species vary somewhat from those conducted within the natural range, their main objective being a determination of best source of seed for a specific location. This is strictly racial selection rather than a study of racial variation in general. Thus, the typical study usually consists of seed from several geographic locations planted in controlled tests on one or a few sites in one area. Inasmuch as there is no local or nearby race of the species, we have no basis for comparisons other than among seedlings of different geographic origin. Sampling is rarely intensive enough to establish the existence of clines or any pattern of the variation throughout the natural range of the species. The results of tests of seed from different geographic locations may require a comparison with local species or other candidates for introduction which may also be planted. Tests of this kind are usually of longer duration because of the necessity for obtaining an adequate sample of weather conditions and other environmental factors under which the species might be planted. Each study of racial variation involving planting outside the natural range of loblolly pine will probably have to stand by itself because results of studies elsewhere do not apply and cannot be transferred. The performance of seed from different geographic locations may or may not conform to the general pattern of racial differences shown by tests within the natural range of loblolly pine.

Virginia

Loblolly pine from four widely separated locations over the South planted in the western part of the State differed in volume growth and form of trees (Kormanik *et al.* 1961). Seedling survival after 15 years was not significantly different among trees from different locations, although survival varied as follows: Arkansas, 93 percent; South Carolina, 77 percent; North Carolina, 83 percent; and Mississippi, 84 percent. Survival differences were significantly different early in the life of the study, or after 1, 3, and 5 years in the field, but not after 10 and 15 years. Damage by diseases and insects was extremely low in all plots. After 15 years in the field, heights differed significantly as follows: Arkansas, 34 feet; Mississippi, 34 feet; South Carolina, 35 feet; and North Carolina, 37 feet. On the basis of volume per tree, trees of North Carolina origin produced 26 percent greater volume than those from Arkansas or Mississippi. Trees from South Carolina produced only 3 percent more than those from Arkansas and Mississippi. Trees originating in North Carolina were 9 percent taller and 7 percent larger in diameter than those from Arkansas and Mississippi, resulting in a volume gain of 26 percent. Height differences were not very great at the end of 5 years, and by the end of 15 years the ranking of seedlots had not changed; thus, the inherent rate of growth was established before the end of the first 5-year period after planting. Trees of Arkansas origin had 15 percent complete forks, while those from Mississippi had 5, North Carolina 6, and South Carolina only 3 percent. Partial forks varied from 23 to 32 percent among seedlots. Stem form on all plots was so poor that only a small percentage (8 to 20 percent) could be placed in classes 1 and 2 for straightness, which included straight trees or those with small crooks that would be outgrown before maturity. Class 3 trees had crooks that could be attributed to either damage from freezing rain or snow. In this class Arkansas trees had 2 percent, Mississippi 5 percent, South Carolina 3 percent, and North Carolina 3 percent. Class 4 had severe crooks or leaning trees. In this group Arkansas had 78 percent, Mississippi 87 percent, South Carolina 82 percent, and North Carolina 85 percent. The study shows that the form of loblolly pine may be so poor when planted in the Piedmont region of Virginia that few if any high-quality trees are produced for saw logs or poles. Similar observations were made in Maryland by Little and Tepper (1959), and in Illinois by Woerheide (1959).

Southern Illinois

Performance of loblolly test plantings from several different areas throughout the South has been compared with that of local shortleaf pine and with some of the hybrids between loblolly and shortleaf pines. These tests show in general quite wide differences in resistance to low temperatures and in height growth (Minckler 1951, 1952, 1953; Woerheide 1959). Seedlings were planted in March of 1949. At the end of the first year, seedlings of southern origin were tallest, but the unusually cold winter temperatures of 1950 to 1951 severely damaged loblolly pine from North Carolina, South Carolina, and Mississippi. Below-zero temperatures in late November were followed by near-zero periods in December and January. On February 2, temperatures reached 22° below zero, the lowest since 1912. Such cold is expected once every 10 to 20 years. In nursery beds, 1–0 loblolly pine from eastern South Carolina were killed, while those from Maryland and Arkansas showed only a slight browning of top needles and negligible killing. Loblolly suffered more than shortleaf, with damage to both species varying by seed source. In the field, loblolly pine trees 1 to 3 feet tall from most southern and southeastern sources showed by far the greatest ice damage. Shortleaf from northern Arkansas, Missouri, Kentucky, Ohio, and Oklahoma showed no freeze damage. Those from northern Mississippi showed slight to moderate injury. Plots of two shortleaf × loblolly pine hybrids with parental stock from Maryland and North Carolina showed no freeze damage. The 2-year height growth for trees from Maryland and Virginia areas was significantly better than that of all other sources. After 3 years, trees from the northern areas were dark green, well formed, and the terminals and branch leaders were intact and straight. Contrariwise, the frost-damaged trees from Mississippi, North Carolina, and South Carolina were ill formed, bushy, spindly, and a lighter green in color because their terminals and branch leaders had been killed. On the basis of survival, height growth, and appearance, trees from Maryland and Virginia were definitely superior for planting on the upland old-fields of southern Illinois. After 10 years, trees from Maryland were tallest and largest on all plots (Woerheide 1959). Stands from Deep South seed areas not only were shorter but had only 65 to 75 percent as much basal area as Maryland trees.

Specific gravity of shortleaf pine wood in southern Illinois averaged considerably higher (0.435) than that of loblolly pine (Gilmore *et al.* 1961). Specific gravities for trees in Illinois were much lower than those in Mississippi. The maximum specific gravities for shortleaf and loblolly pines grown in Illinois barely exceeded the mean of Mississippi data. Also, bulk yield per unit volume for the two tree species is considerably lower in Illinois than in Mississippi. The larger yield per cord in Mississippi of 207 pounds for shortleaf and 216 pounds for loblolly pine amounts to a considerable quantity of pulp in a large-volume mill. On this basis, assuming that a cord per acre per year is produced in both States, approximately 2⅛ tons less wood per acre is produced at pulpwood age (20 years) in Illinois than on a comparable acre in Mississippi. In Illinois, lowest average specific gravity for entire tree contents was 0.362, and the highest 0.500 for shortleaf, with 0.361 and 0.473 for loblolly pine. Little tree-to-tree variation in specific gravity could be attributable to rate of growth alone (Geyer and Gilmore 1965). The usual spacing intervals of 4 to 10 feet had little effect on wood density of loblolly pine at 14 years of age. The difference between the highest and the lowest specific gravity (0.397 to 0.414) was too minor to be of practical importance. Thus, specific gravity cannot be raised by regulating spacing. Forty-nine percent of the variation in wood specific gravity of loblolly pine grown in southern Illinois was accounted for by environmental factors and percent of latewood. Environmental conditions that influenced the availability of moisture, especially during summer, were most important. In a corollary study, neither specific gravity nor percent of latewood was related to seven known geographic seed sources (Gilmore *et al.* 1966; Geyer and Gilmore 1965). Average wood specific gravity for loblolly pine trees in plantations throughout western Kentucky and eastern Tennessee averaged 0.424, with a range of 0.351 to 0.467 (Gilmore 1967). Percent latewood was 27.7, with a range of 20.5 to 34.3 percent. The data substantiate earlier observations showing that the specific gravity of loblolly pine wood decreases from the southern to the northern part of its range and that this decrease is due to environmental factors.

In Illinois plantations Gilmore (1971) found concentration of certain terpenes was higher in southern sources than northern, while other terpenes were highest in trees from the midpoint areas of the loblolly pine range.

Southern Ohio

Loblolly pine height growth was superior to that of shortleaf pine and certain other introduced species (Aughanbaugh 1957). Loblolly pine trees 17 years old were nearly 38 feet tall, and shortleaf trees 34.5 feet. Pitch pine, which was second in diameter growth, was shorter. Shortleaf pine was better than loblolly in one respect—self pruning. It ranks next to loblolly pine in volume growth, with an average increment of 140 cubic feet, or 1½ cords per acre annually. Pitch pine was reported as doing remarkably well, with natural pruning that was rapid and form that could be improved by pruning. White pine's growth rate was good, exceeding that of red pine; red pine required early thinning to prevent growth stagnation. Also, red pine is particularly susceptible to damage by the European pine shoot moth, *Rhyacionia buoliana* (Schiffermüller). Poorest showing of all six species tested was made by Scotch pine, which grew fast in early ages but showed reduced vigor after 17 years.

Tennessee

Loblolly pine seedlings from southeast Tennessee, the Alabama Piedmont, Georgia Piedmont, North Carolina Piedmont, North Carolina Coastal Plain, and South Carolina Coastal Plain were tested. After 5 years, seedlings from the Alabama Piedmont and North Carolina Piedmont had significantly lower survival than other seedlings (Thor and Brown 1962). The loblolly seedlings from areas closest to the planting location had the highest survival but the shortest heights. Seedlings from the Georgia Piedmont were significantly taller than all others. Number of stomatal lines differed by race but not needle length. Frequency of serrations on needle margins, percent dry weight, stomatal frequency, and number of needles per fascicle did not differ. Two groups of trees from the Coastal Plain had fewer stomatal lines than the Piedmont trees. Average of needles per fascicle showed a clinal pattern, with a decrease in number from inland to the Coastal Plain. Wood specific gravity varied considerably within any one seedlot, and seedlings from the Georgia Piedmont had significantly lighter juvenile wood than trees from other areas (figures 72 and 73). Tracheid length varied widely from tree to tree but not among lots from different geographic locations. At 10 years of age significant differences were found among the six different lots of seedlings for height growth, wood specific gravity, and frost damage (Thor 1967). When the temperature dropped below 0° F on three different days, seedlings from the two southernmost areas, South Carolina Coastal Plain and north Georgia Piedmont, suffered the most needle damage. Survival was lowest, 80 and 81 percent, respectively, for South Carolina Coastal Plain and North Carolina Coastal Plain stock, as compared with 90 and 92 percent for seedlings from the North Carolina Piedmont and southeast Tennessee. Ranking by height growth had not changed from the time of establishment to age 10. Heights ranged from 26.6 feet for trees from the South Carolina Coastal Plain to 31.6 feet for trees from the North Carolina Piedmont. Differences in height growth and survival exerted strong effect on the weight of extracted wood in short tons per acre. The lowest yield per acre was 5.03 for trees from the north Georgia Piedmont. Other yields were: South Carolina Coastal Plain 5.17, North Carolina Coastal Plain 5.79, southeast Tennessee 6.68, Alabama Piedmont 6.78, and the highest, North Carolina Piedmont, 8.91. The yield of trees from the Georgia Piedmont was only 56 percent of that from the North Carolina Piedmont trees. The Georgia Piedmont trees had lowest specific gravity and were significantly lighter than those from the Alabama Piedmont. The regional variation in wood specific gravity in this particular study did not follow geographical patterns demonstrated by natural populations. It was concluded by Thor that it was not feasible to determine which population had the higher wood density without actual testing in the local environment.

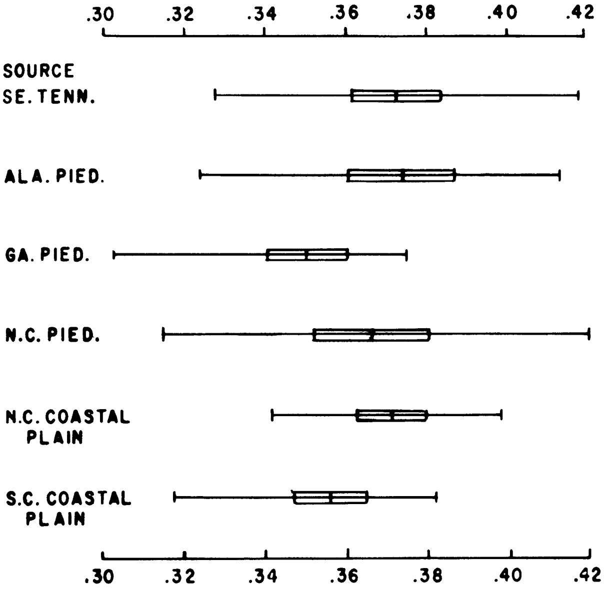

Figure 72.—Specific gravity of loblolly pine juvenile wood varies by geographic source of seed, but the range among trees is much wider. Total range and means of two standard errors are indicated for trees of each geographic location. (Thor and Brown 1962)

In Tennessee, one other racial variation study in loblolly pine showed important differences after 10 years of growth in nine loblolly seedlots outplanted at three locations inside the natural range of loblolly pine and four locations outside the natural range (Zarger 1961). The Atlantic Coast area was represented by seedlots from Maryland, South Carolina, and Virginia; north inland by Alabama,

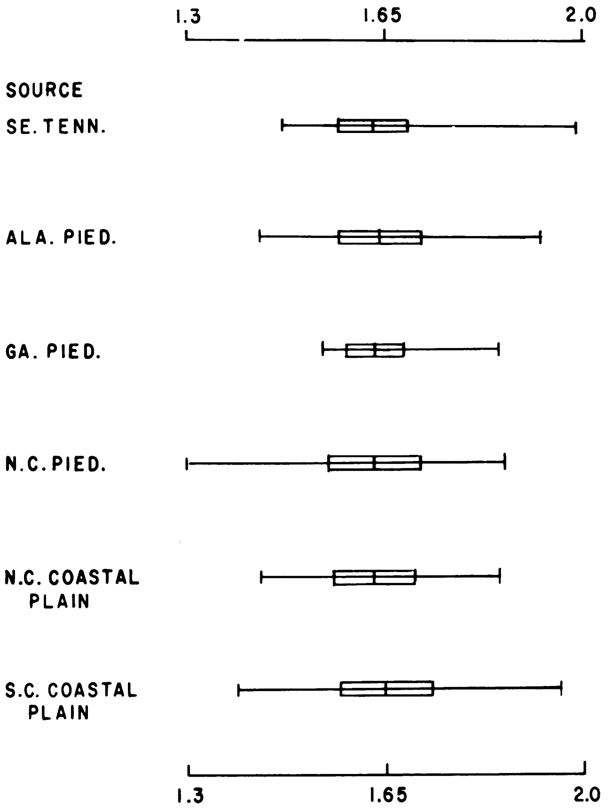

Figure 73.—Tracheid length in millimeters of loblolly pine juvenile wood varied widely among individual trees but not among trees from different geographic locations. Total range and means with two standard errors are indicated for trees of each location. (Thor and Brown 1962)

Mississippi, and Tennessee; and south inland by Alabama, Georgia, and Mississippi. It was concluded that inland races survived better than Atlantic Coastal Plain races. Of the inland races, northwest Georgia, north and south Alabama, and Tennessee trees survived best. It would appear that Atlantic Coastal Plain seed should not be planted outside the natural loblolly pine range until evidence to the contrary is available. The present test also suggests a similar restriction for Mississippi seed. In contrast to results of 5 years, at 10 years there was no significant difference in height between seed sources. Loblolly pines planted inside the natural range of loblolly pine grew 2 feet taller on the average than those planted outside the range. Inland races grew to larger diameters than Atlantic Coastal Plain trees. Of the inland trees, all but those from south Mississippi were generally superior in diameter growth. Trees planted inside the natural range averaged 0.6 inch more in diameter than those planted outside. However, the 5.4 inch average diameter growth of the Arkansas planting exceeded that of all other plantings. Distance between point of seed collection and planting site should not be used alone to evaluate the suitability of seed collection locations. While there is a general decrease in survival with increase in distance, the wide variation in some seedlots suggests that other factors are involved. Neither height nor diameter growth was affected by increase in distance from seed collection area to outplanting location. Range in height growth was wide, with seedlings from Mississippi averaging 14 feet in height and those from north Alabama 22 feet, the latter being tallest of all those tested.

In a subsequent evaluation of a seed source study, it was recommended that most loblolly pine clones for Tennessee seed orchards should be selected from Maryland, Virginia, and North Carolina stands (Rink and Thor 1971). Trees from these areas produced from 25 to 100 percent more wood than Deep South and Coastal Plain trees. Wood specific gravity did not vary significantly, but there was a trend for trees from the northeastern part of the loblolly range to have the highest specific gravity as well as the fastest growth rate.

In the Cumberland Plateau area of Tennessee, almost 80 percent of the trees in two plantations were damaged or killed by a severe freeze in the winter of 1962 and 1963 (fig. 74) (Mignery 1967). Seed probably came from middle Georgia and the lower Piedmont areas. The trees were planted in Rhea County in 1956 and had been growing well 8 years from seed. Diameters averaged 3 inches, heights 20 feet, and a few of the trees were 28 feet tall. In contrast, 6-year-old trees adjoining the Georgia plots from Polk County, Tennessee, about 45 miles southeast of the planting site, suffered only a little damage. The parent trees were growing at about 2,000-foot elevation or some 300 feet higher than the Cumberland Plateau site of the seed source plantation. A year after the freeze, 11 percent of the trees from Georgia were dead, an additional 10 percent were still declining, and 58 percent were apparently recovering but showed damage. Only 21 percent of the trees were uninjured. Increment cores on stem internodes indicated that growth had been unusually slow during 1963. The trees ranged in diameter from 1 to 6 inches, but there was no relation between tree size and the damage sustained. A severe midwinter drought having put additional stress on the trees, it was concluded that for planting in the Cumberland Plateau, seed from local Tennessee areas was much preferred to that from Georgia.

An important factor in loblolly pine silviculture in east Tennessee is the presence of comandra blister rust, *Cronartium comandrae* Pk. Prior to 1951, the fungus was found almost exclusively in the Western and North-Central States (Cordell and Knighten 1969; Powers 1972). Forty percent of sampled

Figure 74.—In Tennessee, loblolly pine trees of lower Georgia Piedmont origin suffered heavy cold damage (left), but trees of local origin were undamaged (right). (Mignery 1967)

stands of loblolly pine plantations 10 years old and younger had infected trees, according to a 1967 survey. Incidence of infected pines was 6 percent, one-third of which were dead. Resistance of various loblolly pine races to comandra rust is unknown at present.

An interesting comparison of the relative cold tolerance of loblolly and longleaf pines from the same location was made in Idaho (Parker 1955). One-year-old seedlings of loblolly pine were planted at two elevations and longleaf pine at one, but only the longleaf seedlings survived the first winter.

Northern Arkansas

Loblolly pine from different locations in the eastern part of the range grew well after extensive top-kill by frost (Shoulders 1952), but volume growth at 15 years varied widely (Maple 1966). Seed sources tested were Tennessee, Georgia, north and east Mississippi, south and north Alabama, Virginia, and Maryland. Average height of different lots ranged only from 39 to 40 feet, but differences in survival (56 to 90 percent) caused a wide range in merchantable volume per acre. Trees of south Alabama origin produced only 12 cords per acre, while those from Georgia produced 23 cords, or nearly twice as much.

South Florida

Survival of loblolly pine 6 years after planting on eight sites south of the natural range was better than that of native and exotic pines tested, and height growth was roughly the same (Bethune 1963a). In January 1955, outplantings of loblolly pine seedlings of the same origin were made at eight Florida locations south of the southern limits of the species. Four planting sites on cutover pine flatwoods were located in the east half and four in the west half of south Florida to insure wide geographic representation. At each site, 392 loblolly pine seedlings 1 year old were planted. Seventy-seven percent of the loblolly pine seedlings survived the first growing season. After 3 years—the first 2 of which were notable for severe drought—the overall survival had dropped to 60 percent. After the third year, mortality was negligible. This survival compares favorably with that of native and exotic pines tested in southern Florida. Height growth at age 6 averaged 5 feet for all locations. On the better sites the trees averaged 8 feet in height. It was considered that the height was not spectacular but growth approximates that of other pine species planted on the same sites. None of the plantations suffered serious insect or disease attack.

Studies Outside the United States

Loblolly pine and other southern pines have been planted extensively for forest production outside the United States in areas where the climate is somewhat comparable to that in the South. Plantations have been made over a number of years in Africa, South America, Australia, and to a lesser extent in New Zealand and Japan. Selection of proper races for planting outside the United States presents somewhat similar problems to that of selecting the proper race for planting in areas adjoining the natural range. This is true because there is no local race for comparison of performance and, also, results have to be compared to the alternative species or races of species that are also candidates for importation. Although choice of species or race can be made on the basis of the homoclime principle (similar climate at seed source and planting site), it is not common that these geographic locations are strictly comparable. There may be differences in soils, and insect and disease pests. Therefore, use of introduced species in foreign countries may be of great importance in forestry programs, but they require somewhat extended periods of observation. The history of racial variation tests of loblolly pine outside the United States is not geographically extensive, nor are the plantations very old.

Perhaps the oldest trials of seed of loblolly pine planted in formal replicated tests outside the United States are those described by Sherry (1947). In 1937, trees from 11 different locations in the United States were planted at 5 locations in the United States and at 8 locations in South Africa. The United States plantings were not completely successful but did indicate trends in growth, survival, and resistance to fusiform rust. After 9 years in plantations at four of the locations in South Africa, there was clinal variation in height growth associated with increasing latitude of the seed source from Florida to Maryland (fig. 75). Seedlings originating in the United States from warm regions, latitude between 30° N. and 31° N., averaged 40 feet in height and those from cool regions, latitudes 37° N. and 38° N., averaged about 30 feet. Later, the 21- to 26-year height growth showed a strong positive correlation with the 9-year data, as described in a personal communication from H. A. Luckhoff (Wells and Wakeley 1966). Trees from areas with warmest winters grew fastest in plantings in both the United States and Africa.

In Australia, on a basis of the first 6½ years, the best sources of loblolly seed for planting were coastal areas of low latitude, such as Florida, which produced up to 30 percent greater height growth and 20 percent greater diameter than trees from the poorest locations, such as Maryland and Virginia (Nikles 1962). In an additional test of trees from 12 different locations, highest volume was produced by trees which had been originally obtained from central Florida but which had been improved somewhat by selection for high pruning (Slee and Reilly 1966). Trees from the South Carolina coastal area, also improved some by selection, produced high yields. The yields from these two areas were significantly greater than for trees from other locations. There was a correlation between performance at Beerwah and distance from the sea at the original source location, with coastal areas generally performing better in the coastal areas at Queensland. In a 9-year-old test in the same location, a Florida lot of seedlings from Silver Springs outclassed the local control in both height and volume growth.

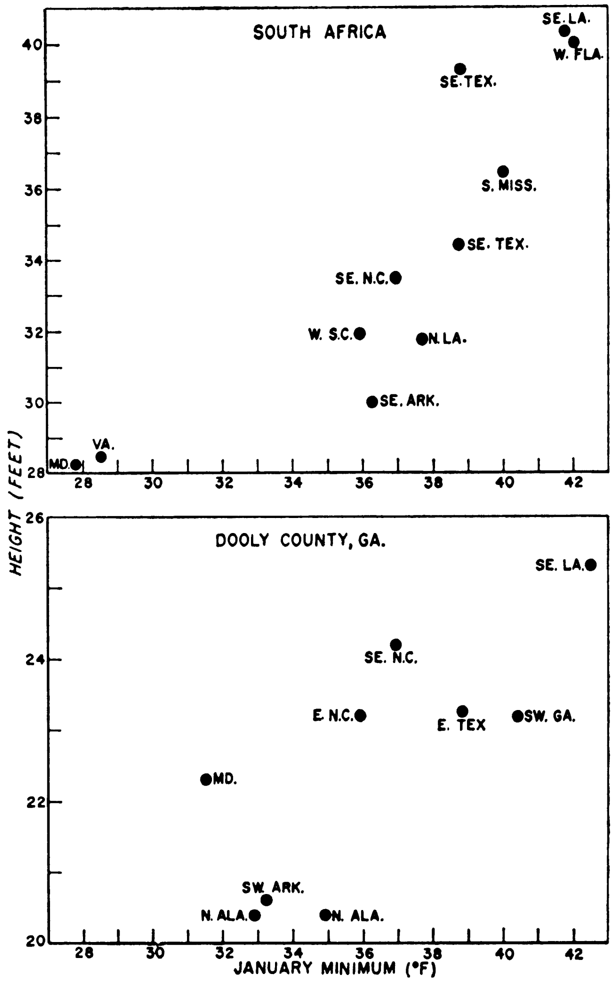

Figure 75.—Height growth of loblolly pine from different geographic locations has about the same relationship with average minimum January temperature at the point of seed origin when planted in South Africa or Dooly County, Georgia. (Wells and Wakeley 1966)

In Japan, loblolly pine seedlots collected from 15 locations in the United States showed important differences after 5 years in height growth and mortality (Iwakawa *et al.* 1964). Trees from the Atlantic Coastal Plain grew faster than those from inland areas. At 5 years, Florida seedlings and those from one mother tree in Maryland were best, with trees from Texas, Louisiana, North Carolina, Arkansas, and Mississippi showing poor height, especially Texas and Louisiana. There was a strong positive correlation between height at the first and fifth years ($r = 0.61$). The seedlings from individual trees in Maryland presented significant differences between mother trees. At 3 years after planting, mortality varied from 5 percent for one lot of trees from Maryland to 100 percent for seedlings from Florida, leading to the conclusion that high mortality of stock from southeastern regions was due to winter cold, as the test plantation in Japan is situated near the northern limit of loblolly pine planting. Seedlings from Maryland, South Carolina, Arkansas, and Texas locations showed low mortality percentages, and those from Georgia, Mississippi, Florida, and Louisiana showed high percentages. In general, trees from more northern or western inland locations having less precipitation showed lower mortality percentages than those from locations from southern rainy regions.

In Korea, extensive use is made of a pitch × loblolly pine hybrid for commercial planting. For the first 5 years of growth, pitch pine from Pennsylvania being the maternal parent, loblolly pine pollen from northern locations such as New Jersey produced hybrids of the best growth because of their resistance to cold (Hyun 1969). Pollen from Virginia and North Carolina produced hybrids that were about as good, but hybrids from southern pollen were damaged by cold, and those from western pollen did poorly. Number of sound seed was low, varying from 6.9 to 20.8 sound seed per cone, but not clinally.

Seed from 24 trees selected for drought resistance in the Lost Pines area of Texas was exported to Rhodesia. After 1½ years of growth, significant positive correlation was seen between the drought resistance of the parent and the height of the seedlings (Banks 1966). The location of the test plantation was in an area having an average rainfall of about 57 inches, but most of the rain was in a 6-month period from October to March, with normally a 3- to 6-month dry spell. Also in Rhodesia, seed from eight different areas was established in replicated trials at Tarka Forest in January 1964 (Southern Rhodesia Forestry Commission 1964) and at Chisengu and Erin Forests during 1964 and 1965 (Rhodesia Forestry Commission 1966). In addition, trials including seed from 12 different locations were started in 1965 and 1966 at Martin, Stapleford, and Erin Forest Reserves. After 1 year and 4 months in the plantation at Tarka, trees from Florida and Louisiana were significantly taller than those from Arkansas, Georgia, Texas, and Virginia. An additional test in Africa was described by Burley (1966) in which 36 different seedlots were to be outplanted on five sites in Malawi in 1966-67.

In Colombia, loblolly pine from Georgia seemed better suited to the location of planting than races from Texas and Virginia (Perez 1967).

Several tests in Africa and other countries were summarized by Burley (1966) based on personal communication because results have not been formally reported. In Kenya, there were barely significant differences in first-year survival among five seedlots (Alabama, Florida, Georgia, Texas, and Virginia) represented by four or five 9-tree plots. In Argentina, at Castelar, Buenos Aires, Georgia is considered the best State of origin for loblolly pine seed but no replicated trials have been established to compare seed from different locations. In Sao Paulo, Brazil, racial variation tests are in progress, but no results are yet available. Replicated trials were established in Uruguay during 1960 with 10 different seedlots of loblolly pine, and throughout the first 5 years trees originating from Texas, Florida, and South Carolina demonstrated superior height and diameter growth. Their success was attributed to close similarities in temperature, precipitation, and growing season between the planting site location and the sources of seed—which were eastern Texas, coastal South Carolina, Georgia, and northern Florida. An additional trial in Uruguay with seedlots from Arkansas, Georgia, Louisiana, and Texas was started in 1967. During the third growing season in an area with an average growing season of 274 days, which corresponds closely to that of Shreveport, Louisiana, late-season growth was roughly related to length of growing season at the place of seed origin (Krall 1969). Late-season growth as a percentage of the yearly total varied from 39.9 percent for trees originating at Bowie, Texas, to 51.9 percent for trees from Bastrop, Texas. In New Zealand (Burley 1966), replicated trials of loblolly pine from 11 different locations were established at two points in 1955; best growth rates, as indicated by unanalyzed data, were exhibited by trees from coastal Georgia, South Carolina, and North Carolina, with poorest growth by Arkansas and Texas trees.

Discussion of Loblolly Pine Racial Variation

Racial differences have been studied on both a rangewide and "local" basis because of the wide geographic range of the species—the kind and extent of inherent racial differences make them important factors in silviculture, tree breeding, and genetics. Also, racial variation in forest pests is being recognized as important (figures 76 and 77).

Silviculture

Foresters must recognize racial differences in loblolly pine in all phases of seed procurement, including that for local use as well as for the import and export trade. For the United States, on the basis of his own and studies of others, Wells (1969) proposed seed collections and planting zones based on 15-year results from the southwide study and other studies (fig. 78). For planting in zone 1, seed should be collected in southeast Texas, zone 2 in southeast Louisiana, zone 3 anywhere within the area, North and South Carolina anywhere within the Coastal Plain of these States, and areas north of zone 2 in inland areas such as northern Mississippi,

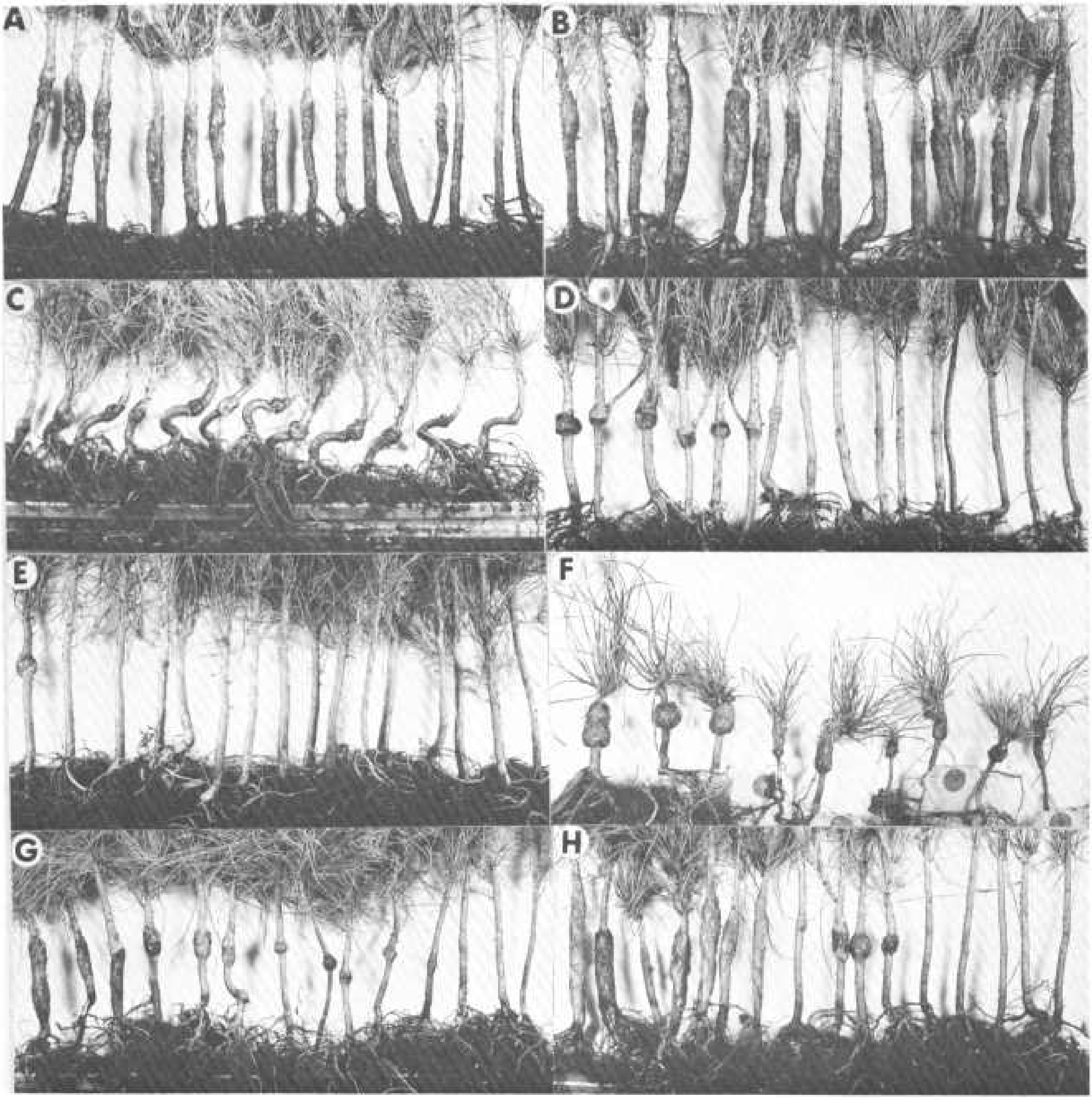

Figure 76.—Gall formation at 12 months following pine inoculations with various isolates of *Cronartium:* (A) slash pine and (B) loblolly pine inoculated with *C. fusiforme* isolate No. 1; (C) shortleaf pine and (D) loblolly pine inoculated with *C. quercuum* Mississippi isolate No. 1; (E) slash pine inoculated with *C. quercuum* Mississippi isolate No. 2; (F) jack pine inoculated with *C. quercuum* Wisconsin isolate No. 1; (G) sand pine and (H) loblolly pine inoculated with *C. quercuum* North Carolina isolate No. 2. (Kais and Snow 1972)

Alabama, and Georgia, or the Piedmont of North and South Carolina.

In mid-latitude areas of the loblolly range, considerable gains over local seed may be made by judicious choice of nonlocal seed, but near the northern and perhaps western extremities of the range, it is most important to choose local seed to avoid what could be a very large loss. Evaluation of races for importation should be based on growth of trees, yields per acre, and tree quality, because most of the economically important traits are not correlated with one another. Some risk may be associated with use of nonlocal seed, but confidence will grow if current studies show similar patterns of

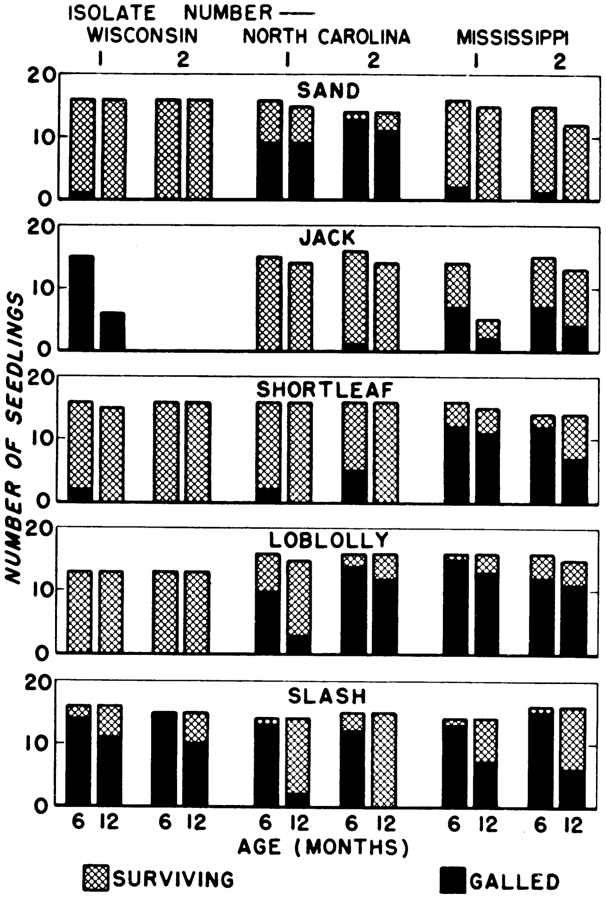

Figure 77.—Gall development on pines inoculated with *Cronartium quercuum* from three geographic sources. (Kais and Snow 1972)

variation as they increase in age. Sometimes advisable is hedging against loss of trees from cold or other factors by mixing seed of two or more promising races or increasing the number planted per acre.

Silviculturists importing loblolly pine seed from the United States should recognize that important races exist. Proof of accurate labeling in respect to location of seed origin should be required. Loblolly pine seed should be obtained from locations with climate similar to that of the planting site if it is not possible to establish local racial selection studies to determine the better races.

The possibility of serious loss in wood production of planted stands as a result of misjudgment in racial selection is well demonstrated and serves as justification for spending considerable time and effort to determine proper races for planting.

Tree Breeding

Tree breeders may be interested in many aspects of racial differences that concern silviculturists and, in addition, those affecting choice of breeding methods. Important gains might be obtained by selection of the proper race for seed orchard clones or for breeding stock and, in addition, probably by selection of plus trees within races, although more research is needed to determine the kind and amount of additive effects.

Many traits exhibit clinal variation, which is helpful in estimating performance in geographic areas where no racial planting tests have been made.

Individual traits such as growth rate, drought resistance, and fusiform rust resistance seem to have developed independently of each other; this complicates evaluation of overall performance of races but provides an opportunity for selection of breeding stock with special traits for intensive and long-range creative breeding projects. It is not known whether these traits can be utilized most efficiently by racial or plus-tree selection or accelerated by selection at both levels.

The indications of differences among stands within "local" races should alert tree breeders to the fact that it might be highly desirable to avoid working in phenotypically poor stands if better ones are available. More investigation is required to indicate the importance of stand effects.

The relationship of population centers, as discussed in the chapter on geographic variation, to racial variation or racial selection cannot be established from results of studies to date. This subject might well receive further study in the northeast and northwest part of the loblolly pine range.

Racial differences in wood characteristics do not appear to be as great as geographic differences or differences in growth rate, although trees in racial tests have not reached maturity.

On a basis of one study by Woessner (1972a), crossing among races to obtain heterosis is not promising. There were indications, however, that hybrids might be suitable for planting on a more diversified range of site conditions than their parents. Seedlings from the Coastal Plain parents grew faster than Piedmont seedlings at the beginning of the growing season but slower in the latter part, indicating racial differences in height growth pattern in loblolly pine. In the study, seedling height at 1 year varied little in crosses between geographic areas but widely in crosses between individual trees within areas.

Genetics

The population dynamics that have led to development of widely varying stands and races at various geographic locations is of considerable interest. The relationship of racial differences in growth, yield, and quality to environmental factors either past or present is not clear. Guidelines in qualitative genetics are not sufficiently well estab-

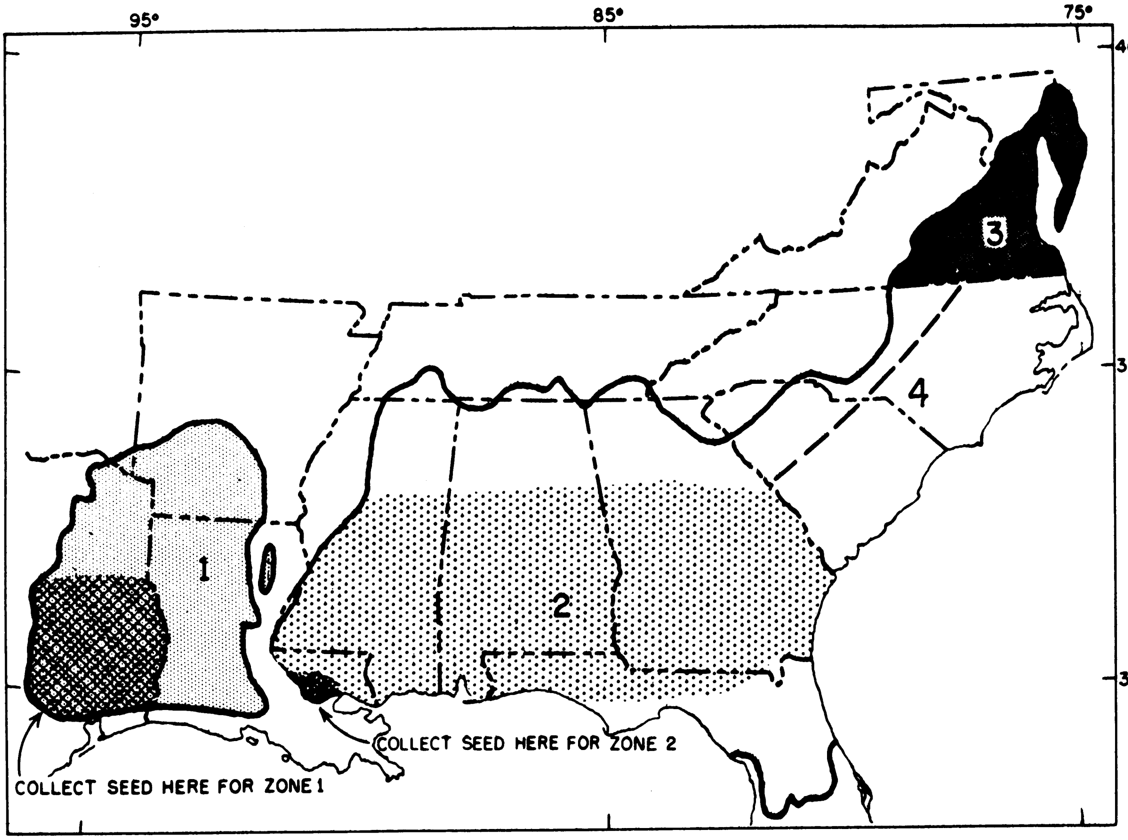

Figure 78.—Suggested seed collection and planting zones for loblolly pine within the natural range as indicated by the solid black line. Seed for zones 1 and 2 could come from the southwest part, zone 3 anywhere in the area, and zone 4, the Carolinas, within the Coastal Plain as distinguished from the Piedmont by the broken line. Seed for planting in areas north of zone 2 should come from northern Georgia, Alabama, Mississippi, or the Piedmont of North and South Carolina. (Wells 1969)

lished to guide tree breeders in the proper selection of mating schemes and breeding methods.

Many problems in quantitative genetics have been indicated by the low sensitivity of racial variation field test designs, but they have not attracted the attention of geneticists.

Results of racial variation studies to date have not defined the interrelationship between loblolly pine and the incidence of fusiform rust. Variation in resistance to rust seems to be discontinuous, with the highest resistance found in races west of the Mississippi. Introgression between loblolly pine and shortleaf pine has been suggested as an explanation for resistance to rust (Hare and Switzer 1969). Heavy loss to fusiform rust in natural stands is limited to part of the loblolly pine range, but it is not clear whether differences among pine races, or environmental factors, or both, confine the pathogen. Even less is known about the relationship of races to insect attack.

Inherent variation in loblolly pine creates problems in taxonomy if precise identification of trees is to be obtained. Inherent differences in many traits of loblolly pine from different locations, as illustrated by the results of racial variation studies, confirm the geographic variation studies of trees and stands in places that the species is quite variable. Furthermore, studies are showing the magnitude of both environmental and genetic effects. The findings are of great economic importance in forestry.

RACIAL VARIATION IN LONGLEAF PINE

The natural range of longleaf pine extends from the southeastern tip of Virginia southward deep into Florida and west to eastern Texas, as shown on the range maps in chapter 1 and wood-volume maps in chapter 5. There is a short extension northward of the longleaf pine range to areas of clay soils in northern Alabama, but generally it is found on the Coastal Plain soils. The range of longleaf pine is more extensive than that of slash pine but less extensive than that of loblolly and shortleaf pines.

Because longleaf pine is somewhat difficult to plant and its seedlings have a delayed juvenile growth stage, longleaf pine has not been planted so often as loblolly and slash. Moreover, loblolly and slash can be readily planted and are suitable for the large majority of sites within the natural range of longleaf. Very little longleaf pine seed has been exported to countries normally including southern pines in their planting programs.

Because of the relatively minor part longleaf pine has played in reforestation in the South, there has been little interest in racial variation or racial selection studies. The southwide pine seed source study, in which 15 longleaf seed sources are represented, is by far the largest longleaf study attempted to date (Wells and Wakeley 1970a). They sampled a greater part of the natural range of longleaf pine, although there was a noticeable omission in the sampling between southern Florida and central Georgia, an area where considerable genetic variation would be expected. Among the 36 plantings distributed from southeastern Virginia to eastern Texas, seed for Series 1, 2, and 3 was collected in 1951 and plantings made during the winter of 1952–53. Seed for Series 4, 5, and 6 was collected in 1955 and plantings made during the winter of 1956–57.

The series were designed to test possible specific causes of genetic variation in longleaf pine. Series 1 and 4 sampled the range of longleaf pine primarily along an east-west transect from central Georgia to eastern Texas as far north as northeastern Alabama and as far south as the central Gulf Coast. This part of the range has three major features that could be expected to cause genetic variation in longleaf pine: the Mississippi River and its accompanying wide flood plain acts as a barrier to gene exchange between the pine populations on either side of it; precipitation is lower in the western part of the range; and temperature is lower and precipitation less in northeastern Alabama than it is near the Gulf Coast. Within the area sampled by Series 2 and 5, two major influences could be expected to cause genetic variation in longleaf pine: (1) the difference in climate between the Carolinas, where northern plantings and the seed collection points are concentrated, and the climate of the central Gulf Coast, where the southern series are located; (2) soil type. Seed collection and planting locations were selected on sandhill and non-sandhill soils (hereby designated "Coastal Plain" soils) to determine influence of soil type on genetic variation. Series 3 and 6 sampled the northern, western, and southeastern extremities of the longleaf range at three intermediate points designed to test the influence of the extremes of climate within the longleaf pine range. Six plantings were established during the winter of 1952–53, but only the Virginia planting survived for 10 years, and even this one has since been lost to flooding caused by dam construction. During the first few years, 10 of 18 longleaf plantings were destroyed by drought, and several others suffered serious damage. Attempts were made to rehabilitate individual plantings or part of them, but by 1955 it was found advisable to reestablish the entire longleaf phase of the study. Of the replacement plantings which were established in 1956–57 in seven areas, all but the one in southern Florida have developed satisfactorily.

Most plantings were sprayed to suppress brown-spot needle blight caused by *Scirrhia acicola* (Dearn.) Siggers. Spraying was carried out at the discretion of the individual cooperator, usually two or three times a year, but in spite of these measures the disease was prevalent in most plantings.

Longleaf pine's characteristic grass stage introduced much experimental variability into the data on performance. At age 10, for example, trees 25 feet tall and trees still in the grass stage were commonly found on the same plot. Under these conditions, the units of analyses, plot means, would have little meaning. Therefore, the smallest trees on each plot were ignored and the mean plot height was calculated on the basis of trees taller than 1 foot at age 5 years and 10 feet at 10 years of age. Calculated in this manner 10th-year height was based on about 90 percent of the trees that had begun height growth. Survival of all trees originally planted was calculated from the first- and third-year data. Many surviving trees remained in the grass stage longer than 10 years, however. While technically surviving, their actual contribution to the stand at maturity will, in all probability, be negligible. Potential commercial value of longleaf pine races is expressed by percentage of trees that have begun height growth after 5 and 10 years in the field. Therefore, the number of trees taller than 1 foot, expressed as percentage of trees originally planted, was calculated. At age 5 there was little correlation between the proportion of trees living and the proportion of trees beginning height growth, but by the 10th year the correlation was very strong ($r = 0.93$ for Series 4, 5, and 6). Apparently many of the trees still in the grass stage at age 5 either died between the 5th and 10th year or became so seriously overtopped by competing vegetation that they were unseen by the observers.

Analysis of results after age 10 by Wells and Wakeley (1970a) and Wells (1969) indicates that geographic patterns of variation are evident in survival, initiation of height growth, total height, volume, and infection by brown spot and fusiform rust.

Survival of the 32,900 seedlings in Series 4, 5, and 6 averaged 71.3 percent after 3 years, 69.1

percent after 5 years, and 57.0 percent at age 10. Trees from the two most western locations, central Louisiana and eastern Texas, survived satisfactorily up to 3 years after planting but suffered more mortality between the 5th and 10th years than did trees from other locations. This heavy mortality could be accounted for by differences in brown-spot infection among trees from different locations, as the western ones were relatively susceptible to brown spot (Henry and Wells 1967). Infection by fusiform rust was very low, which is typical for longleaf pine, but it was higher in trees from locations in Alabama and Georgia (8.1 and 7.8 percent, respectively) than in trees of Mississippi, Louisiana, or Texas origin (4.7, 2.5, and 3.3 percent, respectively). The possibility of introgression with loblolly pine as an explanation for the susceptibility to fusiform rust has not been investigated. In addition, this might be an explanation of the population center for loblolly pine characterized by a concentration of wood volume in southwest Alabama (fig. 46) and for longleaf pine in the western tip of Florida (fig. 52). Two additional centers of population were not sampled in the southwide study.

Average height of trees taller than 1 foot, averaged over all plantings in Series 4, 5, and 6, was 4.7 feet at age 5, whereas after 10 years the average height of trees taller than 10 feet was 20.2 feet. Most of the important genetic variation in height developed between the 5th and 10th years, so this report accordingly was concerned mainly with 10th-year data. Trees from collection locations in the Atlantic coastal region showed a trend of decreasing height growth with increasing annual temperature and precipitation (figures 79 and 80). However, for the same temperature zone (68° F), trees from the south-central part of the range (Alabama and Mississippi) grew much faster than those from Georgia, Louisiana, and Texas.

The most conclusive findings of the study to date are poor performance of trees from the southern Florida area and superior performance in several widely separated plantings of the trees from the three central Gulf Coast locations (fig. 81). Superiority has been expressed in terms of 10th-year heights and in the percentage of trees beginning height growth by the 10th year in the field. On these bases, it is possible to draw a map delimiting

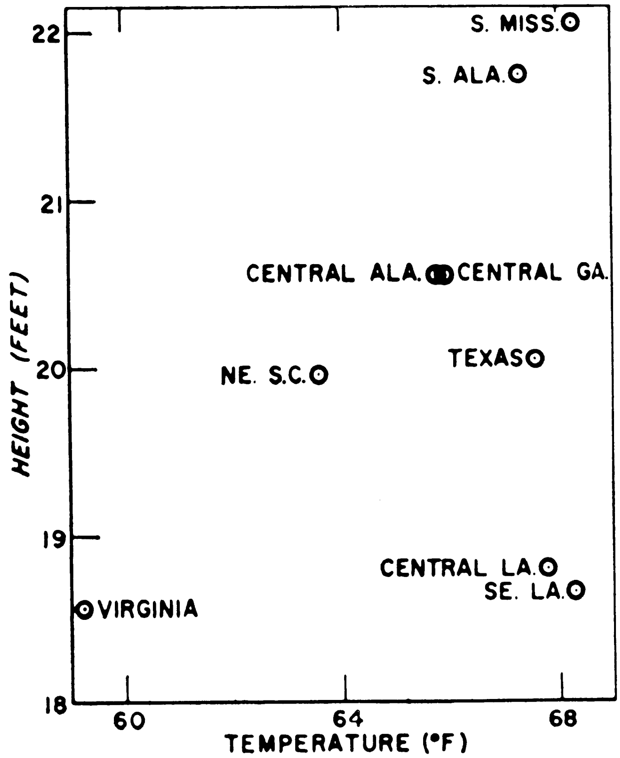

Figure 79.—Height of longleaf pine from different geographic locations in the eastern part of the range varies with annual temperature at the collection point. For the same temperature zone (68° F), trees from southern Alabama and Mississippi grew faster than those from Texas or Louisiana. (Wells and Wakeley 1970a)

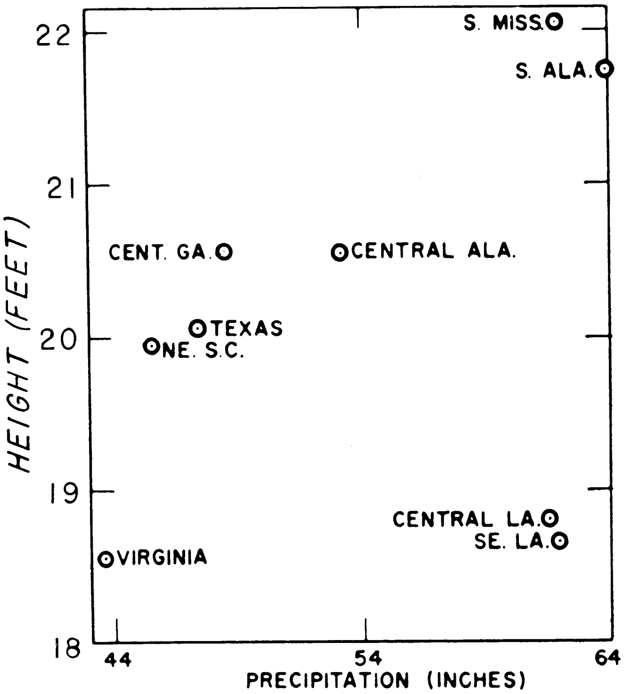

Figure 80.—Height of longleaf pine from different geographic locations varies with the average annual precipitation at the collection point, but for an annual precipitation of 62 inches, trees from south Mississippi and Alabama grew faster than those from Louisiana. (Wells and Wakeley 1970a)

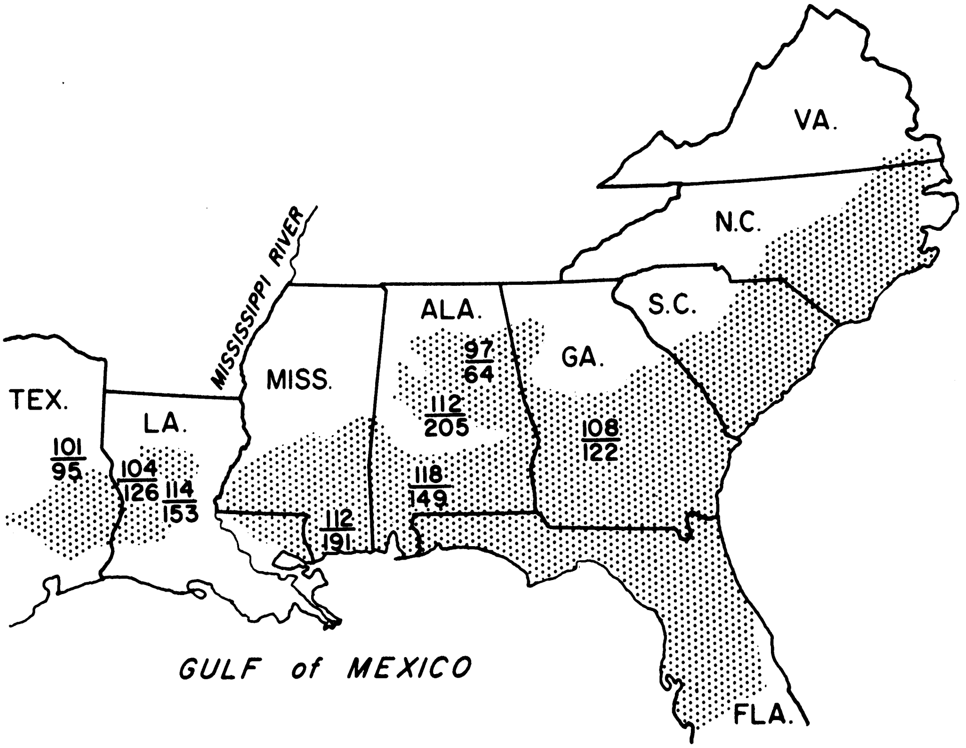

Figure 81.—Tenth-year height (numerator) and volume per acre (denominator) of longleaf pines from southern Alabama seed, expressed as percent of mean of trees from all seed sources represented in planting. Position on map indicates planting location, and the stippled area represents the natural range. Series 1 and 4 combined. Superiority in both survival and height growth contributes to superiority of 22 to 105 percent in wood-volume yield per acre. (Wells 1969)

the zone within which trees from the Gulf Coast areas have performed better than trees from other sources in the study (fig. 82). Growth differences are striking, with wood volume from 22 to 105 percent higher than trees from other sources. A proposal to move seed from the shaded to the stippled area of figure 82 must be viewed with some caution as it involves moving seed into a slightly more severe climate than that of its origin. The 10 years that the trees in the present study have been in the field have not provided all the climatic tests that could be expected during a longer period, and it is therefore possible that the growth advantage shown so far could be nullified in the future. However, maximum seed movements of 150 miles north and 250 miles east and west cannot be regarded as drastic in a region as climatically uniform as the southern Coastal Plain. The plantings from the present study have been subjected to relatively severe weather during the test period. West of the stippled area, use of seed from west of the Mississippi River area is indicated, and on the basis of the present results, seed from or near the eastern Texas counties of Polk, Tyler, or Hardin promises better growth than seed from central Louisiana. The results do not indicate any "best" seed source from areas north or south of the stippled area. They do, however, indicate that there is no advantage in moving longleaf seed north more than 4° of average annual temperature (fig. 82).

The results indicate certain combinations of seed collection and planting locations should be avoided if at all possible. Seed from southern Florida should not be moved into northern Florida or beyond. Present results indicate that such a move would result in almost complete failure. The penalty for not following the other recommendations listed below would probably not be catastrophic, but rather a growth loss of perhaps 10 or 20 percent. 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, at least until further research shows that the two seed collections made by the present study were not representative of the area. Seed from near the extremity of the range in northern Alabama should not be moved south or east more than about 150 miles, and particularly it should not be used near the central Gulf Coast. The superiority of the central Gulf Coast seed when used near the central

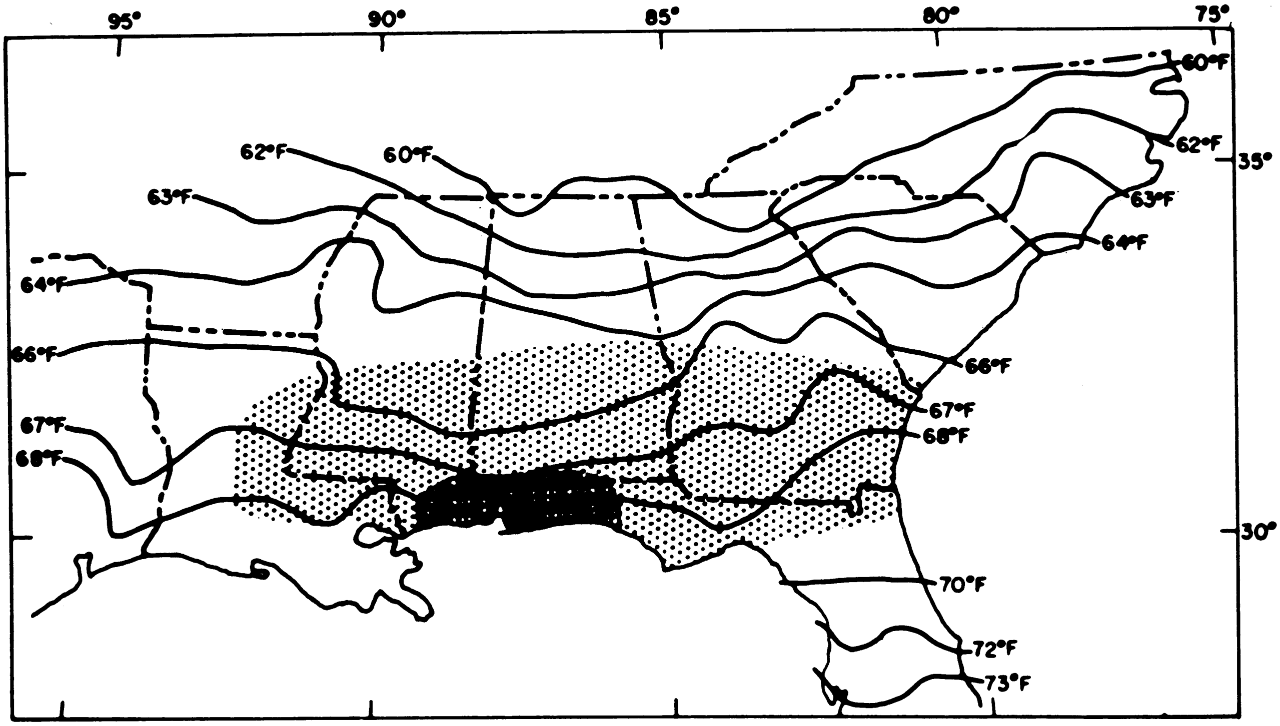

Figure 82.—Optimum longleaf seed collection area (hatched) for plantings to be made within the stippled area. For other locations local seed or seed from areas a short distance south of the plantation should be used. Isotherms of average annual temperature are given as a guide in following the recommendation to avoid moving seed northward to a zone with more than 4° difference in annual temperature. (Wells and Wakeley 1970a)

Gulf Coast is one of the strongest points made by the present study. Similarly, longleaf from near the northern extremity of the range in Virginia or northeastern North Carolina should probably be avoided. Seed from nearer the North Carolina-South Carolina border would be a better choice for planting anywhere in the northeastern part of the natural range.

Additional information on performance of longleaf pine seed from different locations in specific areas has been reported by various authors. In a discussion of the wide differences among races in survival and damage by cold of longleaf pine planted in Virginia (fig. 83), Allen (1961) reported that the damage resulted from cold at 12°, 15°, and 26° F between November 30 and December 3. Also, the plantation included numerous hybrids with loblolly pine, which have different height growth habits from longleaf pine. In the Maryland plantation, trees of Florida origin had significantly lower specific gravity than trees from other areas tested, as well as being less frost resistant (Saucier and Taras 1966). When trees of the Florida origin were omitted from the analysis of variance of specific gravity, there were no significant differences among the other five lots of trees. Wood specific gravity varied from 0.325 to 0.367.

For the longleaf planting in southwest Georgia, the range of seedlings making height growth by the fourth growing season was from 48 percent for trees from Cleburne County, Alabama, to 82 percent for the local race from Treutlen County, Georgia (Collins 1964a). Also, forking of the stem varied significantly at 5 years of age between trees from different locations. Trees from Polk, Tyler, and Hardin Counties in Texas had 1.9 percent forking, while those from Treutlen County, Georgia, had 7.9 percent. However, difference in forking was nonsignificant at 10 years, although it ranged from 4.7 percent of the trees in one race (Rapides Parish, Louisiana) to 15.7 percent (Baldwin County, Alabama). The relationship between tree height at the planting location in Georgia and latitude and longitude was somewhat stronger at the 10th year than at the 5th year (Bethune and Roth 1960; Collins 1964a).

Shoulders (1965) reported that for test plantations in Louisiana, trees from regions with 17 to 20 inches of rain from January through April made the most height growth. In the Texas plantation of trees from six different locations, height ranged from 20.7 feet for trees from Cleburne County, Alabama, to 23.8 feet for trees from Treutlen County, Georgia. However, trees from Georgia av-

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Figure 83.—Longleaf pine seedlings from Hillsborough County, Florida, in Nansemond County, Virginia, planting. These seedlings had less height growth and poorer survival than more northern sources. They were frost damaged and showed a general lack of vigor in contrast to longleaf (in the background) which came from other locations.

eraged only 10.2 percent survival, while trees from Texas local seed source had survival of 40.4 percent.

Early flowering in longleaf pine was found to be related to geographic origin of the seed (Boyer and Evans 1967). Six years after the trees were planted, 71 percent of flowers on trees in the plantation were on those from Richmond County, North Carolina. The seed source study plantation was located in southwest Alabama. However, there was a difference between planting locations: at 10 years of age, trees on all plots at one experimental forest had 92 female flowers in contrast to only 24 on trees at a different location. At 10 years of age, trees from 6 of the 11 geographic locations under test produced from 1 to 67 flowers, but no regional pattern seemed apparent.

In a study not connected with the southwide pine seed source study, Snyder (1961b) found small but apparent differences in the number of fibrous roots of longleaf pine seedlings originating from Georgia and those from states farther west. The number of lateral roots was greater on seedlings from seeds collected east of the line joining Laurens and Echols Counties in Georgia. Snyder and Allen (1962) discussed the importance of differences occurring in the heights of longleaf pine seedling grown at different nurseries in connection with design of racial variation studies.

In an Alabama plantation, local seed from Bibb County, central Alabama, produced 15 percent greater volume than trees from Harrison County, southern Mississippi; and in Mississippi the local seed produced 19 percent more volume than Alabama trees (Snyder and Allen 1968). Also, for the Alabama trees the volume was 11 percent greater for offspring of parent trees growing on productive or cove sites than for offspring of trees growing on unproductive or ridge sites. The results confirm those of the southwide study which indicate longleaf pine in central and northern Alabama is not a highly vigorous race.

In Louisiana, tests of wind-pollinated families for resistance to brown spot showed parent trees growing in Alabama, South Carolina, and Florida transmitted to progeny more resistance than those growing in Louisiana and Texas. Progenies of trees on the Conecuh National Forest in southern Alabama excelled all others in resistance; those from the eastern part of the longleaf pine range, with the exception of North Carolina trees, excelled the local Louisiana trees by a two to one margin (Derr 1971). Thus, some of the resistance to brown spot in the eastern part of the longleaf pine range might be genotypic rather than phenotypic.

Tests with longleaf pine seedlings in Florida under different day lengths showed that seedlings grew larger under long days of 15-hour photoperiod than under a short day of 9.5-hour photoperiod, but showed no significant differences attributable to geographic source, perhaps because they represented a narrower latitudinal range than did seedlings from other locations used in tests with shortleaf and loblolly pines (Allen and McGregor 1962). Longleaf pine seedlings were grown from seed used in the southwide pine seed source study. Seed was obtained from North Carolina, Georgia, Alabama, Mississippi, and Louisiana. Longleaf pine seedlings were exposed to the two photoperiods for less than 6 months. Those under long day became considerably heavier than those under short day. The average dry weight per top was 1.18 g for the long day, and 0.28 g under short day. Roots weighed 0.28 g per seedling under long day and 0.16 g under short day. The short test period and the species dwarf-growth habit probably contributed to the absence of marked differences in growth attributable to geographic origin.

Longleaf pine is not so popular as slash or loblolly pines for importation in countries where southern pine may grow well; consequently, few comparisons of races have been made. In Colombia, South America, longleaf pine of Florida seed grew better than trees of Alabama and Mississippi origin (Perez 1967).

RACIAL VARIATION IN SAND PINE

Sand pine is geographically confined to the well-drained, infertile sands of Florida and the southern tip of Baldwin County, Alabama, as shown on range maps in chapter 1. The major concentration in wood volume of the species is in a 280,000-acre block in north-central Florida. The only other extensive area is in western Florida, between Panama City and Pensacola. Sand pine occurs in isolated stands at two locations between these two large blocks.

Of the two races of sand pine that have been recognized (Little and Dorman 1952a), Ward (1963) has named the western race var. *immuginata*, and the name has been generally accepted. The Ocala race has serotinous cones, grows in even-aged stands, and is phenotypically of poorer form than the open-coned and uneven-aged western race called Choctawhatchee sand pine.

Studies of sand pine seedlings originating from different geographic locations and treated by different fertilizers showed considerable seed source effects (Morris 1967). It has been reported that seed color darkened and seed size increased from east to west (Barnett and McLemore 1966), but Morris found no difference by seedling origin in the number of cotyledons. The most frequent number of cotyledons was five, and the range by individual seedlings was from three to seven. The range in cotyledon number by mother tree was 4.30 to 5.70, and the differences were statistically significant. However, nutrient deficiency symptoms were significantly different both by seedling origin and by fertilizer treatment. The nitrogen treatment alone resulted in stunted growth and prickly needles, a typical phosphorous deficiency. This effect was uniform for seedlings from all different geographical locations. Seedlings with yellow tips which later turned brown were present only in the nitrogen and phosphorus treatment. Seedlings from Walton and Franklin Counties exhibited such symptoms to a significantly less degree than did seedlings from Levy, Marion, and Hernando Counties. Ectotrophic mycorrhizae were completely absent in the presence of 100 p/m of nitrogen. However, the proportion of infection was unaffected by 300 p/m of phosphorus. Seedlings from Walton and Franklin Counties showed significantly more mycorrhizal infection than did those from Levy, Marion, and Hernando Counties. Although the overall root infection on seedlings from Walton County was greater than on those from Franklin County, the latter exceeded the Walton seedlings in proportion of infection in the phosphorus-alone treatment. The relationship between root infection and growth in sand pine is not well known. Seedling shoot growth rates were significantly different by seedling origin, by fertilizer, and by the origin x fertilizer interaction. All shoot growth rates were severely decreased in the nitrogen-alone treatment and mortality was high. All shoot growth rates, with the exception of Walton seedlings, were positively affected by the phosphorus-alone treatment. It was found that all origins responded synergistically to the nitrogen-phosphorus treatment. The nitrogen x Walton and Franklin comparisons were significant; the nitrogen main effect was positive for Franklin and negative for shoots of seedlings from Walton County. The interactions of nitrogen and phosphorus with the Walton and Franklin seedlings are of considerable practical significance, as this relationship reduces the importance of the main effect of fertilizer. It follows that seed origin must be considered before response to fertilizer can be predicted with any degree of confidence.

Over a 12-year period, Ocala sand pines grew taller in west Florida sandhills but were not as resistant to disease and insects as the Choctawhatchee race native to the area (Burns 1968). First-year mortality was high for the Ocala race so that total volume was only 1.9 cords per acre at age 12, compared with 2.6 cords per acre for Choctawhatchee sand pine. Neither growth nor survival of Choctawhatchee sand pine was seriously affected by disease or insects, while Ocala pines were susceptible to shoestring root rot caused by *Armillaria mellea* (Vahl. ex Fr.) Kummer or *Clitocybe tabescens* (Ross 1970) and pitch moths (*Dioryctria amatella* Hulst). Nantucket pine tip moths (*Rhyacionia frustrana* Comst.) attacked trees of both races but with negligible effect. Also, the lance nematode (*Hoplolaimus galeatus*) attacks trees of both races, as demonstrated with potted seedlings (Ruehle 1971).

In Texas, sand pines of west Florida origin (Choctawhatchee race) grew faster than those from central Florida (Zobel *et al.* 1956). In plantations near Columbus, Georgia, and Cheraw, South Carolina, with average annual temperatures of 66° F and 62° F, respectively, Ocala sand pine had much higher mortality from freezing and was more susceptible to tip moth attack than Choctawhatchee sand pine, but there was no significant difference in height growth (Harms 1969). The study was 3 years old when results were evaluated. A summary of differences among races was given in chapter 2, taxonomy.

RACIAL VARIATION IN SHORTLEAF PINE

Shortleaf pine has the most extensive range geographically of all the major southern pines, as shown on the range maps in chapter 1. It does not occur in pure stands with high volume or stocking over large areas, as do some of the other southern pines. A concentration of wood volume occurs in the Piedmont areas of southern Virginia, central North Carolina, and northwestern South Carolina, but stocking is low through north Georgia, Alabama, and Mississippi (fig. 54). In Arkansas, there are population centers in the west central part of the State in the mountainous areas, and in the central part of east Texas near the Louisiana State line. Population-center locations for loblolly and shortleaf show a general likeness in pattern, although the specific centers do not coincide. Racial variation studies will indicate whether inherent differences occur among groups of trees in various population centers.

Shortleaf pine seedlings can be produced at low cost, but, as a result of somewhat slower growth rate, it has not been planted as extensively as slash or loblolly pines. Another factor in limiting use of shortleaf pine in reforestation is its susceptibility to littleleaf disease in certain parts of the natural range from Alabama eastward through Georgia and South Carolina. Because of its limited use in reforestation in the Deep South, little interest has been shown in racial variation studies. However, in the northern part of the natural range and in areas through the central United States north of the range of other southern pines, interest in shortleaf pine as an introduced species has been active for many years.

Because of its wide range and because it grows from extremely low elevations not far above sea level to as high as 3,300 feet in the southern Appalachian Mountains, considerable racial variation may have developed. Investigations have followed somewhat the same pattern as that in other southern pines. The first studies were rather general using limited number of seed from different geographic locations that might be of particular interest to local planters. This was followed by the southwide pine seed source study, which sampled the entire range of shortleaf pine but with limited samples in certain locations (Wakeley 1953b).

In Florida, shortleaf pine seedlings of different geographic origin grown under a short day of 9.5 hours exhibited a clinal pattern in growth, but under long days of 15 hours they showed significant differences more suggestive of ecotypes (Allen and McGregor 1962). Seed for the test was obtained from seven geographic locations used in the southwide pine seed source study. They ranged from Burlington County, New Jersey, in the North, south through Virginia, South Carolina, Georgia, and west through Tennessee, Arkansas, and Texas. At the termination of the experiment, which extended from December through May, all long-day seedlings had fascicle needles, while seedlings under short day had only juvenile foliage. There was no clinal growth pattern under long day, but the seedlings from South Carolina and Arkansas grew significantly more than those from other locations. Height of seedlings from New Jersey under the long-day treatment was 9.2 cm, those from Virginia 9.2 cm, South Carolina 15.6 cm, Georgia 10.6 cm, and Cherokee County, Texas, 10.6 cm. Under the short-day treatment, seedlings from Burlington County, New Jersey, were 2.1 cm, those from Virginia 2.5 cm, South Carolina 3.4 cm, and Cherokee County, Texas, 4.0 cm.

Shortleaf Southwide Study

The shortleaf pine southwide study includes seed from 23 locations and 40 plantings throughout the range (Wells 1969; Wells and Wakeley 1970b). The study is divided into six series based on combinations of seed-collection points and plantings. Plantations of the first three series were established during the winter of 1952–53, but mortality was so high that three more series were established in 1956–57. Generally, the last three series sampled the same areas as the first three, but the surviving 10 plantations from the first plantings constitute valuable replications by year.

In the southwide study Series 1 and 4 sample the shortleaf pine range north and south. Series 2 and 5 sample three distinct geographic areas such as west of the Mississippi River, the Appalachian Mountains in Georgia and Tennessee, and the Allegheny Mountains in Pennsylvania. Series 3 and 6 encompass samples from a longitudinal transect extending from southeastern Oklahoma to South Carolina.

Important racial differences in height, volume growth, survival, and degree of early cone production have been indicated by the shortleaf pine southwide study (Wells and Wakeley 1970b; Wells 1973). Trees from the warmest part of the range have grown faster than all others in Coastal Plain plantings up to 250 miles north of their point of origin. Differences in survival have been small except in the northern plantations, where trees of northern origin were superior.

There is a strong relationship between growth rate of shortleaf pine and temperature of the seed-collection location; also an interaction between seed-collection location and planting location (fig. 84). Trees from southeastern Louisiana and southwestern Georgia, the southernmost collection points, grew much faster than those from other locations, as averaged for three southern plantations, and only slightly faster than averages for five middle-latitude plantings. In the North, however, as indicated by averages for two northern plantations, trees of Missouri and New Jersey origin were already superior in growth rate to those from locations to the South.

Tentative seed-collection and planting zones for shortleaf pine have been proposed by Wells (1969) based on results of the southwide study to date (fig. 85). Seed should be collected in zone 1 for planting in zones 1 and 2. For six test plantations in zone 2, trees from zone 1 seed had about 17 percent more volume than those from zone 2 locations. Also, seed from zone 5 should be suitable for planting in zones 5 and 2. For planting in zone 3, seed should be collected in zones 2 or 3 or the northern half of zone 5. Seed for planting in zone 4 and farther north should be collected only in zone 4. The importance of using only northern seed in zone 4 is emphasized by the fact that trees from zones 3, 2, and 1 had 27, 48, and 76 percent less volume, respectively, than northern trees at age 10.

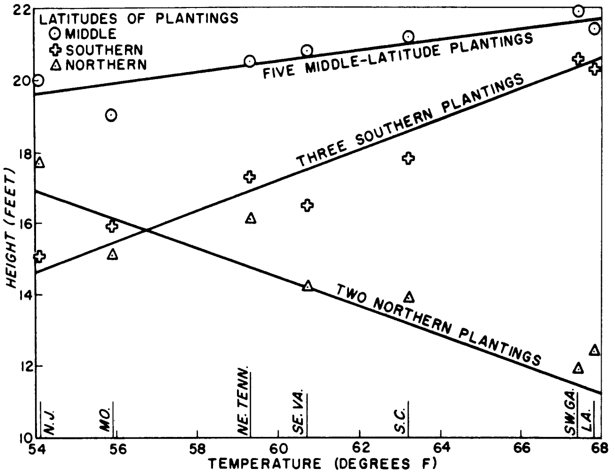

Figure 84.—Strong relationships occur between 10-year height and mean annual temperature at the location of seed origin in southern, northern, and middle latitude plantings of shortleaf pine Series 4 in the southwide study. An important interaction of growth rate with planting location is shown by trees from Georgia and Louisiana, which grow much faster than other races in southern plantings, only slightly better than others in middle-latitude plantings, and much slower than others in northern plantings. In silviculture, selection of the proper race for planting is very important. (Wells 1969)

Reports on certain installations of the shortleaf pine study have given additional information on certain traits other than height growth and survival. Northern seed were best for planting in Missouri (Rogers and Phares 1962). Latitude of seed source was directly related to seedling survival. For shortleaf planted in 1953, survival ranged from 24 to 70 percent; for trees planted in 1957, it ranged from 45 to 84 percent. In both plantings major losses occurred during the first growing season.

In Maryland plantations, shortleaf pine from New Jersey grew much faster than trees from locations farther south and west (Little and Somes 1964). Although height of seedlings from northern areas was relatively low at the time of planting, after five growing seasons the trees were much taller than those from southern locations. Furthermore, survival of seedlings from Webster County, Georgia, was only 41 percent, but from Burlington County, New Jersey, survival was 94 percent. At 11 years, large differences occurred in many traits (figures 86, 87, and 88) (Little 1969).

For the Oklahoma plantations of the southwide shortleaf pine study, Posey and McCullough (1969) combined growth yield and wood quality to evaluate racial performance. They concluded that seed from Ashley County, Arkansas, grew trees superior to local Oklahoma trees on a basis of height growth, d.b.h., survival, tracheid length, and specific gravity of extractive-free wood. Volume growth superiority expressed as tons of extractive-free wood per acre averaged slightly

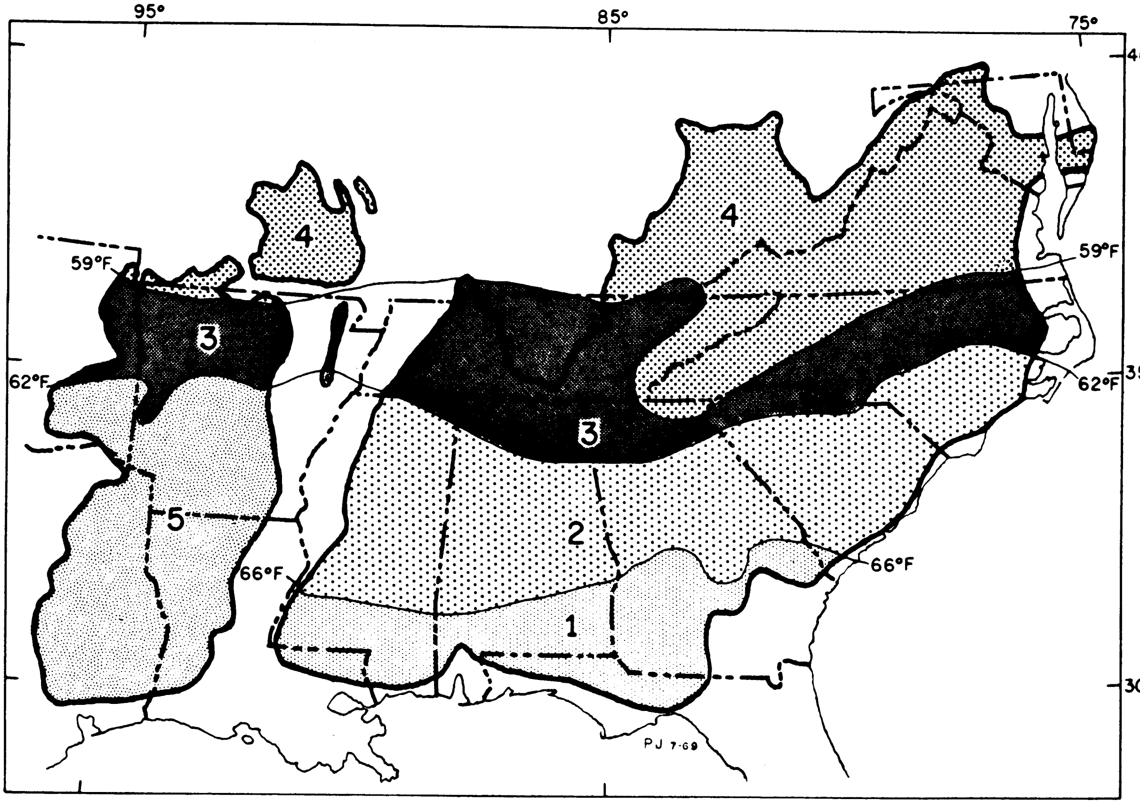

Figure 85.—Suggested seed-collection and planting zones for shortleaf pine. Seed should be collected in zone 1 for planting in zones 1 and 2, and from zone 5 for zones 2 and 5. For zone 3, seed should be collected in zones 2 or 3 or the northern half of zone 5. For zone 4 and farther north, seed should be collected only in zone 4. Isotherms indicate average annual temperature, and the heavy black line the natural range of shortleaf pine. (Wells 1969)

over 20 percent. There were small but significant differences among shortleaf pine races in both wood specific gravity and tracheid length.

Other Shortleaf Pine Racial Studies

Several racial variation studies, many older but none as comprehensive as the southwide study, have shown wide differences in economically important traits.

Aughanbaugh (1950) reported that, on the basis of a plantation in Pennsylvania, seedlings from Morgan County, Tennessee, made superior height growth compared to seedlings from Arkansas, Texas, Louisiana, Mississippi, and South Carolina. At 14 years from seed, shortleaf pine from South Carolina and Mississippi averaged 9.2 to 9.5 feet in height, respectively, and trees from Morgan County, Tennessee, were 14.3 feet in height.

In Ohio, shortleaf pine was second to loblolly pine in height growth but better in respect to self pruning. Shortleaf pine ranked next to loblolly pine in volume growth and was better than pitch pine, red pine, and Scotch pine (Aughanbaugh 1957).

In southern Illinois, shortleaf pine from various geographic locations showed highly significant differences in height and some evidence of differences in foliage color but no difference in survival (Minckler 1950). Shortleaf pines from some locations were taller than loblolly from others, although loblolly was generally the faster growing species. Temperatures near zero in December and January caused light to moderate injury to shortleaf pine seedlings from Tishomingo County, Mississippi, but no damage to seedlings from northern Arkansas, Missouri, Kentucky, Ohio, and Oklahoma (Minckler 1951). From a variety of different geographic locations shortleaf showed much less damage than loblolly. Plots of two shortleaf-loblolly pine hybrids with parental trees in Virginia and North Carolina showed no freeze damage.

On both good and poor sites in North Carolina, individual shortleaf seedlings attained heights as great as the best loblolly pines during early years. Seedlings that were taller after 1 year's growth continued to be significantly taller at the end of 5 to 7 years after planting (Lane 1961).

In erosion-control plantings in north Mississippi, where tests of shortleaf pine and loblolly pine from different geographic locations were being made,

Courtesy of New Jersey Department of Environmental Protection

Figure 86.—Shortleaf pine 11 growing seasons after being planted in New Jersey. Louisiana trees in foreground have low survival and short height in contrast to more vigorous New Jersey trees in the background. This is a good example of the extreme differences in tree growth and wood yield occurring among shortleaf pine races. (Little 1969)

shortleaf from local areas appeared to be a little taller than those from Oklahoma, but there were no significant differences in growth or amount of needle litter produced (Thames 1962). In contrast, loblolly pine from the Lost Pines area in Texas grew much faster than trees from other localities and produced much larger volumes of litter.

From a test in which tops of seedlings of different geographic origin were grafted to Mississippi shortleaf pine stocks, Allen (1969) concluded that rootstocks contribute little to variation in height growth among races. Shortleaf pine seedlings grown in Mississippi showed racial differences in root physiological characteristics such as pigment content, activity of IAA oxidase and peroxidase, IAA oxidase inhibitor, elongation inhibitor, acetone powder, and root respiration.

Introgression with shortleaf pine west of the Mississippi River has been proposed as an explanation for resistance to fusiform rust in loblolly pine (Hare and Switzer 1969), but the effect on shortleaf pine growth does not seem to have been investigated, although it has been recommended that some of the seed be planted elsewhere.

Shortleaf pine planted on littleleaf sites in Georgia, South Carolina, and Virginia showed a trend of healthier trees from locations west to east, and trees from upland locations were healthier than those from Coastal Plain locations (Ruehle and Campbell 1971).

RACIAL VARIATION IN TYPICAL SLASH PINE

Slash pine and longleaf pine are the two most important species in the vast timberlands that seem

Courtesy of New Jersey Department of Environmental Protection

Figure 87.—Shortleaf pine 11 growing seasons after being planted in New Jersey. Missouri trees on the left of the pipe have lower survival, thinner crowns, and smaller size than New Jersey trees at right and illustrate the effect of seed-source latitude and longitude on shortleaf pine. (Little 1969)

to stretch endlessly for great distances in the region of low elevation along the lower Atlantic and Gulf Coasts. Slash pine has the smallest natural range, as indicated by the maps in chapter 1, of the four major southern pines and of the minor ones as well with the exception of pond, pitch, and sand pines. It does not occur in natural stands west of the Mississippi but is often planted.

This species has a large population center in southeast Georgia and adjacent Florida and a small one in south Mississippi and Alabama based on wood volume (fig. 57). Geographic variation has been found in many traits, as noted in the preceding chapter.

The average annual temperature in the slash pine range is higher than for any other southern pine except sand pine, which is largely restricted to Florida. Mean annual temperature for the slash pine range is about 72° F in the South and 66° F in the North, or a difference of only 6°. Climatic factors found to be significant between the natural range of slash pine and the area immediately outside its range are expressions of seasonal frequency and intensity of rainfall (Bethune 1960).

South Florida slash pine, formally recognized by the USDA Forest Service as a variety of slash pine, is found only in central Florida southward to the Florida Keys. Typical slash pine and the variety have different ranges, but there is a gradient in traits where they meet, and no clear distinction in the boundary between the two can be made (Squillace 1966a).

Most foresters agree that slash pine in the two parts of Florida are different, but they do not all agree they should be taxonomic varieties, or, if not, how they should be named. The difference of opin-

Courtesy of New Jersey Department of Environmental Protection

Figure 88.—Shortleaf pine 11 growing seasons after being planted in New Jersey. The New Jersey trees on the left, the local geographic source, display higher survival, denser crowns, and greater size than trees from Tennessee on the right. (Little 1969)

ion about names has an important bearing on racial variation research. To those who cannot accept classification as a variety, differences in traits associated with geographic location represent examples of continuous or discontinuous variation within a species. To others, the differences in traits are merely the characteristics of two varieties and are not continuous or discontinuous variation within a species.

Because of the distinctions made between the slash pine varieties, discussion under the section on typical slash pine will be limited to the area in which the species occurs and in which it has been planted here and abroad. Also, the section will include information from the few studies in which field plantings, including both varieties, were made within the range of typical slash pine. The section of this chapter devoted to racial variation in South Florida slash pine will contain a summary of studies made in south Florida with either South Florida slash pine or typical slash pine.

The best summary of racial variation in slash pine from all investigations was made by Burley (1966) to guide foresters who import seed in various countries. The emphasis in the summary was on the kind of racial variation rather than extent. Studies beginning in 1937 were summarized in detail by the Southern Forest Experiment Station, which at one time had responsibility for Federal forest research throughout nearly the entire slash pine range. Later, Snyder *et al.* (1967) discussed the kind and extent of racial variation. Wells (1969) reported the more recent results of the southwide pine seed source study. A brief summary of racial variation in slash pine based largely on work in the United States was given by Squillace (1966a) as part of his

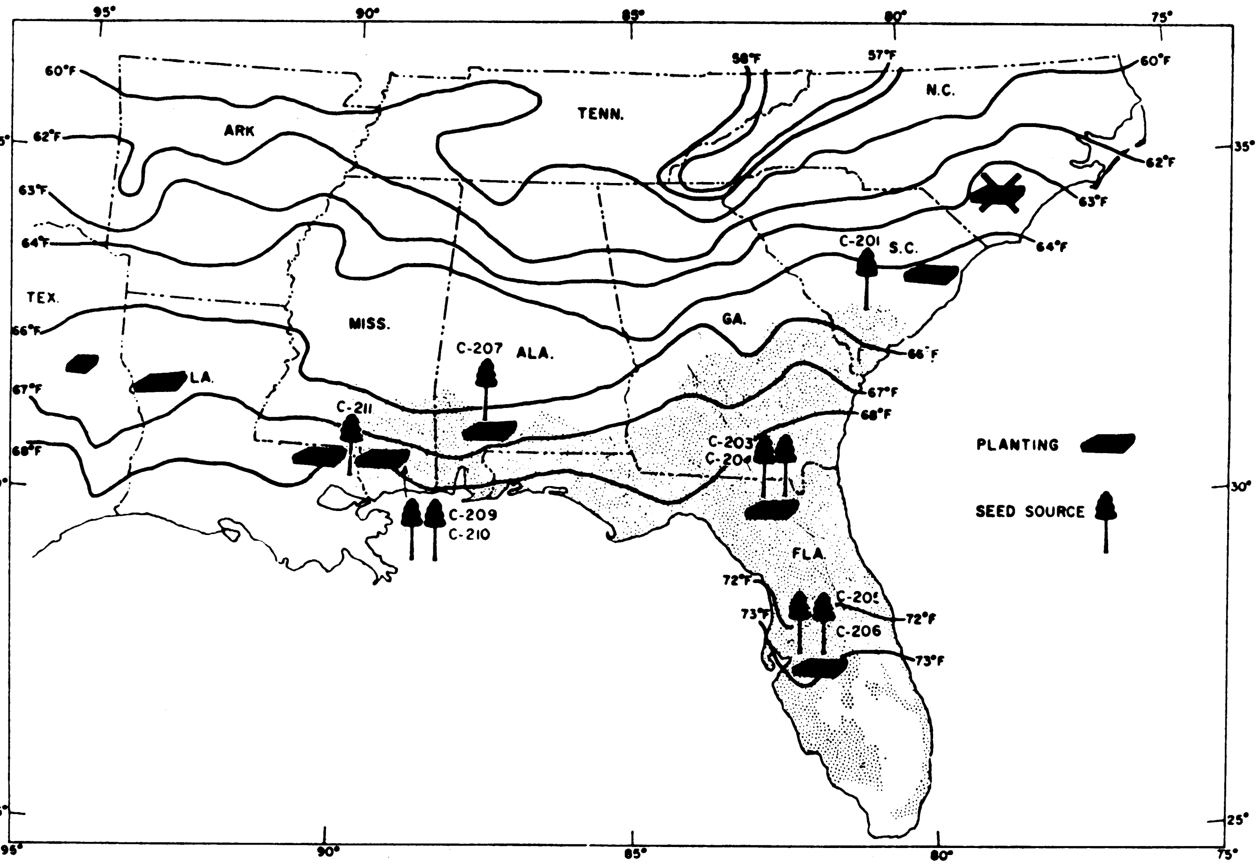

Figure 89.—Slash pine natural range with seed sources and plantings, with reference to mean annual isotherms, in the southwide pine seed source study (X = abandoned planting). Sampling was very thin, as in certain early studies, and was reduced further by failure of seedlings from the central Florida location. The population center in south Georgia was not sampled. The two slash pine varieties are not distinguished on the range map. (Snyder *et al.* 1967)

comprehensive study of geographic and racial differences in morphological traits of parents and growth plus morphological traits in offspring. Later, justification was given for designation of a zone of optimum development for slash pine within which trees are phenotypically and genetically superior in growth rate in comparison to trees in less favorable environments (Squillace 1966b).

So that existing summary papers can be fully utilized, racial variation in slash pine will be reviewed here in groups of studies usually based on a complex of factors such as research organization, geographic location, and individual study. The first group is composed of 10 studies by the Southern Forest Experiment Station prior to 1950, a large study in 1957, and the slash pine phase of the southwide pine seed source study.

Southern Forest Experiment Station Studies

In the period between 1937 and 1949 test plantings or assistance in planting was given in 10 United States and 7 South African studies as part of racial variation, nursery, and plantation disease research. The sources of seed, the planting test design, and the results are given in detail by Snyder *et al.* (1967). The authors discuss results in relation to the design of various studies. The weaknesses of some parts of the studies become important factors when results are compared with those of other studies.

Seed collection points for the southwide study were very widely scattered in relation to both latitude and longitude in the eastern part of the slash pine range, where the range in mean annual temperature is greatest (fig. 89). An additional complication was the low survival of slash pine from south-central Florida, which practically removed it from the tests. Thus, the range in average temperature was only about 2° F, although the southern part of South Carolina is many miles north of northeast Florida.

In the slash pine tests the seed came from only three locations: South Carolina, northeast Florida, and southern Mississippi, with only minor exceptions; these were in the same temperature zones on the main collection points. Test plantations were severely limited and restricted to the three points of seed collection plus areas outside the range in Mississippi, Louisiana, and Texas.

The numerous tests that were established over many years probably should be considered replications of one test rather than independent tests, and they should provide an excellent estimate of racial characteristics of slash pine from the three collection points. The results have a very serious limitation in that they do not provide an estimate of any racial differences that might occur in relation to average temperature throughout the part of the range in which it varies most. Also, the design of the studies does not permit a comparison of slash pine performance from the middle of the population center in southeast Georgia, either north or south, and particularly to the west toward the secondary population center in south Mississippi and Alabama (fig. 57). These very important limitations imposed by the study designs must be recognized when results are compared with those from studies that sampled different parts of the slash pine range, in some cases with much greater intensity.

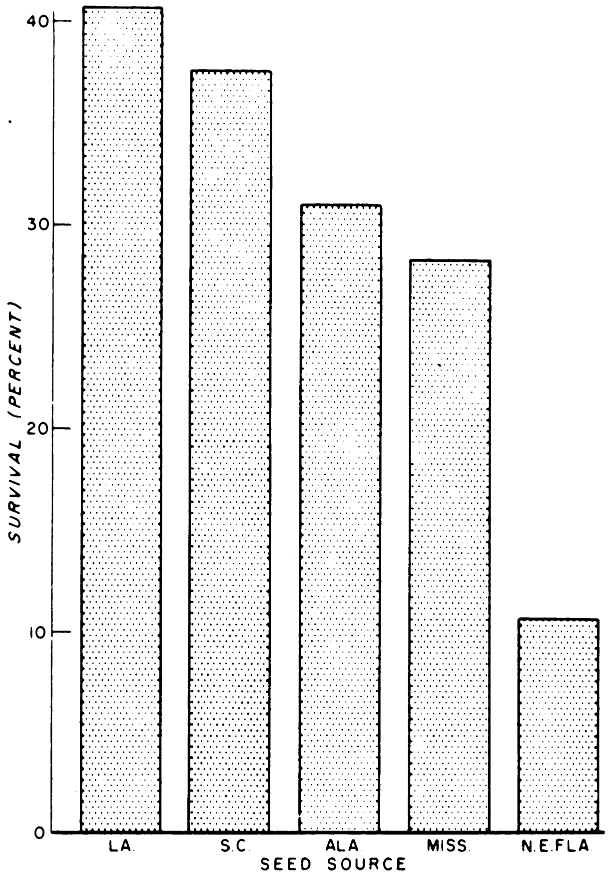

Figure 90.—Tenth-year survival, in a western Louisiana planting, of slash pine from five geographic seed sources. Trees from northeast Florida are not suitable for planting northwest of the natural range because of the low survival and slow growth shown in several test plantings in that area. (Wells 1969)

After an intensive review of a large amount of data from the racial variation studies, it was concluded that significant differences occur in economically important traits such as survival and growth and in certain isolated instances in susceptibility to damage by ice, hogs, and fusiform rust (Snyder *et al.* 1967). In the one study examined, there were no differences among slash pine trees from different locations in oleoresin yield (Barrett and Bengtson 1964), or in wood specific gravity, tracheid length, or amount of compression wood.

Some of the most conclusive evidence from all the slash pine tests was in regard to seedling survival. Trees from northeast Florida and an adjacent area in Georgia seem to have a lower capacity for survival than those from the western part of the range. The difference is not large, but it may be accentuated in areas of adverse climate and site, particularly outside the range, such as in western Louisiana (fig. 90).

Growth did not seem to differ greatly among trees from the three principal regions sampled when planted within the natural range at a limited number of locations. However, when planted outside the natural range, western trees outgrew eastern trees in two out of four tests (fig. 91) (Switzer 1959). Accurate estimates of wood yield in slash pine seem to be as difficult as in other species because of the high experimental error resulting from the interaction of height growth with survival, attacks by pests, and quality of the trees themselves.

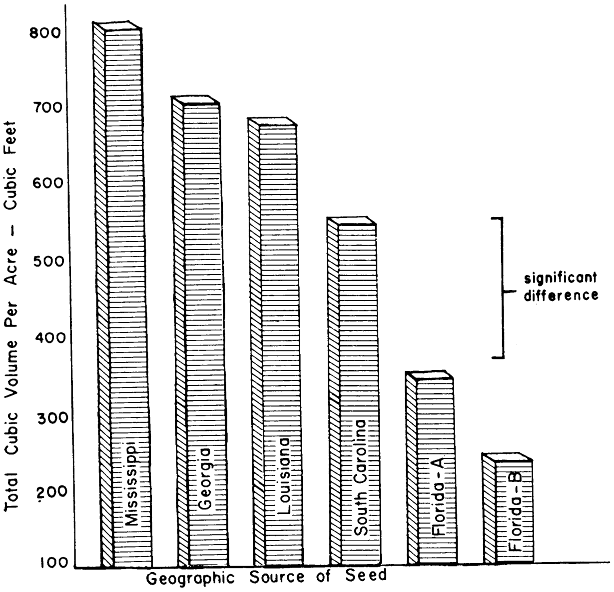

Figure 91.—The average total cubic-foot volume per acre varies greatly with slash pine from Florida, growing slowest at the completion of 11 field growing seasons when planted in northern Mississippi. (Switzer 1959)

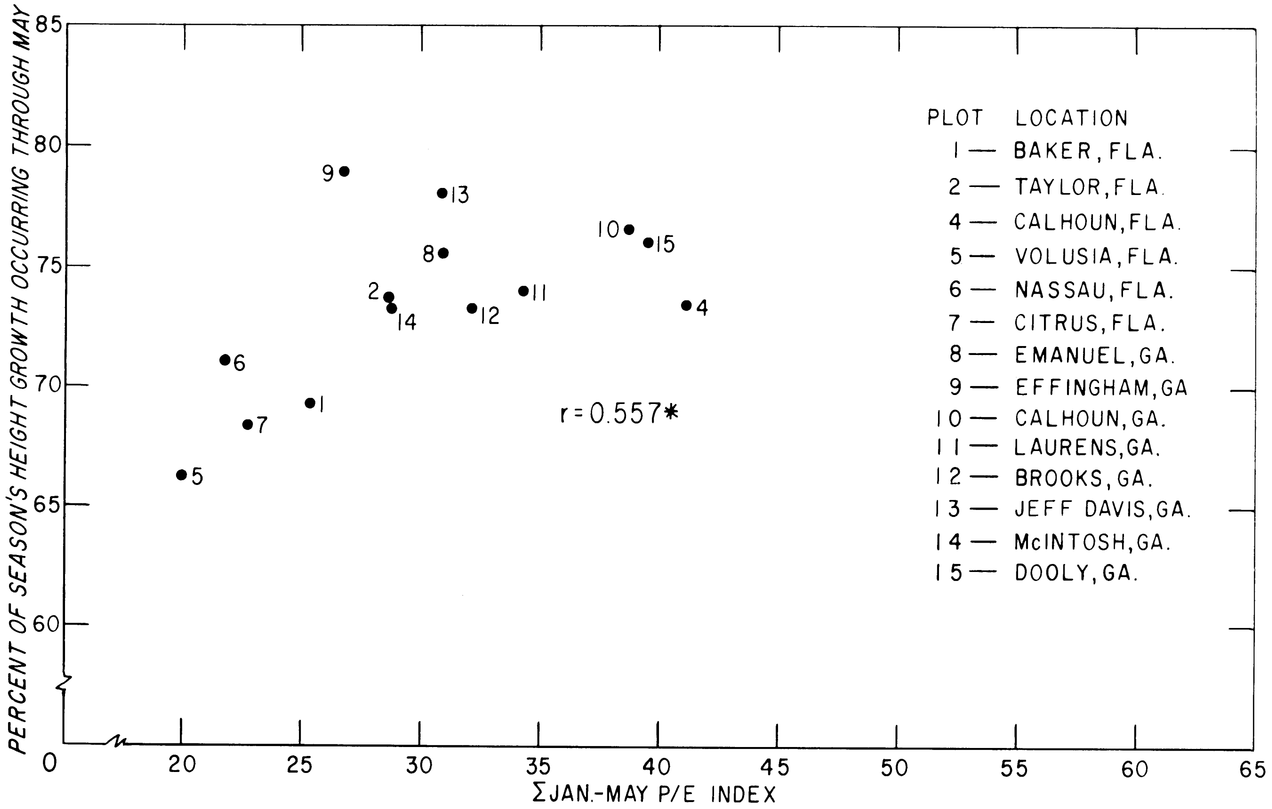

Figure 92.—Correlation of Σ Jan.–May P/E Index, with proportion of slash pine height growth made during early season in racial variation test plantation. (Bengtson *et al.* 1967)

In one test plantation in Louisiana, slash pine from South Carolina and Florida produced 25.0 and 24.4 cords per acre, respectively, while those from one locality in Mississippi and near the Florida line in south Georgia produced 30.5 and 30.6 cords per acre, respectively, or roughly 20 percent more wood; but the differences were not statistically significant (Derr and Enghardt 1960). In one test in which identities of the progeny of maternal parents were kept, heights of various progenies at 7 years varied significantly in one outplanting location, but not in another.

From results of all tests there was no conclusive evidence of differences among slash pines from different locations in susceptibility to fusiform rust infection, but experimental error was high in all cases. In one study susceptibility to rust varied among progeny of various maternal parents.

Other Studies Within the United States

In addition to racial variation studies by the Southern Forest Experiment Station, numerous investigations have varied in size, geographic location, and traits observed.

Slash pine from 15 locations outplanted at 7 locations, all in the Georgia-Florida area, showed large differences in growth, survival, susceptibility to fusiform rust, and minor morphological and physiological traits (figures 92 to 96). Seed germination varied significantly among seedlots from different locations, and seed from one point in Georgia had the highest and one in Florida the lowest (Mergen and Hoekstra 1954). Seedlings from central and northeast Florida and adjacent areas in Georgia had the smallest number of needles with three resin ducts. Number of stomata per millimeter were related to longitude, with seedlings from the eastern locations having the higher number. At the end of 10 years, seed source effects on survival and height growth, and consequently wood volume, were significant, and survival generally increased from south to north but showed no interaction with location of plantations. Trees from the extreme northern and southern parts of the range were, on the average, shorter in height than those from the central or optimum part of the range. Seed source effects on fusiform rust infection were significant, but interaction between source of seed and plantation location was strong, and no geographic patterns were evident. Very large and economically important differences occurred in wood volume yield (Squillace and Kraus 1959; Squillace 1966c; Gansel *et al.* 1971) because of the combined effect of

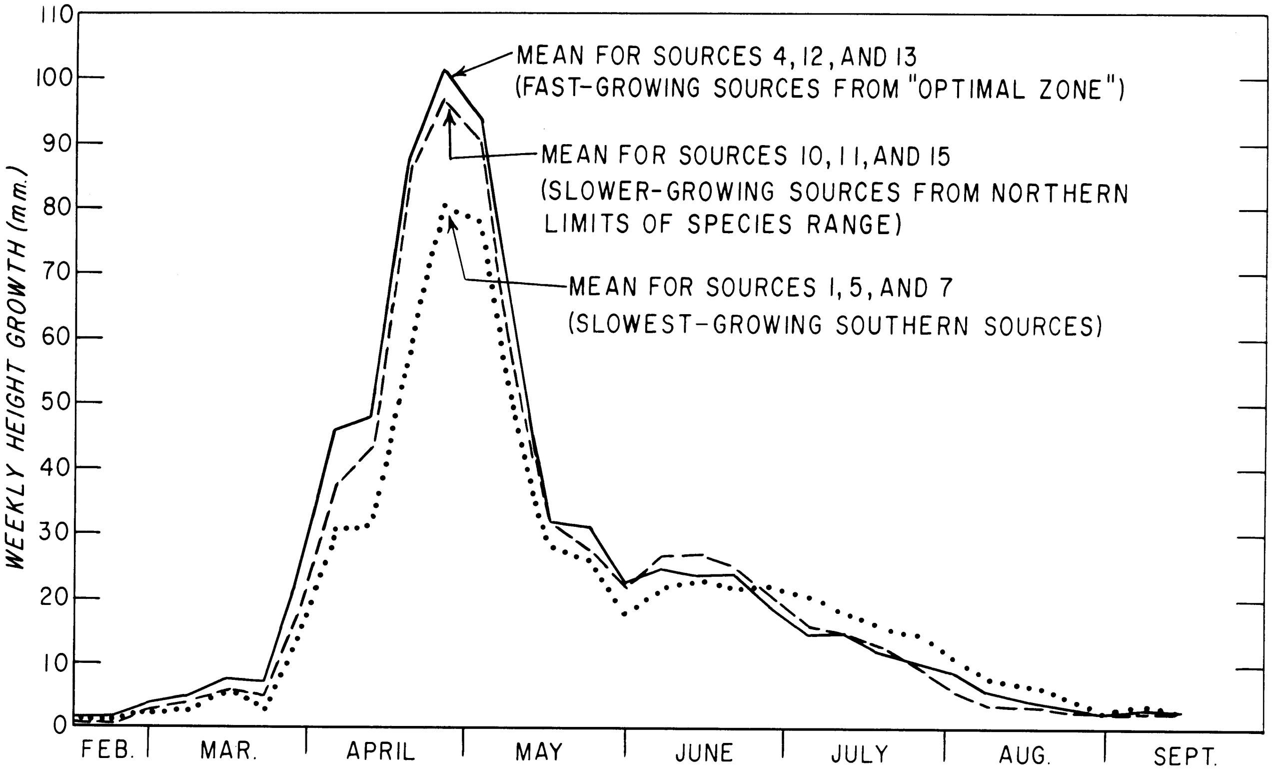

Figure 93.—Comparison of weekly height growth for three representative seed-source groupings shows important racial differences between southern and northern trees in growth rate during the most important part of the yearly growth period. (For source numbers, see previous figure.) (Bengtson *et al.* 1967)

differences in tree growth, survival, and susceptibility to rust. The magnitude of these differences is indicated by the growth in the outplanting installation in Baker County, Florida, the source of seed used many times in early slash pine studies. The local slash pine race produced 175 cubic feet per acre, which is nearly twice that of trees from two locations to the South, which produced 88 and 90 cubic feet per acre. However, the average production of trees from three locations in Georgia was 217 cubic feet, or 21 percent more than Baker County trees. Growth of trees from farther north in Georgia was less than that from the three locations in what was concluded to be the zone of optimum development for slash pine. Growth characteristics were related to geographic location and climatic factors (figures 92 and 93) (Bengtson *et al.* 1967). Oleoresin yield was lowest (76 grams) for trees from Calhoun County, Florida, and highest (130 grams) in trees from Citrus County, Florida, an area near where the ranges of typical slash pine and the South Florida variety meet. This area is known for low gum yields. There was no consistent pattern of variation with geographic location (Gansel *et al.* 1971), but the observations agree with those of Ineson and Rayl (1941) that oleoresin yield in slash pine varies among locations. Oleoresin from the twigs and trunks near the ground in trees of this and one other study showed differences in the components of turpentine, but patterns of variation were not clear except for β-pinene in branch oleoresin, which increased from 10 percent in the trees from the South to 50 percent in those from the North and then decreased; also, β-phellandrene in branch oleoresin decreased from 40 percent in the trees from the South to 10 percent in those from the North (fig. 94) (Squillace and Fisher 1966).

Slash pine from five of the collection points described in the early study (Mergen 1958a) were outplanted in south Florida. After 3 years there were differences attributable to race in survival, height growth, and insect attack (Langdon 1958b). Interim results indicated that slash pine from the central part of the range grew faster than that from the northern part. At age 11 typical slash pine of the most vigorous race had produced 2.2 times more dry weight of wood per acre than South Florida slash pine because of higher seedling survival, faster height growth, and higher wood specific gravity (Saucier and Dorman 1969). If differences among races and varieties continue until the trees reach maturity, it will be one of the few examples of

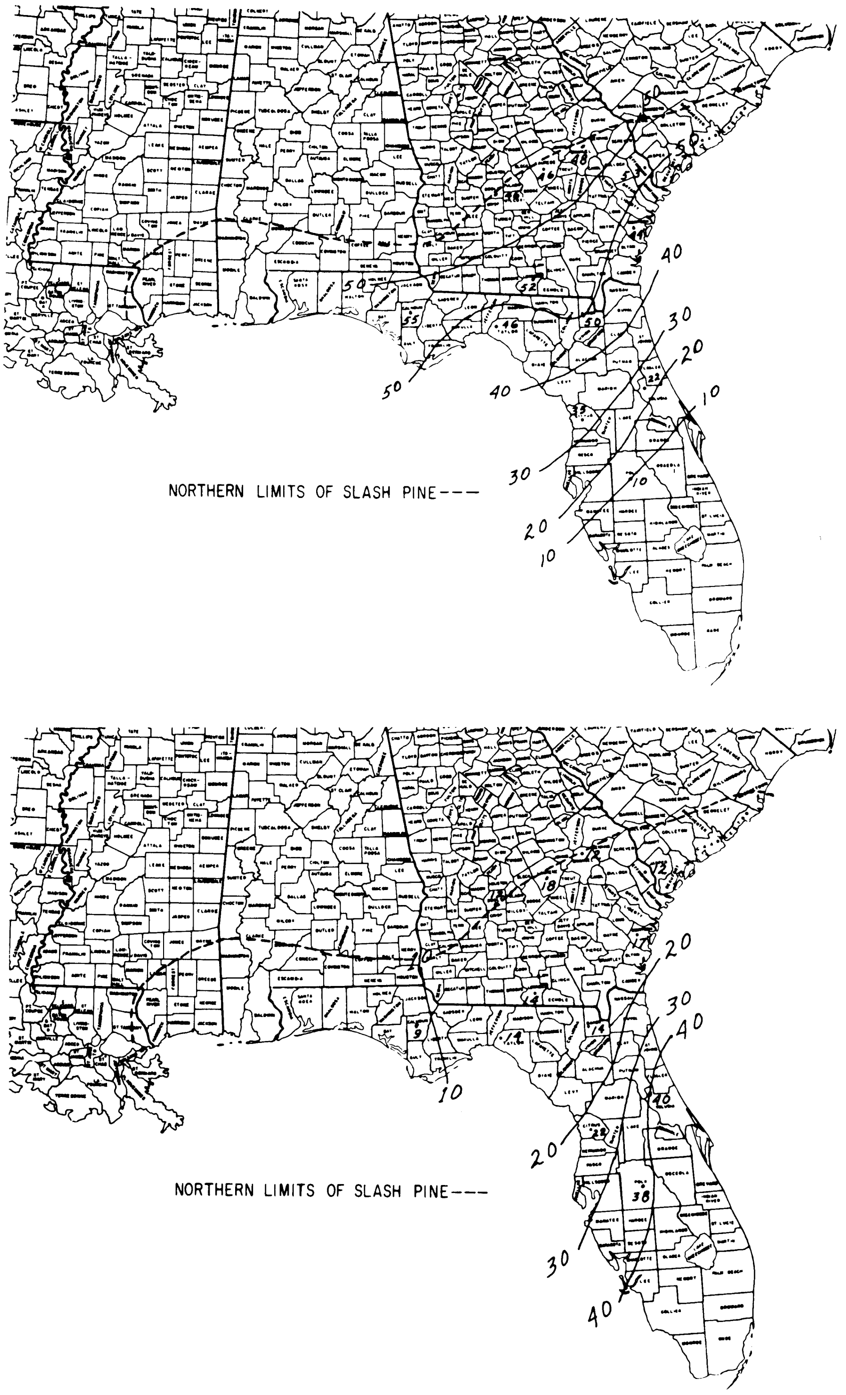

Figure 94.—Top: The percentage of β-pinene in oleoresin from slash pine twigs, but not trunks, is low in central Florida and increases to a high in southeast Georgia and then slightly decreases. Bottom: Average percent of β-phellandrene in twig oleoresin of slash pine varies by geographic location, with high content in central Florida and lower values toward the North, the reverse of the pattern for β-pinene. (Squillace and Fisher 1966)

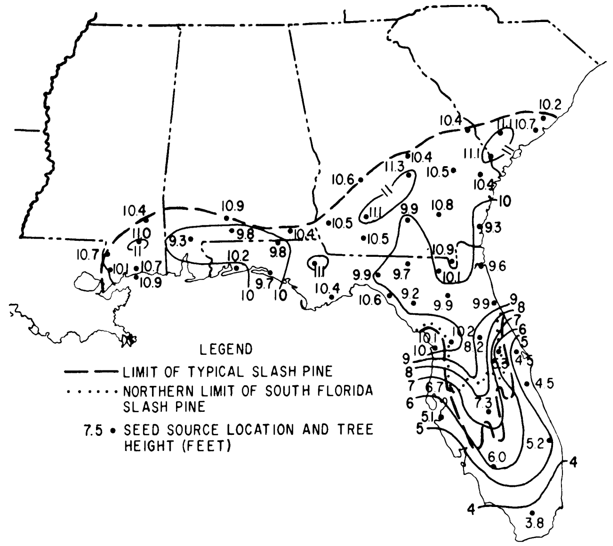

Figure 95.—Geographic pattern of average fifth-year heights at the Lake City, Florida, plantation. (Gansel *et al.* 1971)

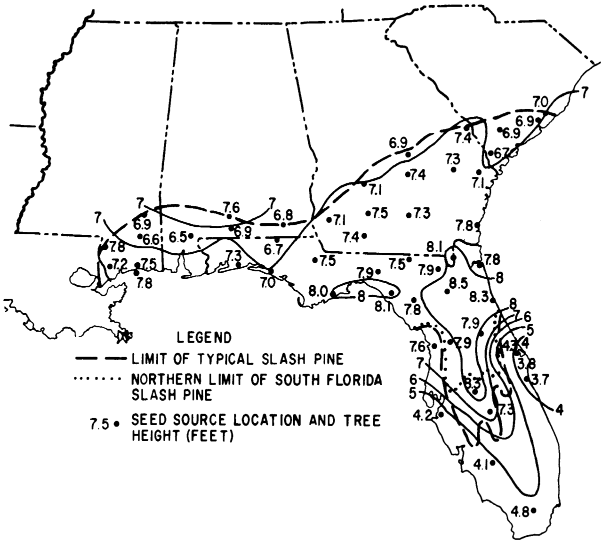

Figure 96.—Geographic pattern of average fifth-year heights at the Fort Myers, Florida, plantation. (Gansel *et al.* 1971)

the successful movement of seed of a southern pine species to an area with higher temperature than the point of origin. In some other southern pines it is advantageous to move seed east, west, or north for planting at a few specific geographic locations, some of which have a cooler climate than the location of seed origin.

The University of Florida cooperative seed orchard project with forest industries has involved slash pine plus trees from many different locations. These trees are propagated at a central point so that the performance of clones can be compared for evidence of racial variation. Oleoresin yield of grafted trees varied among clones, but the geographic pattern of yield followed naval stores productivity zones (Ineson and Rayl 1941), with highest producing areas in the central part of the slash pine range, which is northern Florida and southern Georgia (Goddard *et al.* 1962). This observation agrees with that of Gansel *et al.* (1971) except that variation in oleoresin yield was continuous instead of random. Grafts of trees from the central part of the species range tended to flower more abundantly than those from southern and western extremes (Goddard 1964). Observations for 5 years on 631 trees representing over 400 clones showed that grafts of southern trees averaged 15 conelets per tree, western trees 30 conelets, and central trees 40 to 60 conelets. However, in two racial variation studies, trees from northern locations produced cones earlier than those from southern locations (Gansel 1973). Comparison among plus-tree progenies and racial selections showed large differences among progenies in wood specific gravity (Goddard and Cole 1966) and response to fertilizer (Pritchett and Goddard 1967), but not among slash from one location each in South Carolina, Georgia, and Florida and two bulk seed collections from southeastern Georgia. However, volume growth varied about 25 percent among trees from three bulk seedlots collected at separate areas in Georgia and Florida (Kaufman 1968).

Additional work with seed orchard clones at the University of Florida indicated that progeny of clones from trees at different geographic locations from the Atlantic Coast to Mississippi differed significantly in height growth, and, also, they did not react in the same manner to site differences among the three outplanting locations (Goddard and Smith 1969).

In a small study in Florida, trees at age 9 from parental stock on a wet and dry site showed no differences in growth rate when planted on wet and dry sites at two geographic locations (Gansel 1967).

In Georgia, 3-year-old slash pine trees from seed collected at five locations in Georgia and planted in the northern part of the State showed no statistically significant differences in performance, but trees from coastal areas had 30 percent greater height and 31 percent higher survival than trees from inland locations (Greene 1962b). However, overall survival in the study was low. The combination of faster growth and higher survival of trees from coastal locations should result in large differences in wood yield attributable to location of seed collection. Rust infection was low, probably as a result of the northern location of the planting site.

In a complex study of geographic and racial variation combined, Squillace (1966b) found that a majority of traits showed appreciable stand-to-

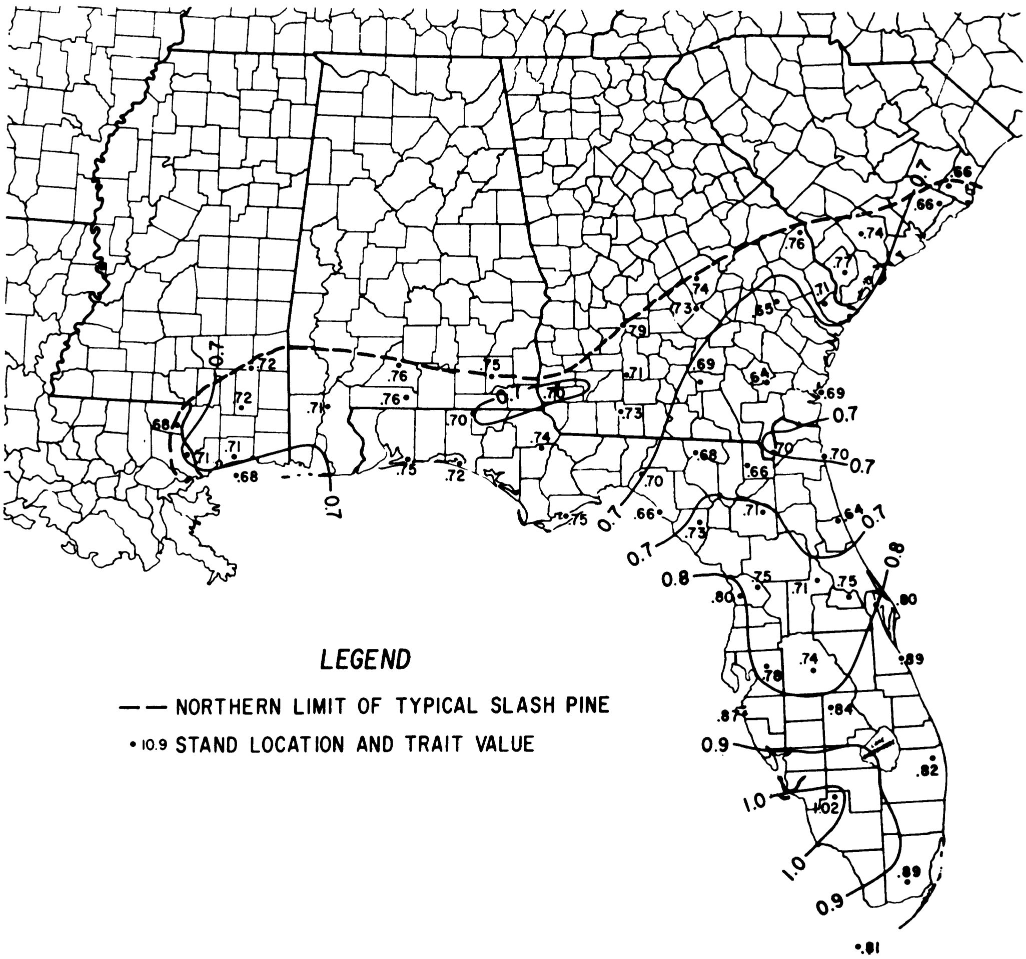

Figure 97.—Stem diameter of slash pine seedlings varies with geographic location but with a reverse trend from that for seedling height. Stem diameters vary from 0.9 to 1.0 centimeter in South Florida slash pine to 0.7 centimeter for typical slash pine in north Florida and south Georgia. (Squillace 1966a)

stand differences and formed a latitudinal gradient throughout most of Florida, with a trend reversal in Georgia or northern Florida, such as indicated for seedling stem diameter, speed of seed germination, and optimum growth (figures 97 to 99). Twelve morphological traits were studied in cones, seed, and foliage of five parent trees at each of 54 stand locations, as were 13 morphological and physiological traits in seedling offspring. For many traits, coefficients of variation were highest among seedlings within mother trees, intermediate among stands, and lowest among mother trees within stands. Later, in fertilizer experiments, trees from coastal locations grew slower, whether fertilized or not; also they accumulated lower concentrations of nutrients than inland trees in the central portion of the slash pine range (Schultz 1969a). In general, the results agree with those of Gansel *et al.* (1971) that there are latitudinal gradients in many traits and there is a center of optimum development in the south Georgia region that coincides with the population center of wood volume.

In the western part of the slash pine range, variation occurred from north to south in 27 needle, twig, bud, and cone characteristics from island, coastal, and inland collections of slash pine in both natural populations and progeny tests, with the exception of needle length, twig spiral length, bud length, and bud scale width (Mergen *et al.* 1966).

In Texas, tests of slash pine geographic races for resistance to drought indicated large differences among groups (van Buijtenen 1969a). Trees from St. Tammany Parish, Louisiana, the western part of the slash pine range, had the highest survival, height growth, and volume growth per acre. Trees of Mississippi, Alabama, and South Carolina were intermediate in performance, and those from Florida were poorest. Volume growth per acre per

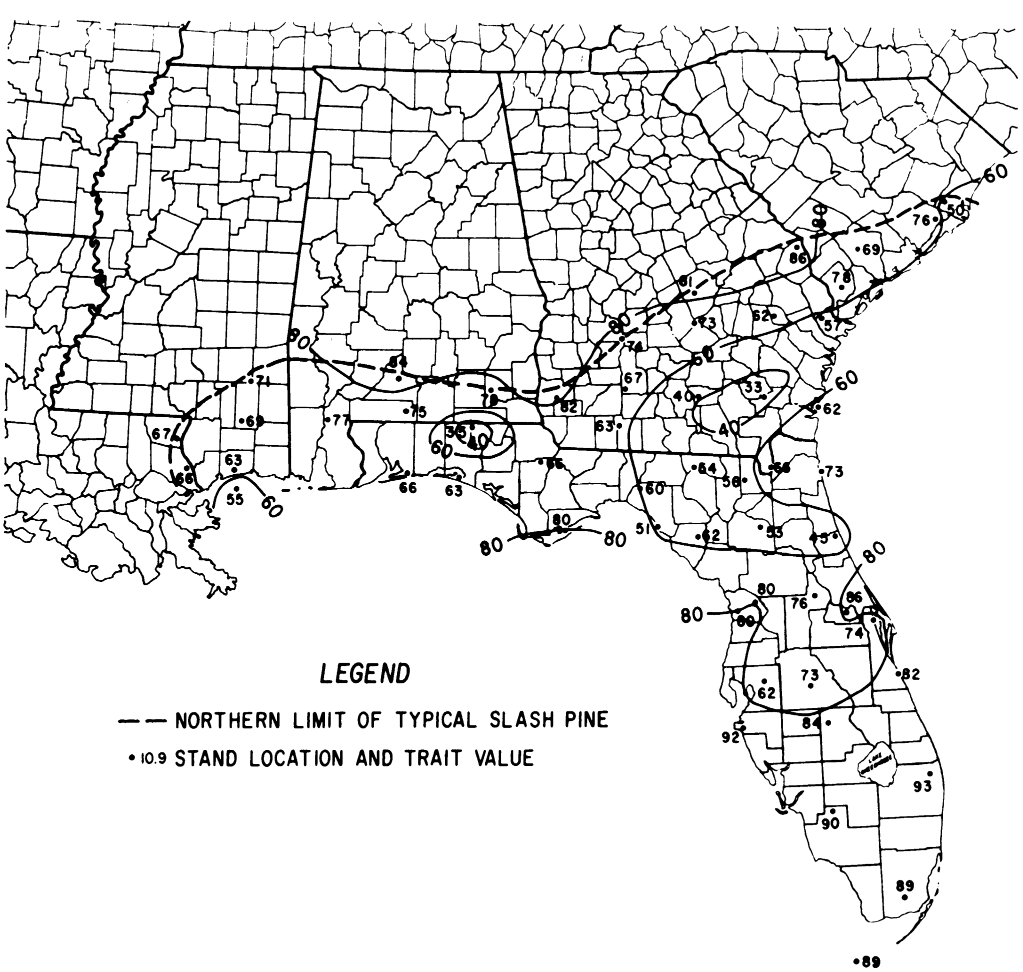

Figure 98.—The pattern of stand variation in speed of seed germination (15-day germination/27-day germination, × 100) shows high values in central Florida, with a decrease northward to a low in southeast Georgia and then a reversal toward higher values near the edge of the slash pine range. (Squillace 1966a)

year varied from less than one-half cord to about 2 cords for the 15-year test period for various geographic races.

Studies Outside the United States

Slash pine has been a favorite for planting in Southern Hemisphere countries, and interest has been stimulated in selection of suitable races because United States studies indicate that important differences exist in volume growth (Burley 1966).

One of the earliest tests was in South Africa. It included seedlots used in early tests by the Southern Forest Experiment Station and gave similar results in that no differences in growth were found among geographic locations (Sherry 1947; Snyder *et al.* 1967). Other studies in Africa were summarized by Burley (1966). An unreplicated trial of tree provenances in Malawi (Africa) indicated that Louisiana trees outgrew Georgia and Florida races during the first 3 years at one site. At another location, the Florida source performed best up to 1.7 years, at which time it was severely attacked by disease. In Kenya, there were no significant differences in first-year survival among eight provenances planted in replicated plots in Muguga. A ninth provenance, Escambia County, Alabama, showed poor growth in the nursery and low survival in the field, but this may have been the result of using an inferior nursery stock. In Rhodesia, trees from three locations (not specified), including two of typical slash pine and one of South Florida slash pine, were planted in replicated trials in January 1964 at one location and at two other locations in 1964–65. Height growth differences between localities were found to be significant, but the major differences were attributable to source of seed. A further replicated trial of five racial selections was

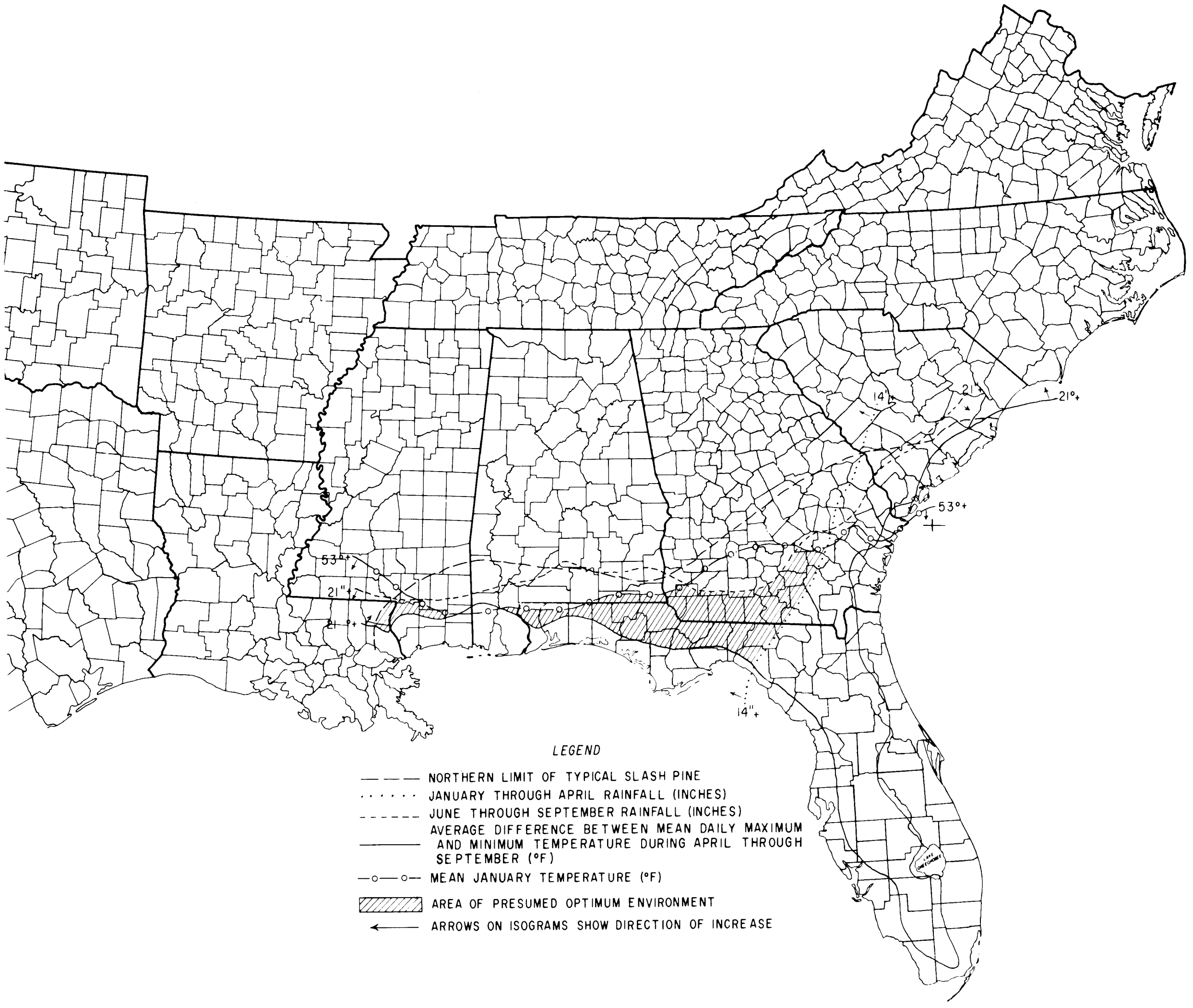

Figure 99.—Delineation of the presumed optimum region for growth rate in slash pine. By "optimum" here is meant the most suitable climate for the species within the range. More suitable climates may occur in areas out of the species' natural range. Likewise, artificially created environments are not considered here. (Squillace 1966b)

established at Lion Hills Forest in 1965 to 1966. Seedlings of some 25 geographic locations were planted at 5 sites during the years 1966 and 1967 in Malawi (Andersen 1967).

In Australia, at Beerwah, the Florida source (Flagler County) and a local control stock had produced significantly larger volumes than nine other provenances at 9 years (Slee and Reilly 1966). Generally, a clinal trend was evident, with southern sources performing better than northern trees. The authors agreed with Squillace and Kraus (1959) that performance depends upon rainfall pattern: the seasonal distribution of precipitation at Beerwah is similar to that in central Florida. In Queensland, Australia, replicated plantings were established at three locations by using trees from northern and western Florida and two coastal Georgia locations together with progeny of selected superior trees of unknown origin (Haley 1960; Nikles 1962). After 2 years the selected progeny were generally tallest, and one coastal Georgia race (Effingham County) was shortest. At one location, after 7 years, differences were slight.

In New Zealand, in a replicated trial of 14 seedlots planted during 1956, trees of one Georgia provenance appeared to have better form than others (Streets 1962).

In South America, slash pine from Georgia seed performed better in both growth and form than did trees of Florida origin in plots at 6,000- to 9,100-foot elevation at three locations in Colombia (Perez 1967).

An unreplicated planting trial at Castelar (Buenos Aires, Argentina) indicated that northern

Florida and southern Georgia were the best sources of slash pine seed. In Uruguay, replicated trials of five provenances were established during 1960 (Burley 1966). During the first 5 years, trees from the Florida and Georgia locations attained greater height and diameter than the material from Alabama and South Carolina. This was attributed to the coincidence of climatic patterns at the planting site and in the source region. In Sao Paulo, Brazil, racial variation trials are in progress, but no assessments have yet been made.

Discussion of Slash Pine Racial Variation

Slash pine has had the benefit of more intensive study of geographic and racial variation than any other southern pine. This happy state of affairs has been the result of a fortunate combination of great economic importance, small geographic range, and energetic investigators. Racial differences occur in important traits, although there have been differences in opinion about the kind and amount because of analyses of data from different studies rather than different analyses of the same data.

In silvicultural practices, foresters must recognize that racial differences occur in slash pine and plan seed procurement accordingly either for local use or importation. Accurate labeling of seed as to geographic location of collection should be required so that collection can be repeated or avoided, whichever is desirable.

Within the range, the gains derived from use of seed from the area of optimum development (Squillace 1966b) will vary with location and will be least, but still an important factor, within the area of optimum development itself. The map of the zone of optimum development is a good reference (fig. 99). For planting in areas north or west of the natural range, recommendations to avoid the use of seed from northeastern Florida in favor of seed from western parts of the range or from South Carolina are well substantiated (Snyder *et al.* 1967). For planting in south Florida, the best races in north-central Florida, such as Alachua County, are best. This is one of the few examples of the successful movement of southern pine seed to a warmer climate than the place of origin.

The probability of serious loss is high because of slow growth and low survival if an unadapted race is used in planting.

The importance of racial variation should be recognized in clonal selection for tree seed orchards, and results of the most recent analyses of racial variation studies should be used to develop the best plan possible for each specific seed orchard program.

In tree breeding work with slash pine, most of the recommendations made for silvicultural programs apply. Tree breeders should try to capitalize on racial selection combined with plus-tree selection to obtain maximum benefits from both. The amount of gain from this practice has not been adequately established by research, but with the large amount of related data available, the opportunity is too great to ignore in creative breeding.

From the viewpoint of population genetics, Squillace (1966b) used the results of genetics studies, climatic factors, and geologic history to develop a hypothesis concerning the development of racial differences in the species. Refinement of the hypothesis to the level of "theory," and still further to that of "law," requires additional study.

Natural hybridization does not seem to be an important factor in development of racial difference in slash pine to the extent suggested for loblolly and longleaf pines.

The reason for variability in the importance of fusiform rust throughout the range of slash pine is not evident from racial variation studies. There was no evidence for variability in the rust organism itself when test inoculations were made on randomly selected seedlings, but plus-tree offspring showed moderate resistance to rust isolates from Mississippi, Texas, and North Carolina and were highly susceptible to those from Alabama and Florida (Snow *et al.* 1969). A later study, in which 10 open-pollinated families were inoculated with cultures of rust from Texas, Louisiana, Mississippi, and Florida, showed 2 families resistant to all the cultures, 3 uniformly susceptible, and the remainder resistant to cultures from some states but susceptible to those from others (Snow *et al.* 1972). Also, it was found that differences in pathogenicity occurred on four slash pine families between cultures of rust collected along a north-south transect in Mississippi and another in Florida and Georgia.

RACIAL VARIATION IN SOUTH FLORIDA SLASH PINE

Research in south Florida with native pine was begun in November 1951 by the Southeastern Forest Experiment Station in cooperation with the Atlantic Land and Improvement Company, the Collier Company, and the Florida Forest Service (Olson 1952). South Florida slash pine appears in narrow bands along both coasts in the north-central part of Florida, but the main body lies across the State in approximately the southern half (Langdon 1963b). It occurs also on certain of the Florida Keys, but not on lower Florida Keys or upper Keys. Formerly, it was found on the north Key Largo but is now extinct. In comparison with other pines in the southern pine region, South Florida slash pine occurs in the area with the highest average annual temperature, the lowest winter rainfall, and about the highest summer rainfall.

Within the natural range of South Florida slash pine, over a million acres is denuded pineland which cannot be reforested naturally because it lacks an adequate source of seed. Another half-million acres is poorly stocked. If new crops of timber are to be grown, planting or some method of artificial regeneration will be required on a big scale. Because of the importance of regeneration in forest management in the area of South Florida slash pine, initial research studies were concerned with sources of seed, site preparation, nursery production, and other activities associated with regeneration.

Growth

The first racial variation study in south Florida consisted of 5 geographic samples of slash pine as part of a larger group from 12 locations in Georgia and Florida (Mergen 1958a; Squillace and Kraus 1959). Results after 3 years showed significant differences in survival, height growth, and insect attack (Langdon 1958b). Trees from Taylor County, Florida, were the tallest at 2.98 feet, followed closely by trees from Volusia and Baker Counties, Florida, and McIntosh County, Georgia, averaging 2.48 to 2.6 feet. The slowest growing lot was from Dooly County, Georgia, with a height of 1.94 feet. Trees from Taylor County, Florida, suffered 23 percent infection from tip moth (*Rhyacionia subtropica*). Volusia County, Florida, had 17; McIntosh County, Georgia, 16; Baker County, Florida, 14; and Dooly County, Georgia, 5, the lowest rate of the entire group. Attacks by sawfly (*Neodiprion* spp.) and pine webworm (*Tetralopha robustella*) varied among seed of different origin, but the effect on health and growth of the trees was slight. Early results from this small study indicated that seed from areas in the central part of the natural slash pine range, near Alachua County, Florida, might grow better in south Florida than those from the northern or southern fringes of the range. At age 11, in contrast to South Florida slash pine, typical slash pine had higher survival, greater height, and higher wood specific gravity (White and Saucier 1966), which contributed to 2.2 times more yield of dry wood per acre (Saucier and Dorman 1969).

In a later study, South Florida slash pine proved to be more resistant to damage from cattle grazing, insect and disease pests (brown spot, tip moth, pine webworm, pine sawflies), and fire, but typical slash pine from the northern part (Baker County, Florida) survived better after planting and had more resistance to wind damage (Bethune 1966). Also, frequency distribution curves for tree heights differed (fig. 100).

Within south Florida, seedlings from Polk County, in the northern part of the range, when planted in Hendry County, which is in the southern part of the range, grew faster and had a higher percentage of trees whose height resembled typical slash pine than did local stock (Bethune and Langdon 1966).

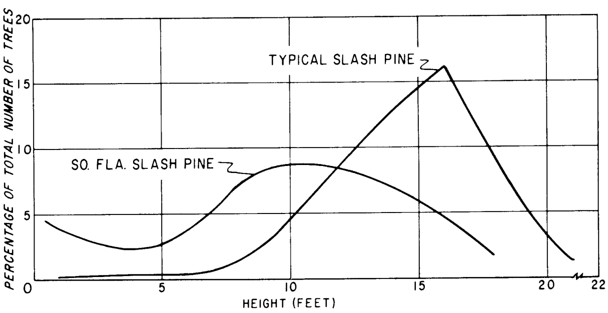

Figure 100.—Height distribution at age 9 of South Florid slash pine and typical slash pine trees. The typical curve for South Florida slash pine reflects differences among trees in initiation of height growth. (Bethune 1966)

Site preparation by ridging caused a 63-percent average increase in height growth of South Florida slash pine but only a 40-percent increase in growth of typical slash pine (Bethune 1963c). Both pine varieties grew better on ridged sites than on unridged sites at all three of the test locations, but there were some differences among sites, with the greatest difference—170 percent—occurring near the town of Frostproof, Florida.

In the large study of geographic variation in slash pine (Squillace 1966b), several stands of South Florida slash pine were sampled (figures 97 and 98). Data for parent trees and progeny were included in the overall analysis instead of separately by variety of slash pine, but there were differences in progeny traits among stands in south Florida.

Pest Resistance

The two varieties of slash pine differ in susceptibility to certain pests, in addition to those mentioned in connection with studies of growth differences. Within the range of typical slash pine, southern fusiform rust is the more important disease enemy, but, in South Florida slash, pitch canker (*Fusarium lateritium* f. *pini*) is the more important (Bethune and Hepting 1963), with individual incident records on over 2,000 trees showing 16 percent infected within a 5-year period.

Test plots in Mississippi showed 4 percent infection by fusiform rust on South Florida slash pine, but 20 and 24 percent, respectively, for typical slash pine from north Florida and Mississippi (Southern Forest Experiment Station 1950). However, in inoculation tests, South Florida slash pine seedlings developed many more fusiform rust galls than typical slash or loblolly pine seedlings (Snow *et al.* 1969).

Survival

The number of seedlings that survive planting can have as much effect on yield of wood produced per acre as do growth and quality of individual trees. In species adaptation plantings, seedlings of South Florida slash, typical slash, longleaf, and loblolly pines planted at eight locations in central and south Florida did not vary appreciably in survival over the 6 years following planting (Bethune 1963a). However, in a comparison of South Florida slash pine from Hendry County with typical slash pine from Baker County in north Florida, survival of South Florida slash pine decreased from 77 percent at the end of the first year to 50 percent at 9 years, whereas survival of typical slash changed only from 77 to 76 percent during the same period (Bethune 1966). Furthermore, typical slash pine showed survival of 85 and 87 percent on sites prepared by ridging and unprepared sites, respectively, compared with 75 and 74 percent for South Florida slash pine on similar sites (Bethune 1963c). Survival may vary among races of typical slash pine when planted in south Florida, as demonstrated in a separate planting where 79 percent of the trees from Baker County survived, while survival of trees from four other locations in the slash pine range in Florida and Georgia varied from 47 to 83 percent (Langdon 1958b).

Resistance to Fire

South Florida slash pine is more resistant to fire than typical slash pine (Ketcham and Bethune 1963). After a wildfire burned over some experimental plots, about 40 percent of the South Florida slash pines survived, although less than 1 percent of the typical slash pines withstood the blaze. About one-third of the surviving seedlings of South Florida slash pine sprouted at the root collar, but these died later after new needle growth appeared below the fire-killed leader. After a different fire, South Florida slash pine from Hendry County showed 27 percent survival, compared with only 17 percent for seedlings from Polk County, which is farther north in Florida (McMinn 1967). The Hendry County trees were smaller than the other trees and had thicker bark, but within each group of trees survival was better among large trees than among small trees.

Wood

Characteristics of South Florida slash pine wood vary widely from those of typical slash pine, as do some of the relationships of wood characteristics with growth. In 11-year-old trees, typical slash pines had 10 percent higher extracted wood specific gravity, 47 percent greater dry weight per tree, 33 percent more latewood but much lower extractive content than South Florida slash pine (White and Saucier 1966). Wood specific gravity increased with tree height and with total tree volume in South Florida slash pine but not in typical slash pine (Saucier and Dorman 1969). The percentage of latewood did not vary with tree volume in either of the slash pines. South Florida slash pine makes appreciable radial growth for a period of about 10 months, much longer than pines farther north, and this may result in high proportions of latewood (Langdon 1963a).

Turpentine

The main differences between the turpentine of typical slash pine and South Florida slash pine, according to Mirov and Iloff (1956), are: typical slash has *l*-α-pinene (61 percent), but South Florida slash pine has only *l*, *dl*-α-pinene (71 percent); typical slash has 34 percent *l*-β-pinene, whereas South Florida slash has 4 percent; and typical slash pine has negligible amounts of *l*-β-phellandrene, but South Florida slash has 19 percent. There are indications, however, that β-pinene and β-phellandrene of oleoresin from twigs may vary clinally with latitude northward from the northern part of the range of South Florida slash pine (Squillace and Fisher 1966); their conclusions were included in the section on racial variation in typical slash pine.

Discussion of Racial Variation in South Florida Slash Pine

On the basis of early results from seedling and sapling trees, separate planting tests have shown the following important differences between South Florida slash pine and typical slash pine, and, in fewer instances, between South Florida pines from different locations within the range: resistance to insects and disease; environmental factors such as drought, site preparation, and wind; growth rate, bark thickness, turpentine components; and wood characteristics such as specific gravity, latewood percent, and extractives. Many traits showed gradients from south to north rather than distinct differences. The biological differences seem well established, although some taxonomic ones remain which seem to depend largely on a definition of terms. The varietal name seems well established and will remain so until there is better agreement on what constitutes a variety.

The finding that South Florida slash has lower wood specific gravity when planted in the North, if it is maintained until maturity, is of interest because the formal varietal name was chosen to emphasize a characteristic trait, highly dense wood. The high content of extractives in South Florida slash pine wood is also of interest, and it remains to be seen what part it plays in the specific gravity of mature wood.

The superior growth of typical slash planted in south Florida is also noteworthy because this is one of the few indications that movement of seed southward might be advantageous. Tests with other species show, for certain locations, that movement of seed northward might be advantageous, but for typical slash pine this does not seem to hold true, either in respect to planting in south Florida or north Florida.

South Florida slash pine has very low stocking and unevenly distributed stands, including those on islands or keys, so that additional racial differences may be disclosed by future studies. This will, of course, have little significance if typical slash is the preferred variety to plant.

RACIAL VARIATION IN VIRGINIA PINE

Growing vigorously on abandoned fields and eroded hillsides, Virginia pine is so rough and limby it was formerly considered an undesirable weed species, with many uncomplimentary local names. But increased economic importance has come with the expansion of the pulp and paper industry in the northern part of the southern pine region. Being not such a minor species as formerly, Virginia pine's natural stands are receiving more research attention, which in turn has been followed by the establishment of seed orchards.

Extensive racial variation may have developed within the species as a result of wide latitudinal and elevational range, as shown by the range map in chapter 1. However, extremely limited geographical variation studies restricted to wood characteristics have shown only minor differences. Racial variation studies have been limited, too.

The Maryland Department of Forests and Parks in 1955 established a study of racial variation in Virginia pine to learn the nature of racial and individual tree variation within the species and to determine those races best adapted to conditions in Maryland (Whitesell 1959). Seed was obtained from 17 locations throughout the range of Virginia pine; sampling was thin in the South, and five successful outplantings were established: three in Maryland, one in Pennsylvania, and one in Tennessee (Genys 1966). Early in the study, variations in form, color, needle length, and duration of growing season were noticed, but detailed measurements were not made. A second study was initiated with collection of seed in 1956 and 1957 from 16 additional locations plus 4 that were included in the first trial.

In the first study, after 7 years the seedlings from Alabama, Tennessee, South Carolina, and Virginia showed high mortality of over 50 percent when planted on a poor site outside the species range (Pocono Mountains, eastern Pennsylvania) (Genys 1966). In the same plantation, trees from locations at higher elevations showed 90 to 100 percent survival. In four other plantations the differences in survival were less significant; the highest mortality rate in the Maryland plantation was among trees originating in Alabama, the most southerly location from which seed was obtained. Height growth difference between the best and poorest seedlots was 20 to 23 percent. In the Pennsylvania plantation, seedlings from some locations at higher elevations in the North showed a more reliable growth rate than seedlings from the South. Seedlings of Atlantic Coastal Plain and Tennessee origin showed a better growth potential in the Maryland and Tennessee plantations than those from northern and more mountainous areas. However, the most southerly seedlings, which were those from Alabama, showed only an intermediate rate of growth.

In Texas, limited arboreta plantings showed that Virginia pines from Tennessee grew much faster than those from Maryland (Zobel, Campbell, Cech, and Goddard 1956).

In connection with techniques used in the Maryland study (Genys 1966), in which one-tree and four-tree plots were used, it was concluded that experiments replicated by "one-tree plots" were less precise to determine the trend of racial variation than the experiment arranged by "four-tree plots." There has been considerable controversy among geneticists concerning the efficiency of field-test designs, and thus it is important to remember that the latter experiment included many more trees but that the precision on a per-tree basis was about the same. It was found also that significant correlations existed between heights of different lots of seedlings at age 7 and the heights at ages 3, 4, and 5 years.

A large-scale, combined geographic and racial variation study of Virginia pine in Tennessee and Kentucky was described by Thor (1964). Progeny of individual trees and groups of trees from 13 different locations are to be grown. In the first phase of the study, extractive content of wood varied among locations. Tracheid length but not wood specific gravity varied among stands and clinally with length, increasing from south to north, although the region sampled is only part of the Virginia pine range. Early results of the study showed growth rate varying among races and families within races (Evans and Thor 1971); wood specific gravity also varied among races but extractive content did not (Rink and Thor 1973).

RACIAL VARIATION IN OTHER SOUTHERN PINES

Racial variation has not been investigated in pitch, pond, spruce, or Table-Mountain pines.

SUMMARY OF RACIAL VARIATION

Racial variation research with southern pines began in 1926 when local loblolly pine seed and loblolly pine seed from three states were planted in Louisiana. From this modest beginning, studies have grown in size and scope to include one with slash pine progeny of five carefully described parent trees at each of 54 locations outplanted at four widely dispersed places.

Studies are established with all the major pines and some of the minor ones within the United States. Elsewhere, studies are underway with loblolly or slash pines in South Africa, South America, and Australia in the Southern Hemisphere and Japan and Korea in the Northern Hemisphere. Most of the studies outside the United States were recently installed to guide seed importation.

Early studies were simple in design, with commercial seed of indefinite origin and with field plantings made at only one or a few locations. Certain designs now require characterization of paternal parents, seed identified by maternal parent in addition to stand, and replicated plots in outplanting at many different climatic locations. A great spirit of cooperation among foresters and researchers in private, State, and Federal forestry has developed to conduct these tests. Test designs have become more sensitive as the need for accurate comparisons of wood yields becomes apparent.

Early tests were designed to sample the kind and extent of racial variation, but now many are made to guide racial selection of seed, seed orchard clones, and breeding stock in limited portions of a species range.

The many studies of racial variation and racial selection in slash and loblolly pines reflect their importance in silviculture and tree breeding, especially seed orchard establishment. Fewer studies occur in longleaf, shortleaf, South Florida slash, sand, and Virginia pines, and none in pitch, pond, spruce, or Table-Mountain pines.

Although strong trends are developing, based on interim results, it has not been possible to relate some results of racial variation studies with different combinations of environmental factors, such as those illustrated by climatographs shown in chapter 1 or the population centers as indicated by volume distribution maps in chapter 5.

The advisability of including silvicultural factors and treatments, such as product objectives and thinning, pruning, and pest control, were important considerations when early studies were designed and, in some instances, still are. Also, the choice of initial spacing of trees within field test plots was difficult to make. Except possibly for control of brown spot in longleaf pine, there are no widely used standands in forest practice for the southern pines; consequently, various investigators used their own best judgment in deciding about the importance of silvicultural practices. It was felt the refinement in techniques could be made in later studies after the gross characteristics of racial variation in each species become apparent. Some silvicultural factors or treatments affect yield—growth on an area basis—and tree or product quality more than average growth per tree.

It has been pointed out in discussions of different tree breeding methods that each may have certain advantages as well as important limitations (Dorman 1962). Apparently, this is true for racial selection in the major southern pine species, the most thoroughly studied, and may apply to the minor species, too. Important gains are to be obtained from racial selection in pine breeding, but they vary by species and geographic location. On a basis of interim results we can say that within natural ranges the highest gains seem to come from planting longleaf pine of southwest Alabama origin in preference to local seed in some areas of Georgia, Alabama, Mississippi, and Louisiana. If sustained, this will be an impressive example of gain from a relatively simple method of tree breeding. Furthermore, additional improvement in wood yields might accrue from plus-tree selection within the superior race of any species. In strong contrast with gains of this magnitude is the probability that local races are best for planting near the edge of the range so that selection of the local race is strictly necessary but only maintains production instead of improving it. In general, real gains would have to come from stand selection, or plus-tree selection, species hybridization, or some other method. Variation in the opportunities for and benefits from racial selection is a good example of the need for careful selection of breeding methods based on relevance to a local problem, and, in addition, to combine one method with others for maximum gain.

Because of the strong influence that the design and size of the study have on results, it is not very meaningful to list traits showing presence or absence of racial variation. For example, some studies, particularly in slash pine, included samples from a very narrow range of climate, and, although test plots were replicated, large absolute differences in wood yields were not statistically significant. Many studies have shown differences as large as 100 percent or more in volume yield that accumulated as a result of differences in survival, susceptibility to diseases, and environmental factors. Variation in some traits was clinal or showed a gradient with cardinal directions, but other traits showed a random pattern.

In general, racial differences have been found to occur in physiological traits, such as growth patterns, oleoresin yields, response to fertilizers, resistance to drought, flowering, resistance to insect and disease pests, and other morphological traits—wood specific gravity, needle traits, and seed traits. Chemical traits that vary are composition of turpentine and extractives in wood.

Traits in ongoing studies are being evaluated, and those relating to flower and seed production must await sexual maturity. Also, traits of growth, stem and crown form, plus wood quality are to be assessed when the trees are old enough.

A major accomplishment was demonstration of the importance of differences in several traits that were small but additive so that total yield of wood was very high. Traits affecting such things as drought resistance, pest resistance, tree growth, and wood specific gravity proved to have this additive attribute.

Racial variation studies have indicated something about the contribution of natural hybrids among species to racial differences. Migration of genes has not been carefully studied to show how this occurred and over what geographic areas. Resistance to fusiform rust in loblolly pine west of the Mississippi as a result of hybridization with shortleaf is an important finding. However, resistance to rust seems to occur at other locations where hybridization is not a strong possibility. In southern Alabama, the susceptibility of longleaf to fusiform rust and its exceptional growth rate might result from hybridization with loblolly pine.

Clinal variation along south-to-north and east-to-west gradients was an important finding. Although there are some indications of discontinuous variation in more restricted parts of the range, all the information is helpful in evaluating genetic relationships, selection of seed orchard clones, parental stock in applied breeding work, and seed procurement in silviculture. The magnitude of losses from use of ill-adapted races is staggering, sometimes causing complete failure of a plantation. Contrariwise, the possibility of gains over use of local seed can be very large, although at present they are restricted in both species and geographic area.

The importance of choosing the proper race of loblolly pine for hybridization with pitch pine for planting in Korea has been demonstrated.

For planting outside the natural range in this country, it is usually not possible to obtain seed from areas with similar climate and site conditions or, in other words, according to the homoclime principle. At some locations, southern pine species have compared favorably with the native species in both volume and tree quality, but in other areas tree form has been poor. Thus, tree form must be considered an important factor in evaluating performance of imported trees.

There is limited evidence that racial and plus-tree traits are additive; that is, plus trees might be found in plus races. If this proves to be true for most races and species, the genetic gains from seed orchards containing the best clones of the best races will be much higher than present estimates, which are based only on traits of local plus trees.

Since racial variation seems to be a special characteristic of a species, a geographic region, and a trait, broad generalities regarding the nature of and the uses for races are not possible. In other words, racial relationships must be defined on a restricted basis if they are to be meaningful in forestry practices.

Relationship between performance of trees when quite young and when approaching commercial size seems to be good in racial studies, but additional periods of observation are needed to show how reliable the early estimates are. They are sure to have a certain reliability inasmuch as performance for some traits is irreversible, but final evaluation of races that survive the juvenile state will probably be based on overall performance expressed in terms of wood yield and tree quality rather than on one or a few traits.

Although not the object of specific studies, a relationship seems to be developing between growth vigor of races and population centers indicated by wood volume concentrations in natural stands: as shown in the chapter on geographic variation, the more vigorous races of slash and longleaf pines come from certain population centers.

Although many southern pine stands are continuous over large areas and pollen is disseminated widely, these conditions have not prohibited the development of racial variation in most southern pine species.

The few test plantings made to date indicate that typical slash pine and loblolly pine might qualify for planting in south Florida. If this proves true, it will be an example of the benefits obtained by moving seed southward. In most other parts of the South, seed might be moved in other directions, depending on species and location, except in the northern parts of the species range, where local seed seems to be best adapted.

The size and complexity of geographic variation is such that it is not feasible to rank traits in order of magnitude of racial differences.

Racial characteristics seem to have developed independent of each other. Thus, races have different combinations of important traits such as growth, form, and resistance to pests. Emphasis on one or more traits that show wide racial differences tends to divert attention from others that may vary almost as much and contribute a great deal to overall yield of wood and tree quality, which after all, are the important economic factors, regardless of the fact that they merely reflect the accumulative or net effect of many individual traits.

Geneticists should do more work in developing study designs that give highly sensitive tests of wood yield, tree quality, and wood quality. This requires more intensive study of traits involved, influence of maternal parents, and field test site variability. Geneticists should also study populations more carefully to develop hypotheses to be tested in future racial variation and racial selection studies.

The contribution of natural hybrids to racial variation should receive further study with emphasis on economically important traits.

Tree breeders in certain locations need to investigate the opportunity for combining selection of races and plus trees for seed orchard clones and breeding stock.

Foresters or tree breeders responsible for importation of seed or pollen in volume may wish to carry out racial selection studies to indicate the best sources of seed for specific planting locations.