CHAPTER 8

LOBLOLLY PINE

Monographs on loblolly pine have described the species in general and the effect of various environmental factors on natural regeneration, planting, cultural practices, and utilization. The monographs of most utility are those by Mohr (1897), Ashe (1915), and Wahlenberg (1960).

TREE GROWTH AND VOLUME YIELDS

The timber crop depends on the inherent factors controlling growth of individual trees as well as those that influence number of trees per acre and their development as a stand. Thus, in addition to height growth, essential aspects are variation and inheritance of traits affecting survival of seedlings, development of crowns, resistance to stem or crown breakage, and tolerance of competition for light and moisture. Attacks by insect and disease pests affect tree survival, and wood specific gravity influences pulp yield and quality and wood quality; these subjects will be covered in separate sections of this chapter.

The wide difference in volume among trees in a plantation and even-aged stand has been widely recognized by foresters. Diameter distribution on 103 plots in a growing space study and its relationship to stand volume growth was studied by Nelson (1964). Plots of the same age, having similar site indices and stocking classes, had distributions that widely varied. For an extreme example, 55-year-old trees varied from 6 to 18 inches d.b.h., while on a 61-year-old plot trees varied only from about 10 to 14 inches. Trees in two plots 30 and 32 years old varied from about 5 to 14 inches d.b.h., but the modal class was quite different. Diameters approached a truly normal distribution on some plots but on others tended to be multimodal, skewed to the right, or skewed to the left.

It is to be expected that diameter distribution curves would be somewhat irregular on small plots because of the relatively small number of trees. However, in plantations where soils, spacing, and age are uniform, both diameter growth and stem form vary widely among individual trees even when average growth rate is high. In a South Carolina plantation, 639 trees on a sample acre produced 48.29 cords of wood in 11 years (Langdon *et al.* 1970). Average diameter was 7.5 inches, but there were 17 trees in the 4-inch class and 28 over 10 inches (fig. 104). Two trees were already 11 inches in diameter, and each had a volume 2.6 times that of the average tree.

Spacing, crown size, soil differences, and other factors can influence growth of individual trees in stands, but in loblolly pine it is obvious that phenotypic selection should concentrate on trees with over twice the average volume as a basis for estimating the genotype. Trees with large trunks and small crowns are preferred. Although trunk volume generally increases with crown size, Rogerson (1964) found a difference of 60 percent in foliage dry weight on planted trees of the same diameter.

Tables of loblolly pine tree height by diameter class, age, number of trees per acre, and site index (Lenhart and Clutter 1971) showed the following relationships: (1) heights varied widely but uniformly in any combination of site, number of trees per acre, and age; (2) range among trees in height increased with age on any combination of site and number of trees per acre; and (3) average height decreased with increasing number of trees per acre on any site. In an intermediate environment, site index 60 and 700 trees per acre, heights at 10 years ranged from 18 to 28 feet, differing by 10 feet; at age 20 from 31 to 54, differing by 23 feet; and at age 30 from 45 to 71 feet, differing by 26 feet. The same relationships apply to diameter distributions.

The combined effect of age, wood specific gravity, stem diameter, and stem height causes extremely wide ranges among individual trees in dry weight of total stem without bark, as shown by Burkhart and Clutter (1971). For example, their data show that 10-year-old trees 3 inches d.b.h. and 30 feet tall weigh 13 pounds, while, at the same age in the same stand, the 10-inch trees 60 feet tall weigh 273 pounds, or 21 times as much. At age 30 the 3-inch tree 30 feet tall would weigh 15 pounds, but the 10-inch tree 60 feet tall would weigh 335 pounds, or over 22 times as much, and the 12-inch tree 75 feet tall would weigh 600 pounds, or over 33 times as much as the 3-inch tree, although they are all growing in the same stand at the same spacing. Diameter distribution tables indicate that trees of these sizes occur.

The diameter, height, and weight tables illustrate that the widely accepted relationships established by silvicultural research are sound in that age, site, and spacing strongly influence growth. They show, also, that there is a constant pattern of variability in growth superimposed on every combination of environmental factors, a concept important in selection and progeny testing. Tree breeders can only exploit the portion of the variability contributed by genetic factors when they create

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Figure 104.—A fast-growing loblolly pine planted stand 11 years old in South Carolina. Diameters vary among trees—the larger trees are over 10 inches—and so do stem straightness and branch size. Although the amount of growing space and other environmental factors affect average growth rate and crown size of loblolly pine, a relatively uniform environment does not insure uniformity, possibly because of inherent differences among trees. (Langdon *et al.* 1970)

new and improved strains. Foresters can utilize environmental factors that best suit their needs—but with the realization that manipulating these environmental factors will not cause trees to be all the same size in forest stands. A major goal of the forest geneticist is to solve the patterns of inheritance of vigor and growth rate.

Physiological and Chemical Differences

Measurements of photosynthesis and respiration have been made in an attempt to relate juvenile performance to that of mature trees. If this can be accurately done, important savings in progeny testing will be possible.

In early studies of the relationship between photosynthesis and respiration and growth in loblolly pine, significant differences occurred among progeny groups, but correlations with seedling dry weight were not evident. Sometimes a small variation in photosynthetic rate was associated with a large difference in growth (Reines 1962; Robertson and Reines 1966; Burkhalter *et al.* 1967). However, when net assimilation rate of seedlings was determined for the entire growing period instead of at one time during the season, a strong correlation with total growth was found (Ledig and Perry 1969). Thus, the concept that net assimilation rate varies throughout the season is most important (fig. 105). Among three full-sib families, two averaged about 800 mg and one nearly 1,400 mg, or 75 percent more dry weight for a 21-week period. However, among all 27 families in the study, there was a threefold variation in total growth. The authors point out that differences in photosynthesis and respiration may influence initial growth of seed-

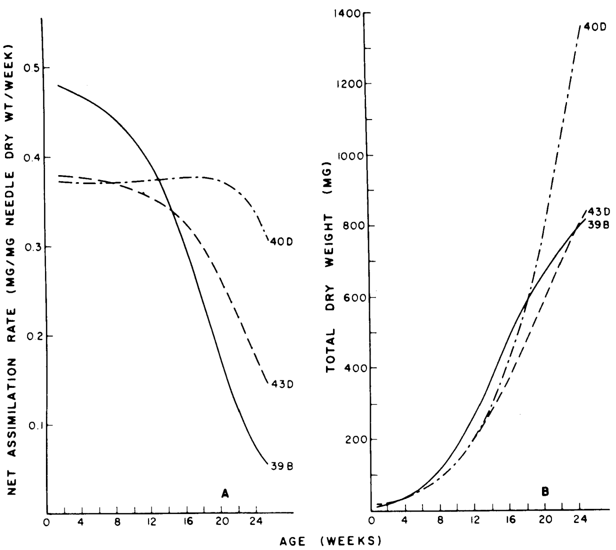

Figure 105.—Variation among three loblolly pine progenies in (A) the course of net assimilation rate and (B) logistic growth curves for seedlings in their first growing season. Growth curves for the progenies cross, and this can be rationalized on the basis of the seasonal patterns of assimilation. With a fairly high and sustained net assimilation rate, progeny 40D produced superior dry weight during a 24-week period. (Ledig and Perry 1969)

lings, but the number of years this is maintained is unknown.

There are other physiological and chemical differences among seedlings that may affect growth of individual trees or survival of planted trees, which will in turn influence wood yield per acre. Winter chlorosis and disruption of the photosynthetic apparatus are affected by both environment and the genotype, as indicated by variation within trees and between clones (Perry and Baldwin 1966). Ability to withstand transplanting shock was found to be related to genetic differences in plant size, plant height, root-shoot ratio, root habit, and root regeneration potential (Beineke and Perry 1966; Ledig and Perry 1966). There was wide variation among trees in reaction to and recovery from cold injury that was not related to tree size in a Tennessee racial variation planting of loblolly pine from Georgia (Mignery 1967). Significant differences occurred among three loblolly pine families in response to clay-suspension coatings used as nutrient sources for 4-month-old seedlings (Tabor and Davey 1966).

Chemical analyses have shown wide variation among loblolly pine trees in nutrient content and dry matter content of needles (Steinhof 1961) and percent reserve carbohydrates of roots of trees in dense stands but not isolated trees (Miller and Kelman 1966). The percent reserve carbohydrates appeared to have no influence on the number of *Fomes annosus* infections which occurred, but the growth of the fungus in each root was inversely related to the percent reserve carbohydrates of the same roots. Dominant trees generally had higher percent reserve carbohydrates than suppressed trees, and current 5-year growth was directly correlated with root reserve carbohydrates.

While studying racial variation in monoterpene composition of loblolly pine, Gilmore (1971) observed wide tree-to-tree variation in terpene fractions, not only among all trees in a seed source study but within a seed source. The range was wide for terpenes occurring in both low or high concentrations. Werner (1972) observed that certain terpenes were strong stimuli for males, while others were attractive to females. The heaviest attacks of male *Ips grandicollis* were related to the greatest concentration of attractive terpenes, which was between 15- and 30-foot levels of the tree stem. Host attractiveness was dependent on the qualitative and quantitative composition of terpenes that were more attractive to insects in injured than healthy trees.

Seed size affects seedling growth in certain pine species and could be a source of error in studies of growth in young plants. However, in loblolly pine the chances of error seem small on a basis of conclusions by Addoms (1937) in sand culture studies. Because of the low correlation between seed size and seedling size for different families, Stonecypher *et al.* (1966) decided no adjustment for seed weight was necessary when estimating genetic and environmental components of variance and covariance. Brown and Goddard (1959) observed that average seed size was variable among mother trees in loblolly pine, but there were no significant differences in seedling size from average- and large-sized seed, although the seedlings from small seed were significantly shorter. The greatest influence of seed size on seedling size was found to be within and not between mother trees.

One component of the growth complex is length of the growing period. Relationships of growth initiation and cessation with temperature, day length, and moisture availability have been generalized for species, but little is known about phenotypic and genotypic differences among trees within a species grown in a similar environment. In southeast Arkansas, an area where late-season rainfall is low, dominant trees in loblolly pine stands began growth earlier, grew faster, and had a longer growing season than intermediate trees (Bassett 1966). In a thinning study, dominant and codominant trees had a longer growing season in lightly stocked stands than in heavily stocked stands (Zahner and Whitmore 1960). In South Carolina, where soil moisture is usually adequate in the fall, 2 percent of the loblolly pine trees stopped growing by September

2, but 23 percent were still growing on November 11 (Harkin 1962). In a Florida racial variation study, length of growing season varied among young individuals and groups of trees from different geographic locations (Perry *et al.* 1966). In the microclimate of a nursery bed in Texas, it was observed that certain seedlings stopped height growth in late August while others grew until October (Bilan 1966). In the greenhouse 29 percent of the open-pollinated seedlings in one family formed terminal buds by mid-October, while the remaining seedlings continued to grow through the entire winter. In several other families 70 to 93 percent of the seedlings formed terminal buds by October 15.

Length of the growing season for individual trees may affect wood specific gravity as well as volume if it prolongs summerwood formation. In a Georgia loblolly pine plantation, the dominant and codominant trees had higher percentages of latewood (43.5 and 43.2) than intermediate and suppressed trees (40.4) (Hamilton and Mathews 1965). Also wood specific gravity was slightly higher for the dominant and codominant than for the intermediate and suppressed trees (0.51 versus 0.49).

Phenotypic Variation

Graded Seedlings

One method of controlling quality of nursery stock has been to grade seedlings before they are shipped to planters. Field checks of graded seedlings have shown the merit of this practice and indicate that the grading process partially estimates inherent growth differences among seedlings. Early work in graded seedlings is summarized in *Planting the Southern Pines* by Wakeley (1954a).

Additional studies have shown that growth differences apparent among seedlings in nursery beds are maintained for several years in the field. It was estimated in Texas that the growing and utilization of medium-sized seedlings would show a $164-per-acre-yield advantage at 11 years over small stock (Silker 1960). Also in Texas, seedlings on three sites showed a strong, direct relation between height at planting and growth over 4 years (Hunt and Gilmore 1967a. 1967b). Height growth and survival of the larger seedlings was of more consequence on the better sites than on the poorer. At the time of planting, seedlings varied from 0.3 to 1.4 feet, and on the best site after 4 years trees varied from 6 to over 12 feet. In naturally seeded areas large seedlings tend to maintain their superiority by faster-than-average growth in subsequent years (Wenger 1955).

The oldest loblolly pine seedling grade study on record showed, after 34 years, pulpwood volume per acre for Grade 3, the poorest grade, 30.7 cords, Grade 2 seedlings 33.9 cords, while Grade 1, the best seedlings, had 78.1 cords, or more than twice the volume of the lower grades of planting stock (Wakeley 1969a). Test plantings were repeated the following year, and after they had grown 34 years, seedlings in Grades 1 and 2 had produced 40.0 and 40.4 cords per acre, respectively, or nearly twice as much as Grade 3 seedlings, which produced 21.5 cords. Superior volume growth per acre was a result of higher survival of seedlings as well as superior height and diameter growth. Fusiform rust infection was not consistently affected by seedling grade.

If seedling survival is an important factor in comparisons of growth, progeny tests must be designed to permit estimates of volume growth per acre as well as volume of individual trees. Estimates of growth based only on height and diameter might seriously underestimate wood yields. Results of silvicultural research have shown that estimating wood yield per unit area is difficult. The use of plots of trees rather than rows or randomized individual trees plus numerous replications, both in space and time, will increase accuracy of volume estimates.

Studies of mycorrhizal fungi are showing that there are wide differences among seedlings in amount of mycorrhizae present on roots and that these fungi are beneficial to growth (Shoulders and Jorgensen 1969; Danielson and Davey 1969). Additional work is needed to learn if there are inherent differences in susceptibility to mycorrhizal infection and if it might be desirable to consider susceptibility in breeding; such studies are underway.

Studies of seedling grades, as well as others in which serial measurements are made of individual trees, provide important clues about the relation of growth of trees in intermediate ages to that of their juvenile years. If the relationship is close, many years can be saved in progeny and other field tests where comparisons of lots of seedlings or families are desired. Such a relationship might lack precision but might be satisfactory to screen seedling lots or individual trees for a group with generally good overall growth performance. This is a problem in progeny test design for southern pine genetics and applied tree breeding research.

Selected Nursery Seedlings

When applied breeding was started in southern pines, indications were that seedlings of exceptional growth rate could be obtained by careful search of nursery beds. However, there were no results from studies of phenotypic and genotypic variation among trees in morphological or physiological traits or resistance to pests to indicate that these were

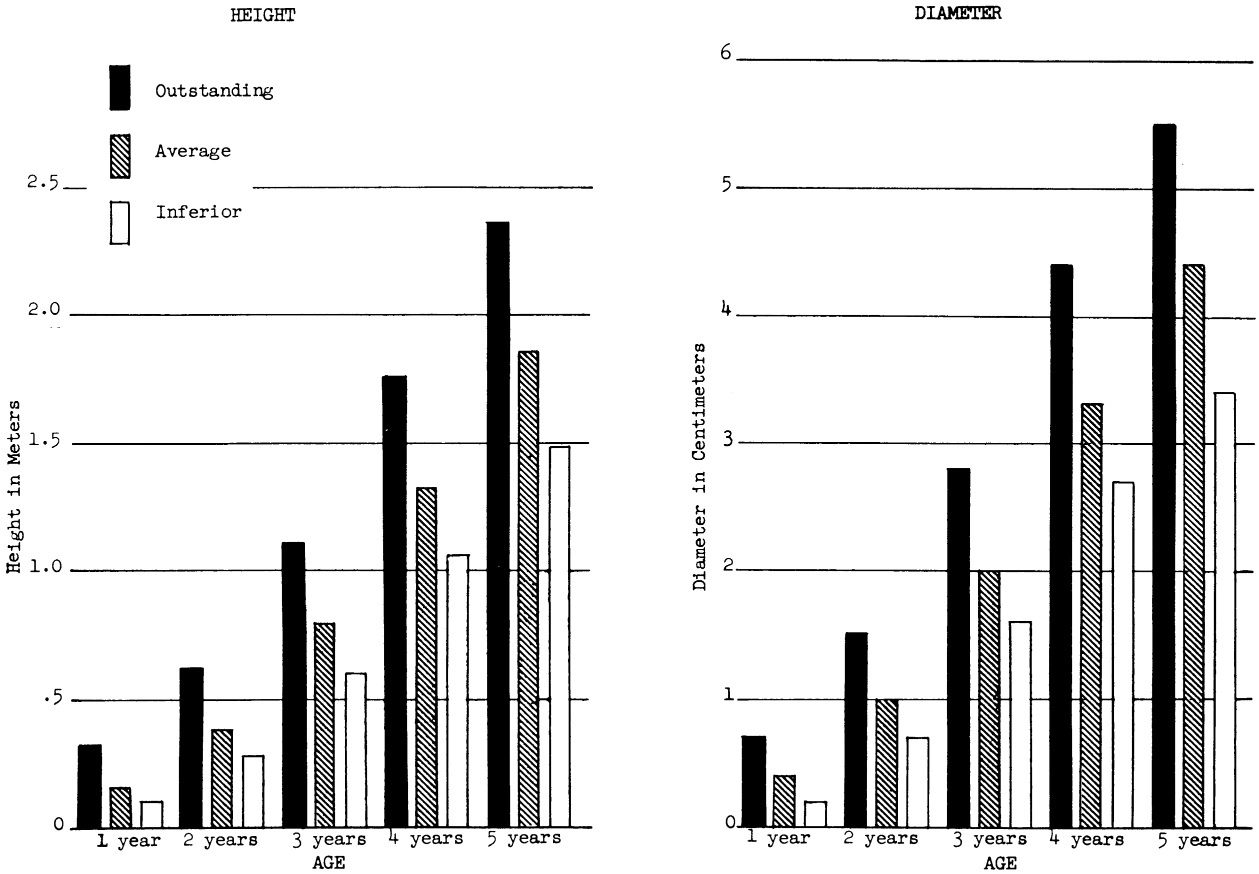

Figure 106.—Loblolly pine seedlings selected for inferior, average, or outstanding growth in nursery beds maintain their ranking over a 5-year period for both height and diameter. (Zobel *et al.* 1957)

also important traits in selection of outstanding nursery seedlings.

In Texas, plus seedlings averaged 25 percent taller than average control seedlings after 5 years' growth (Zobel *et al.* 1957). Seedlings selected for inferior growth rate were about 20 percent shorter than average seedlings (fig. 106). In Tennessee, after 10 years, 68 percent of the plus seedlings were taller than the average control trees but suffered the same kind and amount of damage from snow (Zarger 1965), while after 9 years in a Georgia study the plus seedlings had 25 percent greater volume than controls but the same amount of infection by rust (fig. 107) (Hunt 1967). In South Carolina, 10-year-old plus seedlings were about 30 percent taller than controls (Langdon *et al.* 1968). Thus, phenotypic selection in nursery beds was partially effective for height growth but did not produce any particular gains in other important traits, and often the fast-growing nursery selections had wolf-tree characteristics. The results show, as did those from studies of seedling grades, that growth characteristics established early in life may persist for as long as 10 years, which is a significant proportion of the 15 to 45+ years for rotation age.

Analysis of height-over-age relationships for a 30-year period showed that the majority of loblolly

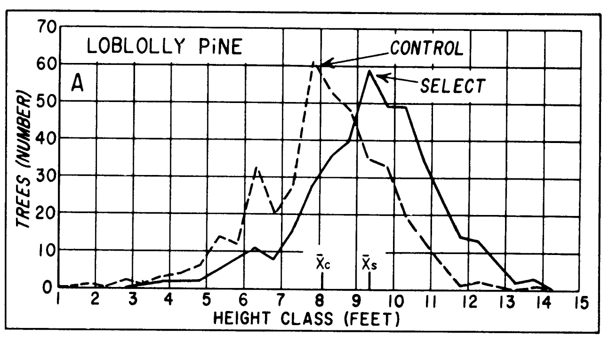

Figure 107.—Loblolly pine selected and control seedlings from nursery beds differ in average height after 4 years but show wide variation among individual trees in both groups. The frequency distribution curves are similar in shape; therefore, variability was about the same within each group. The planting site was an old field with more uniform conditions than are found in woodland sites. (Barber and VanHaverbeke 1961)

pine trees superior in height at the end of the period were well above average since an early age. Certain rare trees were only average in height for 15 years before asserting superiority (Wakeley 1971). This information indicates that early selection for height might be useful on the average but not highly accurate for all individual trees. The fact that a few trees gain an advantage in height after the juvenile period indicates phenotypic variation in the pattern of growth with age, an observation which may be of value in tree breeding. LaFarge (1972) also determined correlations between ages 3, 5, and 15 years and concluded that height relationships for trees or families were not strong. Rust infection did not change much with age.

Genotypic Variation

Foresters are concerned with inheritance of growth from seed used in natural regeneration and forest tree nurseries, whether collected at random or purchased or collected from selected trees in natural stands or from stands converted to seed production areas. Workers in theoretical and applied tree breeding use inheritance data to indicate best sources of open- or control-pollinated seed of improved growth for use in creative breeding of new strains or to improve sources of commercial seed in seed orchards. Geneticists may use inheritance data for growth rate from phenotypically different or similar trees mated according to classical methods for studies of theoretical or applied forest genetics.

Thus, seed for studies of growth must be tested from a wide range of phenotypes for parents that are pollinated or mated differently to meet all the needs for information by foresters, tree breeders, and geneticists. Results are reflected by the choice of study design, age of trees when data are analyzed, and form in which results are presented. Growth differences indicated by height are very conservative because stem diameter also has an important influence on total volume per tree. Furthermore, survival of trees per acre and specific gravity of wood strongly influence dry weight yields in addition to growth of individual trees.

Results of studies in variation and inheritance of growth will be discussed on the basis of the mating design used, which is probably of the most widespread interest.

Half-Sibs of Random Parents

The first progeny test in which growth rate is mentioned was reported by Minckler (1942) in South Carolina, but the plots were subsequently lost by flooding. Among progeny of 105 maternal parents, the 10 families making the slowest growth to age 5 years averaged 5.6 feet, and those with the fastest growth 7.6 feet, or 36 percent greater height. There was no correlation of growth rate with percent survival. In Florida, significant differences of 10 to 20 percent in height growth at 3 years occurred among progenies of trees that had been selected for differences in stem form (Perry 1960a). Adjunct to a racial variation study in Georgia, seed of 11 maternal parents from southeast, middle, and northwest areas planted in middle Georgia showed a height superiority of the tallest over the shortest progeny of 17 to 31 percent after five growing seasons (Barber 1966). The slowest growing family of the slowest growing seed source averaged 8.4 feet in contrast to 12.0 feet, or 43 percent greater height, for the fastest growing family of the faster growing race. These figures indicate that the effects of racial selection and plus-tree selection may be cumulative. Rust infection of families was not correlated with height, and survival was very high; therefore, there was no loss of growth per unit area from an increase in minus traits. An indication of the importance of the maternal parent on growth is given by studies of drought resistance which showed a range in survival of families of 7 to 85 percent when selection was from trees on dry areas (van Buijtenen 1966b) and that there was a direct correlation between drought resistance of the parent and height growth of 1.5-year-old seedlings (Banks 1966). Early results of a large heritability study in Georgia showed a correlation of first- and second-year seedling heights with several growth characteristics of the maternal parent (fig. 108) (Stonecypher 1966). At 7 years greatest gains from mass selection were predicted as 26 percent for wood dry weight, 25 percent for wood volume, and 4 to 8 percent for rust resistance (Stonecypher *et al.* 1973).

Half-Sibs of Selected Parents

Open-pollinated progeny of trees selected for special traits, such as those for seed production areas or clones for seed orchards, have shown wide differences in growth of individual trees and yield of wood per acre. In Texas, progeny of four out of six maternal parents selected for good characteristics had progeny significantly better than the controls, and two progenies were significantly taller than the controls (Goddard *et al.* 1959). In Virginia, 7-year-old progeny of trees selected for growth and form varied from 12.0 feet to 15.9 feet in height, as well as in crown width (Trousdell *et al.* 1963). In South Carolina, at 5 years, seedlings from seed-production-area seed produced 17 to 27 percent more height growth when planted on two different soils (Easley 1963). Within a fast-growing family, cubic-foot volume of individual trees was 0.5 to 2.5 at 7.5 years, with no correlation of volume with wood specific gravity. Seed from seed production

Figure 108.—Control-pollinated progeny 6 months old illustrate striking differences in height growth attributable to parentage. (Cech *et al.* 1962)

areas has, in some studies, produced seedlings with about the same average growth as wild trees, but progenies are more uniform and there are wide differences in growth among progenies of individual trees in the seed-producing areas. In Texas (van Buijtenen 1969c), the 10 highest producing families from trees in seed production areas had 1.82 cords per acre per year, the controls 1.54 cords, and the 10 lowest producing families 1.14 cords for 10 years. The slowest growing individual family produced 0.90 cord per acre per year in contrast to a yield of 2.05 cords, or more than twice as much for the fastest growing family. In the eastern part of the loblolly pine range, open-pollinated seed of carefully selected maternal parents for seed orchard clones produced families that varied from 1.8 to 2.7 tons of dry wood per acre per year for 7 years when grown on an excellent site (Zobel *et al.* 1969). Trees for seed orchards are selected under a much more rigid index for growth than is possible in seed production areas and, also, they must rank high in as many as 10 or more additional traits.

Full-Sib Families

Differential growth rates are established at an early age among control-pollinated families and are quite large, as were those among open-pollinated families. When six males were crossed onto the same female, with all trees being selected as seed orchard clones, family yield of wood per acre per year varied from 1.5 to 2.8 tons, based on equal numbers of trees per acre (Zobel *et al.* 1969). The average yield was 2.2 tons per acre per year. Wood specific gravity was a factor, varying among families from 0.35 to 0.40, but it was not correlated with tree diameter. One of the faster growing families had wood with the same specific gravity (0.38) as the slowest growing family. In average height the families ranged from 27.6 to 31.1 feet, about 17 percent taller.

In Georgia, the best F_1 cross for height growth and wood yield produced the fastest growing F_2 progeny when measured at 2 years of age (Greene 1969). The range in height of 2-year-old F_2 families of 3- and 4-year parents was 6.6 to 9.1 feet, with a wide range in height within families.

Loblolly pine families varied 8 to 10 weeks in duration of growing season when grown at Raleigh, North Carolina (Woessner 1972a, 1972b). Seedling height varied widely among families from crosses among trees within a geographic area but not among trees from different geographic locations, based on measurements of 1-year-old seedlings. Wide phenotypic variation in growth period among individual trees has been observed and was discussed in the section on physiological and chemical differences among trees (Zahner and Whitmore 1960; Harkin 1962; Bassett 1966).

Selfed Families

As discussed in the section on seed production, loblolly pine can often be selfed, although it is normally outcrossed. Few studies have been made of selfing on various traits, but it is indicated that selfed families are more variable than outcrossed and, also, they vary in amount of inbreeding depression (Franklin 1969a; Greene *et al.* 1964).

Clones

Growth of loblolly pine clones has been given little attention, but growth rate the second year in young trees in one study showed a heritability of 86 percent (Brown 1968).

Correlation With Other Traits

Traits inversely correlated with tree or stand growth will reduce yield or quality as well as net returns from management. At present, few obstacles, such as poor wood quality, poor stem form, low resistance to pests, or low planting survival, are apparent in breeding for improved growth rate. There are indications that increased vigor of growth may even improve field survival and early growth. It must be pointed out, however, that strains with exceptionally fast growth—twice the volume growth of average loblolly pine—have not yet been fully tested in large-scale forest management on many sites. Additional information about correlation among traits will be given in the following section on tree-to-tree variation in stem and crown form, resistance to pests, and wood quality.

There is little information available about the cumulative effects of racial plus individual tree selection for growth rate and disease resistance. For certain specific geographic locations, but not all, the combined effect of selection on total wood yield might be large.

Environmental Effects on Growth

In his monograph, Wahlenberg (1960) discusses at length the problem of regulating growth and tree quality under all the complex of factors facing the silviculturist. In fact, many problems in intensive silviculture remain unsolved because of the extremely large number of variables involved.

Outcrossing produces the most vigorous progeny, and selfing depresses growth but has not been tested in combination with all other mating schemes. Thus, genetic factors strongly influence growth and are not overcome by environmental factors. Growth rates seem to be established in nursery beds a year or so following planting and indicate the performance to be expected in following years, but predictions for a wide range in years may be less accurate. If juvenile and intermediate growth stages are highly correlated, progeny testing to screen families for growth rate is facilitated. For accurate comparisons of growth among individual progenies, longer test periods might be necessary.

Phenotypic variation in stem volume is extremely wide in both natural and planted stands, and selection should be concentrated on trees with twice or higher superiority. Because volume ranges are also extremely wide among half and full sibs, mating phenotypically similar parents does not create uniform families for volume growth.

Growth and yield variation among loblolly pine trees has been shown to be a very complex subject which depends on photosynthetic efficiency, length of growing season, vigor in individual trees, field survival, resistance to drought, resistance to pests, and specific gravity of wood in stands. Selection of parents has improved growth of young trees, but phenotypically similar trees produce offspring differing greatly in wood production. It is not clear whether improved selection procedures will increase accuracy of genotype prediction for inherent growth rate or reliance will always have to be placed on progeny tests to indicate combining ability. Theoretically, progeny yields of nearly twice the average might be possible from selecting and crossing superior phenotypes followed by progeny testing to indicate the best combinations of parents.

STEM AND CROWN FORM

Loblolly pine is one of the fastest growing species of the southern pine group widely known for their high volume production, but it has less desirable form in general than certain other species. The branches tend to be long and fairly large in diameter. Some trees in forest stands may have crooked stems, high stem taper, complete or partial forks in the stems, widely varying branch angle, and poor natural pruning, while other trees have exceptionally good combinations of good traits (figures 109 and 110).

In spite of the numerous environmental factors contributing to phenotypic variation in form, much of the bad form has a genetic basis, as indicated by progeny tests. Many of the traits under study are those important in clonal selection for seed orchards and are included in selection criteria (Cech 1959;

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Figure 109.—Open-grown loblolly pine that exhibits poor natural pruning, high stem taper, and stem forking. The strongly ascending branches tend to persist for a long time. Horizontal branching is preferable.

Photo courtesy of North Carolina State University

Figure 110.—One of the highest grade loblolly pines found in selection work for commercial seed orchards. This tree on lands of the Weyerhaeuser Company has high volume, straight stem, good natural pruning, and small-diameter branches.

Dorman 1952; Zarger 1958).

Foresters have been aware of the influence of stand condition on form and growth because this is important in comparisons of silvicultural treatments. General relationships do not apply to specific clones, however, as grafts in seed orchards illustrate that open-grown trees are remarkably uniform and retain the small-branch and slender-crown characteristics of the ortet (fig. 111). Heritabilities of branch characteristics and form are strong in clones, as indicated by estimates in the order of 70 to 80 percent at the end of the second year (Brown 1968).

Wind-pollinated progeny reflect the good and bad branch-length characteristics of the maternal parent, as indicated by studies in Virginia (Trousdell *et al.* 1963) and Texas (Goddard *et al.* 1959). Fast-growing individual offspring may have relatively short branches. Progeny have small branches and knots when the maternal parents have these traits (Von Wedel *et al.* 1967). Progenies of four well-formed families averaged 19 percent smaller branch diameter than did the comparison trees.

Since loblolly pine is used for pulpwood, lumber, poles, and veneer, stem straightness is an important quality factor. Probably the first evidences of the inheritance of stem straightness were observations in Australia that trees from open-pollinated seedling stock of good parent trees had about twice the percentage of well-formed stems, and control-pollinated offspring produced up to four times as many good stems as trees from general seed collections (Queensland State Forest Service 1948). In Florida, controlled pollinations were made among crooked trees and among straight trees (Perry 1960a). At 2 years of age progenies from crosses between straight trees contained four times as many straight seedlings as progeny of crooked parents, and this ratio was maintained to age 7 (fig. 112) (Goddard and Strickland 1964). It was concluded that there were both general and specific combining abilities for stem straightness. It will be helpful in progeny testing if all stem characteristics can be rated at an early age. Because stem crook may influence the amount of compression wood in stems, methods have been studied for measuring it, but subjective rating schemes may be nearly as successful as accurate measurement in categorizing tree straightness (Shelbourne and Namkoong 1966; Shelbourne 1967).

In Australia on fast-growing trees, spiral fluting occurs on some stems (Newman 1956), about 5 percent of the progeny from open-pollination of one tree showing this condition. Spiral growth form is so common in loblolly pine stems that it is difficult to find perfectly straight trees, although from a distance they may seem to have good form. In studies of compression wood there were statistically significant differences between the volume of compression wood in trees with different degrees of corkscrew or spiral form. Gerischer and Kromhout (1964) did not report whether spiral grain in loblolly pine was associated with spiral form of the tree stem.

Morphological characteristics of seedlings in nursery beds are not suitable for predicting form in subsequent years (Brown *et al.* 1961; Bilan 1966; Grigsby 1971).

Although much remains to be learned about the inheritance of forking, stem taper, and natural pruning, it would be unwise to assume these were not under genetic control in applied breeding work. Progeny tests of seed orchard clones indicate that the selection criteria for form characteristics were reasonable, and substantial improvement is being made in form without loss in other important traits.

Probably most of the traits of bad stem and crown form can be bred out of loblolly pine in one or a few generations. After strains with good form are produced, as indicated by families in current prog-

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Figure 111.—Good-form grafted clone of loblolly pine shows short branches similar to those of the ortet. There is close resemblance among individual ramets of the clone in stem form, height growth, and branch angle with the trunk.

eny tests, there might be little opportunity for further improvement. Tree breeders can concentrate on other traits, such as growth rate, that might be improved with each successive generation.

RESISTANCE TO PESTS

In *Loblolly Pine*, Wahlenberg (1960) lists 46 insects and 46 fungi that are economically or potentially important on loblolly pine trees or wood. In geographic areas where a pest is important, resistance must be evaluated with other traits, although increasing number of traits increases complexity of breeding. Creating strains resistant to any particular pest is usually a separate and distinct problem.

Southern Fusiform Rust

This most important pest of loblolly pine is highly destructive on many hundreds of thousands of acres. The disease can be controlled by sprays in tree nurseries but not in the field, and in areas of high incidence nearly all the trees may be infected. Infection not only reduces stocking, but infected trees that do not die may have reduced growth or stem quality. Thus, planting additional trees per acre in certain locations will not compensate for all losses to the disease. Fusiform rust is important only on loblolly and slash pines among the southern pines, and it is most severe in a band extending from northeast Georgia toward the southwest into western Louisiana. Infection rate decreases with distance on either side of the band until it is not a problem in silviculture or breeding (McCulley 1950). A recent survey of rust infection in 8- to 12-year-old plantations shows a higher incidence than was found in earlier surveys (Phelps 1973).

Phenotypic Variation in Susceptibility to Infection

Rust spores carried by the wind may be distributed over large areas. In most stands there are

Figure 112.—Seven-year-old full sibs (left) of straight parents and crooked parents (right) show wide variation in percent of trees with crooked stems. (Goddard and Strickland 1964)

disease-free trees that appear to have escaped infection or have resisted the disease for many years. Racial differences in resistance are indicated, with trees from Texas being notably free of rust when planted in middle Georgia, an area of high incidence (Wells and Wakeley 1966). Selection criteria for most seed orchards specify that parent trees be disease free. This has proved useful, but rigid selection for resistance is difficult because to be effective it should be done in heavily infected stands. Under such conditions there may be a scarcity of trees with the best additional traits required of plus trees. Progeny testing of seed orchard clones permits screening for resistance to rust as well as for other traits when low correlation between phenotype and genotype is caused by selecting parents from disease-free areas.

Genotypic Variation in Susceptibility to Infection

Of great value to applied breeding projects, progeny tests of seed orchard clones from both open- and control-pollination show wide variation among families in rust resistance (Woessner 1965). Also, infection rate varies widely among open-

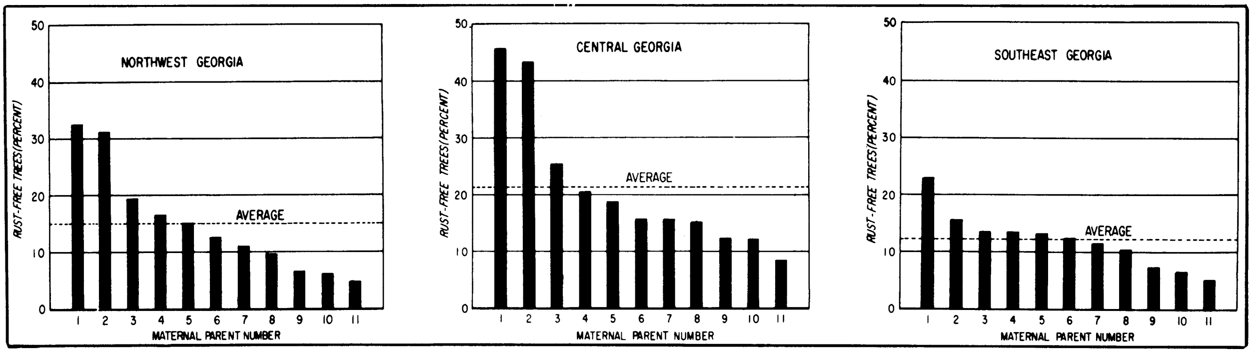

Figure 113.—Rust infection differs among races, but the differences among progeny of maternal parents within race are much greater. Open-pollinated progeny of 11 maternal parents from each of three locations in Georgia were planted in central Georgia. (Barber 1966)

pollinated families of trees chosen at random in different areas, although there are differences attributable to location also (fig. 113) (Barber 1966). A large heritability study in southwestern Georgia, using parental stock from a wild population, showed heritabilities of rust resistance of 0.65 to 0.85, based on family averages, variation from 17.3 to 100 percent infection among families, and positive correlation for resistance among parents and offspring (fig. 114) (Kinloch and Stonecypher 1969). Heritability estimates were remarkably high on all sites tested, although infection rate varied widely among sites. Variation in the pathogen has been studied, as well as variation to susceptibility in the host. Fusiform rust infection varied from 0 to 92 percent among the families of 10 seed orchard clones. Infection in full sibs was correlated with that of the parental clone (Kinloch and Zoerb 1971). When planted in central Georgia, an area of high rust incidence, open-pollinated progenies of two plus trees at Crossett, Arkansas, had 38.5 and 100.0 percent rust-free stems and 9.81 and 12.39 cubic feet of wood volume per plot, in contrast to three progenies from northwestern Georgia that had 5.7 to 14.6 percent rust-free stems and 4.23 to 4.60 cubic feet of volume per plot. The Arkansas trees had higher survival (91.0 and 97.0 percent) than Georgia trees (32.9 to 67.1 percent), and this contributed to differences in volume growth also (Sluder 1973). An open-pollinated progeny test in eastern South Carolina, established to determine wood quality relationships, had a range in infection among the 34 families of 3.6 percent for the least susceptible family to 62.9 percent for the most susceptible family (Matziris and Zobel 1973). Average infection for the 34 families was 25.6 percent.

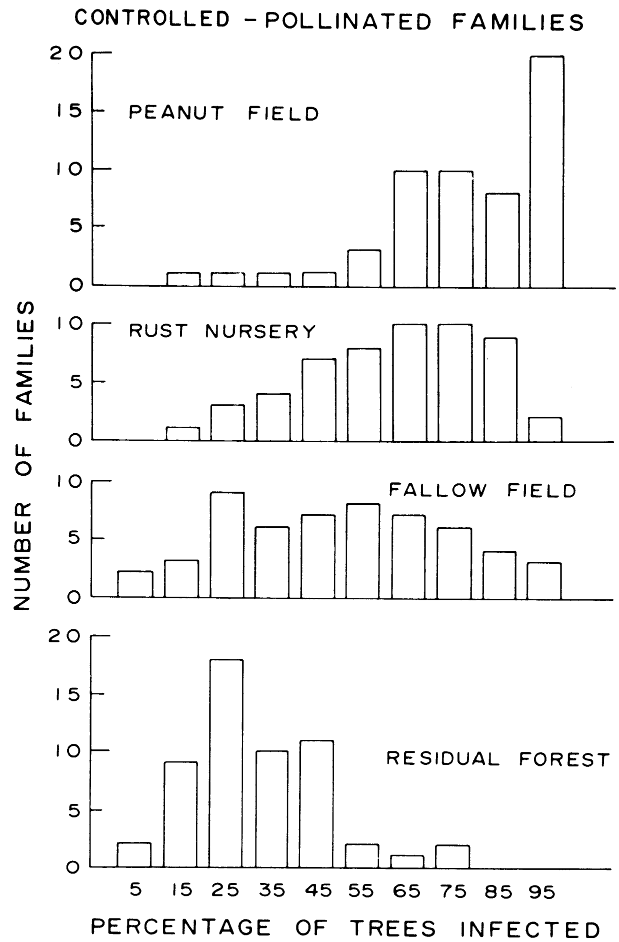

Figure 114.—Percentage of loblolly pine trees infected by fusiform rust varies widely among control-pollinated families and the local sites in southwest Georgia in which they were planted. Susceptible or 'resistant families retained their relative ranking regardless of the average infection rate for the planting location. (Kinloch and Stonecypher 1969)

Relation of Infection to Growth Rate

High incidence of fusiform rust infection in vigorous stands on old fields or in stands that had been fertilized or cultivated had led to fears, summarized from the literature by Goggans (1957), that high growth vigor and infection rate were directly correlated. This relationship has been given special attention in nursery selection studies (Barber and VanHaverbeke 1961), one-parent progeny tests with randomly selected maternal parents (Barber 1966), and both one- and two-parent progeny tests with seed orchard clones (Woessner 1965). From these it must be concluded that infection is only weakly correlated or not related at all to growth rate. Extensive studies on this relationship and possible relations to cultural techniques and fertilizers are still underway. For example, cultivation and fertilization increased height growth in loblolly pine but not incidence of infection (Dinus and Schmidtling 1971).

At present it seems there is no need to sacrifice volume growth to gain resistance to rust. In certain locations in the South, breeding resistant strains, as is being done in industrial seed orchard programs, will result in greatly increased wood volume production per acre.

Minor Diseases

Loblolly pine is slightly susceptible to littleleaf disease, a serious enemy of shortleaf pine at certain geographic locations, but resistance to littleleaf is not a factor in loblolly breeding programs. Indeed, loblolly pine is recommended as a substitute for shortleaf pine on littleleaf sites because of the low risk of loss. Since annosus root rot may become a serious pest of loblolly, studies of resistance are being made. Comandra blister rust occurs in many loblolly pine plantations in Alabama and Tennessee (Cordell and Knighten 1969), but variation among trees in susceptibility has not been determined.

In Louisiana nurseries, seedlings varied in percent with mycorrhizae throughout all grades, and survival of planted seedlings improved in all grades if mycorrhizae were present (Shoulders and Jorgensen 1969).

See section on minor diseases of slash pine for resistance to hard pine gray blight (Kraus and Hunt 1971).

Apparent differences among full-sib families of loblolly pine in susceptibility to *Fomes annosus* were lacking in greenhouse test inoculations (Kuhlman 1972). None of the families showed immunity.

Resistance to Diseases in Species Hybrids

Characteristics of individual parent trees that hybridize with other pine species are given in the chapter on hybrids. The importance of the individual tree is established particularly for fusiform rust infection or resistance in hybrids with shortleaf pine.

Insects

Insects take a vast toll of wood volume in loblolly pine, but outbreaks of pests are variable in time and place. Following rather extensive tests in Texas and Louisiana on resistance to southern pine beetles, there appear to be resistant genotypes. Also, a relationship has appeared between attack by certain insects and inherent differences among trees in rate of oleoresin flow. In a loblolly pine plantation in Tennessee, trees with high oleoresin flow repulsed induced attacks by *Ips avulsus*, and all trees with a measurable flow of oleoresin repulsed attacks by *Ips grandicollis* (Mason 1967). Oleoresin flow was found to vary widely among 8-year-old clones in a loblolly pine seed orchard (Mason 1969). It has been speculated that if oleoresin flow is an indicator of resistance of pines to some bark beetles, then the resistance of low-flowing trees may be significantly lowered during short drought periods, whereas the resistance of high-flowing trees is not seriously affected as long as the minimum level of oleoresin flow is above the threshold needed to repulse attack (Mason 1971). Thus, resistance to certain insects may be affected by inherent traits and inherent traits plus environmental factors.

Tip moth injury to young trees is almost universal, but the effect on total height growth is minor.

In two loblolly pine seed orchards, Sartor and Neel (1971) classified 14 clones resistant and 5 susceptible to coneworms (*Dioryctria amatella* Hulst).

In summary, wide variation among trees has been established or strongly indicated for important pests. Breeding for resistance to fusiform will increase wood yields, but combining resistance with other good traits does not appear to be difficult. For instance, strains resistant to fusiform rust seem possible without sacrificing volume growth. Much additional work on intraspecific variation in resistance to insect and disease pests other than fusiform rust is needed as a basis for intensive breeding.

Although immunity to diseases and insects may be desirable, the forester can live with something less. If he concentrates on carrying out stand improvement measures solely to reduce insect and disease losses, he adds to other problems regarding growth and quality, and he greatly complicates stand treatment.

SEED AND SEED PRODUCTION

The great importance given loblolly pine in tree breeding programs focuses attention on variation and inheritance in several phases of seed production. Age when first flowers are produced, time when conelets mature in the spring, and the volume of seed produced are prime considerations. Flowering in general was discussed earlier in the chapter on sexual reproduction.

In seed production areas, phenotypes selected for good growth and form vary so widely in seed production that collection is not feasible from certain low producers (VanHaverbeke and Barber 1964). It was estimated that limiting collection to trees with 100 cones or more would have required collection from 29 percent of the trees but would have harvested 65 percent of the expected yield. Average number of seeds per cone varied also, averaging 89 with a range from 23 to 135 among individual trees. Wide variation occurred in number of cones produced on trees of similar diameters and heights.

Because phenotypic variation among trees in cone production is a factor in selection of seed orchard clonal stock, some otherwise desirable trees are rejected because of poor seed production history. Rating for seed production is included in tree grading systems for some seed orchard projects (Cech 1959).

Wide variation in seed-producing characteristics of grafted clones illustrates the strong effect of inherent factors (Bergman 1968; Zoerb 1969). It was observed in an 8-year-old seed orchard that average yield per tree among various clones ranged from one for the poorest clone to 268 cones for the heaviest producing clone. Pollen production also varied widely; in the fall clones may vary as much as 50 days in cone ripening and 46 days for opening, but in late clones only 10 days passed. In the spring, maximum receptivity for pollination may occur in some clones before it starts in others (Wasser 1967), which contributes to variation in seed production and unequal crossing among clones. Unequal seed production among clones is undesirable if the poorer clones are the high producers. Seed size and cone length may vary widely among seed orchard clones (Bergman 1968).

Loblolly pine seed have a high degree of dormancy and require stratification at the nursery, but there is some variation among trees in number of seed that germinate without treatment (McLemore and Barnett 1966).

Loblolly pine may become sexually mature at 10 to 15 years of age, but individual seedlings sometimes produce a few conelets at 3 or 4 years (Greene and Porterfield 1962). Artificial crosses among these young trees produced seed of good germination, with progeny that also produced conelets at an early age (Greene 1966a, 1969).

BARK THICKNESS

Pine bark is largely a waste product in utilization but an important protective coating in living trees. Variation and inheritance of bark thickness and volume have been little studied, but Pederick (1970) found considerable variation from tree to tree and among families of young trees. The combined estimate of heritability from several planting tests was 0.60. Ten-year-old trees from the Piedmont had a proportion of bark to wood volume of about 52 percent, compared with about 31 percent for South Carolina Coastal Plain trees, which may indicate some genetic differences among areas.

WOOD PROPERTIES

The heavy, strong wood of loblolly pine is widely used, and thus requirements for various products have influenced the type of studies made in variation and inheritance among trees. Tree stems are sold for poles, piling, or posts. Stems may be divided into parts such as timbers, lumber, or veneer, or further reduced to flakes for flakeboard or to fibers for paper and paperboard of different kinds.

Studies of loblolly pine wood date from Johnson and Roth (1896), who worked on mechanical and physical characteristics, and Mohr (1897), who wrote in detail about the commercial pines of the southern United States, including a discussion of the structure of the wood. In the book *Loblolly Pine*, Wahlenberg (1960) discusses properties and uses in considerable detail.

Forest tree breeding research has concentrated on refining broad relationships already established by sampling stand and individual trees to determine correlation of properties with tree age, between properties in various parts of the tree, and between each of various individual properties. These basic studies have made it possible to estimate wood yield and quality in studies of trees growing in different environments, trees of different ages, trees of similar age growing in the same environment (such as plantations), and trees used in parent and offspring relationships or inheritance studies.

Relationships between growth rate and wood quality factors for the whole tree and between certain individual properties within the tree are of special importance in inventive breeding to create new strains because of the need to avoid improving one or more traits at the expense of other traits. Also, when the effect of various traits is additive, the breeder should estimate the total gain and not just that from one trait. In classical studies of inheritance or heritability, it may not be possible to include all the economically important traits and keep the study size within manageable limits.

Techniques for Studying Wood Properties

In the early stages of breeding research with loblolly pine, many relationships of wood characteristics with position in the tree were investigated. The diagram presented for longleaf pine by Johnson and Roth (1896) showed the relationship of specific gravity with ring number and height in the tree (fig. 115). Lodewick (1933) pointed out the change in wood of the inner rings compared with the outer, and he concluded that the time of change was a characteristic of the tree and not related to width of annual ring. Other summerwood relationships were studied.

To avoid destructive sampling, the correlation of wood properties at breast height with the average for the whole tree was examined and found to be usable (Zobel 1956; Zobel, Henson, and Webb 1960; Christopher and Wahlgren 1964). Also, properties of the outer rings are correlated with those of inner rings for specific gravity (Zobel and Rhodes 1956) and tracheid length (Kramer 1957; Wheeler *et al.* 1966).

The correlation of tracheid length in the branches of trees with that of the trunk is high (Greene 1966b), and tracheid lengths vary within the annual ring (Jackson and Morse 1965a).

Where estimates must be made of wood specific gravity from increment cores, it is desirable to extract the resins to increase accuracy (Taras and Saucier 1967).

Compression wood is generally undesirable in many wood products, but causes are not fully understood. However, significant differences in the volume of visible compression wood occur in loblolly pines with different degrees of corkscrew or spiral growth form of the tree trunk (Zobel and Haught 1962). Percentage of merchantable volume composed of compression wood were: in essentially straight trees 6 percent; in intermediate or average trees 9 percent; in crooked trees 16 percent; and in one excessively crooked tree 67 percent. In South Africa (Gerischer and Kromhout 1964), the cumulative mean of spirality in loblolly pine decreased outward from the pith, and the occurrence of right-handed spirality was 50 percent, the same as in slash pine. In 5-year-old loblolly pine used in inheritance studies, compression wood percent showed low positive genetic and phenotypic correlations with height (0.37 and 0.21), diameter (0.38 and 0.26), and volume (0.74 and 0.40) (Shelbourne *et al.* 1969). Fairly low negative correlations were found with specific gravity (−0.29 and −0.22).

Heartwood may first appear in trees 14 to 23 years old, but there is little volume of heartwood in trees under 30 years (MacKinney and Chaiken 1935;

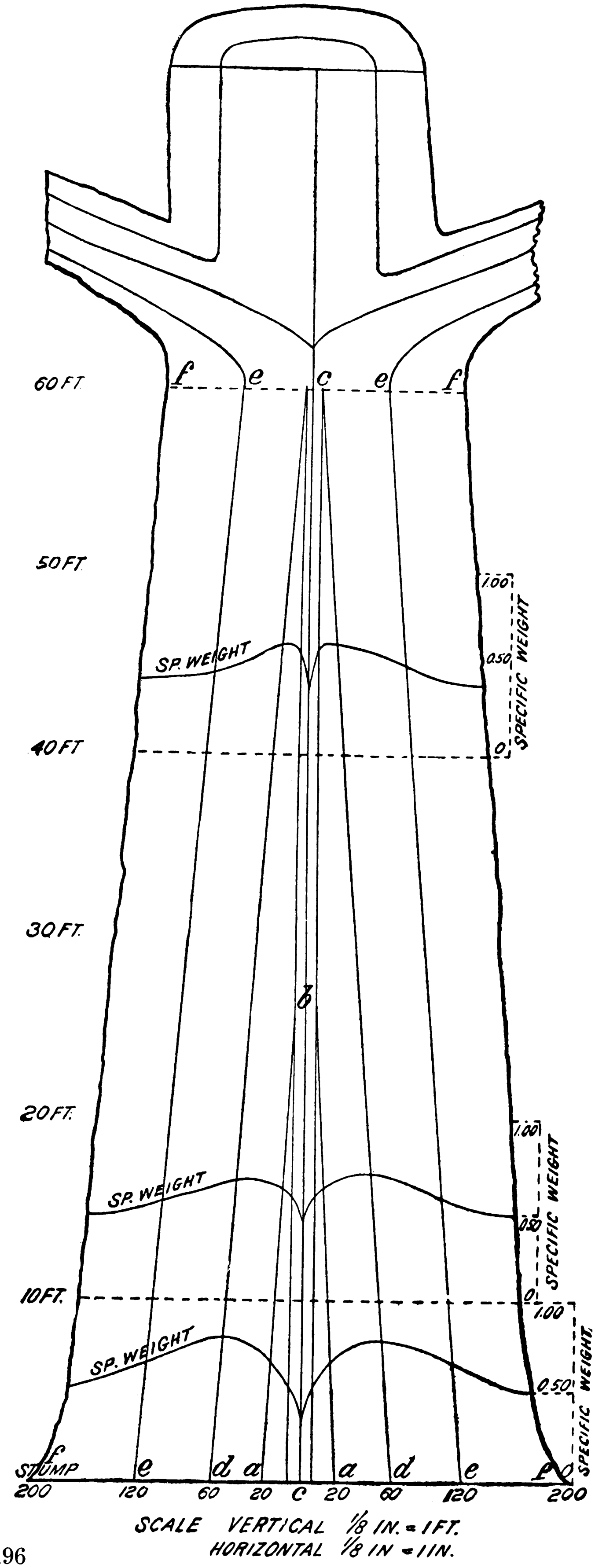

Figure 115.—Schematic section through the stem of longleaf pine, showing variation of specific gravity, or weight, with height, diameter and age at 20 (aba), 60 (dcd), 120 (eeee), 200 (ffff) years. (Johnson and Roth 1896)

Zobel *et al.* 1959). In trees over 30 years old, heartwood content increases rapidly, the amount varying greatly from tree to tree (fig. 116). Certain trees in the 65- to 70-year age class had very little heartwood, but, conversely, no young trees under 30 years had more than 5 percent and most had none. Also, heartwood varied with height in the tree trunk. Formation of heartwood appeared to be at random, inasmuch as it could not be correlated with several environmental factors tested.

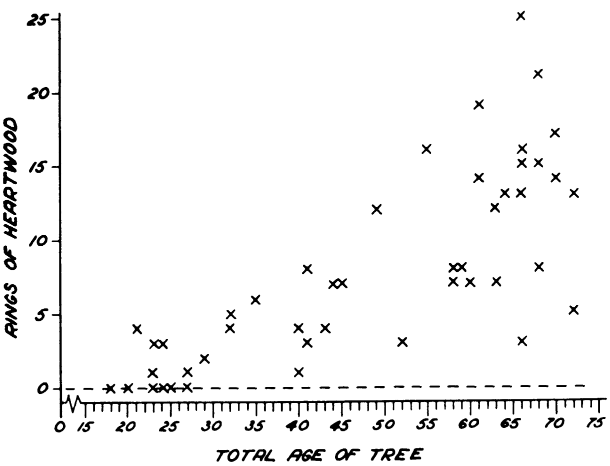

Figure 116.—"Chemical heartwood" for loblolly pine is not in evidence below 20 years of age, and there is very little present in trees younger than 30 to 40 years. After 30 years, heartwood on the average increases with age, but there is wide variation among individual trees. (Zobel *et al.* 1959)

The proportion of latewood increases from the pith outward but decreases from the ground level to the top of the tree in the same annual ring. Latewood may be formed at the ground level starting in June but not until early September near the tree top (Young 1952).

Moisture content in percent increases with height above ground in loblolly pine regardless of whether the tree has high or low content (Zobel, Matthias, Roberds, and Kellison 1967). For example, a tree in the 25-year age class with low average moisture content may have 70-percent moisture in the pulpwood bolt at the ground and 120 percent for the ninth bolt above ground, with percentage based on weight of dry wood (fig. 117).

Cellulose yield of the wood at breast height, like wood specific gravity, has been shown to give a very close estimate of the average yield of the tree (Zobel and McElwee 1958b; Zobel, Henson, and Webb 1960).

Fibril angle in tracheids has an important effect on wood shrinkage and fiber properties and must be included in studies of wood quality. In the summerwood portion of annual rings in 10- to 15-year-old trees, fibril angle increased with width of the ring at breast height and at crown height but at a lower rate at crown height (fig. 118) (Pillow *et al.* 1953).

Among 65 trees from the Coastal Plain of South Carolina, highly significant positive correlations were obtained between tree age and specific gravity, percent summerwood, fiber length, cell-wall thickness, pulp yield, and zero-span tensile strength. But significant negative correlations were obtained between age and percentage of juvenile wood, lignin, and alcohol-benzene extractives (Einspahr, Peckham, and Mathes 1964). These relationships are important in pulping. Also, there were differences in the degree of relationships among factors but not in kind for trees from the Piedmont of North Carolina, in contrast to trees from the Coastal Plain.

Establishment of a wood-properties relationship between various parts of individual trees has been of great benefit in studies of phenotypic variation, selection of plus trees, and investigations of parent and offspring relationships. Also, they have been useful in progeny testing by showing that results based on properties of young trees might be reliable indicators of the characteristics of mature trees, thus making possible a shortening of the generation time in sustained breeding projects. The precision of certain estimates of wood properties can be increased by increasing the number of samples or adding other variables, such as age, diameter, or tree height, if very high precision is desired.

The relationships among wood properties in various parts of the tree have been estimated from samples of numerous trees; to be sure, there is variation among trees in the relationships that will contribute to error, but magnitude of possible error usually can be estimated. Information in the following sections on variation among trees will be helpful in estimating the amount of error.

Phenotypic Variation

The variability of each wood property is influenced by both genetic and environmental factors; therefore, when the environment is relatively constant, value differences closely reflect inherent wood qualities. Some knowledge of tree-to-tree variation in natural stands and plantations has helped us to establish useful guides for studies of the relationship of various wood properties to each other, to quality of products, and to characteristics of offspring. These studies are valuable because of the high economic values of wood quality traits.

Specific gravity of mature loblolly pine wood varies from 0.40 to 0.68 among trees under widely differing environments, regardless of rate of growth or age (fig. 119) (Kramer 1957; Zobel and

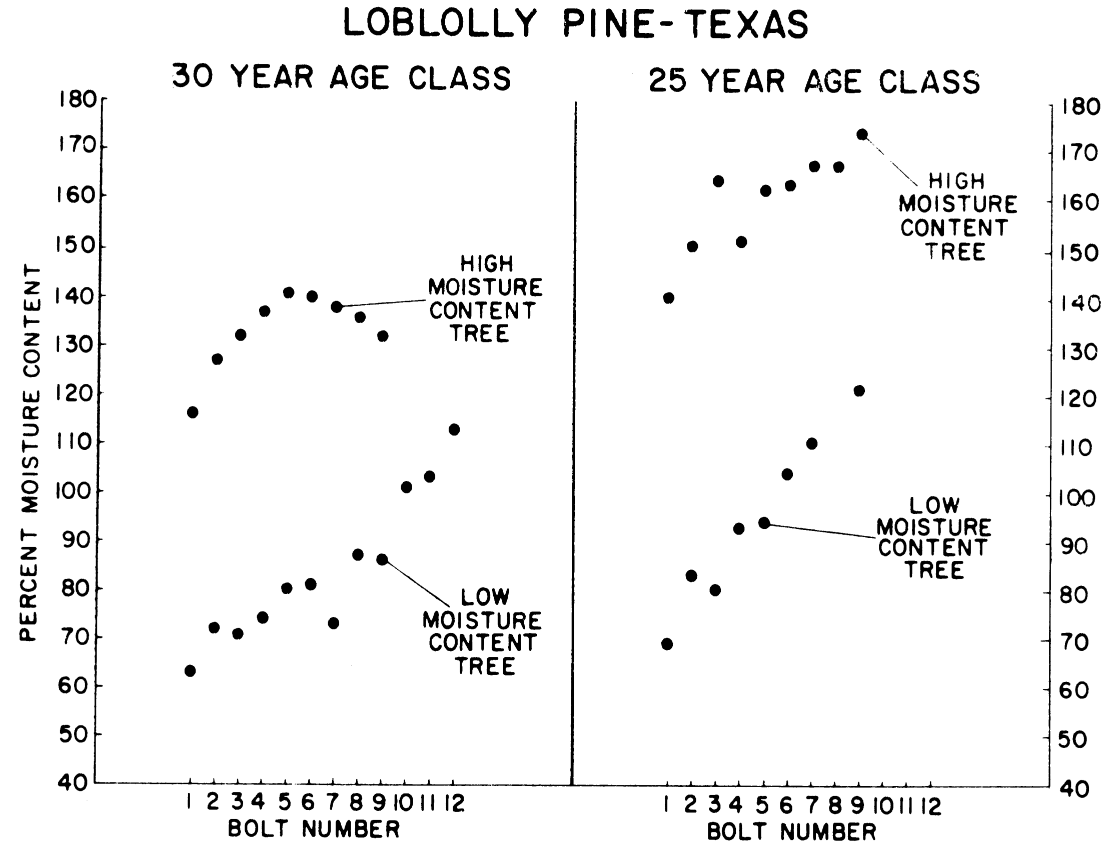

Figure 117.—Moisture content of the wood varies widely among individual loblolly pine trees, but it generally follows the same pattern of increasing from the first pulpwood bolt at the base of the tree through successive bolts above ground, as shown by two trees in two different age classes in Texas. (Zobel, Matthias, Roberds, and Kellison 1967)

McElwee 1958a; Zobel, Thorbjornsen, and Henson 1960).

Tracheid length follows different patterns, varying widely among trees (Kramer 1957; Zobel, Thorbjornsen, and Henson 1960); in juvenile wood it ranges from 2.93 mm to 3.78 mm and in mature wood 4.00 mm to 4.97 mm (Wheeler *et al.* 1966). In Kramer's study with trees 65 to 69 years old, tracheid length increased rapidly with ring number from the pith and then became constant for most trees, but for certain individuals it kept increasing as the tree grew older. In one tree, fiber length decreased with age.

Loblolly pine and slash pine in South Africa had about one-half of the trees with right-hand and one-half with left-hand spirality, while in similar environments *Pinus patula* had predominantly left-hand spiral. *Pinus patula* also had a higher degree of spirality than loblolly (Gerischer and Kromhout 1964). In loblolly pine the decrease in average degree of spiral from the pith to the outer ring was slightly more than in slash pine but not so great as in *P. patula* (fig. 120). Among 47 loblolly pine trees examined, spirality in the second ring from the pith ranged from ¼° to 6°. There were two trees with spirality of ¼° and three with ½°, while the average was 2.25°.

In one study, tree-to-tree variations in both water-resistant carbohydrate and alpha-cellulose were considered large, with a spread of 7 to 13 percent (fig. 121) (Zobel and McElwee 1958b; Zobel *et al.* 1959).

Extractives content of 94 loblolly pine increment cores over a four-state area averaged 6.50 ± 5.37 percent, or a coefficient of variation of 83 percent. This was a larger variation than found in slash, longleaf, or shortleaf pines, but average extractives content did not vary significantly among the four species (Taras and Saucier 1967). In a natural even-aged old-field stand, 23 trees averaged 8.33 percent extractives content, with a standard deviation of 2.37 percent and a range among individual trees of 5.2 to 14.3 percent (van Buijtenen, Zobel, and Joranson 1961).

In an important study van Buijtenen, Zobel, and Joranson (1961) sampled 10 physical and chemical characteristics of 24 trees from a natural stand and computed 31 correlation coefficients among them.

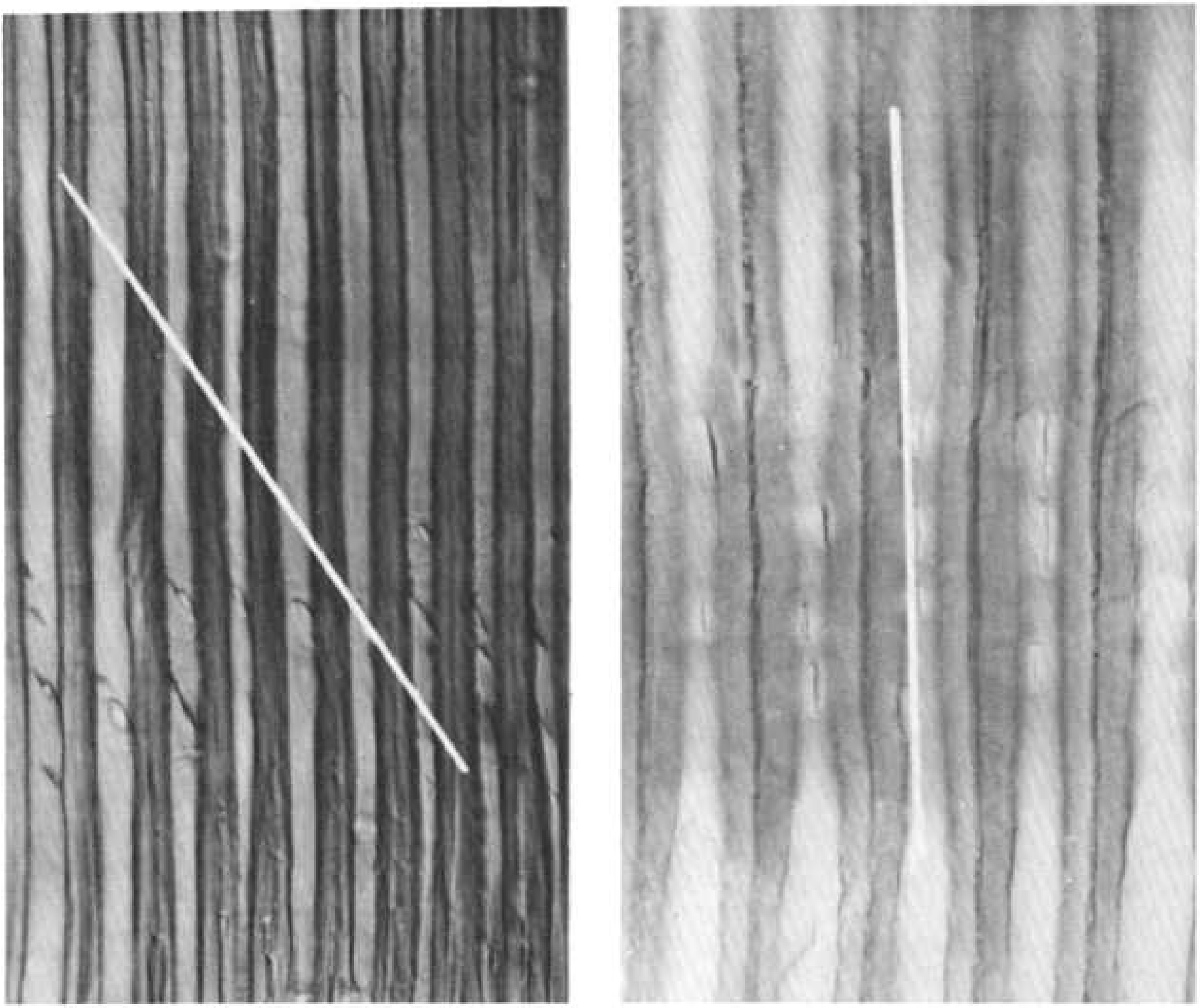

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Figure 118.—In loblolly pine, fibril angle in tracheids generally increases with width of the annual ring, but there are important differences among trees. Large fibril angles (left) and small fibril angles (right) in normal summerwood affect amount of shrinkage in drying wood and properties important in pulping. (Pillow *et al.* 1953)

In addition, handsheets were prepared from the pulp and several properties tested. Of the factors influencing zero-span tensile strength of paper, the strongest influence was exerted by fiber length, specific gravity, alpha-cellulose content, and water-resistant carbohydrates. Of the chemical properties, differences in percent lignin, percent alpha-cellulose, and percent extractives all contribute to differences in pulp yield. The amount of variation from tree to tree was outstanding.

In the paper made from wood of four trees selected for high specific gravity with short or long fibers and for low specific gravity with short or long fibers, it was found that (except for yield) at least 93 percent of the variation of many paper properties could be accounted for in terms of fiber morphology (Barefoot *et al.* 1964). Of the fiber dimensions, summerwood cell-wall thickness was the best single predictor of paper properties. In general, fiber characteristics associated with wood density were predominant in determining paper properties of the pulping fractions examined.

Handsheets of paper made from trees with high specific gravity had lower apparent density, indicating the thick-walled summerwood and compression wood fibers were not collapsing, with the result that open-textured, bulky sheets of low apparent density were produced (Einspahr *et al.* 1969). For the 10-year-old trees selected for extremes of wood specific gravity, increases in specific gravity of the wood were accompanied by increases in tearing strength and reduction in burst and tensile strength in paper.

Kraft paper made from 50 trees varied among trees but not between a group of trees selected for seed orchards and control trees (van Buijtenen,

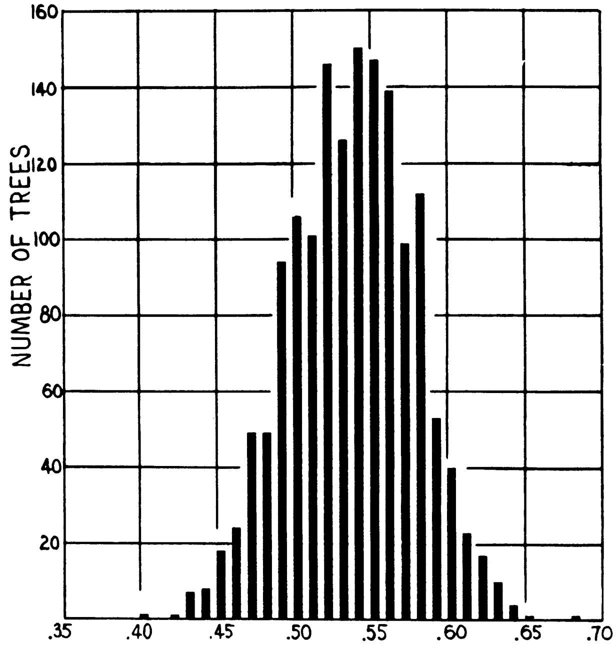

Figure 119.—Wood specific gravity is one of the most important properties of pine wood, and it varies over about the same range (0.40 to 0.65) in different stands, geographic areas, and trees of different growth rate. (Zobel and McElwee 1958a)

Joranson, and MacLaurin 1961). Standard deviations varied widely among 11 wood properties.

Phenotypic variation has proved to be wide for those morphological and chemical traits of loblolly pine that are important in pulping. The magnitude of variation and the correlations among traits are therefore important factors in studies of inheritance and evaluation of individual offspring and family means.

Genotypic Variation

Most progeny tests being fairly young, results are based largely on juvenile growth. However, the correlation of outer wood with juvenile wood is high enough so that early tests are indicative of genetic control.

Analyses of wood property relationships may include correlations with various individual properties and also with growth of individual trees and with volume yield per acre. This permits estimates of the combined effect of wood quality and volume yield, which is of obvious importance in forest management.

Although a wide range of results are reported in studies of genetic factors in wood quality, they generally are in fairly good agreement. A large proportion of the tree-to-tree phenotypic variation shows as differences among families of offspring. How-

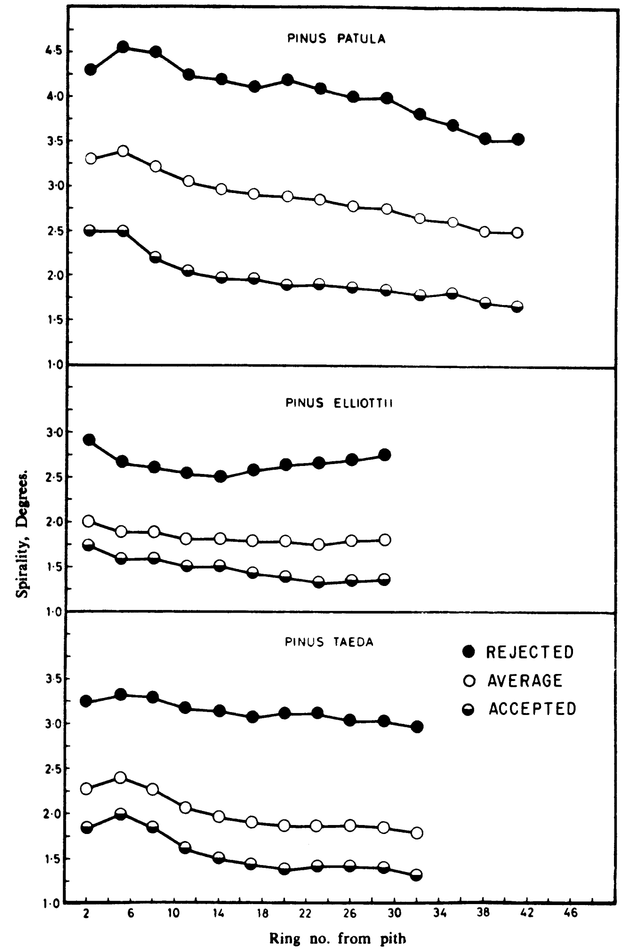

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Figure 120.—Average spirality of wood grain, either right-hand or left-hand, for all trees sampled. Note the wide difference separating trees accepted for breeding and those rejected. (Gerischer and Kromhout 1964)

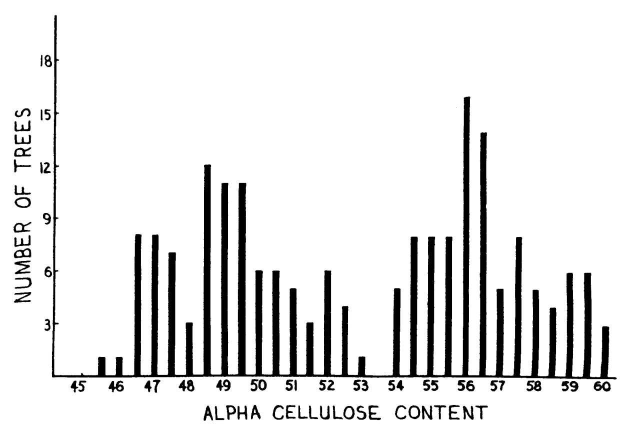

Figure 121.—Variation is always wide in cellulose content among even-aged trees growing on the same site. Left, core wood; right, outer wood. (Zobel *et al.* 1959)

ever, there may be important differences among progeny of phenotypically similar parent trees.

Specific Gravity

For trees 7.0 to 7.5 years old in plantations on three sites, wood specific gravity was 0.38 in two and 0.39 in the third (Zobel *et al.* 1969). A total of 43 open-pollinated families of trees chosen for seed orchards were involved, and family means varied widely. For six control-pollinated families with a common maternal parent, specific gravity averaged 0.38, with a range among families from 0.35 to 0.40. Moisture content averaged 143 percent, with a range among families from 133 to 150. Tracheid length in the last annual ring averaged 3.13 mm, with a range among families from 2.93 to 3.37 mm. Cords of wood produced per acre per year averaged 2.3 cords, with a range from 1.6 to 2.9 cords, and tons per acre per year averaged 2.2, with a range of 1.5 to 2.8 tons.

In this study by Zobel *et al.* (1969), there was no correlation between family means for growth rate in cords per acre per year and wood specific gravity, although the range in values was fairly wide (fig. 122). Also, for trees within a family, growth in cubic feet was not correlated with specific gravity in a fast- and a slow-growing family (fig. 123). Here, there was a wide range in tree size and wood specific gravity in the open-pollinated progeny of plus trees. In control-pollinated families, the correlation of specific gravity with volume was not significant for four, but for the fifth it was +0.447 and significant, which means that specific gravity was higher in trees of rapid growth. Parent trees with low moisture content produced progeny of low moisture content in both open- and control-pollinated progeny. A strong relationship was found between low wood density and high moisture content. No relationship was evident between wood density and tracheid length.

When trees with specific gravity in the range of 0.58 to 0.65 were crossed in Texas and the stemwood of 2-year-old progeny seedlings compared with those from crossing trees with low specific gravity (0.46 and 0.49), it was found that seedlings reflected the specific gravity of the parents (Brown and Klein 1961). Narrow-sense heritability values for specific gravity of 0.56 and 0.72, respectively, were obtained with 100 randomly selected 2- and 3-year-old open-pollinated progenies (Stonecypher *et al.* 1964), and little difference was found for results with 5-year-old progenies when compared with 3-year-old progenies from the same trees (Stonecypher and Zobel 1966). In 5-year-old trees, narrow-sense heritability of specific gravity was 0.73, compression wood 0.95, and volume 0.23 (Shelbourne *et al.* 1969).

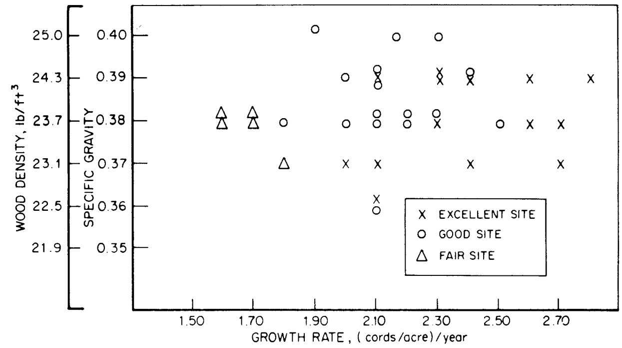

Figure 122.—Average wood density of 35 families is not related to wood volume growth per acre per year over a 7.5-year period in four plantations on three sites. In these young trees, fast growth has not reduced wood weight and related properties such as pulp yield, and neither has slow growth resulted in an increase in these properties. (Zobel *et al.* 1969)

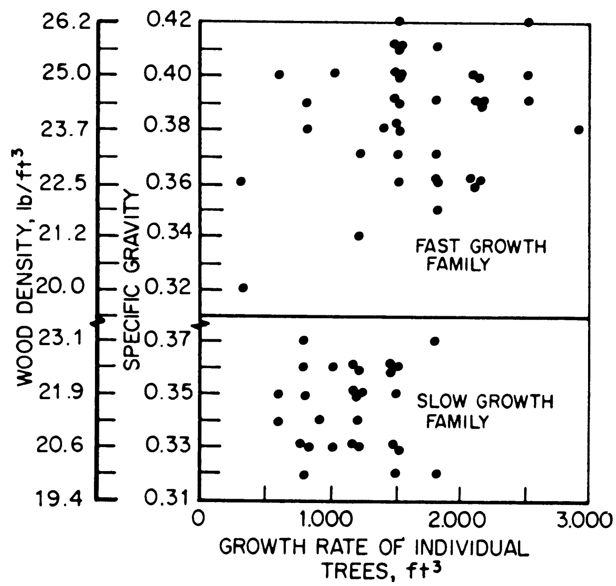

Figure 123.—Individual trees within a fast-growing or a slow-growing family vary widely in wood weight and growth rate, but these two factors are not correlated in these 7.5-year-old families. Although trees may have the same parents, there is always a wide range in rate of growth and wood specific gravity among individual trees. Plantations of improved strains will not be highly uniform for these traits. (Zobel *et al.* 1969)

Juvenile wood of young open-pollinated families is correlated with juvenile wood of the parent (fig. 124). Specific gravity samples of more than 30 maternal parents ranged from 0.38 to 0.54, or a range in pounds per cubic foot of 23.7 to 33.7; progeny means ranged from 0.30 to nearly 0.36 (Zobel, B.J., 1970; Matziris and Zobel 1973). At age 5, correlation of average family specific gravity with specific gravity of juvenile wood of parent trees (seven rings from the pith) was $r=0.694$, and heritability

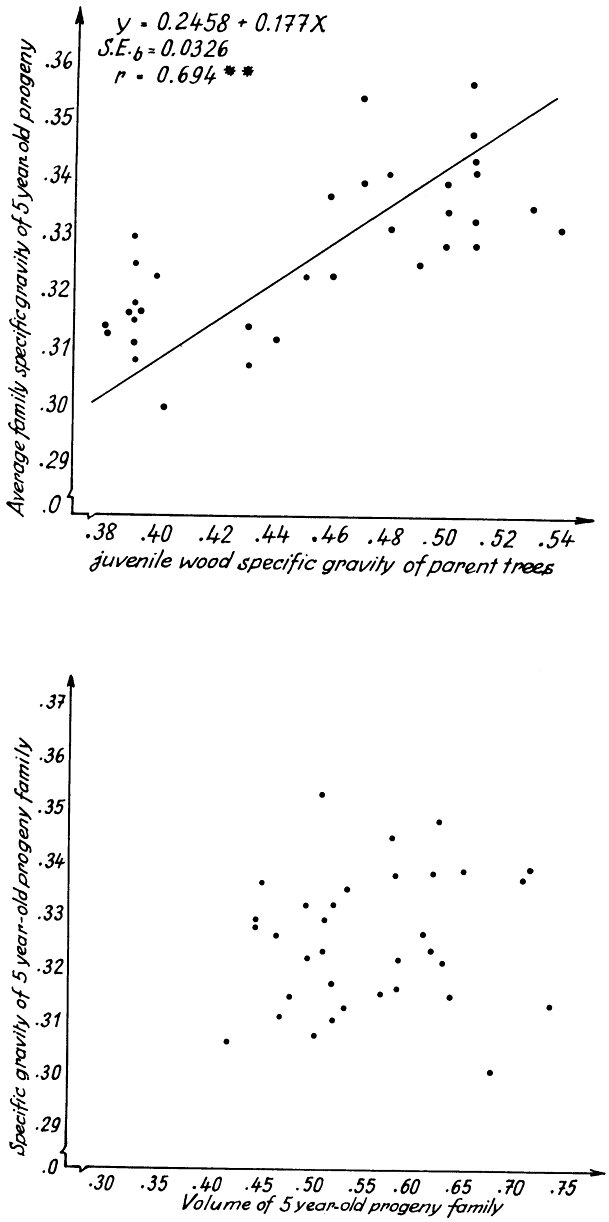

Figure 124.—(Top) Relationship of specific gravity of the juvenile wood of the parent trees (seven rings from the pith) to the juvenile wood of their 5-year-old progeny. (Bottom) Relationship of volume in cubic feet to the weighted specific gravity of the 5-year-old progeny family average. (Matziris and Zobel 1973)

was 0.35. On the basis of progeny test data, heritability was higher, 0.47. A positive phenotypic correlation coefficient of $r=0.242$ was found between specific gravity and tree volume (fig. 124). Because the data indicate that a fast-growing family may have high or low specific gravity, it was concluded that by selection fast growth could be combined, with either high or low specific gravity. For tracheid length, the greatest difference among family means was 0.39 mm, which is large enough to affect quality of paper made from juvenile wood. Tracheid length and wood specific gravity were not correlated—an important conclusion.

From 8-year-old progeny tests in two geographic locations, Goggans (1962, 1964) used heritability values for 19 characteristics in an annual ring as the basis for concluding that the most progress in a selection program would come from emphasis on summerwood tracheid length, percentage of summerwood in the increment core, and specific gravity.

Using the first two rings from the pith as samples, Jackson and Warren (1962) found the correlation of wood specific gravity of parents and offspring to be 0.87 for open-pollinated loblolly and slash pines, and 0.90 for control-pollinated lobolly and slash pines and hybrids of the species.

In 10-year-old clones, three of high specific gravity and three of low specific gravity, heritabilities of latewood and specific gravity were high, but tracheid dimensions were lower (van Buijtenen *et al.* 1968). Marked genetic differences among clones in apparent handsheet density were indicated. Lignin and extractives percent were also under moderate genetic control, as were pulp yield and zero-span tensile strength.

Tracheid Length

In addition to the information given above for the relationship of variation and inheritance of tracheid length to specific gravity, extensive study in Georgia gave estimates of heritabilities for tracheid length of 25 percent for wind-pollinated offspring and 35 percent for control-pollinated progeny (Greene 1966b). Tracheid length of eight parent trees ranged from 1.49 to 1.81 mm, or a range of 0.32 mm in the first-order branch of the current year's growth. There were highly significant differences among progenies in tracheid length when wind-pollinated, control-pollinated, or selfed families were used. In five out of six comparisons, selfing reduced tracheid length in the progeny from that of the parent tree, but each parent reacted differently.

Fibril Angle

As noted in the paragraph on phenotypic variation in loblolly pine wood properties, trees vary in the degree of fibril angle in tracheids (Pillow *et al.* 1953). The fibril angle of open-pollinated progeny of 3 loblolly and 10 slash pines was correlated with that of the parents in a Georgia study (Jackson and Morse 1965b). In control-pollinated progeny, the fibril angle was correlated with the mid-parent average and with the female parent but not with the male parent. Estimates of fibril angle of progeny were based on branch wood samples.

Spiral Grain

In 4-year-old loblolly pine, definite family differences were found in grain spirality when pith was used as the reference plane (Zobel, Stonecypher, and Browne 1967). The smallest grain deviation for a family averaged 4.8°. Differences in spirality among full-sib families were highly significant but not among half-sib families. The limitations in estimating the importance of spiral grain in breeding from performance of young trees were stressed. Excessive spirality of the grain causes warp, twist, and loss of strength in the wood. Loblolly pine in South Africa showed a frequency of right-hand and left-hand spirality of 50 percent, a few trees had a low degree of spiral, and spirality of grain was considered of sufficient importance to be included in selection criteria for breeding work (Gerischer and Kromhout 1964).

Cellulose Yield

Loblolly pine trees of the same age and growing on the same site may differ in cellulose yield (Zobel *et al.* 1966). Also, in forty-eight 5-year-old families, holocellulose percent was 82.8 in one family, but the others ranged from 83.6 to 85.0 percent. However, within-family variability was so great among the eight trees sampled from each open-pollinated family that observed differences between families were not statistically significant.

In summary, the economic importance of wood properties and their variation in loblolly pine is well established. Also there is a growing body of evidence for relatively strong inheritance of many of the characteristics. Many are not strongly correlated, so that selection for each can be made independently. Inasmuch as many are not correlated, the effect of selection may be additive; for instance, increased growth may be accompanied by increased yield of pulp from higher or desirable specific gravity; similarly, increased growth may be accompanied by decreased compression wood, knots, and waste products. As shown in figure 125, certain trees may have both fast growth and a high percentage of summerwood.

There is considerable evidence to indicate that increased wood volume growth need not lower wood quality, although care in breeding must be used. Also, considerable variation is to be expected in forest plantations from improved seed because wide variation exists among trees in both full- or half-sib families.

Environmental Effects on Wood Quality

Studies of variation among trees in wood quality have to be made with recognition of the environmental factors that might influence them, just as was done in studies of growth rate, tree form, and resistance to pests. The more important of these are: soil fertility that influences rate of growth; availability of moisture that might affect rate and length of growth period over the growing season; age of the tree that includes a range from juvenile to mature stages of life; the stocking or number of trees in stands, which influences competition; and lastly, the thinnings or other improvement cuts that might be made during the life of the stand, which influence, the kind of trees removed or left. A description of study material is always given, but the materials vary so much that results among studies are not always comparable.

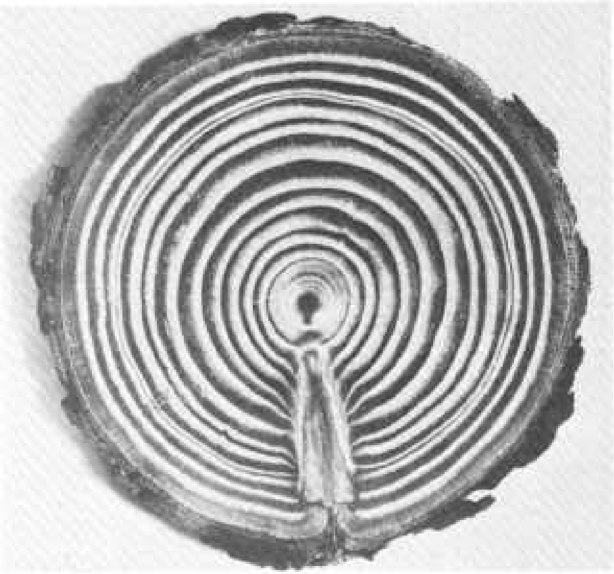

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Figure 125.—Wood specific gravity, one of the most important of all wood properties, varies widely among trees, as indicated by width of summerwood bands, regardless of whether trees grow fast or slow. Correlations of wood specific gravity with other economically important traits are determined to insure that improved trees have a good combination of good traits. (Mattoon 1942)

The range of combinations of strains, silvicultural practices, and environmental conditions is extremely large and nearly impossible to study intensively. However, since combinations of genotypes and environmental conditions influence volume production and quality, they must be considered. Perhaps we will find that the extremes are more important than the small differences.

In a fertilizer study based on 120 trees (Posey 1964), the average tree responded to fertilization with an increase in growth, decrease in specific gravity, decrease in radial wall thickness, and decrease in tracheid length. However, 24 of the trees responded differently from the average and showed an increase in fiber length with a decrease in the other traits (Posey 1965). Also, families may vary in their response to fertilizer application, as was found in young trees (Tabor and Davey 1966).

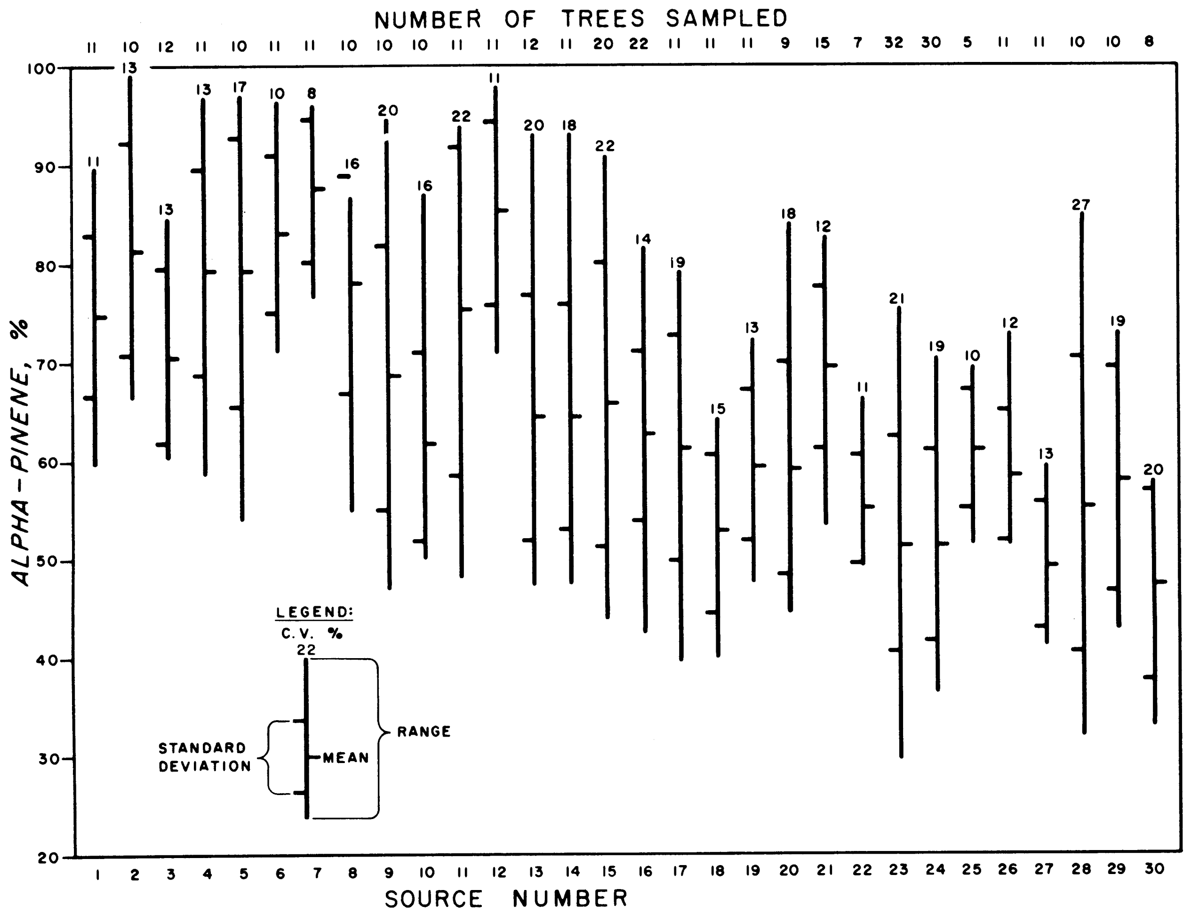
In Arkansas, where summer and fall droughts may occur, the correlation between ring width and soil-water deficits for corresponding years was negative at all heights in the trees, such that the greater the water deficit, the narrower the ring (Smith and Wilsie 1961). Moisture conditions, if critical, may affect both growth and wood quality; it was observed that trees left after heavy thinning and pruning in a 6- by 6-foot Arkansas plantation showed a threefold increase in radial growth and, also, a significant increase in both specific gravity and percentage of latewood (Smith 1968). In an Illinois plantation, Gilmore (1969) found no differences among treatments controlling soil moisture on tracheid length of 18-year-old trees. Zahner (1962) found that container-grown trees in wet soil produced four internodes of growth annually, while trees in dry soil produced only two, and total growth was half that of trees in wet soil. Gross radial growth was more than twice as great in "wet" as in "dry" trees, but the percentage of latewood was much greater in the trees on dry soils. Earlywood specific gravity was the same for both treatments, although latewood of trees in dry soils was somewhat denser than in trees in wet soil. Obviously, the interrelationships among soil moisture, tree growth, and wood properties are complex.

Spacing of plantation trees has only slight, if any, effect on wood quality, but it may on tree quality and volume growth. In Arkansas, wood specific gravity was 0.50 for trees in a heavily thinned plot and 0.51 for controls, although annual growth in diameter for the last 10 years of the study was 0.72 inch for thinned trees and 0.37 for the controls (Bassett 1969). It has been pointed out that growth of large trees is continued longer in the fall than is growth of intermediate and suppressed trees (Harkin 1962; Bassett 1966). Echols (1960) and Banks and Schwegmann (1957) found little relationship between wood specific gravity and tree spacing. Hamilton and Mathews (1965) found that spacing had only slight effect on specific gravity in outer rings but that dominant and codominant trees had higher latewood percentages and higher specific gravity than intermediate and suppressed trees. The relationships of growth periodicity to total seasonal growth, and the proportions of earlywood and summerwood for trees of different growth capacity, are not well understood. Even in the early years, the larger trees in a plantation achieve a volume growth many times that of smaller trees, but it is not clear how this accretion is brought about for either height or diameter growth. No doubt many favorable combinations of growth traits are involved.

OLEORESIN COMPOSITION

Loblolly pine oleoresin in North Carolina averaged 82 percent alpha-pinene—considerably higher than the 70-percent figure reported by Mirov (1961). Fifteen percent was beta-pinene, with only small amounts of limonene plus beta-phellandrene in samples from certain trees at a few locations (Kang 1966). Among individual trees, however, alpha-pinene varied from 50 to 97 percent, and beta-pinene from 1 to 37 percent. In contrast to loblolly pine, pond pine in the same area averaged 28 percent alpha-pinene, 1 percent beta-pinene, and 70 percent limonene plus beta-phellandrene. In hybrids the terpene content closely approached that of loblolly pine instead of being intermediate. Altogether, 76 loblolly pine trees were sampled for oleoresin.

A rangewide study showed wide variation among trees in terpene components of loblolly pine oleoresin, as well as among geographic locations (fig. 126) (Coyne and Keith 1972). Alpha- and beta-pinene account for 90 percent or more of the volatile portion of the oleoresin. The average coefficient of variation for trees at each geographic location was 16 percent for alpha-pinene, 40 percent for beta-pinene, 57 percent for myrcene, and 80 percent for limonene and beta-phellandrene. The average coefficient of variation for beta-pinene in individual trees at various geographic locations west of the Mississippi Delta was 25 percent, which is much less than at locations east of the river, where it was 53 percent. Stands at about one-third of the 30 geographic locations sampled included some trees with no myrcene or limonene, and over half the stands had occasional trees with no detectable amount of beta-phellandrene. Frequency histograms for the 374 trees sampled showed normal distribution for alpha-pinene, beta-pinene, and possibly myrcene contents. Camphene, limonene, and beta-phellandrene concentrations were skewed toward the left. Variation in terpene content occurred among geographic locations and among stands at certain geographic locations, as discussed in chapters on these subjects.



Source No.	State	County	Source No.	State	County
	LOBLOLLY PINE				
1	Maryland	Worcester	16	Mississippi	Wilkinson
2	Maryland	Somerset	17	Arkansas	Clarke
3	Virginia	Southampton	18	Arkansas	Ashley
4	N. Carolina	Hertford	19	Louisiana	Allen
5	N. Carolina	Onslow	20	Louisiana	Calcasieu
6	N. Carolina	Pamlico	21	Louisiana	Livingston
7	S. Carolina	Georgetown	22	Texas	Chambers
8	S. Carolina	Newberry	23	Texas	Hardin
9	Tennessee	Hardeman	24	Texas	Liberty
10	Georgia	Clarke	25	Texas	Tyler
11	Georgia	Wilcox	26	Texas	Cherokee
12	Florida	Marion	27	Texas	Angelina
13	Alabama	Jefferson	28	Texas	Leon
14	Mississippi	Prentiss	29	Texas	Fayette
15	Mississippi	Harrison	30	Texas	Bastrop

Figure 126.—Monoterpene components of loblolly pine wood oleoresin. (Coyne and Keith 1972)

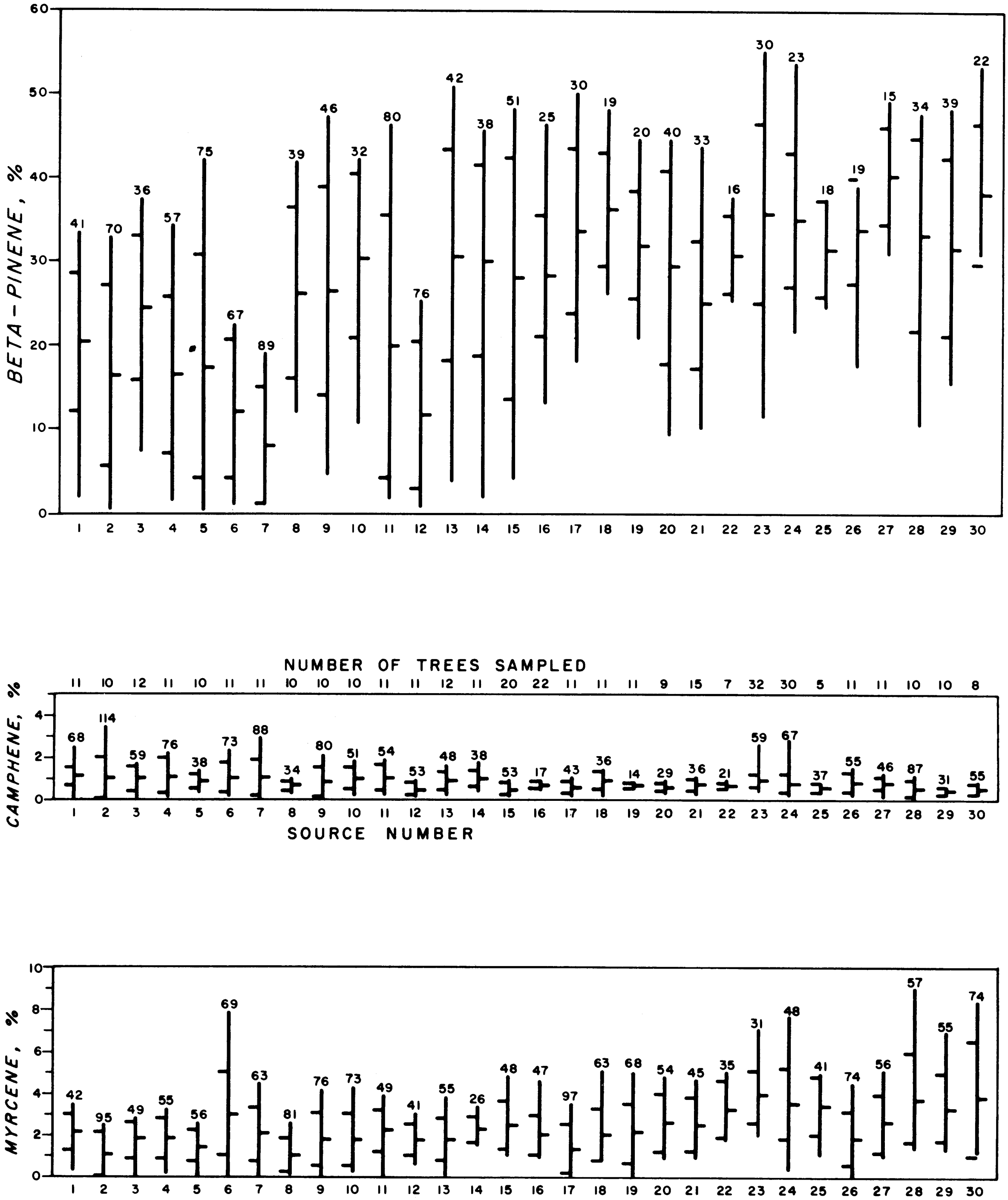


Figure 126.—Monoterpene components of loblolly pine wood oleoresin (continued).

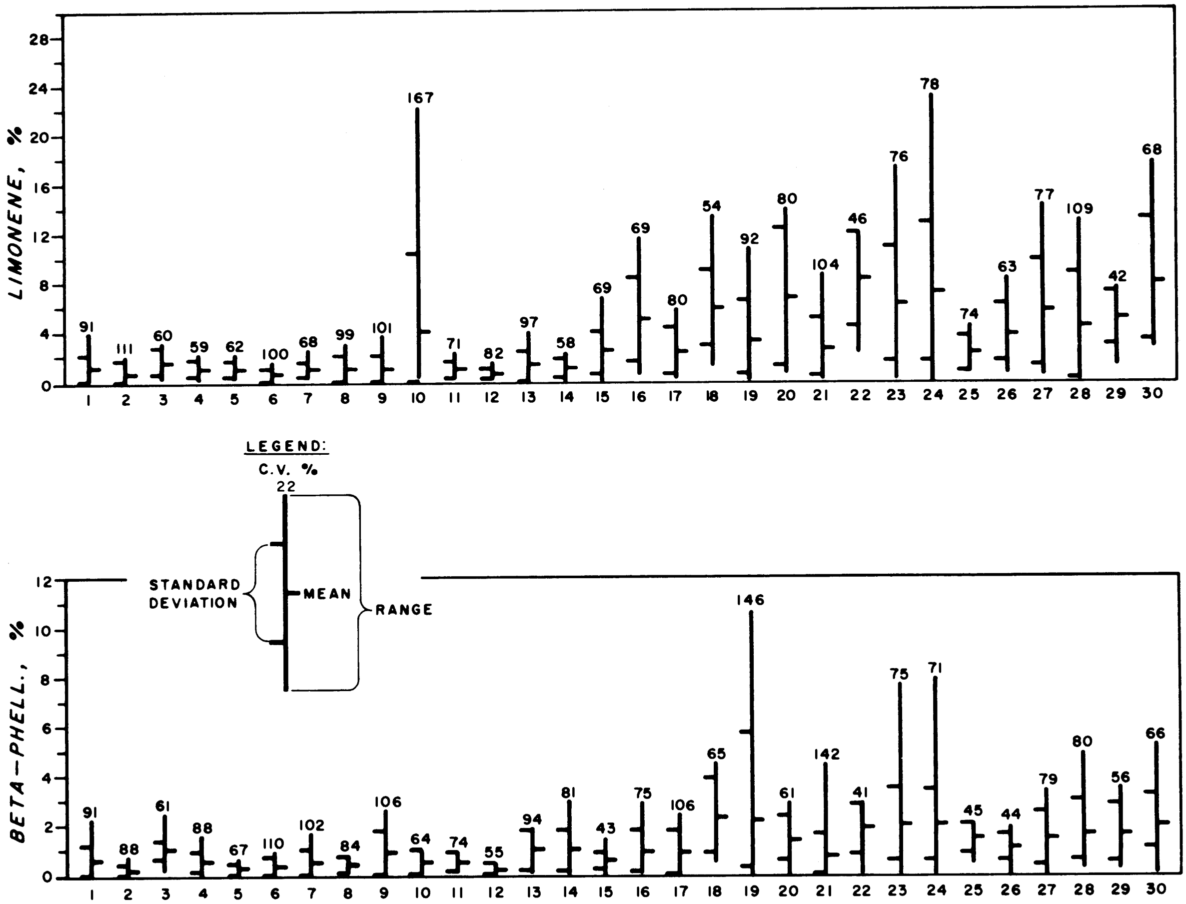


Figure 126.—Monoterpene components of loblolly pine wood oleoresin (continued).