CHAPTER 7

STAND VARIATION

Stand variation is the last chapter of the discussion of variation among geographic locations in southern pines. The first chapters included material on characteristics (phenotypic traits) of trees in different geographic locations without regard to inherent differences. The second chapter was devoted to inherent differences (genotypic traits) among trees from different geographic locations as determined from transplant studies. In the transplant studies, comparisons of performance at one point are made among trees originating at many different locations.

Stand variation, in its turn, may be described as variation occurring among stands of trees within relatively small geographic areas throughout the natural range of the species. Much of the published information on stand-to-stand variation has appeared in connection with geographic or racial variation studies. These chapters should be read in connection with the chapter on stand-to-stand variation in order to obtain details of various studies.

Neither Richens (1945) nor Snyder (1972b) nor Wright (1962) include stand variation definitions in their glossaries. In general, stands have been defined in various studies as groups of trees located relatively close to each other within the natural range of the species and growing under somewhat similar soils and climatic conditions. In some reports of stand variation studies, groups of trees sampled were contiguous so that they might constitute the same breeding population, while others have been disconnected, such as stands occurring on islands or in groups beyond the natural range of the species, for example, the Lost Pines area in Texas.

HYBRIDS

Natural hybridization among species may contribute to stand variation. Although the occurrence of hybrids has been fairly well substantiated, the kind and extent of populations they cause remain undescribed. The location of natural hybrids has been included in the chapter on geographic variation, and the traits of hybrids appear in the chapter on hybrids; they need not be repeated here.

SLASH PINE INCLUDING SOUTH FLORIDA SLASH PINE

In Texas, studies of variation in slash pine plantations showed that strength-property variations within trees, within locations, and between locations presented themselves in increasing order of magnitude (Kramer and Smith 1956). Wood specific gravity varied between 0.46 and 0.54 among the six locations sampled in Texas. Strength properties varied widely, particularly modulus of rapture and maximum crushing strength. The differences in characteristics among plantations support studies showing that racial and tree-to-tree variation occurs in slash pine. From a study of variation in coastal and insular slash pine in Mississippi and Alabama, it was found that differences occurred from north to south among 27 needle, twig, bud, and cone characteristics of 11 island, coastal, and inland collections of slash pine (Mergen *et al.* 1966). In one part of the study, stands on offshore islands were paired with stands near the coast for comparison of various traits. Two of the islands were different from their mainland counterparts, but the third, Cat Island, was not different from adjacent coast stands in spiral length and bud scale length. One of the islands was different from its mainland counterpart, but the other two were not different in number of resin canals and twig diameter. There were no differences between island and coastal stands in bud width.

In Florida, variation in certain morphological characteristics of slash pine among stands tended to be low in the North and high in the South (Squillace 1966b). It was suggested that this may have been partly due to prevalence of islands in Florida during Pleistocene times, causing stand variation through genetic drift, and possibly due to a higher variation among habitats in south than in north Florida. Twelve morphological traits were studied in cones, seed, and foliage from five parent trees in 54 stands throughout the species range, and 13 morphological and physiological traits were studied in seedlings from the parent trees. Most traits showed appreciable stand-to-stand variation. They contributed to a larger pattern of variation consisting of a latitudinal gradient through Florida from south to north, with a trend reversal in the north-central area; this reversal occurred roughly in extreme south Georgia and north Florida (fig. 101). Stand-to-stand variation was relatively strong for cone dimensions, seed yield per cone, seed weight, needles per fascicle, needle length, fascicle sheath length, and hypoderm thickness; this variation was relatively weak or absent for various measures of stomatal frequency and frequency of resin ducts.

Slash pine seedlings from stands on wet and dry sites in Florida did not differ in survival or growth

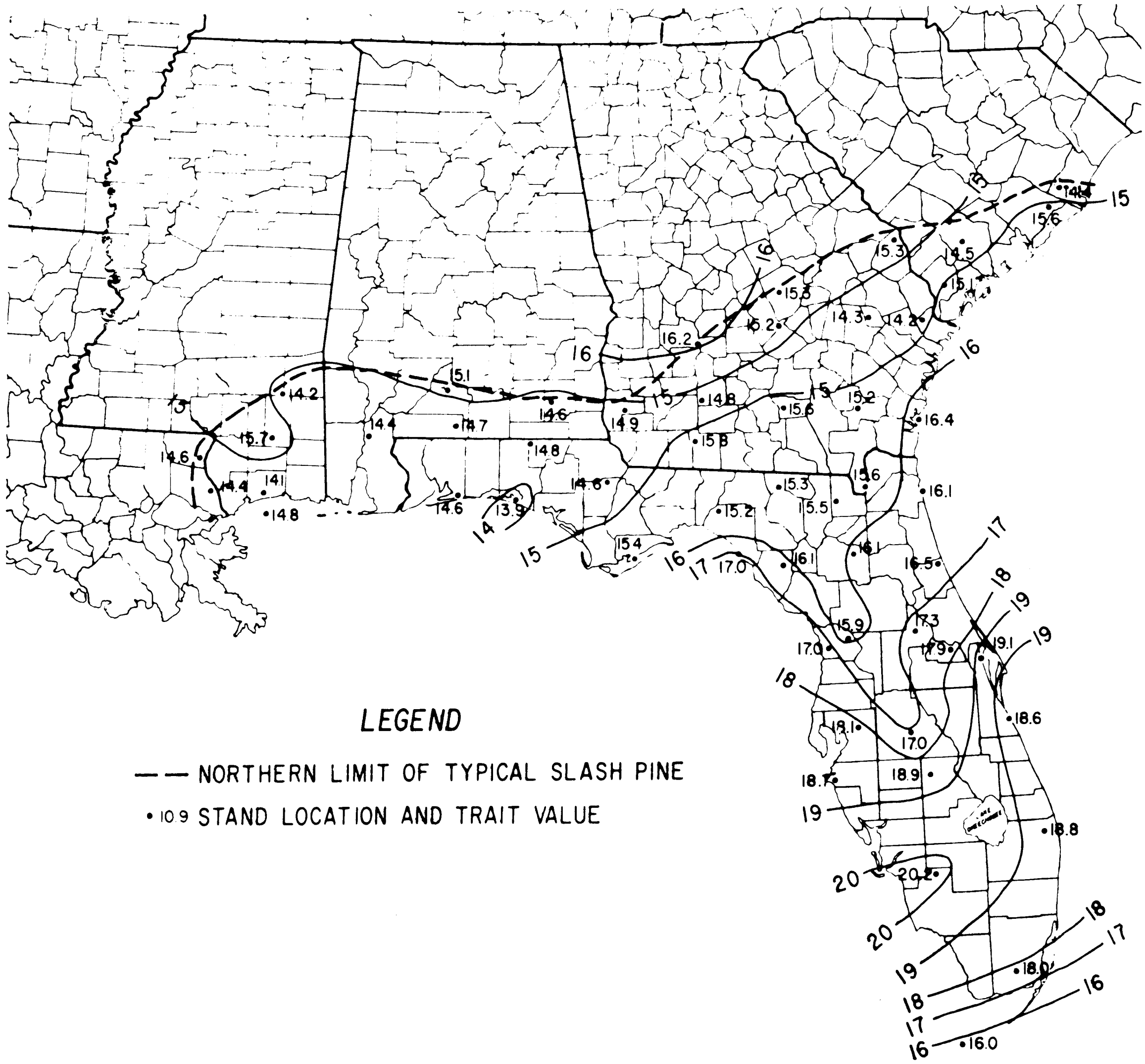

Figure 101.—The pattern of stand variation in needle length (centimeters) in progenies shows small differences among stands within relatively small areas as part of regional gradients. Stand-to-stand differences were found for many seed and foliage traits. (Squillace 1966b)

rate when outplanted at two locations (Gansel 1967). Among geographic areas within the range of slash pine, percentage of summerwood tended to be highest in areas with low pre-season and high mid-season rainfall and in trees on the poorer sites, but within small areas there were no differences in summerwood percentages in trees on wet and dry sites (Larson 1957).

In a Georgia and Florida racial variation study, slash pine seedling survival, height growth, and incidence of rust infection varied clinally with latitude, but oleoresin yield showed random variation (Gansel *et al.* 1971). Young trees from stands in certain counties produced as high as 70 percent more oleoresin during the period of test than trees from other locations.

In south Mississippi, progenies of individual trees within stands and the mean of progenies between stands varied in certain characteristics (Snyder *et al.* 1967). The observations were based on progeny of 37 slash pine trees randomly selected in five south Mississippi stands. Traits varying among stands were: height in the cotyledon stage, seedcoat retention following emergence, height at age 1 year, and weight at age 1. The number of rows of stomata at age 2 and needle teeth per millimeter at age 2 varied among progenies within stands but not between stands. Stands differed neither in seedling survival nor fusiform rust infection.

Progeny of groups of slash pine seed orchard clones varied widely in height growth, although the stands in which the group of original trees were selected were not, in some cases, very far apart (Goddard and Smith 1969).

LOBLOLLY PINE

In Washington Parish, Louisiana, results of a racial variation study in loblolly pine described by Crow (1964) showed that trees from nearby Parishes in southeastern Louisiana differed widely in volume growth per plot and rust resistance. Fourteen percent of the trees from seed from Washington Parish were free of canker, while 48 percent of the trees from Livingston Parish were free from disease. Volume per plot for trees of Washington Parish was 119 cubic feet, and for trees from Livingston Parish 140 cubic feet, or 17 percent greater volume. Survival was practically the same in that it was 66 and 67 percent for Washington and Livingston Parishes, respectively. Trees from Washington Parish were collected 20 miles northeast of the planting site, and those from Livingston Parish were collected 30 miles to the southwest.

Studies of specific gravity and tracheid length of loblolly pine in Maryland and Delaware showed that the same general trends occurring along the southern part of the Atlantic Coastal Plain continued northward, and the results were generally similar with other studies except that one plot in Westmoreland County, Virginia, had very low specific gravity and short tracheid lengths (Whitesell *et al.* 1966).

In the southwide pine seed source study, loblolly pine from Pamlico and Onslow Counties, which are closely adjacent in eastern North Carolina, were outplanted at several different locations throughout the range of loblolly pine. Seedlings from these two counties varied consistently in height growth and survival but not in resistance to fusiform rust (Wells and Wakeley 1966). In Dooly County, Georgia, which is also in the southwide study, loblolly pine from two adjoining counties in Alabama varied in susceptibility to breakage from ice, with 5 versus 13 percent of the trees damaged (Jones and Wells 1969). In southern Mississippi, loblolly pine seedlings grown from seed collected from two or three trees growing in a single stand from four different counties in Texas varied widely in susceptibility to rust infection. Seedlings from three individual trees in Bastrop County varied in rust infection from 7.8 to 11.6 percent, while three trees from Fayette County varied from 12 percent to 16.4 percent infection (Wells 1966). Height growth of progenies of individual trees from the different counties in Texas did not vary appreciably.

Resistance to fusiform rust varied widely among wind-pollinated seedlings of 115 loblolly stands in Mississippi and adjoining areas in Alabama and Louisiana (fig. 102) (Wells and Switzer 1971). For rust incidence, stand variance was 8.75 times as large (0.1294) as among trees within stands (0.0148). Also, stands nearest the Gulf Coast in Alabama and Mississippi were least resistant, and resistance increased gradually to the north and west in a clinal pattern. Stands with a high degree of resistance were located in the Florida Parishes of Louisiana and an area in southwestern Mississippi. The implication is that selection of resistant clones should be based on geographic location, stands within geographic location, and individual trees within stands.

In studies of drought resistance in loblolly pine in Texas, seedlings from the Lost Pines area were consistently higher in survival after 2 years than those from more eastern locations. Seedlings from locations with drier sites on the western edge of the continuous belt of loblolly pine in Texas had good survival also, while seedlings from the Coastal Plain had very poor resistance to drought (Zobel and Goddard 1955). After 5 years in the field, drought-resistant loblolly pines from the Lost Pines area showed greater height growth than the trees from east Texas and Louisiana. There was no apparent difference in bole form and quality between seedlings from the areas in which drought resistance occurred and the more eastern locations (Goddard and Brown 1959). In testing loblolly pines for drought resistance, van Buijtenen (1966b) found that differences in drought resistance between progenies of individual parents selected from sites subject to drought exceeded the average differences in drought resistance among geographic locations. Survival ranged from 7 to 85 percent for progenies of individual trees and from 27 to 50 percent for groups of trees from different locations within the area in which general drought-resistant seedlings occur. Local ecotypic differentiation between locations in areas where drought occurred was shown by the root-growth responses of seedlings from lowland and upland areas relatively short distances apart (Youngman 1967).

Monoterpenes in loblolly pine wood oleoresin varied among stands in both mean values and the range among individual trees within stands (Coyne and Keith 1972). Additional information on this is given in chapters on variation among trees and geographic variation.

Of 13 morphological characteristics of loblolly pine seed, cones, and twigs that differed significantly throughout the range, some showed regional trends, but others varied among stands within regions (Thorbjornsen 1961). Details of the study are given in the chapter on geographic variation in loblolly pine.

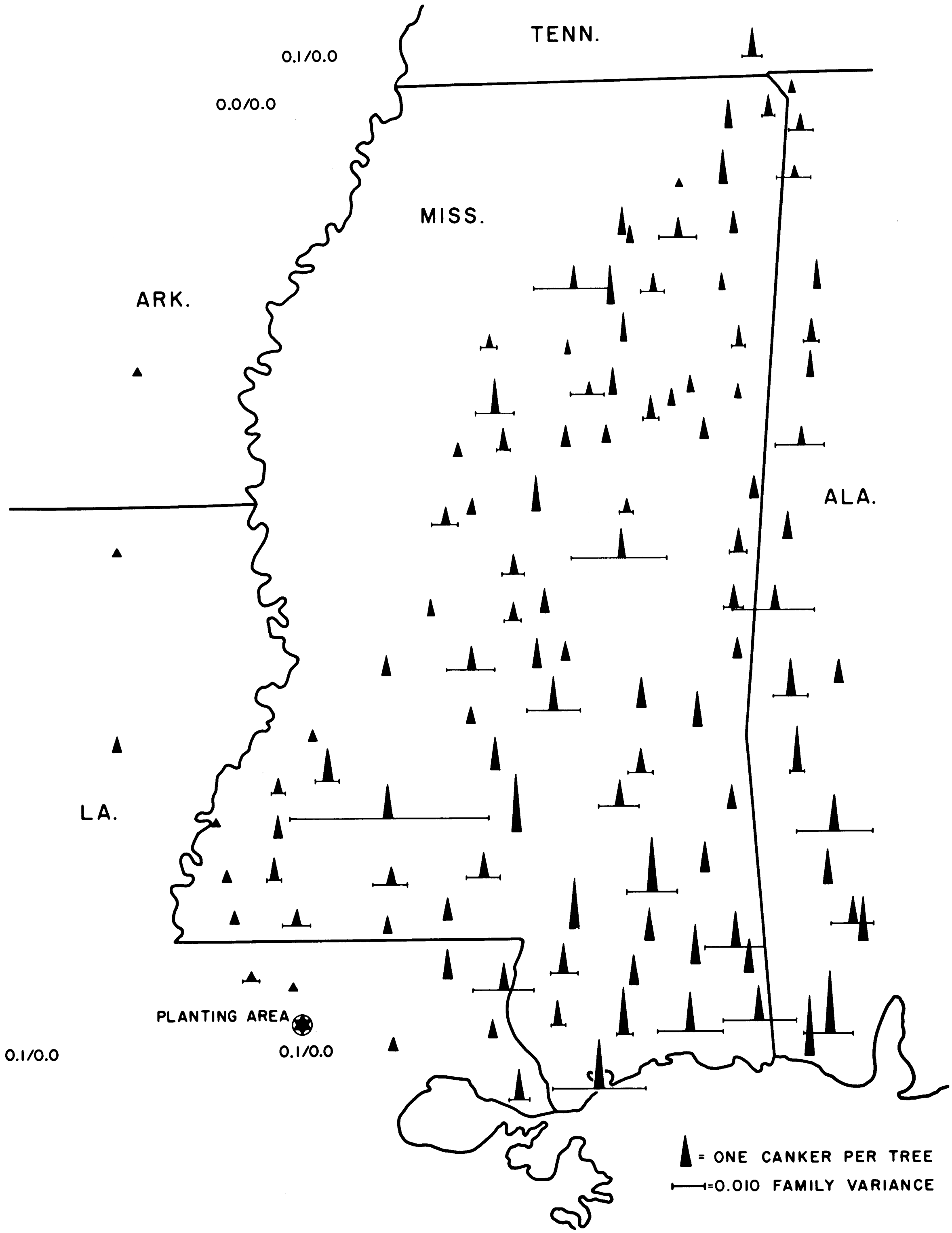

Figure 102.—Average number of cankers per tree at 4 years (vertical triangles) for the progenies of 115 stands of loblolly pine. The horizontal bars represent variation among the (usually) five families from each stand. The fractions indicate canker/variance values too small to depict graphically. (Wells and Switzer 1971)

OTHER SOUTHERN PINES

In a study of wood and growth characteristics of pond pine in the coastal area of North Carolina, there were differences among plots in natural stands and very large differences among trees within the plots in both specific gravity and tracheid length (McElwee and Zobel 1962). Six different locations were sampled, with 3 plots of 10 trees each in each area. Plots were separated by at least 1 mile. In some cases means of individual plots within an area exceeded extreme values of trees on other plots (fig. 103). Considerable difference was shown in the amount of variation within plots. Plot 6–1, for example, showed a spread of specific gravities from 0.51 to 0.58, while plot 6–2 in the same area more than a mile away had a range of specific gravity and tracheid length among plots and very large differences among trees within plots but not among different geographic locations. Also, significant differences in tracheid length occurred among stands several miles apart. No ready explanation was apparent for these tracheid-length differences among stands.

In a Virginia pine racial variation study based on 15 trees in each of 13 stands in Kentucky and Tennessee, differences among stands in specific gravity were largely due to differences in amounts of extractives, and there were no significant differences among stands for extracted specific gravity of the wood (Thor 1964). However, on the Cumberland Plateau and in mountain stands farther north, trees had longer average tracheids than those toward the South, indicating clinal variation pattern in this trait.

Results of a study described by Snyder and Allen (1962) and analyzed at 10 years (Snyder and Allen 1968) show that longleaf pine seedlings from parent trees growing on productive or cove sites produced 11 percent greater volume than seedlings from parent trees growing on unproductive or ridge sites. Bibb County, in central Alabama, near the edge of the longleaf pine range, was the location sampled.

In pitch pine, cones on some trees open soon after maturity, while the cones on others may remain closed for many years, often until the heat of a fire opens them or until the trees have been cut. In southern New Jersey, groups or stands of trees with different cone behaviors may grow relatively close together (Illick and Aughanbaugh 1930).

Pollen grain size in shortleaf pine varied clinally throughout the range, but there were differences among stands (Cain and Cain 1948). In the southwide pine seed source study (Wakeley 1961), differences in growth occurred between young trees from Anderson and Morgan Counties, which are adjacent in Tennessee but differ somewhat in elevation.

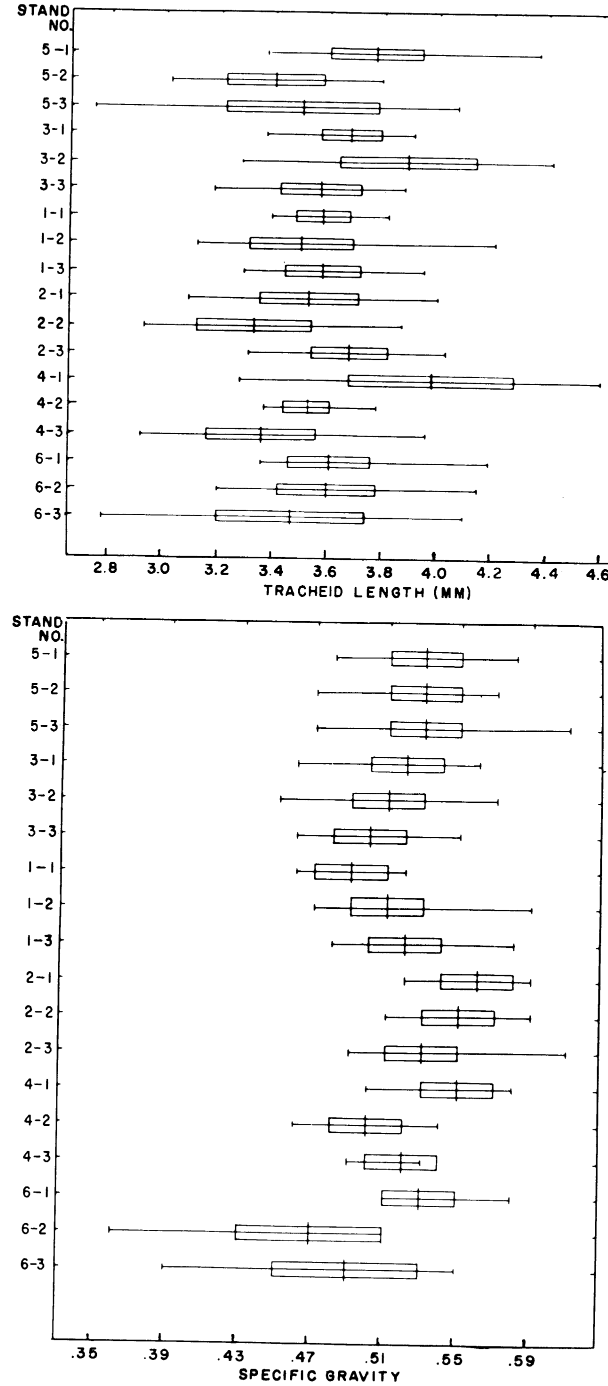

Figure 103.—Tracheid length (top) and wood specific gravity (bottom) of pond pine in stands, plots, and individual trees in eastern North Carolina. (On the vertical scale, the first numeral indicates stand number, and the second indicates the plot within the stand.) The central vertical line is the average for each plot, not closer than 1 mile, within each of six areas sampled, the rectangle represents 2 standard errors on both sides of the mean, and the horizontal line shows the total range of values among 10 trees per plot. The traits varied significantly among trees within plots, and plots within areas, but not among areas or stands. (McElwee and Zobel 1962)

DISCUSSION OF STAND VARIATION

Variation may occur among stands of southern pine within geographic areas so small that the usual environmental factors, such as day length, length of growing season, average temperature, rainfall patterns, and various combinations of these, are inoperative on adaptive traits. It occurs because of the silvicultural system used or because of the genetic makeup or the seeding habit.

The southern pines are not uniform genetically, and traits vary widely among individual trees within families. Thus, stands may reflect characteristics of the trees the seed came from. The pines as a group are very good seed producers, and seedlings will become established in open areas either in abandoned fields or cutover stands. Most stands are clearcut, and seed for restocking comes from individual seed trees or trees at the margin of open areas.

Pollen may be distributed over fairly large areas, but this does not seem to have kept distinct differences among stands from developing. From the standpoint of seed orchard management, this might be important because there has been some concern about the consequences of pollen contamination from outside.

Techniques for estimating stand characteristics may improve as estimates of tree-to-tree differences become more precise. However, such estimates may become more accurate for morphological traits and resistance to pests, which can be estimated visually, than for growth and yield and other physiological traits.

In shortleaf pine, monoterpene composition of wood oleoresin varied among localized populations within counties as well as clinally over the natural range of the species, according to Coyne and Keith (1972) from a study of the relationship of terpenes to pine beetle outbreaks. Additional information from the study is given in chapters on geographic and tree-to-tree variation.

Some of the error in relating racial performance to environmental factors by regression analysis or other methods may be caused by differences among local stands.

Our knowledge of stand variation is in about the same stage as that for racial variation 15 or more years ago. We are certain it may exist, but we do not know what to do about it. It is clear we must take it into consideration and, when planning future studies, draw on results of racial variation as well as tree-to-tree variation to develop sensitive study designs. Also, stand sampling should be a part of racial variation and tree-to-tree variation studies when feasible.

From the standpoint of the silviculturist and tree breeder, it would be wise to recognize that stand differences may occur and to pay heed to the warning signals raised by the appearance of phenotypically poor trees. Stated differently, it would be unwise to ignore the possibility of stand differences merely because there is no research to show that they occur. For academic contemplation, we should have results to discuss, although the risk of pecuniary retribution is not present. In practice, however, it is foolhardy to take unnecessary risks. We cannot use great care in the selection of geographic races and then assume no differences occur among stands within races.

Silviculturists have recognized growth differences among stands as a result of site factors. If genetic factors also cause important differences in height growth, yield, and quality, silviculturists may wish to replace poor stands with improved trees before improving good stands. The large differences in oleoresin yield among races of slash pine indicate how significant differences in major traits might be. Management for naval stores is not as important in longleaf and slash pine silviculture as it once was, but combinations of traits affecting timber yield and quality may be equally large economically. Results of racial and stand variation studies show these differences exist.

Additional work will be needed to show the relative weight, of racial, stand, and individual tree differences when trees are being selected for research purposes, creative breeding, and seed orchard clones. This would be most important for species or locations in which new seed orchard work is planned. Many seed orchard programs have progressed beyond this level of selection. If the three levels are additive, it will greatly affect selection procedures.

Studies of inherent differences among stands within a relatively small geographic area, as compared with regional differences within the range, will indicate whether specific identification of seed collection point is important. Heretofore, little attention was paid to local stands when seed or pollen was collected at specified geographic locations. Collection points will have to be described accurately if stand differences are large and repeat collections are necessary.

The part that species hybridization plays in contributing to variation among stands should be investigated.

SUMMARY OF PART III

Within the range of each southern pine species, regardless of size, there are important differences in climatic factors, such as temperature and rainfall, that influence growth. Growth of individual trees and wood yields per acre have been correlated with several climatic factors. There is variation in other traits, such as oleoresin yield and susceptibility to fusiform, that is only partially correlated with climatic factors. In addition to variation over large areas, stands in the same climatic zones and breeding population differ in important traits, as indicated by the few data available.

Studies of geographic and racial variation have been extremely important in both southern pine breeding and silviculture because of the great differences in wood yields among races. From the standpoint of the geneticist, racial variation within species might be evaluated as viewed from a point in space where the entire range is visible. On the other hand, the forest manager or tree breeder might have to view racial variation from the point on the earth's surface where he is located. For some of his forestry activities, he has to consider from what location or locations he should select seed or breeding stock to move toward him. Thus, these men are concerned with selecting races for their use, which is in contrast to the researcher's job of determining patterns or theories about the origin, kind, and extent of races.

It was emphasized that racial selection as a breeding method for southern pines will result in large gains in yields for certain species only at a limited number of locations, but it is required for all species at all geographic locations to maintain high-yielding races by avoiding ill-adapted races. This is the most important contribution of racial variation research, and it has had a great impact on southern pine silviculture in the past and will have an even greater one in the future.

Racial differences in southern pines create important problems in choosing proper races for foresters importing seed for their country. Many have recognized the problem and are conducting racial selection studies to guide seed procurement. Southern pine races have limited adaptability—they cannot be planted "everywhere" even within their own natural range. However, there are administrative problems involved in collecting seed or establishing seed orchards at specific geographic locations to produce seed for commercial planting in other states or for export. As large volumes of clonal material or special seed on a production basis are needed by one state from another or by foreign industrial or forestry organizations, to whom shall these organizations apply for seed?

There are certain similarities in the shape of the natural ranges of certain southern pine species, but population and climatic relationship studies have not contributed much information explaining the reasons for similarities or differences or why they are not of a random nature.

There are indications, although very limited, that race, stand, and even individual tree characteristics are cumulative. If so, selection of clonal or breeding stock on these three levels will yield important genetic gains. Additional work is required to indicate if this type of selection is feasible and how much investment is justified for each species for each seed orchard project.

Forest geneticists and specialists in experimental designs have much to do to increase the efficiency of racial selection studies. Studies of this type may be of long duration and large size, which means they are expensive but necessary because of the high value placed on wood yields in study results.

Geographic variation and physiological studies should be used to screen races and reduce the number to be tested in field trials. Plot studies are too expensive to be used for determining all the relationships involved in breeding and seed orchard programs with each species.

The importance of population centers and racial and stand variation in relation to incidence of disease and insect attacks should be investigated. Also, we should determine the effect of racial and stand variation, or the additive effects of both, on breeding for resistance to pests. Forest pathologists and entomologists could be much more active in this field of work than they are; this will require increased interest in the host and decreased interest in the pathogen or insect.

Certain southern pines have well-developed population centers based on volume of timber. As yet, there is no explanation for the development of these centers. In slash pine, a species with limited range, the area of optimum development, based on volume, has genetically more vigorous trees, as indicated by planting tests outside the population center. The genetic superiority may have resulted from differences in the type and degree of natural selection. In the areas of optimum development, natural selection may have been relatively strong for growth vigor, whereas in the marginal or more severe environments natural selection may have been relatively strong for resistance or adaptation to the critical environmental factors. However, other mechanisms may be operative. For example, longleaf pine trees in the population center in southern Alabama seem to be genetically superior to other longleaf trees, but the environment in that area does not seem to be different from that adjacent to the center. This suggests that some other factor may be operating, such as introgression with loblolly or with some species from which it obtained not only increased vigor but a low level of susceptibility to fusiform rust to which it is usually resistant.