CHAPTER 13

PITCH, POND, SAND, SPRUCE, TABLE-MOUNTAIN, AND VIRGINIA PINES

Some of the minor pine species make locally important contributions to forestry, although they lack the total volume of the four major species. Seed orchards have been established with pond, sand, and Virginia pines with the hope of attaining benefits similar to those for major species.

Information available is limited largely to estimates of phenotypic variation, usually as a part of studies designed for other purposes. However, it probably would be unwise for foresters, geneticists, and tree breeders to assume that no inherent variation exists among trees merely because it has not been studied.

PITCH PINE

Seed and Cones

Pitch pine seems to vary in many of the characteristics of seed and cones, as do other southern pines. Perry and Coover (1933) observed that large cones had heavier seed with longer wings and that cones varied in size from tree to tree. Cones from the top of the crown were slightly higher in quality than those from other parts. The cones that opened earliest in the season from the same tree tended to be larger than those that opened at a later date. Individual trees greatly above average in both quantity and quality of seed were noted. Illick and Aughanbaugh (1930) observed also that cones on some trees opened soon after maturity, while on others the cones remained closed for many years, often until the heat of a fire opened them or until the tree had been cut. Ledig and Fryer (1972) thought that pitch pines with serotinous cones are homozygotic for a single gene controlling the trait and that the trees occurred most frequently in the New Jersey Pine Plains. In areas where pitch pine and shortleaf pine occur in mixed stands, some natural hybridization takes place. It is not known to what extent this may have affected characteristics of the seed and cones of either species.

While testing effects of gamma irradiation on pitch pine seeds, it was found that there were highly significant differences between trees, and, within the crown, in seed weight, with a highly significant interaction between trees and position (Mergen and Cummings 1965). External characteristics of the seed varied considerably. Seeds of one tree were large, with smooth, shiny black coats, while those of a different tree had heavily etched brown coats. After irradiation, there were significant differences in seed germination between 10 trees and within individual trees. Seeds from the upper crown were generally more sensitive to gamma rays than those from lower positions. Yim (1963) found that the smallest seeds were more sensitive to irradiation damage than larger seeds.

While working on a method for distinguishing pitch pine from pond pine, Clausen (1939) noted wide variation in prickles and, also, needle length among individual pitch pine trees.

Seedlings

Pitch pine seedlings have been observed to vary in their ability to sprout (Little and Somes 1956). Among nonsprouters are those seedlings that never develop basal crook, those that are too young to have well-developed crooks, and those growing on peat-like soils which do not protect them from fire. Some open-grown seedlings may develop basal crooks in their first year, while shade-grown seedlings may take 9 to 10 years. The external and internal changes associated with basal crook formation in pitch and shortleaf pines were investigated by Little and Mergen (1966). Only 2 of 21 seedlings surviving 6 years did not form a typical basal crook. Many seedlings formed incipient crooks during the first summer, others a year or more later. Shortleaf pines usually formed shorter crooks and did so in less time than pitch pine. Open-grown seedlings formed crooks in less time than shade-grown ones. Basal crooks in these two species may be an adaptation to their environment. Both species grow in areas where fires have been common. Survival might often have been limited to seedlings with crooks because basal dormant buds on seedlings lacking crooks would have been exposed to and killed by the fires. Seedlings having crooks and capable of producing sprouts were selected for survival.

Tree Form

Crown and stem form of pitch pine generally is not as good as that in the other southern pines. Very few studies have been made of variation from tree to tree in stands of comparable age and density. However, the species may contain some mutants. Allard (1940) described a globose form of pitch pine growing in natural stands in Virginia. Natural stands in which trees were obviously dwarfed were studied by Andresen (1959), who concluded that this was a case of pseudo-nanism rather than dwarfing because repeated burning seemed to be the cause of the condition and not toxic amounts of soluble aluminum.

Wood Specific Gravity

The average specific gravity of unextracted increment cores of 2,000 trees was 0.474 and the standard deviation 0.047. Thus, the range among trees was about the same as for the major pines (Saucier and Taras 1969; Saucier and Clark 1970). The average tree specific gravity was estimated to be 0.471, but values were lower for trees in New England and New York than in the remainder of the species range.

POND PINE

Wood Properties

The average wood specific gravity of unextracted increment cores of 554 trees was 0.492 and the standard deviation 0.049, about the same variation among trees as in the other southern pines (Saucier and Taras 1969; Taras and Saucier 1970). No geographic trend was indicated.

From a study of wood and growth characteristics of pond pine in eastern North Carolina, McElwee and Zobel (1962) found quite large differences in both specific gravity and tracheid length among plots, and very large differences among trees in a plot (fig. 176). There was no definite pattern between geographic area or depth of organic material and specific gravity or tracheid length in pond pine. The range in latitude was not great, inasmuch as it varied from 34°30′ N. to 36°30′ N. In the study, 10 trees in each of three stands at each of six locations were sampled, making a total of 180 trees. There was considerable difference in plot variation among trees in specific gravity, one plot showing a specific gravity spread of only 0.07 (0.51 to 0.58), in contrast to another plot in the same area only a mile away, which exhibited variation over twice this range (0.36 to 0.51). In the 180 trees sampled for the pond pine study, the range of specific gravity was 0.36 to 0.61, with most of the trees having specific gravities between 0.45 and 0.61. Several exceptionally low specific gravity trees were found in the southern and westernmost geographic areas. Tracheid length, like specific gravity, varied among individual plots within an area: in one case, stands had trees with longer tracheid means than another stand within 1 mile distant and also significantly longer than stands in another area. Tracheid length had a variation pattern similar to specific gravity among individual trees, and much individual variation was found. It was difficult to obtain reliable age information because most of the trees were of sprout origin. Age measured in this way accounted for only about 3 percent of the tree-to-tree variation in specific gravity and, to all effects, was of minor importance. There was a very small but significant relationship between rings per inch and specific gravity. The small correlation value indicated that only about 7 percent of variation in specific gravity could be accounted for by differences in growth rate. Some plots had significantly lower amounts of compression wood than others, the spread ranging from 44.8-percent compression wood in area No. 1 to 10.9 percent in area No. 5. Percentages of compression wood are on a cross-sectional area basis at 4½ feet and do not represent the proportion of compression wood volumes in the entire bole.

Oleoresin Composition

The oleoresin of pond pine is unique for the high proportion of limonene and low proportion of alpha- and beta-pinene (table 2). Trees in North Carolina averaged 28-percent alpha-pinene, 1-percent beta-pinene, and 70-percent limonene plus beta-phellandrene (Kang 1966). Among 77 individual trees sampled at 10 geographic locations, alpha-pinene varied from 8 to 63 percent, beta-pinene from 0 to 2 percent, and limonene plus beta-phellandrene from 25 to 91 percent. In hybrids of loblolly and pond pines, terpene composition is similar to that of loblolly pine instead of intermediate with the parents, as is found for many morphological traits.

Other Characteristics

In North Carolina stands, Kang (1966) found variation among trees in 26 traits of cones, seed, needles, wood, and seedlings. Differences were greater among trees for the traits than among geographic locations. Seventy-seven trees and 10 geographic locations were sampled.

SAND PINE

Cones and Seed

Geographic and individual tree differences in cone opening in sand pine were described by Little and Dorman (1952a). Observations of cones on sand pine made in January indicated that sand pine in eastern Florida and central Florida—Ocala race—were largely closed-cone types and that the cones did not open on the tree when mature, while those in western Florida—Choctawhatchee race—were

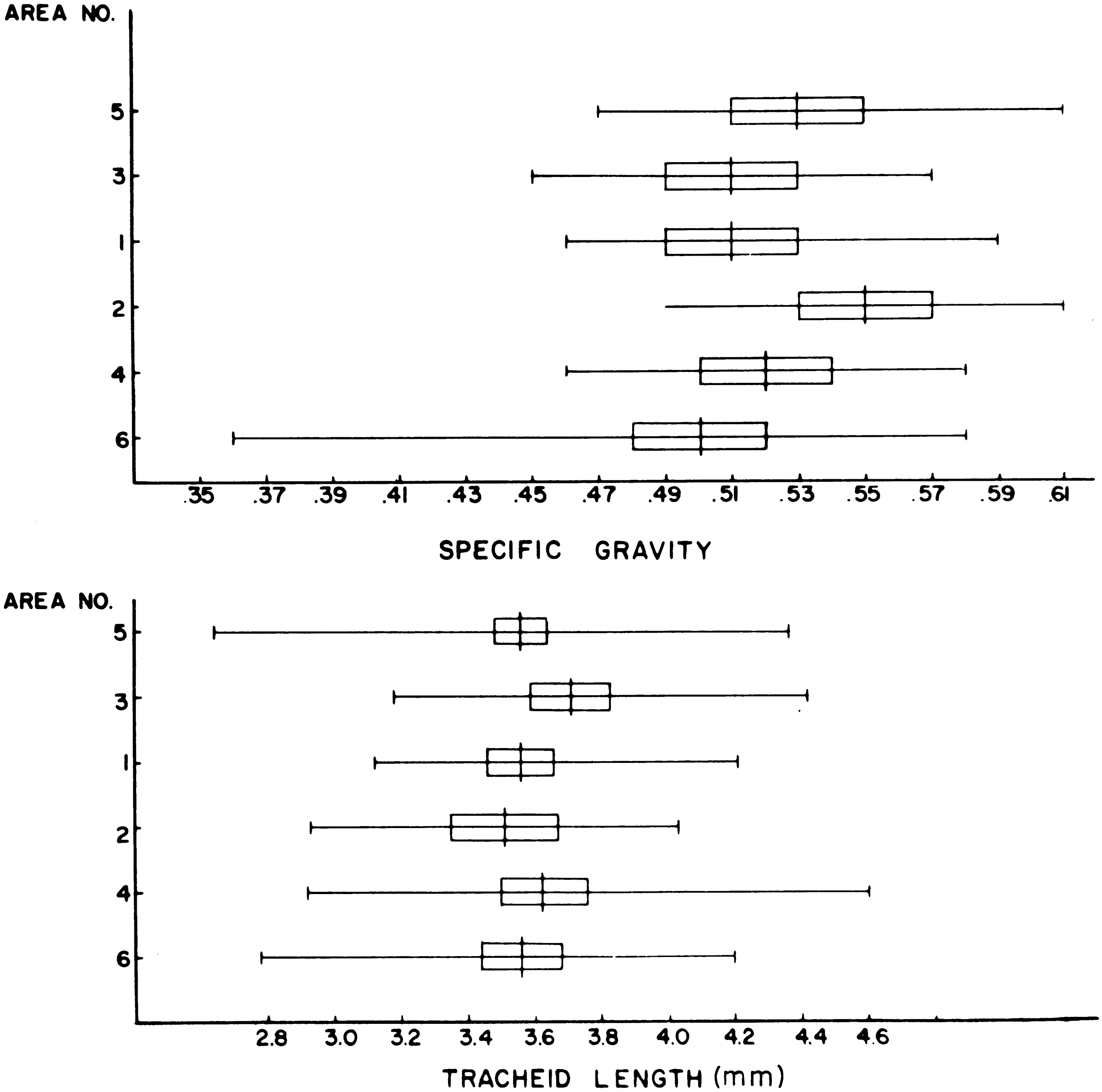

Figure 176.—Variation in specific gravity and tracheid length in pond pine among areas and trees within plots. The central vertical line is the average for the area; the rectangle represents two standard errors on both sides of the mean. The horizontal line shows the total range of values found for each area. The arrangement of areas is from northeast to southwest in the North Carolina Coastal Plain. (McElwee and Zobel 1962)

largely the open-cone type in which cones on the majority of the trees opened in the fall after becoming mature. No morphological differences between trees and specimens of sand pine needles of the two races were found at that time. Other differences are given in the chapter on racial variation.

Cones per bushel in Choctawhatchee sand pine average 1,010 and vary from 630 to 1,310; in Ocala sand pine they average 830 and vary from 450 to 1,100. Wide tree-to-tree variation occurs in size, coloration, and yield of seed. Ocala seed average 47,200 per pound and vary from 26,000 to 67,000; Choctawhatchee seed average 56,100 per pound and vary from 40,800 to 58,900. Seed yield may be about 0.62 pound per bushel of cones, but in Ocala sand pine the cones from individual trees had yields of from 0.3 to slightly over 1 pound. Some of these differences are perhaps caused by the sand pine characteristic of frequently setting two or more whorls of cones in a single year (Barnett and McLemore 1965).

Root Rot Susceptibility

Planted and natural stands of sand pine in Georgia and Florida may have root rot primarily on intermediate and suppressed trees and occasionally on dominant trees of the Ocala race, while the Choctawhatchee race has been disease-free even when planted on the same site. The root rot is caused by *Clitocybe tabescens* (Fr.) Bres. (Ross 1970).

Needles

An unusual specimen of sand pine was observed on the west coast of Florida, in Franklin County, in association with normal sand pine (Woods and Dawsey 1955). The "needles," normally in fascicles of two, appeared to be single and terete. Closer examination revealed that each single needle actually consisted of two separate ones cohering tightly by their adaxial surfaces. When the tips were teased apart, the needles could be stripped one from the other and completely exposed. They were relatively straight, rather than greatly twisted and curved, as is normal for the species. The growth habit of the tree was otherwise normal. Microscopic examination showed that the cohering surfaces were bound together by an adhesive that apparently withstood solution by alcohol and xylol.

Hybridization and Oleoresin Composition

Attempts to hybridize slash and sand pines showed that certain combinations of the three trees used of each species would produce more sound seed than others (Saylor and Koenig 1967). Also, sand pine seedlings used as controls for the hybrids varied widely in chemical composition of the volatile fraction of the cortical oleoresin. Proportion of alpha-pinene varied from 33.2 to 44.8, beta-pinene from 55.2 to 66.3, camphene from 0 to 1.4, and myrcene from 0 to 1.0. There was no beta-phellandrene.

Growth Rate and Form Class

In a 28-year-old plantation, 22 trees, or 5.3 percent, had cubic-foot volumes of 250 percent greater than average (figures 177 and 178). The three largest trees, however, had a volume of 15.0 cubic feet and the average tree only 5.2 cubic feet. Form class ranged from a low of 64 to a high of 89 percent, average wood specific gravity for rings 11 through 20 was 0.51 (Burns and Brendemuehl 1969).

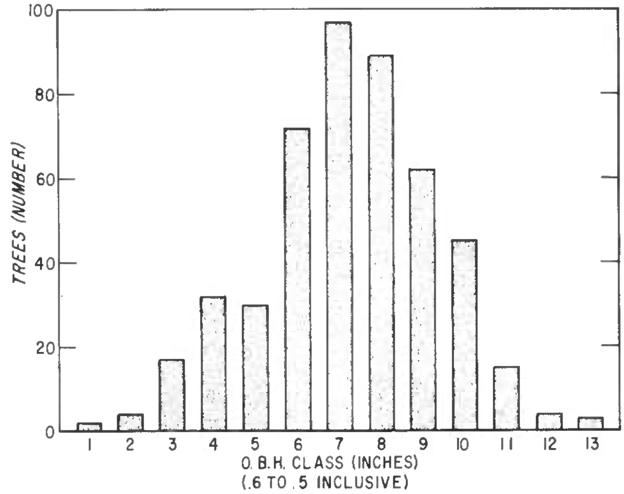

Figure 177.—Diameter frequency distribution in sand pine at plantation age 28. (Burns and Brendemuehl 1969)

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Figure 178.—Sand pine plantation in Florida after 28 years. Stem and crown form are not as good as in the major southern pines, but plus trees can be selected for small branches, rapid natural pruning, stem straightness, and fast growth. (Burns and Brendemuehl 1969)

Wood Specific Gravity

The average specific gravity of unextracted Ocala sand pine increment cores was 0.439 (standard deviation 0.037) for 523 trees. For Choctawhatchee sand pine, specific gravity was 0.485, with a standard deviation of 0.045 (Clark and Taras

1969). For 151 trees averaging 48 years of age, specific gravity was 0.48, the standard deviation being 0.042 (Saucier and Taras 1969). Superior trees selected for good growth and form averaged 0.490, and the comparison trees 0.476. The variation among trees seems to be about the same as in other southern pine species.

Spiral Grain

In logs of individual trees, amount of spiral in the grain varied from about an inch per linear foot to 3.2 inches per foot. The inner wood of the trees had smaller slope of spiral than outer wood (Paul 1932). In slash pine, Gerischer and Kromhout (1964) observed that spiral grain was almost constant from pith to bark, but in loblolly pine it decreased outward. Thus, the pattern of variation from the pith outward seems to vary among sand, slash, and loblolly pines, on a basis of these limited studies.

SPRUCE PINE

Seed Dormancy

Seed of two trees showed a large difference in dormancy. Stratification was effective in breaking dormancy (McLemore and Barnett 1967).

Wood Specific Gravity

The average specific gravity of unextracted increment cores over the entire range of the species was 0.443, with a standard deviation of 0.041 for 1,152 sample trees. The range of variation among trees was about the same as for other southern pines. The specific gravity for the entire tree was 0.426, as computed from regressions (Taras and Saucier 1968).

TABLE-MOUNTAIN PINE

Cones and Seed

Cone and seed size and other features differ widely among individual trees. Time of cone opening varies among trees (Zobel, D.B., 1969, 1970).

Wood Specific Gravity

The average specific gravity of unextracted increment cores over the entire range of the species was 0.470, with a standard deviation of 0.033 for 750 sample trees. The whole-tree specific gravity was 0.485. The variation among trees was about the same as in other southern pines (Clark and Saucier 1969).

VIRGINIA PINE

Seedling Growth

Nursery-grown seedlings of Virginia pine vary widely in growth potential, as shown by tests of seedling grades. Seedling survival was nearly 90 percent for the premium grade and only 40 percent for culls (Meekins 1964). Seedling growth varied among open-pollinated families of trees in several stands sampled in a combined geographic, racial, and single-tree variation study (Evans and Thor 1971; Rink and Thor 1971).

Tree Form

Generally, Virginia pine has poor stem and crown form because of crook, forks, and poor natural pruning, but individual trees with a good combination of good traits of form in addition to superior volume growth have been located. Seed orchards have been established with clones of these trees (fig. 179) (North Carolina State College 1958).

Wood Properties

The average unextracted specific gravity of Virginia pine wood was 0.449, with a standard deviation of 0.055, about the same range in variation as found in other southern pine species. The sample included 2,114 trees throughout the natural range (Clark and Wahlgren 1970). The whole-tree specific gravity was estimated to be 0.447. Superior phenotypes selected for National Forest seed orchards averaged 0.502, while the comparison trees, with smaller volume and average form, averaged 0.496 (Saucier and Taras 1969). Thus, trees with superior growth may have typical wood weight.

In a study by Thor (1964), variation among trees within stands was significant at the 0.1-percent level for all characteristics studied. Specific gravity after extraction among trees ranged from 0.39 to 0.62. Individual trees ranged in tracheid lengths (25 years from the pith) from a low of 3.2 mm to a high of 4.6 mm. Only 4 of the 13 trees with specific gravity of 0.58 or more had small amounts of extractives. The amounts varied from 2.1 percent in the lowest tree to 20.6 percent in the highest tree. Tracheid length at 10 years and at 25 years was highly correlated. Samples were obtained from 15 trees in each of 13 stands in Kentucky and Tennessee. At 6 years, differences in specific gravity among families were only significant at the 10-percent probability level, and extractive content was statistically nonsignificant. Specific gravity of progeny was correlated with that of the maternal parent (0.091) but not extractive content (Rink and Thor 1973).

No significant relationship was found to exist between radial growth and specific gravity before extraction of soluble material; after extraction, there was a significant correlation, where radial growth accounted for almost 7 percent of the among-tree variation in specific gravity. Rapid growth rate was associated with large amounts of extractives in the tree, but it did not appear to cause a serious reduction in tracheid length. There was no significant correlation between specific gravity and tracheid length. The effect of extractives in the pulping process was discussed, and it is suggested that extractives be incorporated as a factor in a selection program for Virginia pine. Trees with rapid growth, low extractives, and high specific gravity would not be too difficult to find.

Cones and Seed

Observations over a period of 20 years (Slocum and Miller 1953; Sucoff and Church 1960; Snow 1960) have shown that Virginia pine produces cones every year; once a tree starts producing cones, annual production follows unless the position of the crown and the canopy changes. Virginia pine produces cones in all portions of the crown. Studies of seed production show that it varies from year to year, but it is nonrhythmic. Virginia pine trees differ enormously in the number of cones they produce; also, there are wide differences among entire stands in annual cone production. Release of mature Virginia pine appears to stimulate seed production. Cones of Virginia pine average 2,244 per bushel but may vary from 1,600 to 2,816 per bushel. Samples taken from 88 trees showed variation of 67,132 to 114,761 seeds per pound. The best guide to future seed production of individual trees is past production history. Virginia pine seedfall began in late October and continued until May and sometimes longer. However, most of the seed fell during the first 3 months; each year the normal rate of total seedfall is different. Cones from different trees vary considerably in size.

In 6-year-old open-pollinated Virginia pine families, over 90 percent of the trees were flowering, and there were significant differences among 30 families observed (Bramlett 1971). Heritability estimates over a 2-year period were 0.59 and 0.65 for female and 0.48 and 0.44 for male flower production.

Figure 179.—Excellent Virginia pine phenotypes are tall, small limbed, and have fairly well-pruned boles. The tree shown here is 36 years old, 69 feet tall, and 10.5 inches in diameter. Trees in the background are typical for the species. (North Carolina State College 1958)

Oleoresin Yield

Although Virginia pine is not considered economic for naval stores production, tree-to-tree variation in oleoresin production is of interest as an example of extreme variation occurring in this particular trait. Gum flow and pitch-soak in Virginia pine following Fusarium inoculation was reported by Hepting (1954): 49 trees in western North Carolina averaged 11 grams per week for a 27-week period from one fungus-treated streak. The highest season-long yields of oleoresin from an individual tree, when compared with average yields of other Virginia pine trees at three locations, varied from about three times to nine times the average yield.

SUMMARY AND DISCUSSION OF PART IV

Genotypic and phenotypic variations in traits are reviewed for each major and minor southern pine. Special techniques developed for use in studying variation and inheritance have been briefly described. Emphasis has been placed on economically important traits and those essential in breeding.

Variation among trees has been studied in the southern pine more than any other group of pines. More research, however, has been done with slash and loblolly pines than all other species combined, and most of the work has been on traits such as volume growth, wood properties, resistance to pests, tree form, and oleoresin yield.

Gains in wood yield and quality from breeding within a species depend on the kind and amount of natural variation between trees in traits, heritability or inheritance of the traits, selection of economically important traits, and the interrelationships or correlations between all the various traits. For this reason, all these aspects of variation among trees have been stressed.

VARIATION AND INHERITANCE OF TRAITS

A large number of physiological, morphological, and chemical traits has been shown to be variable, either by phenotypic surveys in natural or planted stands or by progeny tests. The same traits are variable among all the species, but, as stated, certain traits have been studied more than others. Phenotype and genotype are often highly correlated. Many traits such as vigor, resistance to pests, wood specific gravity, branch size, stem crook, and others combine to influence wood yield per acre and tree value.

The range of inherent variation in the southern pines is much wider for some traits than others, regardless of species. In terms of growth and yield of products, progeny of certain parents produce twice as much wood or oleoresin as average trees. In contrast, wood weight, lignin content, or cellulose content may vary from under 5 to 20 percent or higher. Stem form may vary from crooked to straight, forked to unforked, wide sweep to straight, and high to low taper. Crown form varies from small to large branch angle, small to large branch diameter, and poor to good natural pruning. Resistance to fusiform rust in loblolly and slash pines, to brown spot in longleaf, and to littleleaf in shortleaf may vary from high susceptibility causing death to high resistance facilitating volume production.

Heritability estimates for various traits differed among studies because conditions were not constant. Average heritability estimates for each trait are not meaningful, but most of them are consistently high and indicate that substantial progress could be made in breeding. Most broad-sense heritabilities were within a range of about 0.40 to 0.90, and narrow-sense heritabilities from 0.10 to 0.50.

Phenotypic and genotypic variation among trees is so wide in the southern pines that sampling methods must be prepared accordingly by taxonomists, plant physiologists, wood technologists, and others if their results are to be "meaningful" as an "average" for the species. Estimates of the range in variation in each trait have been used to establish selection criteria for special trees.

Correlations of genotype and phenotype have been generally higher for certain traits such as crown form, stem form, wood specific gravity, and oleoresin yield; they have been lower for others such as volume growth, resistance to pests, or chemical composition of the wood. For metrical traits, estimation of the plus-tree genotype has been most accurate if selection was carried out in mature stands with uniform environmental conditions. Selection for resistance to disease has been most accurate when carried out in stands with high exposure to the pest, in other words, stands characterized by high incidence of infection.

Although correlation of genotype and phenotype may be high, families sometimes differ when similar phenotypes are mated. The difference among families perhaps indicates important differences among the parents in combining ability. The necessity for selecting trees with good combining ability, or breeding value, is well established, but little is known about the range in variation among trees in combining ability.

Width of the range in variation for each trait seems to be closely regulated. This makes it possible to compute the number of trees that must be examined to identify a specified number of plus variants. Also, the range of variation for each trait can be predicted among offspring or strains used in commercial planting. Contrary to common belief, examination of several thousand trees in selection work might not reveal trees that rate higher for a particular trait than occur in a group of a few hundred trees. However, trees with a better combination of several desirable traits would be found in a large, rather than a small, group.

The variation within families or groups of families from crosses among plus trees or seed orchard clones is an important factor in recurrent selection and in silviculture but is often overshadowed by the emphasis placed on family means.

Minus variants for some traits are so bad in southern pines that the trait cannot be ignored while concentrating selection on one or a few traits, such as growth rate and crown form, to make greatest gains. Crown form, stem form, seed production, and perhaps other traits make certain trees unusable, although they rate very high in one or more other traits. Thus, it is advisable to select *against* some traits while selecting *for* other traits. The possibility of including some trees completely unusable in breeding is often overlooked in discussions of the advantages of concentrating on one or a few traits to make the greatest genetic gain. One method of selection may not be suitable for all tree species or for seed orchard clones or breeding stock within species.

Many traits in the southern pines vary continuously or quantitatively, indicating several genes are involved. Thus, frequency distribution curves for progeny trees or those in uniform plantations are normal in shape. Curves that may represent the additive effects of more than one trait—oleoresin yield in slash pine and tree volume in slash and loblolly pines, for example—may have a long tail to the right or toward improved performance, which is characteristic for this type of genetic effect. The frequency distribution curves for myrcene and other monoterpenes in slash and loblolly pine oleoresin are not normal in shape but bimodal, which indicates a different type of inheritance.

Resistance to pests is difficult to express by frequency distribution curves, but progeny tests indicate that several genes may be involved.

Genetic variances have mostly been of the additive type rather than dominant or epistatic, in the few instances where they were computed. Progeny from wind pollination and controlled crosses and selfs seem to vary about the same for certain traits but not all traits; only a few comparisons of this type, however, are possible. Mating like trees to like for high oleoresin yield or wood specific gravity has produced offspring with higher than average performance but with rather wide range among individual offspring. Close crossing may reduce but not eliminate variability among trees, in comparison to that found among trees in wild stands.

RELATIONSHIP AMONG TRAITS

Most traits in the southern pines are inherited independently and are not negatively or positively correlated. This situation promises large gains in breeding but creates some problems by making it necessary to consider several traits at once in parental stock. Fears that breeding for high oleoresin yield would result in short-lived trees or that improving growth rate would lower wood specific gravity and lumber grade while increasing susceptibility to disease are without foundation as long as all important traits are considered in the process. Inasmuch as improvement in one trait will not result in corollary improvement in another, as would occur if they were positively correlated, it is necessary to have several good traits in parents. When selection of this type (index selection) has been done, gains in growth, stem and crown form, and resistance to pests have been obtained. In certain slash pine progeny tests, trees have grown faster and survived better than controls because of resistance to fusiform rust and other pests, and the additive effect of a few good traits resulted areawise in much higher than average volume growth.

The necessity for evaluating several traits has complicated progeny testing because volume growth and tree quality may take much longer to accurately estimate than would survival, resistance to pests, wood properties, and other traits when performance in juvenile and mature trees is correlated.

The silviculturist has some but not unlimited opportunity to remove from a stand the fast-growing trees that are undesirable because of disease, poor form, or low-value wood. The tree breeder, on the other hand, can be far more selective in choosing breeding stock to create strains with many good traits. The tree breeder can search among the entire group of fast-growing trees within stands for those with superior growth plus good form, acceptable wood quality, and freedom from disease. Such selection is possible because form, wood quality, and susceptibility to disease are not highly correlated with growth rate. The subject of relationship among traits from the viewpoint of the silviculturist is quite different from that of the tree breeder—causing much confusion when wood and tree quality in relation to growth rate is discussed only in general terms instead of in detail.

The mental picture stimulated by mention of breeding for improved growth—a tree with long limbs, no natural pruning, high stem taper, diseased parts, and wide growth rings—is wrong. This is an inherently average tree made bad by a poor environment and poor silviculture. By contrast, trees with improved growth rate visualized by tree breeders produce higher than average wood yields per acre, with no decrease in tree quality or wood properties. In fact, certain traits of crown and stem form as well as wood quality may be improved over the average for the species. Trees with this combination of good traits have been selected and photographed by tree breeders. To make economically important gains in timber yields, it is not necessary to discover the very largest or very best formed trees for breeding. Results of numerous progeny tests with southern pines show this important fact.

Researchers have estimated correlations among traits in wild trees under typical field conditions. Studies of the most value in the future will be those concerning maximum volume growth and traits of tree form and wood properties. Improved growth rate is the goal in breeding, but it must not be achieved at the expense of tree and wood quality.

Manipulation of several important traits to create greatly improved offspring is one of the most important and complex subjects in applied breeding with southern pines.

INFLUENCE ON SELECTION METHOD, BREEDING METHOD, AND MATING SCHEME

An objective of research in variation is to obtain information that will guide genetic improvement of southern pines. We have learned that many economically important traits vary among trees, that the range of variation is wide, and that trees in the minus part of the frequency distribution curve for certain traits, such as stem forking, stem crook or seed production, may be valueless in breeding. The relationship between economic value and variation gradient is very high for traits such as volume growth, oleoresin yield, or wood specific gravity (in pulping) but rather low for others such as tracheid length, stem taper, branch angle, or bark thickness. Also, the correlation between certain traits is negative, for some it is positive, but for many others there is no correlation.

Thus, for seed orchards and breeding projects, variation in southern pines is such that selection by an index method, based on numerous traits, has advantages over selection by the tandem or independent culling level methods. But a combination of selection by independent culling levels and an index system is used in seed orchard projects and is effective in producing large increases in wood yield. Selection by an index based on only two or three traits does not have much merit.

Tree-to-tree variation is of the kind and amount that makes selection and crossing within species more efficient as a breeding method to improve wood yields than do species hybridization, mutagenesis, or introducing foreign species. However, for improvement of certain traits, selection combined with another method such as hybridization might be efficient.

Variation among trees influences effectiveness of mating schemes such as crossing like trees, crossing unlike trees, or selfing to improve certain traits or groups of traits to improve wood yield.

The advantages and limitations of various selection systems, breeding methods, and mating schemes are enumerated in Part VI.

ENVIRONMENTAL EFFECTS

Soil fertility, soil moisture, and growing space seem to have slight, if any, effect on the number of traits that vary or on the range variation among trees, although the subject has not been intensively studied. When differences in these broad environmental factors are associated with geographic location, changes in the level of a trait may vary somewhat but not among trees on the local site. Thus, uniform environments are required for selection work and progeny testing.

Broad-sense heritability percentages are high for many traits, indicating that variation caused by environmental factors within study areas is low. Also, parent-offspring correlations are usually significant, showing that phenotype and genotype of parents are similar.

The belief is common that most differences among trees in plantations or even-aged natural stands on level areas are a result of environmental factors differing over distances of a few feet. But facts from inheritance studies demolish such suppositions. Although much importance has been attached to environmental effects, little use has been made of environments to control or eliminate differences among trees. Site quality has been used to forecast timber yield, and growing space has been regulated to control average growth of stands, but these do not change the relationship of traits among trees or make stands uniform.

Improving trees genetically is a more effective course of action for increasing tree growth, areawise volume production, and tree quality than is improving the environment by irrigating or fertilizing, but there seems to be no reason why the two approaches cannot be combined when techniques are perfected.

VARIATION AMONG TREES AND GEOGRAPHIC VARIATION

Many of the traits that vary with geographic location, such as growth rate, wood properties, oleoresin yield, and resistance to pests, vary among trees in stands. For many traits the differences among trees are larger than among geographic locations. Indications are that racial and plus-tree selection should be combined to achieve maximum gains in breeding.

A SIGNIFICANT POTENTIAL ASSOCIATED WITH VARIATION

Because striking improvement over the average has been obtained in tree growth, tree form, oleoresin yield, and resistance to pests by crossing carefully selected plus trees, these results indicate also the importance of the individual tree in other methods of breeding such as mutagenesis and species hybridization. Countries importing southern pine seed should try to obtain it from the best trees as well as from the appropriate geographic location.

Although striking gains have been obtained in certain traits, the full potential in improving several traits has not been realized in seed orchard projects. Some seed orchards contain many clones and serve widely scattered planting regions; thus, the problems in clonal selection and progeny testing are both large and complex.

The limits of recurrent selection in improving certain traits have not been established. A satisfactory level might be attained in one or two generations for traits important in stem and crown form or resistance to fusiform rust, but improvement of other traits such as tree growth, areawise wood volume production, and oleoresin yield should be emphasized as far as possible. Improvement in wood yield by recurrent selection might be brought about by improving single traits as well as using the additive effect of several morphological, physiological, and chemical traits.

Inasmuch as most traits vary continuously, mating like to like trees or selfing will not produce uniform progeny. Thus, the silviculturist cannot expect highly uniform stands, although overall performance is improved.

IMPORTANCE OF VARIATION AMONG TREES IN SILVICULTURE

It has been shown that many of the differences among trees, often attributed to environmental factors, are genetically controlled. This means that silviculturists must consider the characteristics of individual trees whenever choices among them are made. Trees with one or several bad traits may be inherently bad, and those with good traits may be inherently good.

Not being able to progeny-test trees to obtain proof of genotype as research workers might do, the silviculturist has to be guided by assumptions. He assumes that poor growth or form in certain trees might be a result of poor environment or heredity or both and discriminates against them rather than take a chance that the traits result only from poor environment. The silviculturist should give preference to trees of good growth and other desirable characteristics because he can assume that they are inherently good and will produce good offspring. The trees he may choose under this system may not be quite as good as they appear, but they present to the observer no evidence of faulty genetic constitution. The silviculturist should not get involved in small and meaningless distinctions but proceed on the basis that there is something to gain and nothing to lose in assuming that a tree's outward appearance indicates its genetic makeup.

The discussion shows that tree breeders have demonstrated a genetic solution to problems in improving growth and quality that have proven hard to solve by manipulating environmental factors. Tree breeders have shown that it is not necessary to increase growing space, which results in large crowns and low tree quality, or to improve growth rate, or grow trees slowly to insure good wood properties and resistance to pests.

WORK NEEDED

There is a need to extend the type of studies that are so productive in loblolly and slash pines to other species. The maximum range in many of the traits should be established to guide selection procedures and crossing patterns. The relationship among traits, particularly additive effects, needs further study to guide breeding procedures and indicate alternate ways of achieving results if blocks occur in certain approaches. Techniques should be perfected for creating extremely fast growing, synthetic varieties with high-quality wood so that they can be applied in large-scale seed orchard and breeding projects. Estimates of inheritance for use in predicting genetic gains should be prepared to guide recurrent selection used in most seed orchard breeding programs. Current inheritance data are based on parent trees in natural stands, and thus results may not apply to trees in advanced generations that are being produced in seed orchard projects. Diagrams of the steps in phenotypic and genotypic recurrent-selection breeding methods are given in the chapter on organization of southern pine breeding in Part VI. The breeding of strains with fast growth, slender crowns, and faster natural pruning required additional silvicultural research in the relationship of yield to age, site, and stand density. All silvicultural research heretofore has been with wild-type trees, and the results may not apply to improved strains. The importance of selecting for combining ability or breeding value should be determined.