CHAPTER 11

SLASH PINE

Slash pine has been the most commonly planted pine within most of its natural range and certain adjacent areas. The species produced large wood volume, could be used for naval stores, was easy to plant, and could be managed in even-aged plantations. In recent years loblolly pine has been preferred over slash pine for some areas because of its fast growth and the decreased importance of naval stores. As slash and loblolly pines are two giants in southern pine forest management, a large amount of forest genetics and tree breeding research has been done with each.

Slash pine, like loblolly, is suitable for most of the wood products made from southern pines and is a source of oleoresin for naval stores; consequently, tree, wood, and oleoresin quality are important in addition to wood yield. Thus, correlations among traits are important. The most important enemy is fusiform rust, which also attacks loblolly pine, but slash pine does not suffer from tip moth as do loblolly and shortleaf, brown spot as does longleaf, or littleleaf as does shortleaf. Stem and crown form are probably better than that of loblolly pine but, perhaps, not quite so good as those of longleaf and shortleaf pines.

Susceptibility to fusiform rust is the main weakness to overcome while breeding for wood yield and quality, but the disease is an important problem only in the northern part of the range (fig. 135). With the most limited natural range of any of the major species and most of the minor species, racial selection as a means of genetic improvement is a possibility but may be of lesser value than in other species.

South Florida slash pine, a formally recognized variety of slash pine, is discussed in a separate chapter because of its geographic isolation from the typical variety.

Slash pine characteristics were described by Mohr (1897), silviculture by McCulley (1950), and silvics by Fowells (1965).

TREE GROWTH AND WOOD VOLUME YIELD

Most of the growth and yield relationships of individual trees and stands discussed for loblolly and other pines apply to slash pine. Growth of an individual tree is influenced by a very complex assortment of individual traits, and growth of a stand from seedling age to maturity is even more complex. Evidence is accumulating from research about the number of factors involved and the importance of each. Silviculturists have worked for years in attempts to understand just the environmental factors concerned. Addition of genetic factors has made some parts of the problem a little easier to understand and others more difficult.

For natural stands, growth studies seem to have stimulated interest in the phenotypic variation among trees in growth rate. Forbes and Bruce (1930) made special note of the percentage of trees in diameter classes above and below average and the variation in these percentages with average diameter and stocking. For overstocked stands, a higher percentage of the trees is below than above average, and in understocked stands the reverse is true. Meyer (1930) used stand tables available for comparisons of diameter distributions among species, in less detail for slash pine than shortleaf pine, and concluded that the attributes of curves were characteristic of the individual species. Clutter and Bennett (1965) developed diameter distribution tables for old-field slash pine plantations by age, site, and density as an aid to: (1) forecasting the number of merchantable stems per acre for either pulpwood or sawtimber; (2) predicting the number of trees per acre large enough for naval stores production; (3) determining optimum spacings for multiple-product combinations; and (4) evaluating harvest costs.

Wood volume varies widely among slash pine trees in even-aged stands and plantations, as indicated by a few examples from phenotypic surveys. Although spacing, soil nutrients, and soil moisture influence tree volume growth at different locations in the forest, slash pine trees at any one location where the environment is relatively uniform (such as level old fields in the Coastal Plain) may vary widely, and some of the difference between trees may be a result of genetic factors. Environmental factors may cause differences in growth of trees among stands, but a relatively uniform environment does not insure uniform growth of individual trees within a stand. Tree diameter varied from 4 to 18 inches in a 20-year-old stand being converted to a demonstration seed orchard in a Florida old field. Removing the slow-growing and undesirable trees raised the average volume of the trees left for seed production to twice that of the average tree of the original stand (Mergen and Pomeroy 1953). Diameters ranged from 6 to 14 inches among 202 trees on a 1-acre plot in a 16-year-old Georgia plantation. The largest trees were 55 percent larger in diameter and 130 percent larger in basal area than the average tree. In another 5-acre plantation, the tallest tree was 30 percent taller than the average tree after 8 years (Dorman 1952).

In studies of growth rate in relation to wood specific gravity in planted stands, wide ranges in tree size have been sampled for regression analyses (Squillace *et al.* 1962; Saucier and Dorman 1969).

Wide variation in diameter among trees is indicated in comprehensive tables of distribution in relation to age, site, and spacing to aid foresters in silviculture and timber management of slash pine plantations (Clutter and Bennett 1965). As an example, with 700 trees per acre 25 years old and site 70 feet, the prediction of diameter distributions is for 11 trees in the 5-inch class and 4 in the 11-inch class, with other sizes spread within these extremes. It was found that mean diameter decreased as trees per acre increased, but diameter increased as site index increased, and the range in diameter distributions did not change to any extent with these variables, although the tails of the curves were not well defined (table 5). However, other reports indicate wide spacings increase the diameter range among trees (fig. 147) (Nelson and Bennett 1963). If the amount of growing space does affect range in variation, trees of similar plus genotype may have a different phenotypic superiority rating when selected in closely or widely spaced plantations.

The coefficient of variation for d.b.h. in 10-year-old slash pine decreased from nearly 15 percent for theoretical plot sizes of 2 trees to about 3 percent for 20 trees (Evans *et al.* 1961). Curves of the coefficient of variation in relation to number of trees for total height, clear length of stem, and bark thickness tended to stabilize at about 20 trees per plot; consequently, plot sizes of about 25 trees or more were needed in progeny tests for good estimates of growth. The coefficient of variation for clear length of bole was higher than for the other three traits measured.

As the table of diameter distributions indicates, the range in diameters among trees on any site may be roughly about the same on an acre with 200 trees as one with 900 trees. In other words, the superiority index, based on the average tree, of individual trees available for selection may increase only until a few hundred trees are examined; thus, surveys of additional hundreds may not disclose trees with much greater genotypic superiority than those occurring among the first few hundred examined. These conclusions are based on the assumption that local environmental factors such as growing space and soil fertility are constant.

It is often assumed that the more trees examined in surveys for plus trees, the greater the genotypic superiority will be of the best trees located. As frequency distribution curves indicate, this assumption may not be true for individual traits. However, it still holds for selection criteria based on rating for a combination of traits. A large number of trees must be examined to locate a few trees with the best combination of many desirable traits.

Estimates of diameter distribution in slash pine stands indicate that trees up to 50 percent larger in diameter and 100 percent volume occur frequently. This information provides a base for selection of seed orchard clones and parental stock for inheritance studies. Trees of high vigor may have minus traits making them unsuitable for breeding purposes, but the problems of correlation among traits and isolation of individual factors of growth and yield are subjects for future sections in this chapter.

Physiological and Chemical Differences

Measurements of photosynthesis and respiration, as well as chemical composition of seedlings and patterns of seasonal growth, have been made in attempts to define components of the growth complex.

Photosynthetic Efficiency

Some of the early tests showed little relationship of photosynthesis and respiration with growth in seedlings (Reines 1962; Robertson and Reines 1966), but later studies showed differences among families of seed orchard clones that may have come from different geographic locations (Burkhalter *et al.* 1967). Also, rates of apparent photosynthesis and respiration were found to be higher and efficiencies lower in larger than in smaller slash pine seedlings. Wyatt and Beers (1964) found that seedlings from two plus trees showed a significantly faster-than-average increase in carbon dioxide uptake with age. Indicated net photosynthesis of plus-tree progeny at 764 days from seed averaged about 58 percent greater than controls. After 3 years, the plus-tree progeny had more stemwood than controls. Similar relationships were found for loblolly pine by Ledig and Perry (1969), who showed also that season-long tests were necessary because rates of net assimilation and dry weight growth vary widely at different times during the growing season.

Chemical Composition

Differences among individual seedlings within families and among families in chemical composition have been observed, but chemical content had little relationship with growth rate (May *et al.* 1962). Progeny means based on an average of five seedlings per family for nitrogen varied from 0.587 to 1.049, calcium from 0.095 to 0.122, and phosphorus

Table 5.—*Diameter distributions by age, site, and stand density for slash pine plantations of the Middle Coastal Plain of Georgia (Clutter and Bennett 1965)*

Trees per acre (number)	Site	Diameter class (inches)															
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
		Number															
	40				9	31	52	58	41	9							
	50					5	21	40	53	49	28	4					
200	60						3	14	30	45	50	40	18	1			
	70							1	9	23	37	45	44	31	10		
	80								1	6	16	29	40	43	37	23	5
	40			8	41	78	93	66	14								
	50				4	26	59	83	79	45	5						
300	60					2	16	43	68	78	64	28	1				
	70						1	10	30	54	71	70	49	16			
	80								6	21	42	60	68	59	36	8	
	40		2	34	92	131	108	32									
	50			1	19	64	108	118	77	14							
400	60					10	43	84	109	98	51	5					
	70						5	28	63	93	101	78	31	1			
	80							2	18	47	76	93	88	59	17		
	40		14	81	157	167	79	2									
	50			6	49	117	157	129	41								
500	60				2	29	83	132	141	93	18						
	70					1	16	58	105	132	118	63	7				
	80							9	39	81	114	122	94	39	1		
	40	1	42	150	222	162	23										
	50			20	97	181	193	103	6								
600	60				9	61	136	181	154	58	1						
	70					4	37	99	153	164	114	29					
	80						1	22	70	123	153	139	80	12			
	40	6	93	237	264	100											
	50		1	49	164	245	197	44									
700	60				24	108	199	220	134	15							
	70					11	69	151	202	180	83	4					
	80						5	43	110	170	186	139	46				
	40	21	174	330	250	25											
	50		7	97	248	295	149	4									
800	60			2	52	172	264	233	77								
	70					27	114	212	244	169	34						
	80						13	74	160	219	207	114	12				
	40	55	287	403	156												
	50		20	171	341	304	64										
900	60			7	97	252	321	204	20								
	70				2	53	174	277	268	123	4						
	80						27	116	220	265	206	65					

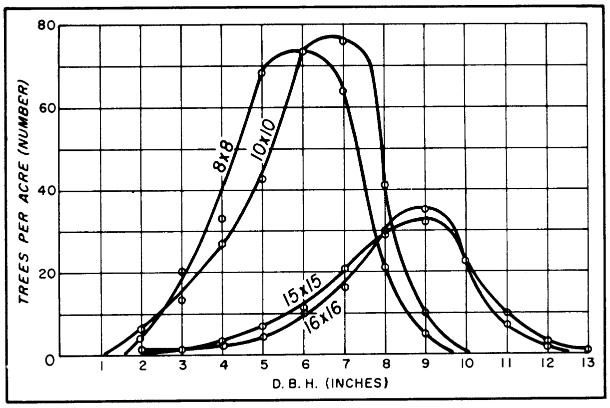


Figure 147.—At 14 years of age in plantation slash pine, wide spacings produce trees of larger diameter and wider range in diameter than narrow spacings. (Nelson and Bennett 1963)

from 0.150 to 0.214 in percent of dry matter in stems.

Length of Growing Season

Slash pine seedlings in nursery beds vary widely in the date on which terminal buds are formed in the fall, and this influences yearly height growth. Also, plantation trees begin and end diameter growth on different dates (Harkin 1962). In a young South Carolina plantation, 16 percent of the trees began diameter growth between January 27 and February 10, 50 percent were growing by February 18, and all of them by March 6. In the fall, 6 percent had stopped growth by September 8, 37 percent by October 21, and 81 percent by November 11. Both slash and loblolly pines in dense stands grew rapidly in the early season and then slowly thereafter, but loblolly pine in the open grew rapidly throughout the growing season. Soil moisture may be more favorable to late-season growth in South Carolina than in Arkansas, where it has been shown to be a factor with loblolly pine, as discussed in the chapter for this species. Length of growing season could contribute to proportion of earlywood and latewood among trees, but this subject has not been studied in slash pine.

Phenotypic Variation

Phenotypic selection for size among nursery seedlings has shown differences in survival and in growth rate of seedlings that are maintained for years. The relationship of seedling growth to seed size and mycorrhizal infection has been investigated as part of studies in seedling performance.

Graded Seedlings

Grades for slash pine seedlings have been in use for many years, as well as those for species discussed in preceding chapters, because it was a favorite of tree planters. In general, differences in survival and growth rate among grades have been large.

Because of the numerous progeny tests with individual slash pine parent trees, performance of graded seedlings is probably more important for juvenile-mature growth relationships in progeny testing than as an indicator of genetic differences among trees. Thus, growth of graded seedlings will be discussed in brief form.

On sandy sites near Aiken, South Carolina, after 5 years, grade 2 seedlings were 10.1 feet and subgrades of grade 3 were 8.2 to 9.2 feet; survival was 88.3 percent and 63.0 to 83.8 percent, respectively (McGee and Hatcher 1963). In southwestern Alabama and southeastern Mississippi, larger seedlings (3/16 inch in diameter at the root collar) had better growth and survival than small seedlings (less than 1/8 inch at the root collar), but medium-sized seedlings differed from the large seedlings only with respect to less growth (Swearingen 1963). In Argentina, seedling size had no effect on survival, but large seedlings were 25 percent taller than medium and small seedlings after 2 years (Cozzo 1964).

In southeastern Louisiana after 34 years, the oldest seedling grade study of record, pulpwood volumes in cords per acre were as follows for grades 1, 2, and 3, respectively: 55.8, 52.7, and 39.7. In a second study established 1 year later, volumes were 75.4, 51.0, and 24.8 cords, respectively (Wakeley 1969b). Superior volume production of the higher grades was a result of moderately faster growth plus substantially higher survival. Degree of fusiform rust infection, an important factor at times in seedling survival and, thus, in volume growth per acre, was not consistently affected by seedling grade. A majority of the trees with superior height at age 30 in planted stands may gain their superiority at an early age (Wakeley 1971). Thus, early selection might be as accurate for locating phenotypes with high and sustained growth rate as later selection but not for trees that may improve their growth superiority at a later date. However, the latter group of trees might be relatively unimportant in intensive breeding if trees possessing the same growth superiority can be identified after only a few years' growth in progeny tests.

For families and trees within families, correlations between measurements taken at 3, 8, 14, 18, and 25 years were weak between the 3rd and 25th years for total height, but they increased rapidly thereafter for height, d.b.h., stem volume, and oleoresin yield (Squillace and Gansel 1972). Average wood volume per plot at 15 years was highly correlated with volumes at 8 years in 27 open-pollinated slash pine progenies in Georgia where rust incidence is high (Sluder 1972). Additional information is given in the section on variation among trees.

Seed size could be a factor in seedling growth and, consequently, in progeny testing, but tests show little, if any, effects. Shoulders (1961) found that small seeds produced smaller seedlings than medium or large seed and fewer plantable seedlings, but the overall performance of the seedlot was the same whether the seed was sown, mixed, or separated into size classes. In a 500-pound lot of seed, about one-fourth averaged 12,700 seed per pound, one-half about 15,900, and the remaining one-fourth 20,800 per pound. Cozzo (1967) found germinative energy was greater for large-sized classes of seed, but after 4 to 6 months, initial height differences were not significant.

Mycorrhizae have an important beneficial effect on survival of slash pine seedlings of all grades. The percentage of seedlings with mycorrhizae decreased with seedling grade in a Louisiana study. It was concluded that morphological grade represents the most important combination of characteristics by which plants with high survival may be selected, but mycorrhizae and grade provide better criteria than grade alone (Jorgensen and Shoulders 1967). Growth of slash pine in Argentina was significantly greater on soil inoculated with mycorrhizae than where it was not, and it was thought that mycorrhizae assist in the assimilation of elements present in the soil at low levels (Braga and Myers 1967). The relationship of mycorrhizae to growth rate in superior slash pine progenies has not been investigated.

Selected Nursery Seedlings

Selection of large seedlings in nursery beds is one method of obtaining plus trees of superior vigor. Although selection for height can be rigorous, the period of growth is short; and tree form, resistance to pests, and wood properties cannot be evaluated. Results of nursery selection in slash pine have been variable.

In one study with 84 seedlings averaging 50 percent greater height than controls, average height and survival did not differ after 5 years. Selection was at the rate of about 1:25,000 seedlings (Foulger 1960). Selection of 34 super seedlings at the rate of about 1:23,000 yielded trees 23 percent taller than controls after 8 years, but survival of select trees was only 35 percent, in contrast to 66 percent for the controls. Infection by fusiform rust was low and did not differ in the two groups of trees. None of the select seedlings was taller than the most vigorous controls (Bengtson 1963).

In a large study with 373 select seedlings chosen at a ratio of 1:146,000, height differential of controls and selects was 1.6 feet, and the selects averaged 22 percent greater cubic-foot volume after 9 years. The two groups of seedlings did not differ in survival or percent infection by fusiform rust. Certain of the select seedlings were taller than any of the controls. Height frequency distribution curves were roughly similar in shape to those for loblolly pine included in the study (fig. 106) (Barber and VanHaverbeke 1961; Hunt 1967).

The results of nursery selection in slash pine are in general similar to those for other southern pine species: a small number of trees with high vigor are identified, but they may not have improved form, pest resistance, or wood properties.

Genotypic Variation

The preceding discussion of differences among trees in growth was restricted to stands and plantations and also to seedlings without regard to parentage or other factors that may influence performance. Next, we will give estimates of inherent differences among trees based on performance of the offspring. Difference among individual trees can be obtained by planting tests comparing progeny such as half sibs from wind pollination, full sibs from controlled pollination, seedlings from selfing different trees, and rooted cuttings or grafts forming clonal lines.

Half-Sibs of Randomly Chosen Parents

From the viewpoint of the forester or silviculturist, variation in growth of seedlings from different mother trees is of major importance, since stands are regenerated with seed of individual trees and seed for nursery use must be collected from individual trees.

Large differences in height and volume growth occur among individual slash pine trees in natural stands and plantations, as shown in preceding sections in this chapter. Comparison of progeny of trees chosen at random might indicate something of the range among the parents. However, a large number of trees would have to be chosen to insure samples of the lower and upper range. Furthermore, the sample may be biased because trees of low or slightly below average vigor may not bear seed or may have been lost from the stand as a result of competition or other factors not operating at random in the stand.

The full range of inherent variation is largely of academic interest because the forester has no alternative but to evaluate the trees in place in any stand and make a choice among them. A low percentage of highly vigorous slash pine, particularly in young or highly stocked stands, may produce little or no seed, but slash pine is such a good seed producer in general that this is rarely a problem.

Comparison of progeny from maternal parents chosen at random has been incidental to other studies. More emphasis has been placed on performance of offspring from selected trees because of greater importance in tree breeding and genetics. However, large differences in growth among progenies have been demonstrated. At the end of the first growing season, progeny means ranged from 18 to 35 cm for maternal parents throughout the northern part of the range; 12 to 30 cm for trees in the intermediate part of the range; and 8 to 27 cm for trees in the southern part, which included South Florida slash pine (Squillace 1966b). This information was obtained from a sample of five trees from each of 54 stands throughout the range, with the restriction that each tree had to be a dominant or codominant and producing seed. Coefficients of variation for total height were lowest (11.7 percent) for progeny means among mother trees within stands, intermediate (22.2 percent) among seedlings within mother trees, and highest (24.0 percent) among stands. Thus, seedlings not only varied widely in average height per family but varied also among individual seedlings within each family. Heritability based on wind-pollinated progeny was estimated at 18 to 35 percent, depending on basic assumptions, and 31 percent for control-pollinated families.

Slash pine progeny families 15 years old varied in average stem volume from 6.0 to 8.4 cubic feet, or 40 percent more. Total average heights ranged from 38 to 42 feet (Squillace and Bengtson 1961). Control-pollinated offspring of the same eight maternal parents varied from 6.5 to 9.4 cubic feet, or over 44 percent larger. Maternal parents had been selected for high yield of oleoresin without regard to volume, but they were in the range of intermediate size classes among trees large enough to be worked commercially for naval stores in natural stands.

Half-Sibs of Selected Trees

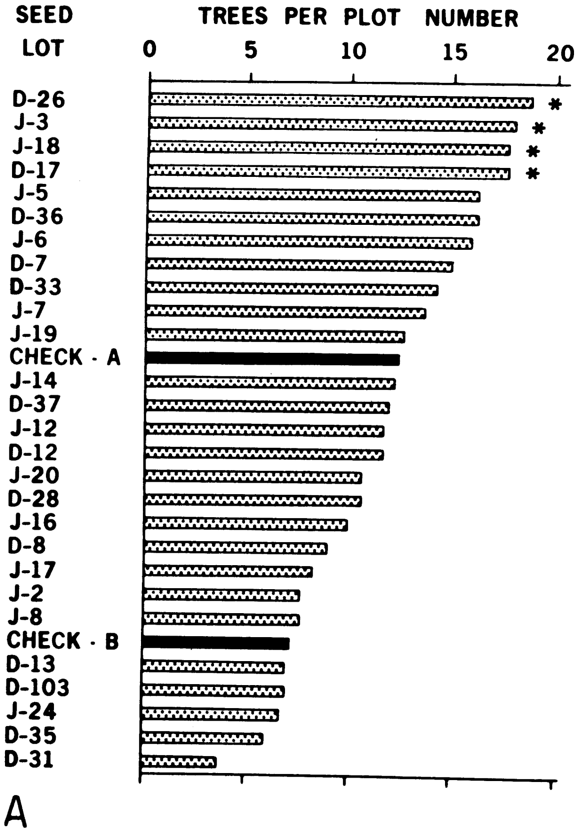
Growth of open-pollinated progeny of selected trees may provide the forester with useful data upon which selection of maternal parents can be based. This is true if trees are selected under the stand conditions and the traits with which he works.

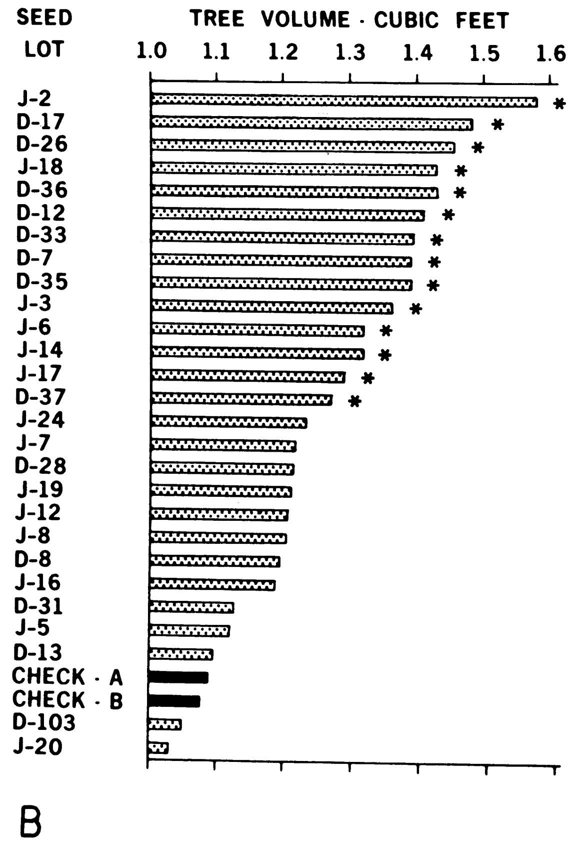
Information available to date shows that growth of offspring is roughly correlated with that of the maternal parent, but there may be important differences among progenies of fast-growing phenotypes. After 5 years, seedlings of five selected mother-tree lines varied from 15 to 18 feet in height (Kaufman 1968). Height varied widely within families. Families varied significantly in response to cultivation and fertilization.

As a basis for selecting seed orchard stock, the Ida Cason Callaway Foundation in Georgia conducted extensive open-pollinated tests of slash pine trees selected in planted stands north of the natural range. At 7 years of age, heights among families varied from 16.8 to 21.6 feet for all trees and 17.5 to 22.2 feet for disease-free trees (Barber 1964). The slowest growing family was the offspring of a tree with fast d.b.h. growth and intermediate height growth (14.4 inches d.b.h. and 44 feet tall at 15 years). The tallest families were from parent trees 11.2 and 11.8 inches d.b.h. and 59 feet tall at 15 years. In a 7-year-old study, narrow-sense heritability was 34 percent for height and d.b.h.; in an 8-year-old study, it was 20 percent for height and 6 percent for d.b.h. Total height at 2 years correlated well with height at 7 and 8 years in two different plantings. Progenies that grew fastest had the highest survival. There were differences among progenies in natural pruning, crown width, number of crooked trees, and percent infected by fusiform rust. Because of high experimental error, only the taller families were significantly superior to the controls, although 25-tree plots or larger and 3 or 4 replications were used.

Also in Georgia at 8 years of age, open-pollinated progeny of good slash pine phenotypes varied significantly in individual tree volume and wood volume per plot. The difference in plot volume was large because the number of trees per plot varied as a result of rust infection. Several families were significantly better in growth than the best of two commercial controls (Webb and Barber 1966). The fastest growing families produced twice as much volume per unit area as the best of two controls. Seven families of a total of 27 produced significantly more volume, averaging 81 percent more (at the 5-percent probability level) than the best control (fig. 148). Heritability of individual tree volume growth was low, $h^2 = 0.16$. Infection by fusiform rust was such an important factor in volume growth that only 45 percent of all trees were considered potentially merchantable. The overall conclusion from the study was that mild selection and use of open-pollinated seed produced an improvement over commercial checks of 19 percent in individual tree volume, 19 percent more merchantable trees, and 46 percent more volume per unit area. At 15 years the progenies from all selected trees showed only a 30-percent improvement in wood volume and the best 10 progenies an improvement of 84 percent. Cubic-foot plot volume varied from 23.21 to 134.5 for plus-tree progenies, survival from 12 to 64 percent, and rust-free trees from 0 to 92 percent (Sluder 1972).

We can conclude that open-pollinated offspring of individual slash pine maternal parents will vary widely in tree growth and volume yield. Progeny of certain superior phenotypes will make outstanding growth, but either good or poor performance of offspring of individual maternal parents is subject





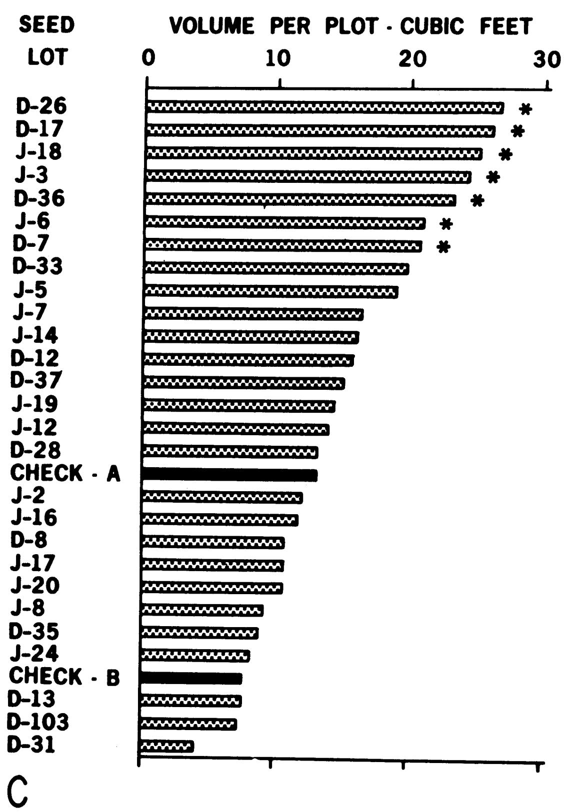


Figure 148.—Open-pollinated progenies of slash pine vary widely in number of potentially merchantable trees per plot, number free of stem infection by fusiform rust (A), average volume of individual trees (B), and total wood volume per plot, which is an expression of the combined effect of tree size and number of trees per plot (C). (* indicates progenies producing more trees, larger trees, or more wood volume per plot, at the 5-percent level, than the best check lot.) (Webb and Barber 1966)

to large error. Inasmuch as it is well established in plant and animal breeding that the maternal parent can influence offspring, it is well to recognize this relationship in silviculture. In addition to growth rate, other economically important traits, such as crown form, stem form, natural pruning, and resistance to rust, must be considered, and these will be discussed in future sections.

The cause of error in estimating maternal parent-offspring relationships is not clear. It may arise, in part, from the genetic makeup of the parent tree, as mentioned earlier. Also, pollination may be a very important factor, influenced by variation in amount of pollen and time of pollen shedding.

Full-Sib Families

The increase in precision with which two parents are evaluated is accomplished at the expense of the number of trees that can be tested. This is the reason there are so few progeny tests for estimating inheritance of growth and other important traits. Making controlled pollinations is laborious; also, cones must be observed, seed handled carefully, nursery beds supervised closely, outplanting done carefully, and so on. In spite of high costs and other difficulties, control-pollinated progeny tests provide estimates of the large gains possible in breeding slash pine. The large seed orchard programs depend on results of these studies for justification. The costs of breeding are high, but the rewards are great.

At 5 years of age, progeny height was highly correlated with average height of both parents (Webb and Barber 1966). Height superiority of parent trees was computed from height of the plus tree and the average of adjacent trees in planted stands. The regression of offspring height on mid-parent superiority in feet was very similar for progeny planted in 25-tree plots replicated 4 times, or 5-tree plots in rows replicated 5 times (figures 149 and 150).

In a Florida study after 5 years, control-pollinated offspring of plus trees were significantly taller than the controls (Peters and Goddard 1961). Heritability of vigor was roughly estimated at 15 percent. Selfed progenies were significantly shorter than any cross-pollinated progeny. In a comparison of seed orchard clones, nine families 4 years old averaged 40 percent greater dry weight production, and the range among families was 13 to 65 percent (Goddard 1968). In an additional plantation, 5-year-old trees in 15 families averaged 11.8 percent gain in volume. Roguing the five poorest clones in a seed orchard would have raised the average to 20.4 percent. Gains per family varied from minus 10 percent to plus 48 percent average dry weight of bole wood.

In a polycross test of seed orchard clones, the commercial controls ranked next to the lowest in height growth in two plantations of 19 progenies each at 5 years of age (LaFarge and Kraus 1967). However, only a few of the families were significantly taller at the 5-percent level, although average heights ranged from 12 to 14 feet. A pollen mix from 30 clones was used, which may have held down the range in height among families. Certain progenies had slender crowns, as indicated by the crown width over total height ratio, and others indicated increased resistance to fusiform rust. It was concluded that the polycross tests gave a good indication of the clones with the best combination of height growth, crown form, and resistance to rust.

Selective breeding with slash pine has been underway in Australia for many years (Sherry 1958). Progeny tests planted before 1948, which were mainly with wind-pollinated seed, were summarized by McWilliam and Florence (1955). These and more recent tests were reviewed by Haley (1957) and Nikles (1962). A report on 6- to 10-year-old progeny from plantings made in the period from 1952 to 1957 was prepared by Nikles (1966). In the plantations established 1952–57, 59 full-sib, 42 wind-pollinated, and 20 selfed families were available in all. Seed for the control stock was the same as that used commercially and came from 160 of the most vigorous, well-formed trees per acre. The progeny tests with full sibs involved 59 families from 25 parents. Subjective rating of bole straightness showed on the average 7 times the number of trees of a defined high standard (8+ out of a possible 10) in these progeny, as compared to the checks of commercial stock, which averaged 26 trees per acre with 8+. The gain in volume per acre increased with age, reaching 243 cubic feet per acre, or about 23 percent greater, at 9 years and appeared to be still rising. Gains realized in the wind-pollinated progeny tests were smaller but considerable. Twice as many trees scored 8+ for straightness compared to checks which averaged 22 per acre with 8+, and in one large progeny test the gain in volume was 123 cubic feet per acre. Evaluation of the breeding qualities of parent trees was attempted by comparison of their general combining abilities for straightness and volume. Estimates for 14 parents involved in the more comprehensive full-sib tests showed great variation in their capacities to produce superior offspring, indicating progeny test selection to be potentially of great benefit. When all the data within each of the three types of progeny test (full-sib, wind-pollinated, and self progeny) were pooled, 15 parents were found to be represented in all three types of test. A significant difference between the means for straightness of the full-sib and self-pollinated progeny was found; the respective means were 176 and 157 trees per acre with 8+. The wind-pollinated progeny mean was 65. The three types of progeny test differentiated the same trees, with few exceptions, into groups of parents characterized by (1) excellent straightness, (2) very poor straightness, (3) very high vigor, and (4) about average vigor. Specific combining abilities for straightness and volume were calculated for 30 crosses, resulting in high values in 10 and 3 cases, respectively. However, the most outstanding single crosses encountered did not show high specific combining ability, and those with high specific combining ability were relatively poor in absolute terms. No information was obtained on infection by fusiform rust because the disease does not occur in Australia.

In evaluating gains from mass selection as practiced in Australia, it should be kept in mind that the phenotypic level of the controls was higher than that of average trees or trees selected at random.

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Figure 149.—Large-crowned slash pine may not have fast height growth. Although growing at the edge of a plantation, height is average compared with other trees with less growing space. Offspring of a cross of this tree (Jones 25) with another average tree (Jones 26) grew much slower than progency of fast-growing phenotypes, as indicated by the regression of offspring height over mid-parent height in figure 150.

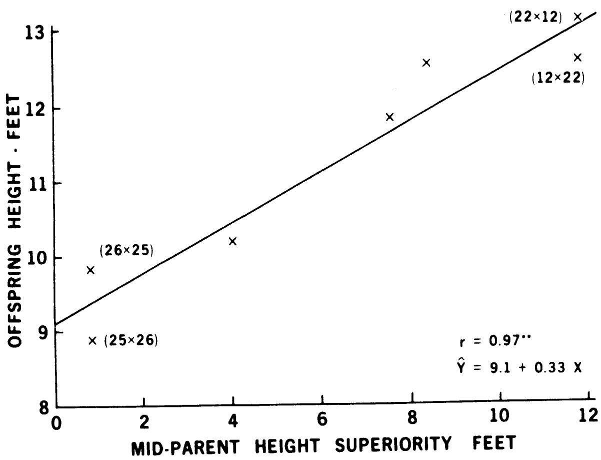

Figure 150.—Height of young slash pine progeny is highly correlated with the average height superiority, based on the stand average height, of the maternal and paternal parents. Progeny heights in reciprocal crosses were similar, indicated by parent tree number, whether the parents were average or greatly superior to average in height growth. (Webb and Barber 1966)

Also, the controls would be considerably better than what is called commercial seed in the United States.

The three types of progeny tests used in Australia gave somewhat similar results in indicating the breeding value of plus trees. But this was not the case for certain trees, which indicates that slash pine trees not only vary in vigor and some morphological traits, but vary also in the relative magnitude of the three kinds of associated genetic variance—additive, dominance, and epistatic. Thus, the more intensive and sophisticated the breeding work, the more intensive the progeny testing should be.

Selfed Families

In forest genetics and tree breeding research, selfing is usually studied to determine the extent of self compatibility, average effect of selfing for a species on growth and other traits, utility of selfing in creating new families or strains singly or in combination with other mating systems, and utility of selfing for creating individual trees with exceptionally good traits within selfed families. In *Principles of Plant Breeding* (Allard 1960), breeding methods for normally self-pollinated species are discussed in chapters separate from those dealing with cross-pollination. Results of selfing in contrast to outcrossing are discussed in the chapter on genetic effects of various mating schemes and are not germane to the discussion here of differences in vigor among slash pine trees.

Slash pine is a cross-pollinated species in general, but a small amount of selfing occurs in forest stands, and some trees can be selfed with controlpollinations. It has been shown in the small amount of work done to date that individual trees vary in amount of natural selfing and that families from artificial self-pollination vary widely in growth rate. In other words, individual trees vary widely in the way they respond to selfing. Also, there is a very wide range in vigor displayed by individual seedlings within selfed families.

Amount of natural selfing in seedlings of 11 trees varied from 0 to 27 percent. Seedlings of nine trees showed 5 percent or less selfs, and two families 23 and 27 percent. The estimates were based on the frequency of albino seedlings. When one albino carrier was selfed, an approximate 3:1 ratio of normal versus albino seedlings was obtained (Squillace and Kraus 1963). Self-fertility, expressed as percentage yield of seedlings from self-pollinations versus outcrosses, averaged 18 percent and ranged from 4 to 36 percent for seven slash pine trees (Kraus and Squillace 1964b).

Height growth of 5-year-old selfed progeny of a high-vigor tree was significantly slower than progeny from crosses among trees (4.54 feet versus 8.77 feet), and the range in selfs was from less than 2 to 9 feet in height, which is not unusual (Peters and Goddard 1961). Also, progeny of a selfed tree selected for high gum yield were shorter than those from outcrossing, although heights of the more vigorous trees did not greatly differ (Mergen 1954f).

The average of several 9-year-old slash pine families indicated a decrease in vigor and oleoresin yield with an increase in inbreeding coefficient from 0 to 0.5, but in certain families inbreeding depression was very low (Gansel 1971).

In Australia, selfed families varied in height growth, indicating (as do full-sib or wind-pollinated families) that the trees had high combining ability for vigor and stem straightness (Nikles 1966). In the nursery bed in Mississippi, seedlings varied in height among parent trees, and those with the tallest selfed progenies also produced the tallest wind-pollinated progeny (Snyder 1968). Among 12 trees classed as moderately self-compatible, height of seedlings varied more in the selfs than in wind-pollinated families, although the coefficient of variation was the same for both progenies of one tree and less for the selfs in one other tree.

Results of selfing studies to date all indicate that slash pine does not self readily, selfed progenies may have low vigor, selfed families vary in height, and selfing does not produce individual high-vigor trees. Correlation of growth rate in trees and families produced by selfing has not been studied, nor has the large number of other traits important in tree breeding.

Clones

The difficulty of vegetatively reproducing slash pine has probably been the largest obstacle in the

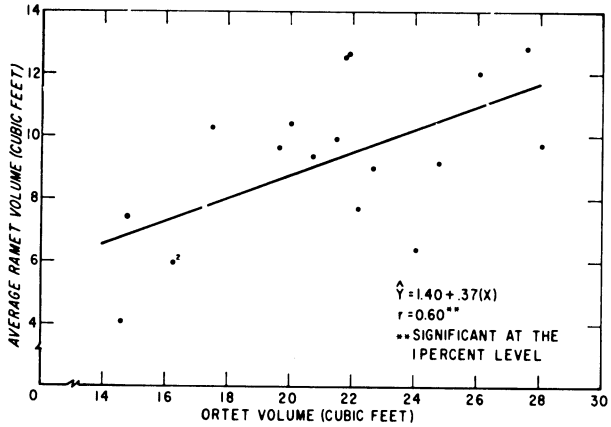

Figure 151.—Volume regression of 12-year-old air-layered ramets of slash pine with 23-year-old ortets grown from seed. Ramets had 85 percent higher wood volume if they were taken from ortets with 71 percent higher volume than smaller ortets. (Schultz 1972)

use of clonal lines in estimating variation among trees, interaction between genotype and environment, and relationship among traits. However, in one study under north Florida conditions, trees in a progeny test for oleoresin yields were cloned by air layering. At age 9, the fastest growing clone averaged 8.9 cubic feet in volume and 39 feet in height, or 3.7 times the volume of the slowest growing clone, which averaged 2.4 cubic feet and 30 feet in height (Schultz 1969b). At age 12, volume differences among clones were still large, and the ramet-ortet wood volume correlation was $r = 0.60$, highly significant (fig. 151) (Schultz 1972). Ramet volume at age 7 was highly correlated with volume at age 3, and at age 12 with age 4, $r = 0.80$. Range in volume of 23-year-old ortets was about 14 to 28 cubic feet. Thus, the correlation between genotype and phenotype was high. The ortets were not selected to represent the entire range in volume among all the trees in the progeny test plantation. The ortets were the same age when propagated, and ramets grew as rapidly as seedlings, but ortet age and ramet growth were shown to be inversely correlated in a separate and small study (Franklin 1969c).

Rooted cuttings to preserve phenotypes selected for high, average, and low oleoresin yield show differences among clones in height growth, volume growth (because of larger diameter and higher taper), stem straightness, and branch size (fig. 152).

On the basis of the limited data given here, clonal tests may be a device for estimating genotype of wild trees and the range of variation. Growth of seed orchard clones might serve as the basis of initial roguing for vigor, tree form, and probably other traits.

Correlation of Growth Rate With Other Traits

Tree growth and yield per unit area are the most important traits with which tree breeders and foresters work. Maximum wood yield from improved strains can be obtained only if there is no loss to disease, or some other trait affecting survival of trees, or reduction of tree or wood quality that lowers value (fig. 153).

Traits negatively correlated with growth (that is, an increase in one trait results in a decrease in other traits, such as resistance to disease or stem straightness) present formidable obstacles to progress in breeding. Fortunately, no high correlations of this type have been encountered in slash pine, but there might be some with a low correlation. Traits positively correlated with growth (an increase in vigor produces an improvement in certain other traits) facilitate progress in breeding, while the lack of correlation among traits (they combine at random) presents problems but does not create important obstacles. Most of the relationships between growth ratio and other major traits in slash pine seem to be of the latter two types, although many are not precisely established.

In contrast to researchers concentrating on one trait, tree breeders and foresters are largely concerned with the performance of the entire tree and stands of trees. The overall performance is important although more difficult to evaluate than individual traits (Dorman 1967), and clonal selection for seed orchards may be based on 10 or more traits (Cech 1959). However, breeding plans can be designed to place emphasis on important traits, such as resistance to rust infection or drought or a product such as oleoresin.

It has been mentioned in this section on growth variation among trees that fast-growing families, in comparison with controls, may have higher field survival, better average resistance to rust infection, acceptable form, and wood of good quality. Examples are given of improvement in growth rate plus one or more important traits. When Barber (1964) ranked 15 open-pollinated families and 4 control lots of seedlings 8 years old for eight characteristics, he found certain groups were high or low for all traits. Thus, some families inherited the good combination of good traits, including height growth, for which the maternal parent was selected. Performance for only 8 years may be questionable, but the trees averaged over 20 feet tall; and some foresters think in terms of a rotation of 20 years for slash pine. Results of the study have an important bearing on the benefits of selecting trees for multiple traits.

Additional information about correlations among traits will be given in the following reviews of variation among trees in traits such as stem and crown

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Figure 152.—Clones from rooted cuttings of selected slash pine trees vary widely in wood volume, oleoresin yield, crown form, and stem form. Wide inherent differences among forest-grown trees and close similarity within clones are demonstrated. The two large trees in second row from right were cuttings from the largest tree in one stand; other clones were from trees with average volume but differing in branching characteristics. Trees with small branches, fourth row from the right, may make good height growth but small diameter or stem volume growth. Thus, stem taper is important in selection.

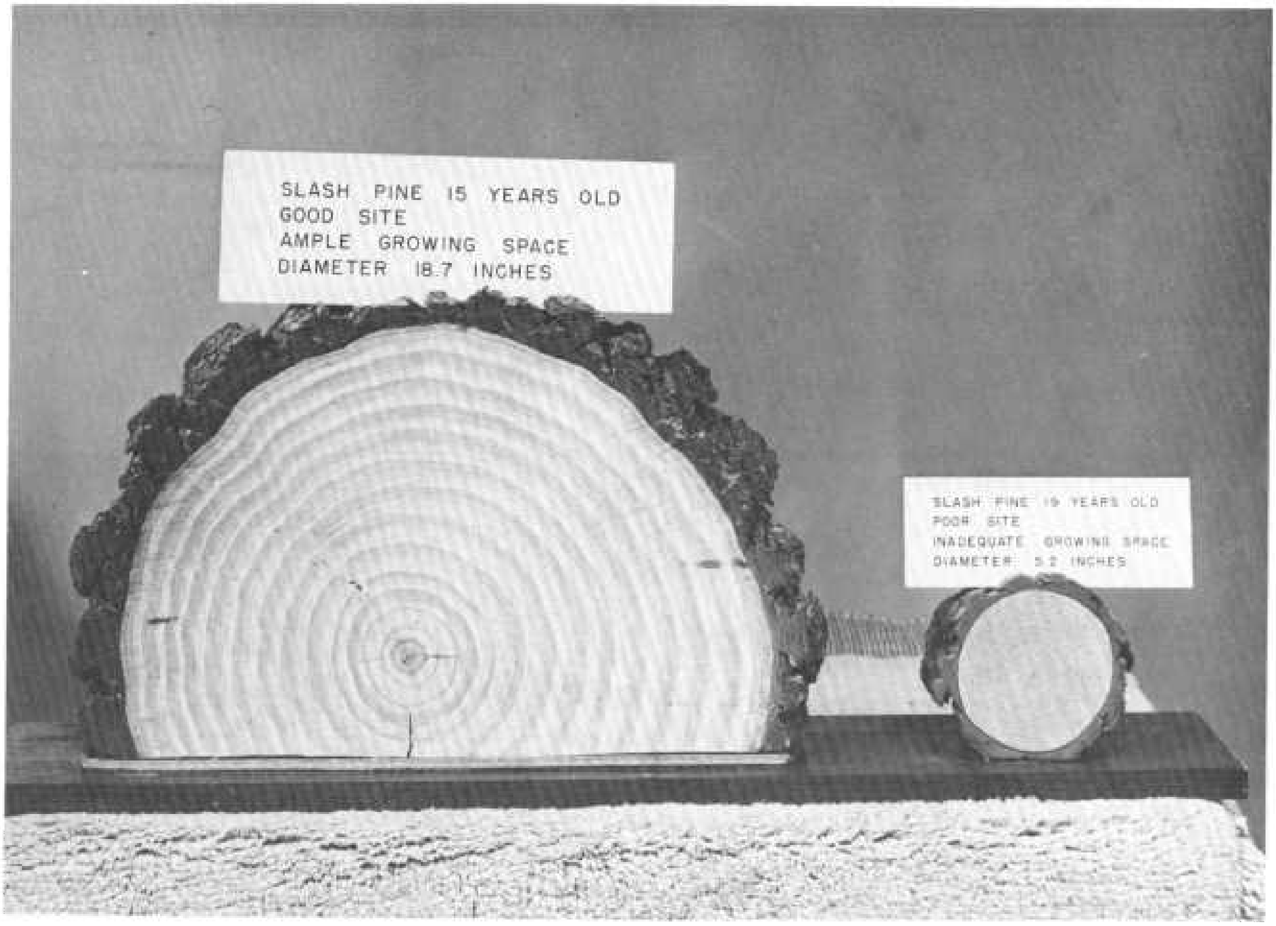
form, resistance to pests, wood properties, and others. This is an important subject deserving intensive study.

Environmental Effects on Growth

At one time it was widely accepted among foresters that environmental factors were responsible for obvious differences among trees in growth form, resistance to pests, and wood properties. Forest tree breeding and genetics research have shown that environmental factors are important but that genetic factors play a far more important role than expected.

Research has shown also that there are inherent differences among trees in the response to certain environmental factors. As shown by Clutter and Bennett (1965), site and spacing strongly influence diameter growth (table 5). Progeny tests reviewed here also show large differences in growth due to genetic factors in the same general environment of each test plantation.

Genetic factors are responsible for differences among trees or progenies to environmental conditions other than spacing and site. For example, survival of 14 slash pine families ranged from 36 to 93 percent, while the commercial controls were 80 percent, indicating large differential response to drought during the first year in the field (Schultz and Wilhite 1969). Height of commercial seedlings was 1.17 feet, and the average for all families was 1.50 feet, but the difference was not significant.



F–478010

Figure 153.—Sections from the butts of two slash pine trees showing extremes in growth. (Pomeroy and Cooper 1956)

Progeny from crosses of individual trees selected for growth and form were among the tallest in the test, 1.7 feet, or 45 percent taller than the control. A few of the taller families had survival higher than the commercial control. Beineke and Perry (1966) found large differences among open-pollinated families in their ability to withstand planting shock and found, also, that there were differences in plant size, plant height, root-shoot ratio, root habit, and root regeneration. The results show that the factors causing some progenies to survive well at one time of the year are not correlated with good survival at other times of the year.

In fertilizer studies with slash pine clones, it was found that trees of several clones grew 20 to 50 percent more when fertilized than not fertilized, but other clones were either unaffected or adversely affected by fertilization (Schultz 1969b). The clones varied widely in their ability to utilize added nutrients.

Open-pollinated families vary in their ability to absorb nutrients, as shown by a study with potted seedlings in Texas (Walker and Hatcher 1965). In Florida in three tests, it was found that certain progenies made poor growth in unfertilized soil and responded well to fertilizer application, while others made good growth in unfertilized soil but were little affected by fertilizers (Pritchett and Goddard 1967). However, certain families made good growth in unfertilized soil and responded well to fertilizer also. After 5 years, height of untreated seedlings of 12 progeny lines and 3 bulk seedlots used for controls was 4.38 meters, and those given fertilization, cultivation, and irrigation (the most effective of seven treatments) averaged 5.55 meters, or 27 percent taller. Among the 12 progeny lines, height growth increase varied from 9 to 55 percent. After additional studies involving field as well as greenhouse tests, Goddard and Smith (1969) also concluded that slash pine families varied in response to cultural treatments. Differential response to cultural measures such as fertilization, detected by field tests 3 to 5 years old, were not strongly indicated by year-old seedlings. Also, they found that greenhouse performance of families or lines was not related to growth in the field.

Growth rate of individual trees within families is controlled by genetic factors as well as that of families. Wide variation occurs within families whether open-pollinated, cross-pollinated, or selfed. Choice of parents for mating will change the average growth rate of slash pine but will not make trees uniform for growth rate. This is typical for polygenic traits. Certain environmental factors may act with genetic factors to increase range in growth rate among trees in planted stands over inherent differences.

Concluding the discussion of variation and growth in slash pine, all the evidence shows that inherent rate of growth varies widely among slash pine trees and that large gains by breeding are possible. Growth rate improvement can be supplemented by improvement of other traits. Considerable improvement in yield is possible by phenotypic selection, but accurate evaluation of breeding value to obtain the largest gain is possible only by progeny testing.

STEM AND CROWN FORM

The general form of slash pine is probably better than that of loblolly pine but not quite so good as in longleaf and shortleaf pines. Stem straightness is fair to good but not excellent, stem taper is good, natural pruning is good, and branch size and angle are fair to good. These are only approximations but show that slash pine is generally favored in its natural range for its good quality and wood yield. Trees with extremely bad traits can be rejected if certain products are the aim. Extremely bad form results from stem crook, stem forking, poor natural pruning, or large branch size. Variation in stem and crown form are of sufficient importance to be a factor in silviculture and, also, in breeding.

Inasmuch as stem and crown form are important, their relationship with wood yield and other traits such as resistance to disease must be determined. Studies in inheritance of growth and other traits may include estimates of form also, as an indicator of tree quality. A decrease in stem or crown form, although small, might occur by chance with a decrease in resistance to disease or drought, to substantially lower the yield and value of progeny.

Problems have been encountered in studies of inheritance of stem and crown form in relating variation in characteristics to economic value. This phase of tree breeding research is continuing for various management objectives such as pulpwood or sawtimber. Some traits show continuous variation from very good to very poor, such as branch size and natural pruning. Stem forking may occur as a single defect or be repeated more than once. Form characteristics can be measured but not easily. In some instances ocular estimates are acceptable. It is easier in some instances to illustrate by photographs rather than mathematically the magnitude of differences among trees of traits in the stem-and-crown-form complex.

Environmental effects on crown size, natural pruning, and stem taper are well known, but in evenly spaced planted stands on a uniform site, close observations will reveal differences among individual trees. Freezing rain, diseases, hurricanes, and other environmental factors may change tree form but may affect stands as well as individual trees and can be recognized.

Phenotypic Variation

Slash pine is often found in even-aged natural or planted stands; therefore, comparisons in form among trees are easily made. Apparent differences in crown size and other traits encouraged research workers in oleoresin production and breeding for improved oleoresin yield to evaluate form as well as tree size.

Stem Forks and Straightness

An estimate of phenotypic variation among trees was made in a 20-year-old Florida plantation. Nearly 10 percent (811 trees) had at least one fork in the stem, and more than 25 percent of these had multiple forks. About one-third of the trees without forks had crooks or sweeps of varying degree. A total of 8,496 trees were examined (Mergen 1955c). In a later study of 363 trees among the group that rated high for oleoresin yield, about 3 percent were straight, 84 percent slightly crooked, and 12 percent very crooked. For branch thickness, 10 percent were classed as "fine," 75 percent as "medium," and 15 percent "thick." The trees were 20 years old (Squillace 1966c). Oleoresin yield was not correlated with tree form; about the same proportion of trees in various stem straightness and branch thickness classes were found among groups of trees rated as high, medium, and low yielders.

Natural Pruning

Evans *et al.* (1961) found that the coefficient of variation was higher for clear length of stem than for total height, d.b.h., or bark thickness in a 10-year-old plantation when they were preparing estimates of optimum plot size for progeny tests. For a plot of 20 trees, the coefficient of variation for clear length was about 7 percent, and for total height 3 percent.

Branch Angle

The angle of branches with the horizontal varies widely in slash pine. Although not directly correlated with economic value, branch angle can influence natural pruning as well as the number and size

Figure 154.—Slash pine branches orientated at a high angle with the horizontal maintain their tips in areas of high light intensity and do not prune as rapidly as branches in a horizontal position. Trees with slender crowns, such as the tree on the left, often grow as rapidly as trees with poorly formed crowns. (Barber and Reines 1956)

of knots which are important for pulpwood, poles, and saw logs (figures 154 and 155). Trees with short branches of small diameter and growing at nearly a right angle with the tree trunk are preferred for seed orchard clones and breeding stock if they are available with no sacrifice in volume growth per acre. The effect of growing space on rate of natural pruning is strong but will not overcome inherent defects. If all trees in a stand are of good general crown form, selection of crop trees for volume growth, freedom from disease, and other traits is facilitated.

Genotypic Variation

Silviculturists are interested in the inheritance of form characteristics in open-pollinated offspring, as was pointed out in the introduction to the discussion of tree-to-tree variation in growth rate. Certain tree breeding projects use one-parent progeny tests to screen plus-tree candidates for seed orchards. The information about inheritance of stem and crown form applies to problems in silviculture because maternal parents with a wide range of traits were used. Additional information is available from control-pollinated progeny and vegetatively propagated clones.

Half-Sib Progeny

In studies by the Ida Cason Callaway Foundation, there was a strong relationship between the traits of stem and crown form of offspring and the maternal parent (Barber 1964). Also, the relationships were strong in studies established in 2 successive years with seed of the same parent trees. Most trees were selected for a combination of good stem and crown form traits with good growth (figures 156 to 159), and poor stem and crown form with fast growth (figures 160 and 161). Crown form of progeny of good maternal parents is good (figures 157 and 159). There were large differences among families of 8-year-old trees in pruning height, and the performance of progeny in successive studies was similar (fig. 162). Ratio of crown diameter to total height varied from 0.38 to 0.54. Progeny of certain maternal parents shown in photographs are indicated in the figures. Tree C–6, whose progeny is identified with other families, was similar to C–4 (figures 160 and 161) in that it was fast growing, but natural pruning was poor and the branches long and large. Narrow-sense heritability estimates for natural pruning and crown width were 16 and 64 percent, respectively. Most of the variation in crown width, stem crook, and natural pruning was independent of height growth. There were significant differences among families in the number of trees with complete or partial forks in the stems of the young trees, although none of the maternal parents had the defect. It was concluded that selection of slash pine trees with a combination of good stem and crown form with high growth rate was possible, but variation among trees within families would remain wide.

Stem taper, although not intensively studied, probably varies among trees and should be considered in intensive selection of breeding stock. Among 115 half sibs of a tree above average for growth and form, there was a difference of about

F-522861

Figure 155.—Slash pine trees in a progeny test for oleoresin yield vary widely in number of branches, branch angle, branch size, and rate of natural pruning. Four trees to the left of the tree in the immediate foreground illustrate differences in these branch traits.

1.5 inches in stem diameter for trees of the same height throughout a range in heights from 18 to 30 feet. For six trees 29 and 30 feet tall, d.b.h. varied from 5 to 6.5 inches, which made the basal area of the largest tree 68 percent greater than that of the most slender tree (Barber and Dorman 1964).

Comparison of half-sib progenies in Florida at 4 years showed significant differences for branch diameter and branch angle but not for branch length. Heritability estimates were 18, 13, and 33 percent, respectively, for the three traits (Strickland and Goddard 1966b). It was pointed out that branch length and branch diameter were directly correlated with tree volume and that selection for good crown form should be accompanied by rigid selection for wood volume.

Selection for stem straightness in Australia was highly effective, as summarized in the preceding discussion of breeding for growth rate, and resulted in an increase in the number of trees with a combination of good traits (Nikles 1966).

Full-Sib Progeny

With important differences among trees in stem and crown form traits established by open-pollinated progeny tests, it is to be expected that full-sib families present in stands from seed orchard seed or produced by selective breeding would have marked improvement in form. Also, differences among families should be distinct if crosses are made among extremely good phenotypes and other phenotypes with less desirable form.

One of the first estimates of inherent defects in stem crook in full sibs came from progeny tests for oleoresin yield. One tree selected for high oleoresin yield had observable crook in the lower stem. Young offspring from this tree, either as a maternal or paternal parent in crosses with straight trees, had 50 percent more trees with crook than families of the same straight-stemmed trees in other crosses (Mergen 1955b).

Crown form as well as growth rate and resistance

466894

Figure 156.—Fifteen-year-old slash pine, C–37, with high vigor and good form. Although growing very rapidly, it has pruned itself well. The branches are not overly large and the trunk has little taper. The tree is 12.7 inches in diameter and 54 feet tall. This is an extremely good phenotype. Open-pollinated families are identified in the following figure, showing the range in crown width and natural pruning. At age 22, wood specific gravity at breast height was 0.52. (Dorman 1952)

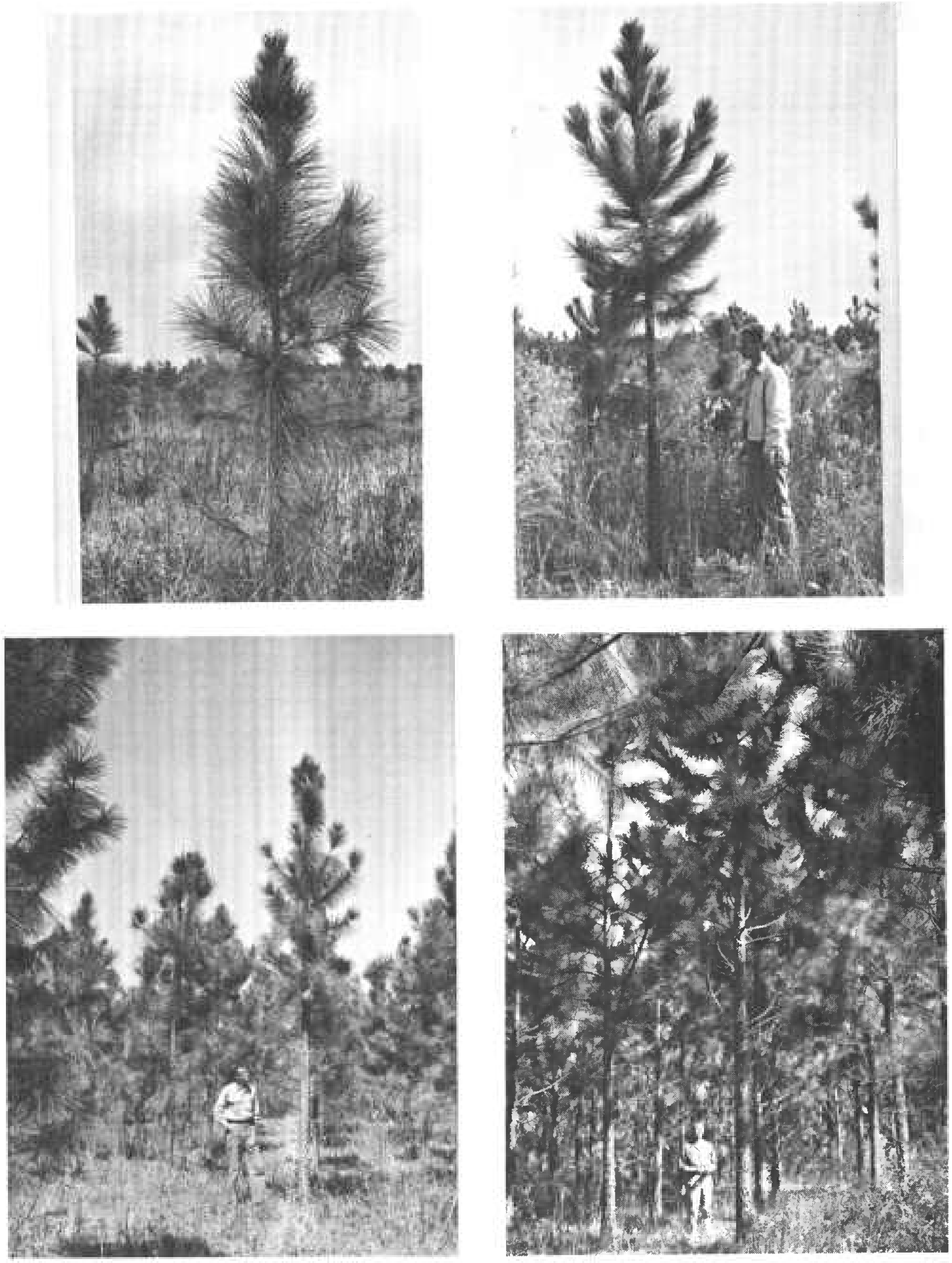


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Figure 157.—Fast-growing open-pollinated offspring of slash pine C–37 shows the tendency for good form and rapid natural pruning at an early age. Other trees in the same family have long branches or partial forks in the stem. These photos were made 3, 5, 6, and 9 years after planting. (Barber 1964)

F–522863

Figure 158.—Slash pine superior phenotype C–50 with excellent height growth, good branch characteristics and natural pruning, and about average diameter. Trees to the left of the banded tree are poorly pruned, and the branches are long and large in diameter. At age 15, C–50 was 8.7 inches d.b.h. and 56 feet tall. The photograph is at age 20. (Barber 1964)

to pests were estimated by polycross tests to rank clones of breeding value in seed orchards of the Georgia Forestry Commission. Although selected under a standard rating scheme, the grafted clones varied in form, and it was necessary to rank the clones for overall performance so the poorest could be removed. The full-sib progenies varied in the ratio of crown width to total height, and many in two separate tests had more slender crowns than controls, which were commercial lots from representative areas in the State (fig. 163) (LaFarge and Kraus 1967). A pollen mix of 30 clones was used, which may have reduced the extremes in

F–522864

Figure 159.—Open-pollinated offspring of superior phenotype C–50 have uniformly narrow crowns, nearly horizontal branches, and excellent height growth. (Barber 1964)

good and poor-formed families, but gave a good estimate of general combining ability. One clone, Telfair G–37, had nearly columnar crown (fig. 164), and the offspring had the most slender crown of all progenies and, also, was rated high for height growth and resistance to fusiform rust. Crown form may be very uniform in control-pollinated progeny of well-formed phenotypes (fig. 165).

Clonal Lines

Plantations of vegetatively propagated trees on a uniform site present the best opportunity for comparing the form of phenotypes selected in forest stands. It is necessary to establish the upper portion of the range in form as a goal to be reached when breeding for fast growth, wood quality, resistance to pests, and other traits deemed important at the time. When trees were selected in progeny tests for cloning, the ramet characteristics were significantly correlated with ortet characteristics for stem crooks per foot of trunk, degree of stem crook, size of branches, and crown-width ratio (Gansel 1966). Estimates of broad-sense heritability obtained from analysis of variance of two clonal plantations were: number of crooks per foot, 0.29 and 0.47; degree of crook, 0.30 and 0.38; size of branches, 0.31 and 0.48; and crown width/height ratio, 0.40 and 0.47. Yield of oleoresin was not significantly correlated with any of the crown and stem form characteristics studied.

Stem and crown form of trees planted at wide spacing did not vary among clones, although volume of fast-growing clones was three times that of slow-growing clones (Schultz 1972).

Ideal crown and stem form, expressed by seed orchard clones planted at wide spacing for a wide

466895

Figure 160.—Fifteen-year-old slash pine with high vigor but very poor form. It has been growing nearly an inch a year in diameter, but it is poorly pruned, the branches are large, and the stem has excessive taper. The tree is 13.6 inches in diameter, 48 feet tall, and it is one of the largest trees in the plantation. This C–4 tree is growing within a few feet of good phenotype C–37. (Dorman 1952)

F–522865

Figure 161.—Open-pollinated offspring of minus phenotype C–4 often have crooked stems with high taper and poor natural pruning and long, large, and crooked branches, while other trees, at left, have straight stems and large crowns. (Barber 1964)

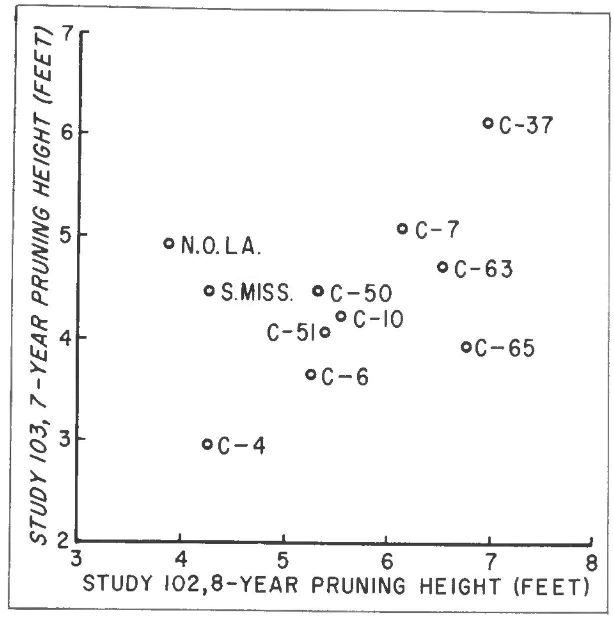

Figure 162.—The relationship of pruning height in studies 102 and 103 for lots with common maternal parentage. Average height at 7 years ranged from 17 feet for C–6 and 18 feet for C–4, to 22 feet for C–37. Groups identified by name are controls. Certain maternal parents and offspring are shown in preceding photographs. (Barber 1964)

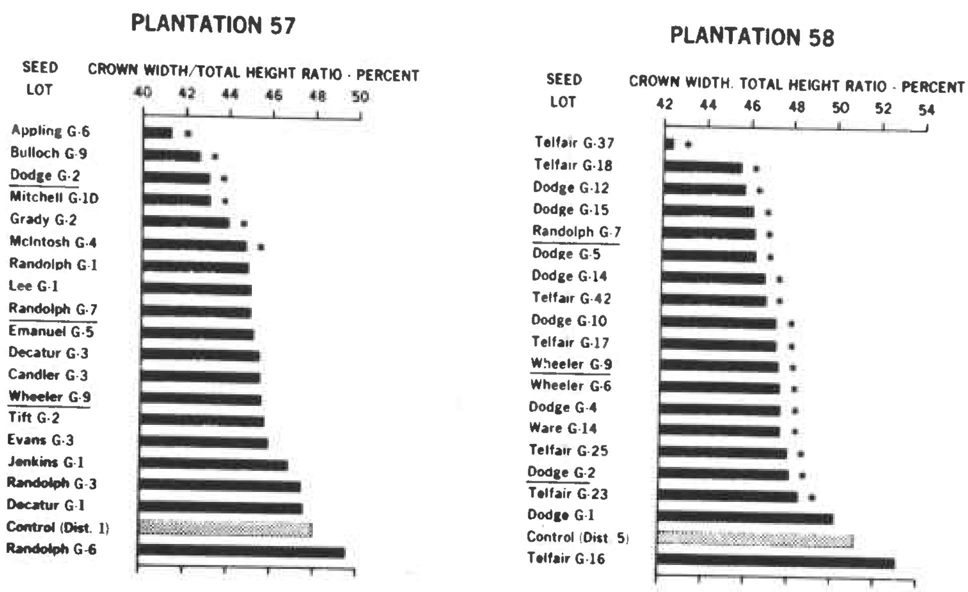

Figure 163.—Progeny lines and controls in plantations 57 and 58 ranked according to the crown width/total height ratio. Underscored progenies are common to both plantations. (* indicates progenies with significantly narrower crowns, at the 5-percent level, than the control.) (LaFarge and Kraus 1967)

Photo courtesy of Georgia Forestry Commission

Figure 164.—Highly vigorous, well-formed, disease free grafted slash pine clone 6 years old in a Georgia Forestry Commission seed orchard. Progeny of this clone are superior in growth rate, crown and stem form, and resistance to disease. This clone demonstrates the feasibility of selecting for a good combination of good traits.

variety of forest products, may not always be best, although still acceptable for seed production.

Correlation of Tree Form With Other Traits

The relationship of growth rate, oleoresin yield, and resistance to pests to stem or crown form has been noted in connection with details of tree-to-tree variation. Although most progeny test results are for rather young trees and this relationship may change, no important problems have been encountered in combining good traits of form with others. This facilitates breeding because tree form in slash pine varies from excellent to bad, which means low-value products.

We can breed for volume growth and expect to get little or no stem crook or partial forking; on the other hand, if we breed for small crown size, we will almost certainly get a reduction in volume growth. The relationship of crown size in extremely small-branched and well-pruned genotypes to tree growth and, what is more important, to volume growth per acre remains to be established. However, if value of forest products is increased by improving tree form, this might offset a loss in growth. If it is possible to achieve a gain in both, so much the better.

Small differences in stem and crown form may be low in economic importance. Thus, tree breeders should not let small problems in breeding for form interfere with work on traits influencing volume growth per tree or per acre that are highly correlated with forestry returns.

Although environmental factors can influence tree form, the inheritance of good and bad traits is so strongly indicated that silviculturists should act on the assumption that phenotypically poor-formed trees will more often than not produce poor-formed offspring.

Indications are that bad form might be bred out of slash pine in one or a very few generations. When improved strains have good stem and crown form, breeders can concentrate on other traits. A possible exception might be in the case of strains being bred for certain high-value wood products. It must be noted that breeding for improved form is quite different from breeding for tree growth and wood volume yield, which might require several successive generations for any substantial increase.

RESISTANCE TO PESTS

Insect and disease enemies of slash pine that affect wood volume growth and value of trees must receive major attention of tree breeders because they offset improvements in other traits. Pest enemies that reduce flower, cone, and seed production may be important in seed orchard culture also.

Small losses to pests might be overcome by adjusting silvicultural treatments, for example, increasing trees planted per acre, but large losses that make the difference between a well-stocked stand and a plantation failure are difficult problems (fig. 166).

Slash pine volume growth and tree quality are often greatly reduced by fusiform rust, the most important enemy. Slash is also severely attacked by annosus root rot but in small areas. Susceptibility to littleleaf has been shown, but slash pine losses

F–522151

Figure 165.—Full-sib slash progeny with good combination of good traits from crossing two superior trees. The offspring have uniformly good form.

F–522866

Figure 166.—In this 12-year-old slash pine plantation, near Cordele, Georgia, nearly half the trees were infected with fusiform rust, about 12 percent were dead, and losses are expected to increase. (USDA Forest Service 1958)

are very low. Trunks of slash pine are attacked by various beetles, and flowers and seeds are injured by a variety of pests. The species does not share longleaf's susceptibility to extensive damage by brown spot, nor shortleaf's to littleleaf, nor the tip moth damage suffered by loblolly and shortleaf pines. Slash and loblolly pines are about equally susceptible to fusiform rust in planted stands over large areas such as Georgia, South Carolina, and Mississippi. A recent survey of rust incidence was summarized by Phelps (1973).

Variation and inheritance of resistance among individual trees will be discussed for various pests because each one presents a specific problem in tree breeding.

Southern Fusiform Rust

An important portion of the natural range of slash pine and the area in which it is extensively planted outside the range falls within the zone of highest severity of attack by fusiform rust, as given by McCulley (1950) and Wakeley (1954a), also illustrated in the chapters on variation among trees in loblolly and longleaf pines, and by the map from Phelps (1973). It has been estimated that fusiform rust destroys 97 million cubic feet of potential pine growth each year (Neelands 1962).

Slash pine seedlings in nursery beds can be protected from fusiform rust by spraying, but there is no effective treatment for planted or naturally seeded stands. Thus, genetic control seems the only feasible method to date. In a Georgia plantation 6 years old, 66 percent of the branch infections 0 to 4 inches from the main stem spread to infect the stem within a year (Harms 1961). In a Georgia plantation with 32 percent of the stems infected by rust, only 14 percent of the infected trees had potential for early sawtimber production, and 91 percent of all mortality was attributed to rust (Jones 1972).

Phenotypic Variation in Resistance

Rust spores are produced in great numbers and wind disseminated; thus, most young trees are exposed. Infection each year may be high or low because it depends greatly on weather conditions (Siggers 1949), but some trees are not infected after repeated exposure. In the Alabama Coastal Plain region, slash pine plantations 5 to 8 years old averaged 48.6 percent infection, while those 9 to 12 and 13 to 16 years old averaged 45.8 percent and 36.8 percent, respectively (Goggans 1957). In the Alabama Piedmont, which lies north of the area of highest severity for fusiform rust, infection was 24.9 percent (Goggans 1949). In both areas, infection percent in slash pine was not significantly different from that in loblolly pine.

In southeastern Louisiana, infection of tree trunks varied from 23 to 39 percent of the trees in the study, but it was not related to different spacings or seedling grades (Wakeley 1969b). A survey of slash pine plantations on certain forest industry lands from South Carolina to Mississippi provided the basis for ranking counties in six classes of infection, from 0 to 15 percent and from 60 to 75 percent. In northeastern Florida, infection rate was low, increasing to the North, with several counties in the northern part of the slash pine range in Georgia classed as having 60 to 75 percent of trees infected (Goddard and Strickland 1970). Thus, damage to slash pine varies from low to high among geographic locations and among trees within stands.

Genotypic Variation in Resistance

Although trees free of infection can be found, inherent resistance in them is suspect because the trees were perhaps lightly infected and the branches pruned before the stem was involved, or the trees could have escaped exposure by some unusual combination of environmental factors. It was not until progeny tests indicated wide differences among families in kind and amount of infection by fusiform rust that genetic factors were seriously considered as contributing to variation. Early progeny tests with slash pine were located in northeastern Florida, where infection rate is low and families were not exposed to rust.

In an area of high incidence of infection in Georgia, offspring of maternal parents free of rust varied from 38 to 91 percent trees infected at 3 years in field plots. At 6 years, percent of trees free of rust among controls and families was 19 to 88. Significant differences occurred among families and between families of rust-free parents and controls (Barber 1964). The maternal parents were selected in plantation at 15 years of age, and lower branches were naturally pruned on many trees. Rust infection in progenies was only weakly correlated directly with height growth.

Inoculation techniques had to be developed for precise tests of resistance. Early tests with these methods showed variation in susceptibility among open-pollinated families of selected trees. Jewell and Mallett (1964) found that families of two rust-free parents were 40 to 50 percent infected over a 2-year period of tests, while those of a third rust-free tree and three infected trees were 89 to 99 percent infected. With a method described for all-or-none traits by Goddard and Arnold (1966), heritabilities calculated were: Resistance to initial infection 0.199 ±0.092; resistance to disease development after infection 0.253 ±0.121; and combined resistance to canker formation 0.237 ±0.100 (Arnold and Goddard 1966). These results were based on tests involving 22 open-pollinated families of selected trees.

Field plots in Georgia, where rust incidence is high, had a higher percentage of rust-free trees in six control-pollinated families than in any open-pollinated group after 5 years (fig. 167) (Webb and Barber 1966). Among 3 commercial control seedling lots and 18 control- or open-pollinated families, rust-free trees varied from 60 to 98 percent. Six of the 11 control-pollinated progenies and 2 of 7 of the open-pollinated progenies had more disease-free trees than the best control group. At 15 years, 27 open-pollinated families varied from 0 to 92 percent in number of rust-free trees, and wood volume per plot was highly correlated with percentage of rust-free trees. There was an average of 141 percent more rust-free trees in the 10 best progenies over the controls (Sluder 1972).

Also in Georgia, a polycross test of seed orchard clones with a pollen mix of 15 clones showed wide variation among families in susceptibility to rust (LaFarge and Kraus 1967). Several families that ranked high for resistance to rust were in the top ranks for height growth and crown form also. The pollen mix may have held down the extremes in percentage resistance or susceptibility but was a useful device in screening clones for overall performance.

Test plantings in Georgia and Florida to rate a large number of seed orchard clones for resistance to rust showed wide variation in infection rate for open-pollinated seedlings from seed orchards or from controlled pollinations among clones. Consistent disease ratings for half-sib families were evident at relatively high levels of rust, and full-sib families at low levels of rust infection. Ratings for resistance to rust infection were more consistent for full-sib than for half-sib families (Schmidt and Goddard 1971).

Jewell and Mallett (1967) used nursery inoculation techniques for testing resistance. They observed 48 percent infection in families from crosses

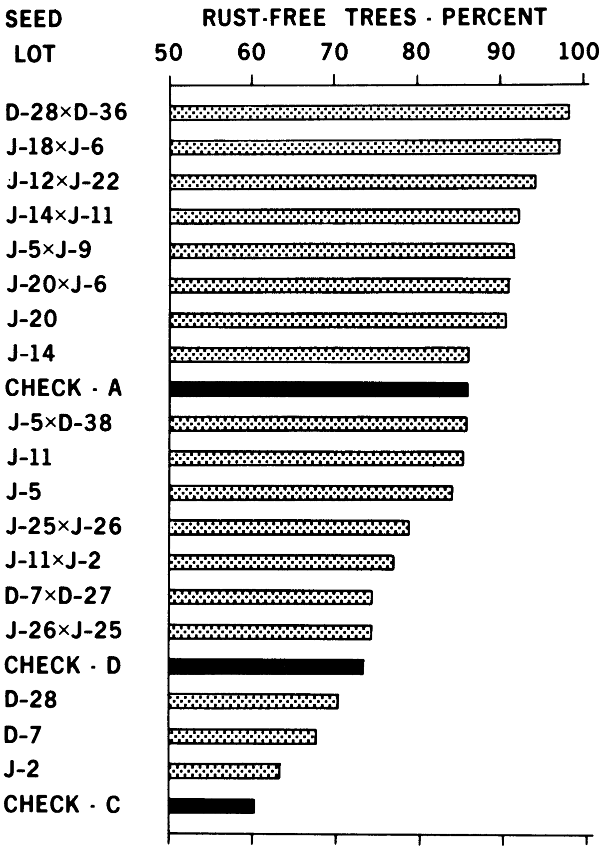

Figure 167.—Open- and control-pollinated progenies and commercial checks varied significantly in percent of trees free of rust, but the checks contained fewer rust-free trees. (Webb and Barber 1966)

of rust-free trees, 72 percent in crosses of rust-free with infected trees, and 97 percent in families of crosses among infected trees. Thus, nursery inoculation and field tests are in agreement in showing that wide variation exists among slash pines in resistance to fusiform. The relationship between the two types and utility in creating resistant or immune strains with good growth and form are less well known.

Seed of disease-free trees is a better risk than that from infected trees. Some disease-free trees may be phenotypically resistant and not produce offspring with meaningful resistance, but trees with visible evidence of infection are obviously susceptible. Progeny of controlled crosses of disease-free trees give the best estimates of the amount of resistance that might be obtained from the use of seed orchard seed.

In the section on geographic variation in slash pine, studies were reviewed showing differences in resistance among certain families after inoculation with rust cultures from different geographic locations.

Relation of Infection to Growth Rate

Early observations of rust infection patterns in stands and plantations indicated fast-growing stands had more infection than slower growing stands used for comparisons. Increased growth rate may have been attributable to site, cultivation, fire, and so on. The observations on this subject were reviewed briefly by Goggans (1957). The possibility of a negative correlation between susceptibility to rust infection and growth rate caused concern among tree breeders. Thus, special attention has been given to growth rate in tests of resistance.

Evidence is accumulating that fast-growing trees may sometimes have more infection, based on open-pollinated progeny tests, but that certain families and individual trees may have not only fast growth but also high resistance to rust (Barber 1964; Webb and Barber 1966; LaFarge and Kraus 1967; Kraus 1973). Fast-growing trees in planting tests of nursery selections and seedling grades have not shown that fast-growing trees have more infection than slow-growing trees (Barber and Van-Haverbeke 1961; Wakeley 1969b). Cultivation and fertilization increased rust incidence and height growth in slash pine, but the more resistant populations remained consistently less infected than their susceptible counterparts regardless of treatment (Dinus and Schmidtling 1971).

Although wide variation in susceptibility to rust has been demonstrated in slash pine, a large job remains to be done by tree breeders to utilize resistance in improving seed orchard clones. This must be done before improved strains become economically significant in forestry practice in the slash pine region.

Minor Diseases

Breeding for resistance to minor pests may not be justified at this time because more important traits for yield have higher priority, but it would be wise to insure that breeding does not increase susceptibility to minor pests. Should this occur, losses to minor pests could offset some of the gains from improvement of other traits. Some of the minor pests that have been observed to vary in attack among individual trees will be mentioned.

There have been few studies of variation and inheritance to mycorrhizae, but it has been observed in studies of seedling growth that mycorrhizal condition as well as seedling grade could improve first-year field survival of slash pine seedlings (Jorgensen and Shoulders 1967). Seedlings have been observed to differ markedly in the species and frequency of fungi associated with their mycorrhizae. Most root systems appeared to be dominated by one or two symbionts. Roots of one seedling yielded seven different mycorrhizal fungi

(Zak and Marx 1964). Tests with control-pollinated, half-sib progenies of slash pine inoculated with *Thelephora terrestris* and *Pisolithus tinctorius* showed that parents of seedlings influence the degree of ectomycorrhizal development and that certain ectomycorrhizal associations can benefit certain progenies more than others (Marx and Bryan 1971). The relationship of mycorrhizal condition to seedling growth and survival is of interest because this may be a situation in which breeding for increased susceptibility to a fungus improves performance rather than reduces it. However, these are still speculations.

Hard pine gray blight caused by *Hypoderma lethale* Dearn. was observed to vary widely in infection rate among slash and loblolly pine progenies in Georgia. Based on components of variance of progeny means, heritability estimates ranged from 0.71 to 0.85 in separate polycross tests for slash pine, and in loblolly pine 0.86 to 0.90 for wind-pollinated progenies; half-sib progenies were 0.94 to 0.98. On a scale of 1 to 5, representing infection classes of 10, 30, 50, 70, and 90 percent, three loblolly pine progenies rated 1.2 to 1.7 for low susceptibility, and three rated 4.7 to 5.0 for high susceptibility over a 2-year period. In slash pine, families with the lowest infection incidence were rated 2.3 to 3.0, whereas the highest infection rated 4.3 to 5.0. No relationship was found between total height and intensity of damage from infection (Kraus and Hunt 1971).

Phenotypic variation in susceptibility to root rot caused by *Polyporus tomentosus* var. *circinatus* was recorded in two slash pine plantations at Athens, Georgia. The root rot was present in 29 percent of 182 trees with basal cankers, 5-year radial growth having been reduced up to 24 percent. Removal of all basal cankered trees during thinning should be considered, according to the author (Boyce 1967).

No strong differences among full-sib families of slash pine in susceptibility to *Fomes annosus* were observed in greenhouse test inoculations. None of the families showed immunity. Susceptibility did not vary with oleoresin-yielding ability of families (Kuhlman 1972).

Insects

In the field of resistance to insect attack, few observations have been made concerning variation and inheritance, but some small amounts of information are available. Merkel *et al.* (1966) observed the number of *Dioryctria* cone attacks on slash pine in relation to size of the cone crop. Correlation analysis showed that the number of *Dioryctria* attacks was positively correlated with the mature cone crop but that the number of cones attacked among trees, after adjusting for the effect of cone-crop size, was highly significant.

Large differences among trees occurred in infestation by a seedworm (*Laspeyresia anaranjada* Miller) in Florida (Merkel 1967a). Fifteen trees had an average infestation of 80, 76, and 67 percent per tree for 3 consecutive years, but 3 of the trees averaged only 47, 42, and 44 percent, or about half that of the 3 trees with the highest rate of cone infestation. Cone infestation by *Dioryctria amatella* (Hulst) and *D. abietella* (D. & S.) on 10 slash pine over 3 years was consistently low or consistently high independently of the total mature cone crop per tree; this suggests there might be inherent differences among trees in resistance to coneworms (Merkel *et al.* 1966). In a slash pine seed orchard Sartor and Neel (1971) classified five clones resistant to coneworms and two clones susceptible.

Stem infestation of young trees by *Dioryctria amatella* was studied in a clonal plantation and two progeny tests. In one study, large differences (0 to 42 percent) occurred in the degree of infestation among clones, the average being 13.6 percent; progeny ranged from 0 to 15 percent, with an average of 7.8 percent. In an additional study where all nine progenies had a common maternal parent, progenies ranged from 2.5 to 32.5 percent infestation, with an average of 19.7 percent. Two of the three clones with inherently high oleoresin yields were relatively susceptible, but the third was relatively resistant (Merkel *et al.* 1966).

Pitch moth attack on stems of slash pine clones was observed to vary greatly in Florida. Ten percent of high-oleoresin-yielding clones were attacked, while 5 percent of those in the low-oleoresin group showed evidence of attack. Within the high-oleoresin group, some clones appeared resistant, although others were highly susceptible (Schultz 1969b).

Preferential attack by the black turpentine beetle (*Dendroctonus terebrans*) on slash pine trunks in northeast Florida was observed by Smith (1963), who determined that previously attacked trees were, conservatively, 12 to 16 times more attractive to attack than those previously unattacked. Inherent differences among trees in susceptibility to attack have not been studied.

Resistance in Species Hybrids

Slash pine has certain disease enemies from which other major southern pines are free. Thus, hybridization among species is one possible method of achieving resistance in improved strains. However, it has been shown that the individual tree, either slash pine or the one to which it is mated, strongly influences the degree of resistance in the hybrid (Jewell 1966; Schmitt 1968). Offspring of crosses between slash pine and other species are described in the chapter on species hybrids. Geographic location of slash pine parent trees and those of other species may influence inheritance of resistance, as shown in the chapter on racial variation.

Wide phenotypic variation among trees has been shown to occur with regard to disease and insect enemies, and strong inherent resistance occurs in a few individuals. Inherent resistance to fusiform rust, the most important enemy of slash pine, has been consistently demonstrated in open-pollinated progeny, control-pollinated progeny, and species hybrids. Creative breeding to produce highly resistant strains with good traits for tree growers remains to be accomplished, but the groundwork has been laid. High susceptibility to disease and insect attack apparently occurs in connection with improvement of certain important traits, but some clones, families, and individual trees exist where this is not true. Thus, breeding for a good combination of good traits is possible, but tree breeders should make sure they are not also including bad traits.

FLOWERING, SEED, AND SEED PRODUCTION

Fortunately, the widely planted slash pine species is in general a good seed producer, requiring no special silvicultural treatments for regeneration. To be sure, it is not as good in total seed production as loblolly pine, but it is better than either longleaf or shortleaf. In any event, its seed production characteristics have assumed vital significance in the intensive breeding programs aimed at creating improved strains.

Seed Production

Open-grown and vigorous slash pine seedlings may produce an occasional conelet 3 years from seed, but consistent flowering does not begin until trees are nearly 15 years of age and crowns are large. Grafted clones of good seed-producing ortets may produce conelets after 3 to 5 years and pollen catkins a few years later. However, inherited frequency and abundance of flowering vary widely among clones.

In young slash pine seed orchard clones, 22 percent of the trees produced conelets the fourth year following planting and 77.1 by the eighth year. Grafted trees planted at 15- by 15-foot spacing had lower flowering per ramet and a smaller proportion of ramets flowering, but production per acre was higher than with wider spacing because of the greater number of trees (Goddard 1964). In 14- to 17-year-old rooted cuttings, broad-sense heritability was 0.50 for cone yields, and in 4- to 6-year-old air layers, heritability was 0.49 for flower production. Narrow-sense heritability for cone yield was 0.13 in 16-year-old control- and wind-pollinated progeny. The narrow-sense heritability indicated a low additive genetic component (Varnell *et al.* 1967). Significant interactions have been found between clones and treatments such as fertilization, irrigation, and cover cropping in affecting male and female flowering as well as nitrogen content of foliage (Barnes and Bengtson 1968; Bengtson 1969; Schultz 1971).

In seed production areas where trees are free of crown competition, cone yields vary widely among trees and strongly influence cost of collection (Webb and Hunt 1965).

Inbreeding or selfing lowers seed quality. Seed yield per cone, germination percent, and rate of germination are inversely correlated with inbreeding coefficient (Squillace and Kraus 1962).

Slash pine can be hybridized with certain other species, but seed yields are low and strongly influenced by the individual tree because of incompatibility (Critchfield 1962; Snyder and Squillace 1966).

Seed and Cone Characteristics

In addition to seed yields, seed and cone size vary widely among individual slash pines. In a seed production area, seed of individual trees varied from a low of 10,368 per pound to 25,699 per pound, averaging 14,418 (Webb and Hunt 1965). However, seed weight seems to have little effect on seedling growth. In a one-parent progeny test, seed of maternal parents varied from about 26 to 43 grams per thousand seed, but height of trees, varying from 22 to nearly 26 feet at 8 years, was not correlated with seed weight (Barber 1964). After 1 year in the field, seedlings from small, medium, large, and unsorted seed did not differ significantly in survival or height (Shoulders 1961).

Of a variety of seed size and color characteristics that have been studied, those having the highest heritabilities and the most likely to be useful in identification of individual trees were seed length and thickness, seed dimension, color, speckling, wing length, and wing ratio (Kraus 1967a).

Slash pine cones vary in shape from short ovoid-conical to long ovoid and in seedcoat from smooth to rough as a result of thick scales armed with short, stout spines (Mergen and Pomeroy 1954).

BARK THICKNESS

Tree bark is generally a waste product, thus lacking the importance in tree breeding attached to other traits which influence fiber yield. Variation in bark thickness can induce error into wood volume estimates because it is a substantial part of the wood-plus-bark volume.

Phenotypic variation in bark thickness seems to be fairly wide. In a study relative to plot size in progeny testing, bark thickness in a planted stand was determined in addition to total height, d.b.h., and clear length. For all these traits, the coefficient of variation decreased as theoretical plot size increased to about 20 trees (Evans *et al.* 1961).

In a one-parent progeny test, bark thickness of 8-year-old progeny seemed to be related to that of the maternal parent, but the number of families was small (fig. 168). The range in bark thickness for the maternal parents was about 0.8 inch to over 1.5 inches. The relationship of bark thickness to diameter inside bark varied among the 8-year-old families studied (Barber 1964).

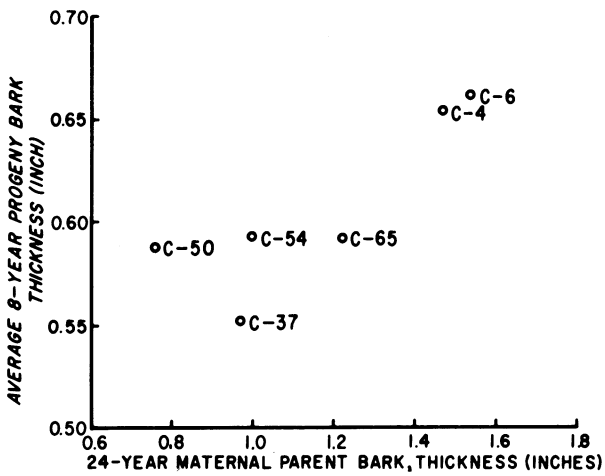

Figure 168.—The relationship of progeny bark thickness to maternal parent bark thickness. (Barber 1964)

Bark thickness was observed to vary among control- and wind-pollinated offspring and among clones. Two estimates of narrow-sense heritability from the progeny data were 57 and 33 to 67 percent. Broad-sense heritability was estimated to be 52 percent for the clones. In 15-year-old clones, bark thickness varied from 0.43 to 0.67 inch when corrected for differences in diameter (Squillace and Bengtson 1961).

WOOD PROPERTIES

The wood of slash pine being similar to that of other major southern pines and used for the same variety of products, problems and techniques in breeding for improved quality are comparable to those discussed for other species. Most of the information for techniques of studying wood properties and evaluating relationships of properties within trees given for loblolly pine is particularly applicable to slash pine and should be reviewed. Only a few additional sources of information and examples of certain minor differences among species will be given here.

Techniques for Studying Wood Properties

Estimates of the wood specific gravity and cellulose yields for the entire tree stem can be obtained from increment core samples of the wood at breast height. The correlation coefficients of breast height specific gravity with total bole specific gravity were r = 0.905, for water-resistant carbohydrates r = 0.901, and alpha-cellulose r = 0.800 (Zobel, Henson, and Webb 1960). The relationship of breast height specific gravity to total tree specific gravity in slash pine obtained by Taras and Wahlgren (1963) differed slightly from that obtained for longleaf pine.

In an Australian study involving 13 slash pine trees, there were high correlations between cell length and micellar angle, percent latewood and basic density, ring width and cell length, and ring width and basic density (Dadswell and Nicholls 1959).

Pulp properties, such as tear factor, breaking length, burst factor, and sheet density, for a whole tree can be accurately estimated from a limited sample of wood taken at 5 and 15 feet above stump height (Wangaard *et al.* 1967).

The relationship between corewood volume and certain chemical components at breast height and total volume was slightly higher for slash than loblolly pines (Zobel *et al.* 1959). Tracheid length variations occur within annual rings of slash pine, and the formation of latewood fibers starts at various distances from the beginning of the annual ring (Jackson and Morse 1965a). Spirality of grain in slash pine is almost constant from pith to bark, but in loblolly pine it slowly decreases outward (Gerischer and Kromhout 1964).

Differences in wood specific gravity between extracted and unextracted material were not significant among species but ranged from 5.85 percent for slash pine, 6.50 percent for loblolly, 6.72 percent for shortleaf, to 7.36 percent for longleaf pines (Taras and Saucier 1967).

Phenotypic Variation

The information given here was obtained from trees in natural stands or plantations and not from trees within families.

Wood Specific Gravity

Considerable differences in summerwood and specific gravity were found to exist between individual trees as well as plots in various parts of the slash pine natural range. None of the between-tree variation could be accounted for by such factors as total age, total height, crown-height ratio, tree spacing, or tree radius (Larson 1956). Wet and dry sites were sampled at each geographic location. The results were obtained as part of a study of the effect of environment on the percentage of summerwood and specific gravity of slash pine. As shown by the photographs of increment cores (fig. 58) in the chapter on geographic variation in slash pine, certain trees have wide annual rings and high summerwood percent and specific gravity. For example, in the plate on the right, the second core from the left was from a tree near Lake Butler in north-central Florida, and the data are as follows: 30 years old, 9.9 inches d.b.h., 82 percent summerwood, and 0.73 wood specific gravity. The core third from the left was from a tree near Ocala in central Florida, with data as follows: 22 years old, 12.2 inches d.b.h., 78 percent summerwood, and 0.63 wood specific gravity.

Later, Saucier and Taras (1969) sampled slash pine selections for seed orchards and comparison trees. For 198 trees averaging 34 years of age in Florida, average specific gravity was 0.57, and the range among trees was 0.46 to 0.70. Average diameter was 10.8 inches. The range among trees in Alabama, Louisiana, and Mississippi was similar to that in Florida. The average specific gravity for all comparison trees was 0.535, and for superior trees with approximately twice the volume it was 0.532.

Within less extensive areas than the natural range, trees vary widely in specific gravity, as indicated by values of 0.35 to 0.80 for 576 slash pine at ages 5 to 65 years in Mississippi (Mitchell 1959). In southern Florida, 11-year-old planted typical slash pine varied significantly in specific gravity from 0.46 to 0.65 among trees in a planted stand on an upland level site (Saucier and Dorman 1969). In northern Florida, the range in specific gravity of comparison trees and a group of plus trees was 0.40 to 0.67, although the plus trees were growing 2.6 times as fast as the comparison trees (Perry and Wang 1958). Planted trees in a northeastern Florida plantation varied from 0.50 to 0.65, and specific gravity was inversely correlated with diameter ($r = -0.01$) (Squillace *et al.* 1962).

The range in variation among trees in specific gravity indicates the characteristics of trees available for selection and quality of wood products obtained from natural stands. The heaviest wood is about 50 percent heavier than the lightest. The wood specific gravity of many of the young trees in natural stands compares well with the range of 0.56 to 0.68 for trees 150 to 200 years old, as studied by Mohr (1897).

Extractives

The specific gravity of unextracted increment cores is higher than that of extracted cores, in slash pine the difference being about 5.85 percent. The wide variation among individual trees in extractives is indicated by standard deviation of 3.58 percent. Correlation coefficient for the relationship between extracted specific gravity and unextracted specific gravity in slash pine was $r = 0.91$.

Spiral Grain

Planted trees in South Africa showed the angle of spiral grain was almost constant from pith to bark, while in loblolly pine it decreases outward. In slash pine about half the trees had right-handed spirality and the other half left-handed spirality, with variation among trees ½° to 5° (Gerischer and Kromhout 1964).

Pulp Properties

Significant differences occurred among 24 randomly selected slash pine in Georgia for paper strength properties of tear, burst, tensile strength, and stretch (Einspahr *et al.* 1962) and among 7 trees for tear factor, breaking length, burst factor, and sheet density (Wangaard *et al.* 1967).

Fibril Angle

Trees of the same age and similar in vigor, as expressed by diameter, size of crown, and early increment in basal area, differ in the size of fibril angles in comparative annual rings from the pith (Hiller 1954). Fibril angles among three branches of the same whorl did not differ in a Georgia study, but the angle was different among different trees (Jackson and Morse 1965b).

Genotypic Variation

With phenotypic variation as a basis for selecting study trees, inherent differences among trees in wood properties have been shown by comparing clones and wind- and control-pollinated families.

Wood Specific Gravity

Grafted clones, with three annual rings, from ortets with specific gravity ranging from 0.53 to 0.70 and averaging 0.59 varied significantly in both specific gravity and tracheid length. The range in specific gravity among clones was 0.30 to 0.40, and heritability for four methods of computation was 0.46 to 0.63. Variation within clones was much less than variation among clones (fig. 169) (Zobel *et al.* 1962). There was no association between stock and graft for either specific gravity or tracheid length, or for the relationship between specific gravity and tracheid length.

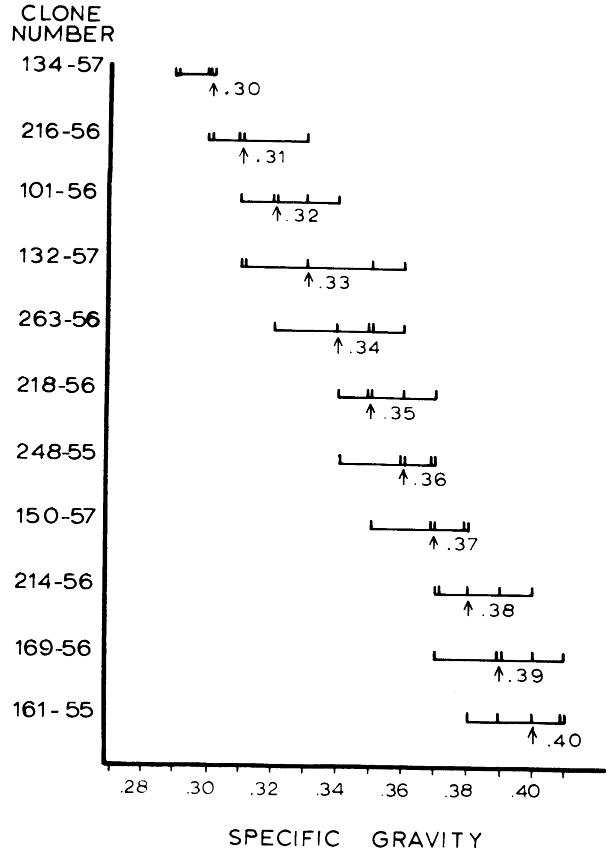

Figure 169.—Variation in specific gravity within and among young slash pine grafted clones. The 11 clones shown here had average specific gravities from 0.30 to 0.40. Note the spread of values of the five trees (ramets) within a clone and the complete lack of overlap between high and low specific gravity clones. The arrow and number indicate the average for the five ramets of any one clone. The short vertical lines indicate the position of each ramet in a clone. (Zobel *et al.* 1962).

In 5-year-old grafted clones from 24 slash pine trees ranging only from 0.579 to 0.597 in specific gravity, estimates of heritability for 11 characteristics of the wood were 0.25 to 0.84. Correlations between several wood and fiber properties such as fiber length and fiber strength, specific gravity and percent summerwood, pulp yield and lignin and extractives indicate that expected gains from breeding are not independent and are not entirely additive. The 136 correlations between wood, fiber, and handsheet characteristics showed that both direct and inverse relationships existed. Genetic gains, as computed, varied among wood properties (Einspahr, Goddard, and Gardner 1964). Close attention should be given to the various relationships among individual traits before objectives are established in breeding for improved wood and pulp properties.

In 12- to 14-year-old clones of rooted cuttings of seven trees selected for high, average, or low oleoresin yield (not for wood characteristics), broad-sense heritability for specific gravity was 0.73 and summerwood percent about 0.48. The range in specific gravity among trees was low, the correlation of wind-pollinated offspring with clones being 0.51, and control-pollinated offspring 0.44, both nonsignificant. The control-pollinated progeny means varied from 0.49 to 0.52, while individual trees within progenies usually encompassed a spread of about 0.10. Narrow-sense heritability in control-pollinated progeny for specific gravity was 0.56 and for percent of summerwood 0.26 (Squillace *et al.* 1962).

The parent-offspring correlation for specific gravity in 13 families was significant, and narrow-sense heritability of specific gravity was 0.43. There was no indication of a relationship between volume growth and specific gravity of progeny means that ranged from 0.084 to 0.153 cubic foot, or 82 percent greater volume (Goddard and Cole 1966). Thus, contrary to well-established opinion, fast growth did not result in wood of low specific gravity.

Tracheid Length

Studies with clones and progeny have usually paralleled those of specific gravity and indicated important inherent variation among individual slash pine trees. Zobel *et al.* (1962), studying specific gravity in young clones, found tracheid length varied significantly among clones, from 2.32 to 3.01 mm (fig. 170). Einspahr, Goddard, and Gardner (1964) showed high ortet-ramet fiber length correlation and computed correlations among many wood and fiber characteristics. Echols (1955) concluded that tracheid length was under rigid genetic control, observing that they were 20 percent longer in certain progeny groups than others. Fibril angle was correlated with tracheid length ($r = -0.956$) but not ring width. However, in a much larger study, tracheid length was negatively correlated with growth rate ($r = -0.34$) and specific gravity ($r = -0.16$). In these trees, radial growth versus specific gravity had a negative correlation coefficient ($r = -0.22$) (Strickland and Goddard 1966a).

Slash pine open-pollinated progeny from parents with relatively long tracheids have relatively longer tracheids than progeny of parents with short tracheids. Tracheid length varied between 1.09 and 1.57 mm in the parents, and progeny means varied from 1.05 to 1.27 mm (Jackson and Greene 1958).

Fibril Angle

In wind-pollinated progeny the correlation of fibril angle with the parent was high ($r = 0.877$) and also in control-pollinated families with the average

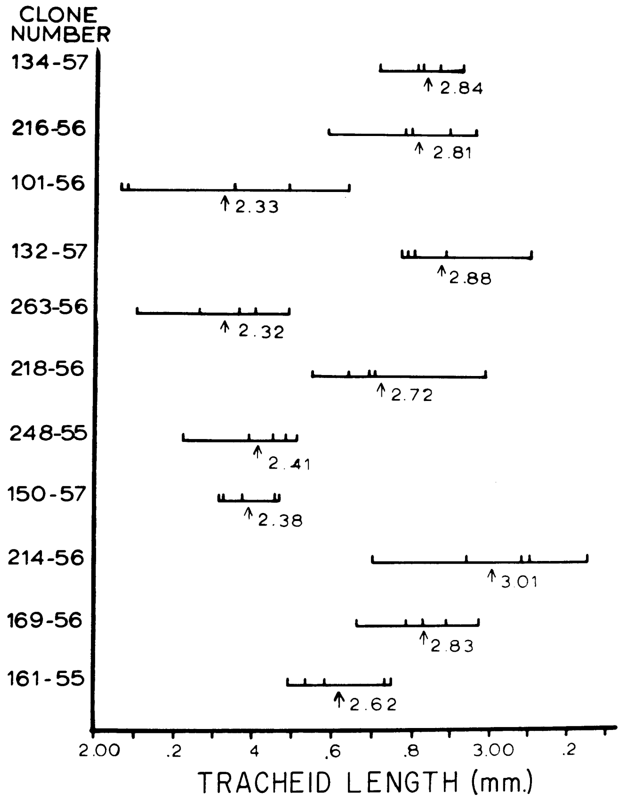

Figure 170.—Variation in tracheid length between and within slash pine clones. The clones are the same as those arranged for increasing specific gravity in the preceding figure. The figures show that tracheid lengths were independent of specific gravity, since the pattern of increasing specific gravities is not evident here. The arrow points to position of mean value for the five ramets of each clone. (Zobel *et al.* 1962)

of both parents ($r = 0.689$). Estimates of fibril angle were based on branch wood (Jackson and Greene 1958; Jackson and Morse 1965b).

Extractives and Tall Oil

A genetic gain of about 12 percent has been predicted, based on family plus mass selection for oleoresin yield. A proportional increase in tall oil yield can be expected because of the high phenotypic correlation ($r = 0.7$) between extractives yield and tall oil yield (Franklin *et al.* 1970).

Environmental Effects on Wood Quality

Environmental factors can influence wood properties directly or in connection with some other factors such as growth rate. The subject is difficult to study, in addition to which results are hard to apply because of the complex relationships among a large number of wood properties and environmental factors. Rangewide relationships were discussed in the chapter on geographic variation. A few local studies summarized here are only indicative of some of the relationships.

In a study of the effect of environment on the percentage of summerwood and specific gravity of slash pine, Larson (1956) found that the only stand variables that could account for any of the between-plot variation were those related to the moisture-holding capacity of the soil. He observed that high moisture-holding capacity, hence good site, produced the lowest percentage of summerwood after adjusting for differences in rate of growth among trees. However, Goddard and Strickland (1962) found no relationship between wood specific gravity and moisture holding capacity of the soil, and Miller (1959) found none between specific gravity and site. In Louisiana, late-season soil moisture showed a significant effect on the width of slash pine summerwood (Foil 1961). In three plantations 10 years old and one 17 years old on soils of different moisture relations, summerwood varied inversely with tree age but was apparently unaffected by the range of stand basal areas in the plantations studied. The width of the summerwood band during a given year was most strongly correlated ($r = 0.435$) with soil moisture level during October. Summerwood width was correlated with July, August, and September rainfall but values were low ($r = -0.246$ to $r = 0.268$) and with spring rainfall in all spring months except May, but values were lower than those for fall-month periods ($r = 0.164$ to $r = 0.183$). The study areas in general were in locations characterized by low soil moisture levels during September and October.

In some fertilization studies, slash pine has responded to treatment. McGregor (1957) found that an addition of 500 pounds of nitrogen per acre increased the growth of slash pine by 36.6 percent. Gilmore and Livingston (1958) found that an increase in growth rate followed a light application of NPK but that there was no significant increase in pulpwood volume after 19 growing seasons. Williams and Hamilton (1961) found that slash pine on the deep sand soils of the lower Coastal Plain of Georgia receiving supplemental fertilizers produced annual diameter increments over two growing seasons which were 26 percent wider than increments for the same period from unfertilized trees. Accompanying this growth rate was a 3- to 7-percent reduction in both the percentage of latewood and specific gravity. No significant difference occurred in the wall thickness of earlywood tracheids between fertilized and unfertilized trees. The changes attributed to treatment were primarily due to the addition of nitrogen and not phosphorus.

Suppressed slash pine with very small crowns may have discontinuous growth rings (Larson 1956).

OLEORESIN PRODUCTION AND COMPOSITION

Extraction of oleoresin from slash and longleaf pine trees for turpentine, rosin, and other products has been economically important in the Deep South for decades. Production has changed according to supply and demand and is currently downward as yields increase in byproducts produced by the pulp and paper industry. A history of the industry has been given by Ostrom and Squires (1949) and of production outlook by King *et al.* (1962).

Yield of oleoresin, produced commercially by wounding the tree, is influenced by the way the wounding is done. Uniform production methods must thus be used in studies of variation and inheritance in breeding for increased oleoresin yield. Past research in extraction methods and future trends has been given by Harrington (1965); the relation of yield to size and number of resin ducts, viscosity of oleoresin and exudation pressure within a tree has been summarized by Schopmeyer (1953). In plantations and natural stands, yield is correlated with tree diameter, length of live crown, ratio of crown length to total height of tree, and viscosity of resin (Schopmeyer and Larson 1955; Barrett and Bengtson 1964). Oleoresin yield and chemical composition vary over different parts of the tree (Kurth and Sherrard 1931; Roberts 1970).

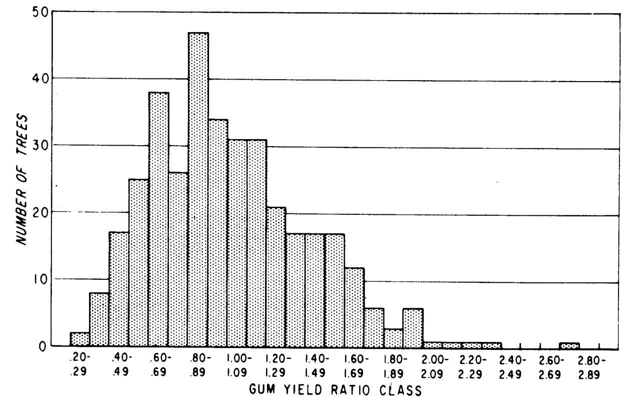

Figure 171.—Frequency distribution of gum yield ratios (yield of tree/average yield of trees of same d.b.h.) of 20-year-old planted slash pines. Basis, 363 trees. (Squillace 1966a)

Phenotypic Variation

Research in methods of extracting oleoresin (gum) according to face width, streak height, streak depth, year of work, season of year, and other variables provided an excellent opportunity to observe the wide variation in yield among individual trees. Oleoresin yield may have been the first trait in forest trees for which most of the environmental factors that might influence it were determined before tests of genetic factors were attempted.

Wyman (1932, p. 9) summarized the prevailing beliefs which showed the need for carefully controlled tests of oleoresin yield and composition. He states, "One of the most striking points that has come to light in the naval stores experiments conducted by this Station is the degree of variation which is found in the yield of gum from individual trees. It is not unusual to find trees alike in all external characteristics varying in their gum production by 100 percent and in some cases even 300 percent." Wyman describes a study of two slash pine trees selected for their similarity in external characteristics but with oleoresin yields differing by 100 percent over a 4-year period; he used the trees to examine wood characteristics that might be related to oleoresin production. Otte (1930) selected a high-yielding tree producing 2.03 times as much oleoresin as a comparable low-yielding tree for a study of the relationship of chemical composition to yield.

Yield of trees in a relatively uniform planted stand illustrates the variability of oleoresin yield (fig. 171). The best 5 percent of the trees produced an average of about 2.0 times the average, and the best 10 percent about 1.8 times the average. At the other extreme, a few trees produced less than 0.40 of the oleoresin of average trees (Squillace 1966a).

Genotypic Variation

Starting in 1941, the first information about inherent differences in oleoresin yield among individual slash pine trees came from breeding to improve yield for the naval stores industry. Outstanding phenotypes for yield were selected in natural stands; controlled pollinations were made among low-, average-, and high-yielding trees; methods were developed for rooting cuttings; and a clonal plantation was established with low-, average-, and high-yielding lines (Mitchell *et al.* 1942; Curry 1943; Dorman 1947a).

Oleoresin Yield of Clones

Heritability of yield in clones used in selective breeding for yield was 0.90; the trees are shown in figure 152, illustrating differences in form and growth. Yield among 13 clones after adjustment for tree size varied from 158 grams to 1,293 grams (Squillace and Bengtson 1961). Among 373 seed-orchard grafted clones in Florida, 4.3 percent had yields over 2 standard deviations from the mean, or an average of 1.82 times the average of all the clones. Certain clones had yields nearly 5 standard deviations above the mean (Goddard and Strickland 1965), and broad-sense heritability was 0.89 (Peters 1971). Among 137 seed orchard clones in Georgia,

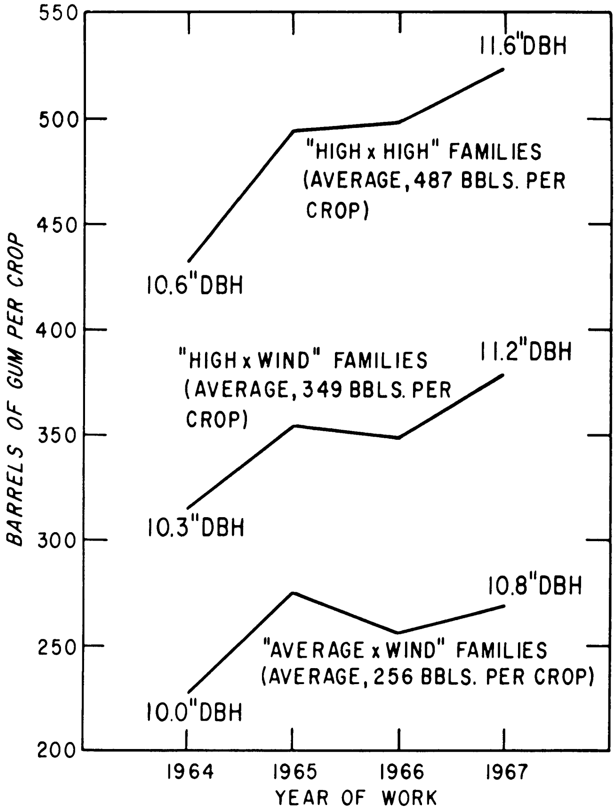

Figure 172.—Family means for oleoresin yield varied according to phenotypic characteristics of the parents, increased more with each year of work in high-yielding than low-yielding families, and did not cause a reduction in diameter growth of high-yielding trees during the test period. (Squillace and Harrington 1968)

yields ranged from 40 to 298 grams, and 5 clones were twice the average or more in yield (Gansel and Darby 1966).

Oleoresin Yield of Progeny

Progeny tests for oleoresin yield show that phenotypic selection is fairly accurate. Offspring of average phenotypes for yield averaged 256 barrels of oleoresin for a crop, based on 10,000 trees; offspring from wind-pollinated high-yielding trees averaged 349 barrels; and control-pollinated offspring of high-yielding trees averaged 487 barrels, or 91 percent more than average (fig. 172) (Squillace and Harrington 1968). The yield tests were started when the progeny were 19 years old, with commercial methods of extracting oleoresin being used (fig. 155).

In subsequent years we were able to evaluate progeny for oleoresin yield capacity at an early age in view of the high correlation of seedling yield with that of commercial-sized trees (Squillace and Gansel 1968).

Oleoresin Composition

Variation among trees in composition of oleoresin is important because of the products derived from pulping, discussed earlier under wood variation, and chemicals from crude oleoresin. Also, chemical composition may be a factor in resistance to insects or diseases, although the subject has not been well investigated.

Variation in oleoresin of individual trees was noted in early research. Black and Thronson (1934) found differences in optical rotation and other variations, and Otte (1930) found various deviations from the average in oleoresin from trees with high, medium, or low yields.

A tree with yellow oleoresin was found in Florida, although normally it is clear and colorless. The beta-phellandrene content of the turpentine fraction of its oleoresin was unusually high, 40.5 percent in contrast to 7.0 percent or less in average turpentine. Also, the turpentine yield of oleoresin was only 15 percent instead of 22 percent. All seedlings derived from selfing the tree produced yellow oleoresin, but none was produced from wind- or control-pollinations with trees producing typical oleoresin (Kraus and Squillace 1964a).

In clones of rooted cuttings, variation among ramets was small, but it was rather large among clones for alpha-pinene, beta-pinene, and beta-phellandrene in both stem and cortex oleoresin (Squillace and Fisher 1966). Parent-offspring regression coefficients for all the constituents of cortex oleoresin, except beta-pinene, were high (0.63 to 1.04), but those for beta-pinene in cortex and stem oleoresin were low (negative in the case of beta-pinene). To test the range of variation among trees, more trees were sampled and frequency distributions prepared (figures 173 and 174). The distributions for alpha-pinene in both cortex and stem oleoresin and for beta-pinene in stem oleoresin were normal, suggesting multigenic control for the compounds. The distribution for beta-pinene in cortex oleoresin was skewed to the left but was continuous and had a single mode. The distributions for myrcene in cortex oleoresin and beta-phellandrene in both cortex and stem oleoresin were definitely abnormal, being skewed and having a tendency toward bimodality (Squillace and Fisher 1966). Additional study indicated variation in content of beta-pinene and myrcene was controlled in two alleles at a single locus, with high amounts being dominant over low. No evidence of linkage between genes causing segregation for beta-pinene and myrcene was obtained. Myrcene and alpha-pinene content were negatively correlated (Squillace 1971).

Oleoresin exudation pressure and viscosity have been studied in slash pine because of the possibility of a relationship with yield. Among 215 trees, 2 had pressures of less than 5 atmospheres, while others

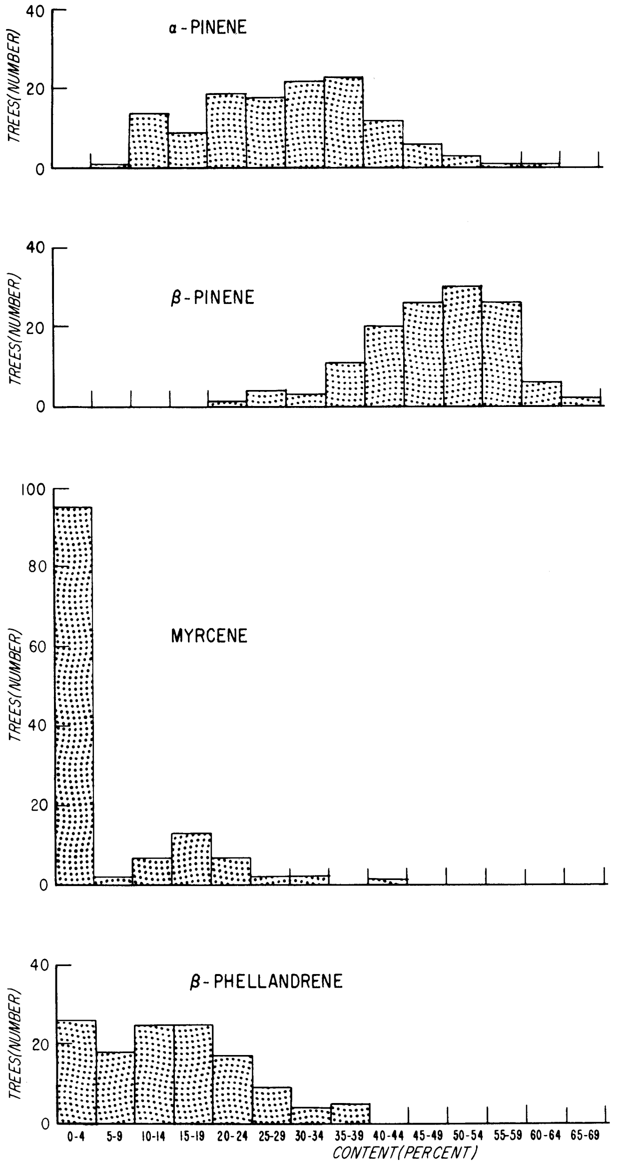

Figure 173.—Frequency distributions for the major constituents of turpentine in slash pine cortex oleoresin. Basis, 129 trees. (Squillace and Fisher 1966)

varied up to 12 atmospheres. The control-pollinated progeny over mid-parent correlation coefficient for exudation pressure was 0.68 (Bourdeau and Schopmeyer 1958). Broad-sense heritability of oleoresin viscosity was high, as indicated by ramet-ortet correlations of 0.56 to 0.67 during April, June, and August (McReynolds 1971).

Levopimaric acid content of slash pine oleoresin varied from 22 to 32 percent among 14 clones sampled, and broad-sense heritability was estimated to be 0.61. In five slash pine families, means varied from 22 to 26 percent, but the differences were not statistically significant. Trees with high oleoresin yield tended to have high levopimaric acid content (Squillace *et al.* 1971).

Chemical components of slash pine oleoresin vary regionally, as discussed in the chapters on geographic and racial variation.

Relationship Among Traits

Because slash pine is important for a wide variety of wood products, the relationships among trees that are extreme deviants for high oleoresin yield, fast growth, good stem form, good crown form, good or special wood properties, or resistance to pests are of greater importance than those of a general nature applying to oleoresin yield and extraction methods and to tree size in general.

Oleoresin yield as a rule increases as tree diameter or crown size increases, but certain trees of average size or smaller produce more than large trees. Trees with exceptionally high yields and rapid volume growth are not common, but they do exist. Among 4,050 trees in a 20-year-old plantation, 1 tree was found with 2.5 times the normal oleoresin yield and wood volume, and another with 2 times the average volume and 50 percent higher oleoresin yield. Both trees were straight, with small branches (Squillace 1966a). Among slash pine clones no correlation was found between stem straightness or branch size and oleoresin yield, and it was concluded that a decrease in tree quality will not follow breeding for oleoresin production (Gansel 1966). In Florida, 16 seed orchard clones of 373 originally selected for superior growth and crown and stem form were also outstanding in oleoresin yield (Goddard and Peters 1965; Peters 1971). In Georgia, 5 of 137 seed orchard clones selected for good growth and form were twice the average or higher in oleoresin yield (Gansel and Darby 1966). Studies are underway on the relationship between oleoresin yield and wood volume growth and resistance to fusiform rust. Since Florida is not an area of high incidence of rust attack, strains of trees developed there are not exposed to rust. Relationships between wood volume growth and wood properties were discussed in the section on wood.

No negative correlations among traits are apparent to delay simultaneous improvement in several traits if time is available to locate the trees. The lack of positive correlations among traits means additional work is required in selection and, furthermore, this complicates the choice of mating schemes and progeny testing designs, but the rewards for effort exerted seem very great.

In summing up the work on slash pine and gum, we can say that as oleoresin yield and composition are among the most variable traits studied in slash pine, important gains have been made by selective

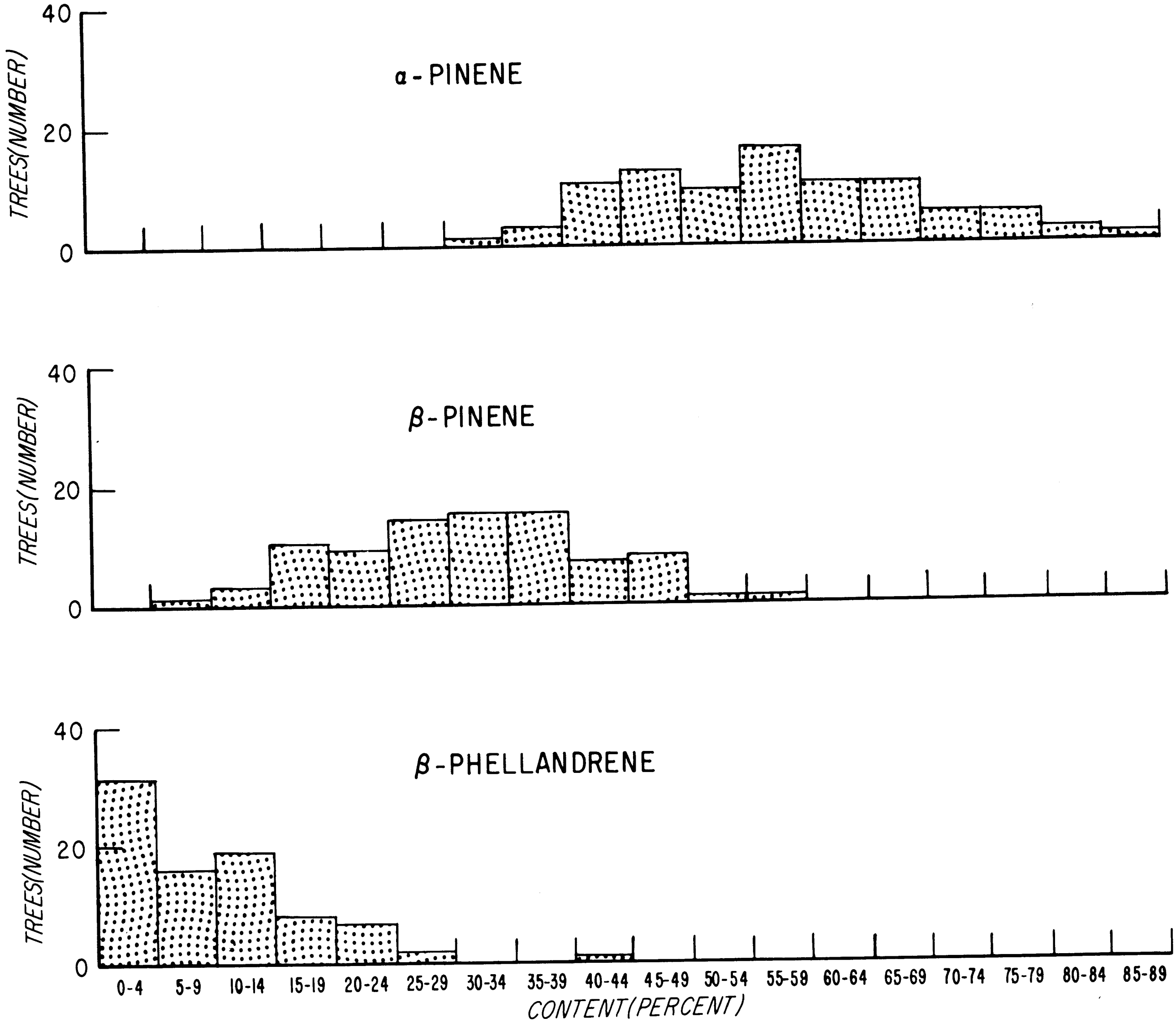

Figure 174.—Frequency distributions for the major constituents of turpentine in slash pine stem oleoresin. Basis, 84 trees. (Squillace and Fisher 1966)

breeding. Plantation trees and seed orchard clones have been selected with a combination of high oleoresin yield, wood volume growth, and stem and crown form.

OTHER TRAITS

Needles and Buds

Phenotypic variation was wide for needle characteristics among individual trees sampled in many stands at various geographic locations. Among the traits measured for cones, seeds, and needles, coefficients of variation in percent were highest for needles (110.0) and seeds per cone (39.4) and lowest for needle length (6.5) and hypoderm layer (6.7) (Squillace 1966b). Parent-progeny regressions were fairly high, 0.32 to 0.81, for needle length, needle bundle volume, needle divergence, needles per bundle, fascicle sheath length, and bud scale length in clones and control-pollinated offspring (Sorensen 1964). The clones were significantly different in all six traits and progeny in all traits except number of needles per bundle.

Greenhouse seedlings with needle anomalies known as *fused* or *curly needle disease* have been observed, and it is thought the condition is related to faulty nutrition (LaCroix 1962).

As a result of extensive observations of full-sib slash pine seedlings, it was determined that heritability was 0.99 for hypocotyl color index based on components of variance, and for half-sib family heritability it was 0.90. Based on regression of wind-pollinated half-sib families on combining ability of female crosses plus stand combining ability divided by 2, it was 0.91 (Snyder *et al.* 1966). All seedling classifications were based on cotyledon color according to the following descriptions and color classes: *Albino;* white. In laboratory tests, only one seedling with pure white cotyledons was seen. The term was applied to only the whitest seedlings with no hypocotyl color, and these seedlings wilted and died after a couple of days of exposure to the sun. *Xantha;* yellow. These seedlings had bright yellow cotyledons and vivid cherry-pink hypocotyls. They lived several weeks if weather was favorable. *Green xantha;* greenish-yellow. These seedlings were similiar to xantha but greener, with less vivid hypocotyls and higher survival potential. *Viridis;* light green. Hypocotyls were normal pink. Some seedlings died, but some which had virescent cotyledons were able to survive. Observations were made on the frequency of variant seedlings among approximately 7,380,000 slash pine seedlings in a south Mississippi nursery. Proportions of seedlings varied from year to year. In 1963, there were no *albino* seedlings, but there were 17.2 *xantha,* 37.9 *green xantha,* and 41.7 *viridis* variants per million seedlings. In 1965, variants per million seedlings were as follows: *Albino* 2.2, *xantha* 25.0, *green xantha* 46.0, *viridis* 123.8. Snyder *et al.* (1966) suggest that the observed frequency of the *albino* class may have been more in 1965 than in 1963 because of the warmer, less cloudy conditions which existed. Under such conditions, some seedlings may have bleached to a lighter color. The difference between the 2 years in frequency of the *viridis* also suggests environmental influences. In both years the *viridis* frequency was largest, although some of the slight deviations from normal green were difficult to detect in outdoor illumination. It was suggested that some of the chlorotic seedlings may have been a result of environmental conditions rather than mutants. This was based on observations of seedlings grown in unfertilized soils; the seedlings were highly chlorotic but assumed normal color after fertilization with nitrogen. Simple Mendelian inheritance, often with deviant segregation ratios, was found for cotyledon mutants based on the four classifications used. When 18 carriers were intercrossed, a common gene was found in only 2 neighboring trees, this indicating, if monogenic inheritance is assumed, that the same phenotypes are produced by several non-alleles.

Propagability and Breeding

Variation among slash pine trees of traits important in breeding and seed orchard establishment has been noted. Variation in success of grafting and rooting was discussed in the chapter on vegetative propagation. Variation in amount of natural selfing and ease of cross breeding were discussed in chapters about sexual reproduction and interspecific hybridization.