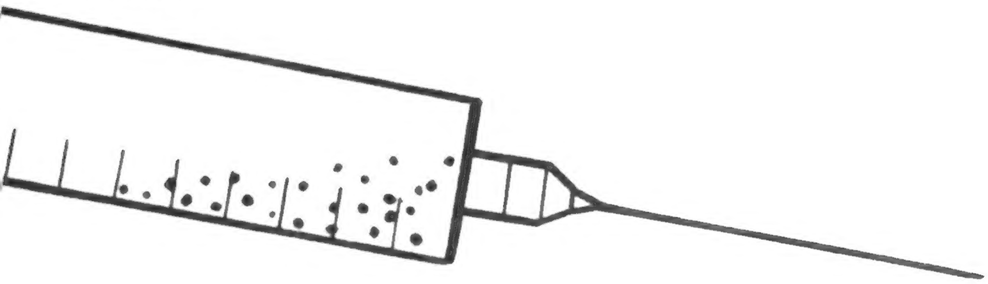
# of SLASH PINE



Research Paper
WO–20

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Issued October 1974

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Dorman, Keith W., and A. E. Squillace.
1974. Genetics of slash pine. USDA Forest Serv. Res. Pap. WO-20,20 p.
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OXFORD: 174.7 *Pinus elliottii*: 181.52, 165.41, 165.52, 165.53. KEYWORDS: Slash pine, genetics, tree improvement, sexual reproduction, controlled pollination, geographic variation, racial variation

Research Summary
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Slash pine has a more restricted range than shortleaf, loblolly, or longleaf pine, but it is of major importance because of its fast growth, high-quality wood for many products, high yield of oleoresin for naval stores, and large area of pure stands. Much of the early genetics research in the South was with this species, and this paper summarizes 168 references from the literature.

Male and female flowering parts are found on the same tree. Flowering may begin as early as 2 years and full production in about 10 years. Seed production is high, yield per cone is high, artificial pollination is relatively easy, and the seed may be stored many years. The species is usually cross-pollinated, but appreciable amounts of selfing may occur.

Vegatative propagation for seed orchard clones is best accomplished by grafting. Trees for experimental purposes may be produced by rooting cuttings or air layers. Rooting needle bundles is extremely difficult.

Geographic variation occurs in a clinal pattern. Stemwood specific gravity increases from north to south and west to east. Rate of growth increases in a general pattern from south to north. Variation occurs also in several cone, seed, needle, and oleoresin characteristics.

Among individual trees, variation is wide in stem volume, stem straightness, pruning height, branch angle, crown width, branch thickness, bark thickness, wood specific gravity, extractives content, oleoresin yield, physical and chemical traits of oleoresin, resistance to diseases and insects, response to fertilization, flower production, and seed and needle traits. Estimates of narrow-sense heritability are variable but sufficiently high to make breeding profitable. Broad-sense heritabilities are generally higher than narrow-sense heritabilities.

Most economically important traits vary continuously, and selection for seed orchard clones is based on an index of 10 to 12 traits. Trees with defects such as disease infection, forked stem, crooked stem, or unfruitfulness are rejected for use in seed orchards regardless of other good traits they may have. Undesirable traits may vary along a gradient, but this variation is not a factor in selection because defect-free trees can be found.

Economically important traits generally are not highly correlated, and seed orchard clones have had to be chosen with strong emphasis for desirable traits and, at the same time, strong pressure against undesirable traits.

Hybrids with certain other major and minor southern pines have been produced, but they are not of major importance in breeding. Seed yield of hybrids may be low.

Range-wide breeding programs are being conducted, and important gains in wood yields are indicated. First-generation seed orchards are producing seed for a large part of the planting program, and second-generation orchards are being established. Seed is produced in grafted orchards of carefully selected and progeny-tested clones. Major emphasis in breeding has been on improving growth rate, tree form, oleoresin yield, and resistance to fusiform rust, with wood quality an additional goal in certain projects.

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Rows of 25-year-old slash pine clones illustrate differences in branch diameter, branch angle, branch length, crown shape, stem straightness, and stem volume growth. The two large trees in the second row from the right are a fast-growing clone, but their oleoresin yield is less than one-third that of the clones selected for high yield in the three rows to the left.

GENETICS OF SLASH PINE

Keith W. Dorman and A. E. Squillace[1]

INTRODUCTION

Slash pine (*Pinus elliotti* Engelm.) is one of the most important species of the southern pine region. Two varieties are generally recognized: the typical variety, *P. elliottii* Engelm. var. *elliotti*, and the South Florida variety, *P. elliottii* var. *densa* Little & Dorman. The former extends from the Coastal Plain of southern South Carolina to central Florida and southeastern Louisiana, whereas the latter grows only in central and southern Florida (fig. 1). However, the distinction between varieties is not always clear. Many traits vary clinally from south Florida to northern portions of the species range, but other types of clinal variation occur (Squillace 1966b). These gradients emphasize the importance of specifying the exact location of seed sources and of avoiding generalizations applying specifically to one variety or the other. Both varieties are considered in this report.

Taxonomists have placed slash pine in the Subsection *Australes*, which contains eight species in the southeastern and eastern United States, two in the West Indies, and one in both the West Indies and adjacent Central America (Critchfield and Little 1966). Availability of closely related species has enhanced opportunities for interspecific hybridization.

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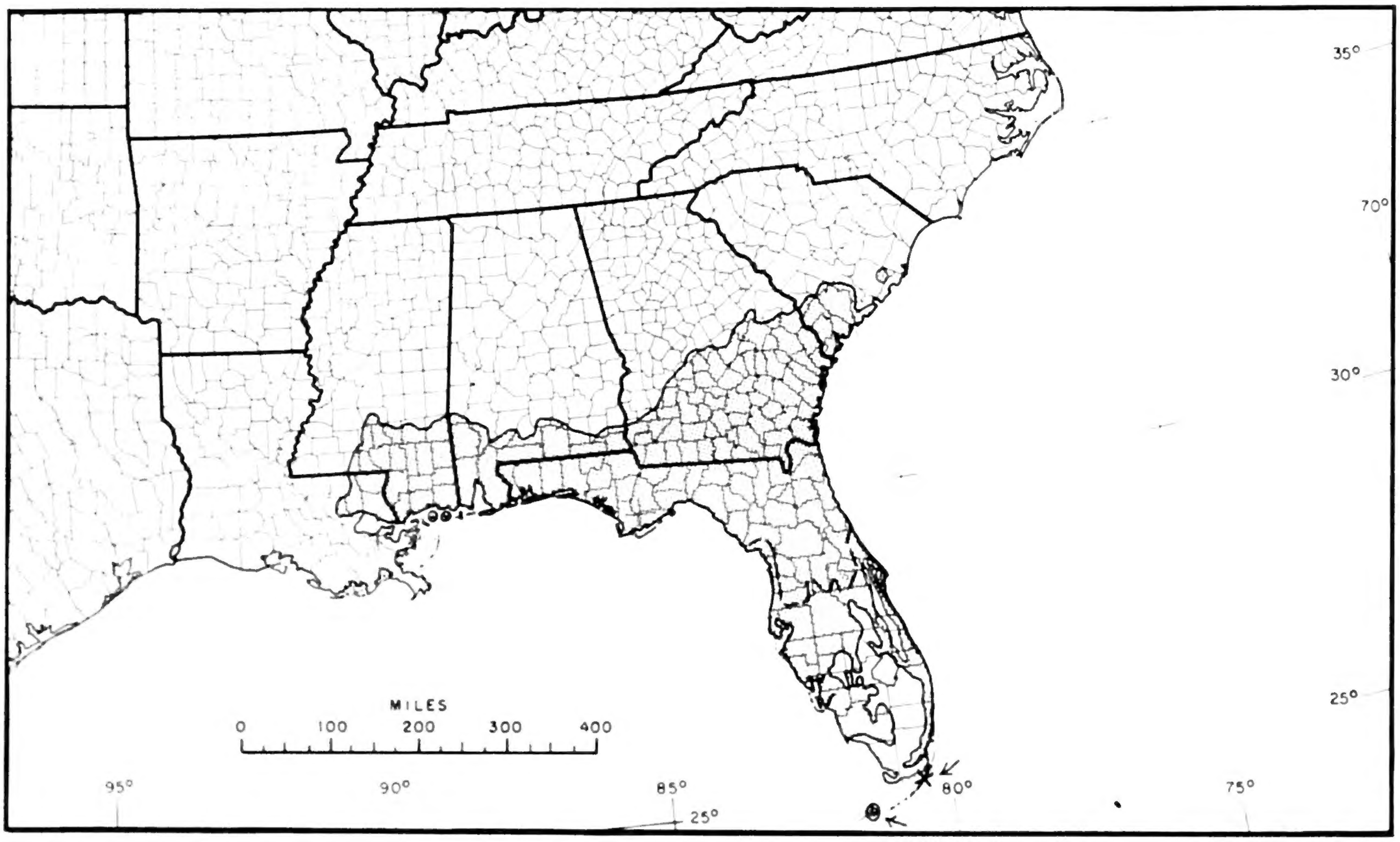

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Figure 1.—The range of slash pine (Fowells 1965). The variety in southern Florida extends northward to the broken line across the state.

Slash pine is used for pulp, lumber, poles, and oleoresin (gum naval stores) production. It is a favorite of forest managers because it is easy to plant and can be handled in pure, even-aged stands with rotation ages as low as 20 to 25 years, in addition to having high wood utility. Slash pine is widely planted within its range and in adjoining areas. It has also been planted successfully in southern Africa, South America, and Australia.

Slash pine is strongly multi-nodal in growth habit and begins rapid height growth soon after planting. Crown closure occurs at an early age, and natural pruning takes place even at wide spacing; consequently, trees reach commercial size and quality in a few years. Seed production is high and consistent at ages 10 to 15 years if crowns are large.

Volume growth is strongly influenced by site conditions, but the species grows well near sea level on soils which are seasonally water-saturated and on drier soils at higher elevations in the Coastal Plain. In volume growth, it ranks among the highest of all southern pines. In the southern part of the slash pine range, summer rainfall is very high and the winter rainfall is very low, but in the northern and western parts the seasonal distribution of rainfall is much more equally divided.

Fusiform rust (*Cronartium fusiforme* Hedgc. & Hunt ex Cumm.) is a serious disease of slash pine in nursery beds, where it can be controlled by spraying, and in young plantations, where it cannot be economically controlled. Losses to fusiform rust are often severe throughout the range, except in central and southern Florida. In Georgia, where most of the wood volume of slash pine occurs, average incidence of rust infection in 12-year-old planted stands was 50 to 72 percent, about the same as in loblolly pine (*Pinus taeda* L.) plantations (Roth and McComb 1971). However, there were sizable areas with less than 25 percent infection, whereas other areas had over 75 percent. Breeding for resistance is an important part of most improvement programs. Both slash pine varieties have other disease enemies, but they are not serious. Slash pine suffers only slight and intermittent damage from insect attack. Resistance to insects is not an important objective in breeding, but conelets and cones must be protected in seed orchards.

When slash pine is planted north of its natural range, it suffers from ice damage. Some breeders are working on this problem.

Slash pine is a diploid and is generally stable in chromosome number and structure. However, irregularities do occur, as indicated by studies of interspecific hybrids (Saylor 1967).

This paper summarizes technical information about the genetics of this important species, some of it is common to other pines and some unique to slash pine.

SEXUAL REPRODUCTION

Reproductive Development

Slash pine is monecious in flowering habit, but large variation occurs in the degree of maleness or femaleness among individual trees (Schultz 1972). Occasionally, bisexual flowers occur. Highly vigorous individuals may produce conelets as early as 2 years of age,[2] but most trees do not produce conelets in appreciable quantities until about age 10 in open stands and age 20 in other stands. Production of conelets in vegetatively propagated trees usually takes place earlier than in seedlings, with numbers sufficient for controlled pollination occurring at 2 or 3 years and commercially important quantities at 7 years (Dorman and Kraus 1967; Schultz 1972).

Most female cones are initated during late August, whereas most male cones are initiated during July and early August (Mergen and Koerting 1957; Eggler 1961). Female cones first appear as swellings on the apex of vegetative buds in late December or early January. Conelets are fully developed by late January in Florida but not until late February in northern portions of the species range (Dorman and Barber 1956). Male cones can first be seen as small knobs around the bases of vegetative buds in late fall.

Slash pine conelets are borne singly or in groups of two to four (occasionally more), usually on primary and secondary shoots in the upper crown, whereas staminate cones occur in clusters on secondary and tertiary shoots in the mid or lower crown.

Heavy cone crops occur about once every 3 years, but appreciable numbers of cones are produced almost every year. Pollination is by wind; heavy rain and subfreezing tempera-

[2] Office reports, Study G-62, on file at Southeastern Forest Experiment Station, Naval Stores and Timber Production Laboratory, Olustee, Fla., April 23, 1968, and March 28, 1972.

ture reduce seed crops. Cone insects and diseases may take about half the crop regularly and all of it intermittently and locally (Merkel 1961).

Time of flower maturity and flower- and seed-producing capability vary widely among trees in seed production areas and clones (Webb and Hunt 1965; Goddard and Strickland 1965; Bengtson 1969). Acceptable forecasts of seed crops can be made by counting 1- and 2-year-old cones (Webb and Hunt 1965). The method is useful in identifying trees with good cone crops, where cone collection is most profitable.

Although slash pine pollen can travel long distances, Wang, Perry, and Johnson (1960) reported that the amount falling at a distance of 400 to 500 feet is only 2 to 5 percent of the amount at the source. The authors recommended isolation distances of at least 500 feet for seed orchards of slash pine. In a study in which pollen catkins were removed from trees within such an orchard, wind-borne pollen from stands more than 400 feet away was sufficient to pollinate the female flowers effectively (Squillace 1967). Until the results of further research are obtained, the recommended 500-foot zone is considered acceptable. However, considerable contamination can be expected in early stages of the orchard or at other times when pollen production is low.

Seeds from wild trees vary in size, ranging from 12,700 to 20,800 per pound (Shoulders 1961). Seeds from seed orchards are usually larger, averaging 14,000 or less per pound. The effect of seed size on seedling growth is not sufficient to be a factor in progeny testing.

Some cultural methods have been effective in increasing flowering in young trees and clonal seed orchards. Wide spacing is desirable (Florence and McWilliam 1956; Goddard 1964), as is moderate application of fertilizer mixtures (Hoekstra and Mergen 1957; Bengtson 1969; Goddard and Strickland 1965).

Cross- and Self-Pollination

Normally, slash pine is a cross-pollinating species, but appreciable amounts of selfing can occur under natural conditions. In a study involving the use of chlorophyll deficiencies as gene markers, the percentage of selfs in wind-pollinated, viable seed from 11 mother trees varied from 0 to 27 percent, with an average of 6 percent (Squillace and Kraus 1963). Empty seeds were not considered in the study, and, because these more often result from selfing than from crossing, the degree of actual self-fertilization was higher than the degree of production of selfed, viable seed.

Kraus and Squillace (1964b) showed that appreciable numbers of selfed seedlings can occur even if self-pollen is mixed with an equal volume of an outcross-pollen mixture in controlled pollinations. Their data suggested that there may be some competition between self- and outcross-pollens or between embryos resulting from selfing or outcrossing, but the effect, if any, is relatively minor. When equal amounts of self- and outcross-pollens are available, the yield of selfed seedlings will be far less than the yield of outcrossed seedlings. This disparity apparently results because abortion of selfed ovules is far greater than abortion of outcrossed ovules after fertilization, as judged from the low yields of viable seed obtained in selfing in comparison with those obtained in outcrossing in separate matings. The authors speculated that, if 20 or more clones are used in a seed orchard, the yield of selfed seedlings will probably be only slightly greater than that which occurs in natural stands under comparable spacing. However, the reduction in yields of sound seed as a result of selfing will probably be a more serious problem (Franklin 1971).

In comparison with crossing, selfing and other types of inbreeding reduce yield of filled seed, seed germination, and seedling growth (Mergen 1954b; Squillace and Kraus 1962; Peters and Goddard 1961; Snyder and Squillace 1966; Snyder 1968; Gansel 1971).

Controlled Pollination

Pollination in slash pine can be carried out according to methods described by Cumming and Righter (1948), Perry (1954), Mergen, Rossoll, and Pomeroy (1955), and Goddard and Allen (1955). Four stages of ovulate flower development were recognized by Snow, Dorman, and Schopmeyer (1943) and five by Campbell and Wakeley (1961) as being useful in controlling pollination of southern pines. The development of conelets and catkins is closely related to temperature, which may vary widely during January and February in the slash pine range (Dorman and Barber 1956).

Pollen should be collected shortly before normal shedding or when some of the catkins on the tree begin to shed. When squeezed, unripe catkins exude a clear fluid, whereas ripe ones exude a thick, yellow curd. Pollen must be dried quickly, in plastic sausage casings (Mergen, Rossoll, and Pomeroy 1955) or kraft paper bags. Impurities can be removed by straining the pollen through a 60–mesh soil sieve or dress-lining cloth.

Fresh pollen is preferred over stored pollen. When fresh pollen is not available because of differences in time of flowering among species, pollen can be stored until the next year. Pollen of several southern pines has been successfully stored for 15 years (Stanley, Peterson, and Mirov 1960). Desiccation for 15 minutes at 5 mm. of vacuum will reduce moisture content of pollen to a safe level for storage (Snyder 1961). Silica gel is also an effective desiccant. For storage, pollen should be kept in small, partially filled bottles stoppered loosely with cotton plugs. The temperature under storage should be at freezing or slightly above.

Because pollen variability may vary among lots, particularly after storage, it should be determined before the pollen is used. Pollen of fairly low percentage of germination can be used if the volume applied is increased proportionally. Distilled water is a good medium (Dillon and Zobel 1957), although other materials may give better germination (Echols and Mergen 1956). Estimates of percentage of pollen germination may be made after 72 hours at about room temperature.

Temperatures of about 115° F. are required for sterilization of pollen (McWilliam 1959), but Hodgkins (1952) suggested 180° F. for 15 hours because there is variation among trees in tolerance of pollen to heat.

Survival of cones from controlled pollinations may be less than 40 percent, and seed yield per cone may average about half that of cones from wind-pollination (Snyder and Squillace 1966). These factors are important when planning the number of bags needed to produce a specified number of seed. Certain cone insects can be controlled by chemicals (Merkel 1969) and certain cone diseases can be controlled by bagging (Jewell 1957). Banding tree trunks with metal has protected cones from squirrels (Texas Forest Service 1957).

Because tree climbing to control pollination and collect seed is strenuous work, special equipment has been developed for transporting small items and ladders (Johansen and Arline 1958; Cech 1961). Truck-mounted extension ladders are widely used; hydraulic lifts are better but much more expensive. Safety rules developed for tree climbers should be followed (Snyder and Rossoll 1958).

Seed Handling

Slash pine cones ripen in September of the second autumn after pollination; they should be carefully observed and collected when fully ripened or when the specific gravity is about 0.90 (Wakeley 1954). This practice is necessary for producing seed of high quality. However, because wide variation occurs among trees in cone opening, average dates for cone collection may be too late for certain individual trees or clones. Time of ripening also varies from year to year.

Techniques for the extraction, dewinging, drying, storage, and stratification of seeds have been developed for slash pine because of the importance of this species in commercial planting (USDA Forest Service 1973).

Nursery beds for slash pine seedlings should be fumigated to control pests and promote the growth of desirable mycorrhizal fungi (Danielson and Davey 1969) which might improve field growth of seedlings (Shoulders and Jorgensen 1969). Seed is planted in mid-spring on mineral soil, covered by pine needles or similar material, and watered. Weeds must be controlled and rigid watering schedules followed to ensure prompt and even germination. Spraying will protect against disease pests. Seedlings may be lifted in the late fall and outplanted with bare roots.

Adequately dried seed in tight containers will remain viable for many years in cold storage, which facilitates the use of the same lot of control seed for progeny tests over many years.

A vacuum sowing device for planting a specified number of seed in rows in experimental nursery beds has been described (Barber 1957).

ASEXUAL REPRODUCTION

Vegetative propagation has been used in slash pine breeding for studies of broad-sense heritability and the establishment of clone banks and, most important, of seed orchards. Efficient methods of propagating the species are needed for large-scale use under field conditions, but there is also a place for intricate techniques suitable for use on a small scale in research to produce special stock.

In certain species, it has been possible to produce individual plants with half the normal chromosome number by treating sex cells such as pollen. These unusual plants are then manipulated still further to double the chromosome number and form a homozygous plant. Initial attempts to culture pollen grains of slash pine and other tree species have been unsuccessful, but the work is continuing (Brown 1967).

Rooting

Rooting cuttings.—Initial attempts to develop techniques for rooting of cuttings were made in connection with breeding high-yielding strains for oleoresin yields (Curry 1943). These attempts were successful, but the percentage of rooting was low (Mitchell, Schopmeyer, and Dorman 1942). It was found that the ability to form roots varied among trees; 1- and 2-year-old seedlings rooted more readily than older trees, complex treatments were necessary, and rooting was better in the fall or winter than during other seasons. Additional studies (Mergen 1955b; Greene and Reines 1958; Reines and Bamping 1962) tested combinations of chemical treatment, environmental factors, and season of collection, but the percentages of rooting have been low and inconsistent.

Cuttings may form only one or a very few rootlets, but height growth of plants is rapid (Dorman 1947) and faster if the cuttings are from young rather than older trees (Franklin 1970).

Rooting needle bundles.—Needle bundles of slash pine can be rooted, but, as with cuttings, the percentage of success is very low and inconsistent (Zak and McAlpine 1957). Additional tests with various combinations of season of collection, light, temperature, chemical treatment, rooting media, and pretreatment of the twig have not improved the rooting success (Reines and Greene 1956–57; Reines and McAlpine 1960; Mergen and Simpson 1964; Hare 1965). Some of the needle bundles that root do not form a terminal bud or make normal height growth.

Rooting air layers.—Slash pines can be successfully air layered under certain conditions. When undetached twigs of 5- to 17-year-old slash pines in Florida were girdled and treated with a rooting hormone, 85 percent of them rooted (Mergen 1955a). However, when twigs of 17- to 26-year-old slash pines in Georgia were subjected to a similar treatment, they failed to root during the first 11 months after treatment (Reines and Greene 1956–1957). Age of tree, concentration of rooting hormone, geographic location of tree, and season when treated affect rooting success (Hoekstra 1957; Hoekstra and Johansen 1957; Slee 1967).

Grafting

Grafting slash pine scions from mature trees into seedling rootstocks in the field or nursery is the most widely used method of establishing seed orchards. Cleft grafting is most popular and is done in early spring. The percentage of successful grafts can be high, but skill in grafting, in control of temperature, humidity and light in the covering of new grafts, and in timing of stock cutbacks are important factors influencing successful union (Mergen 1955b; Greene and Reines 1958; Slee 1967; Perry 1960). Bottle grafts have been highly successful but require more care than other types (Mergen 1955b; Greene and Reines 1958).

The Georgia Forestry Commission has developed an efficient method of grafting slash pine for seed orchards (Wynens 1966). One-year-old stock plants are grown in a nursery at 1- by 1-foot spacing, and grafting is carried out in the spring. The cleft grafts are covered by a moisture-retaining bag, and the plants are irrigated under overhead shade. Successful grafts are transplanted to the field as balled stock.

Slash pine scions can be collected from mature trees with a rifle (Beers 1957) and shipped long distances if packed in ventilated plastic bags with dry moss and a small amount of damp moss to supply moisture (Perry and Wang 1957).

Graft incompatibility is common in slash pine (Otterbach 1963; Slee 1967), and, as shown by a survey of pine seed orchards, 11 percent of all clones may suffer from phloem blockage and 7.5 percent may die as a result of graft union incompatibility. Graft incompatibility is an inconvenience rather than a major obstacle in the establishment of seed orchards.

Grafts between slash pine and other pines are possible, but no important benefits have been obtained thereby (Mergen 1954a; Slee 1967; Allen 1967; Schmidtling 1971).

VARIATION AND INHERITANCE

Geographic and Racial Variation

Although slash pine has a more limited natural range than other major southern pines, it nevertheless spans about 8 degrees of latitude and 10 degrees of longitude. Several climatic factors vary greatly over the area (Bethune 1960; Squillace 1966b). For example, mean January temperatures range from as low as 50° F. in the north to as high as 70° F. in the south. Seasonal distribution of rainfall also shows distinctive north-south clinal patterns. The optimum climatic zone for growth is presumed to be in the north-central portion of the species range (Squillace 1966c). Because the climatic factors vary continuously, clinal patterns of variation in tree characters are expected, and this was indeed found to be the case in most studies.

Survival.—Survival capacity of seedlings originating from different geographic sources increases from south Florida to the northern extremeties of the species range (Langdon 1958; Squillace and Kraus 1959; Snyder,

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Figure 2.—Rows of 25-year-old slash pine clones illustrate differences in branch diameter, branch angle, branch length, crown shape, stem straightness, and stem volume growth. The two large trees in the second row from the right are a fast-growing clone, but their oleoresin yield is less than one-third that of the clones selected for high yield in the three rows to the left.

Wakeley, and Wells 1967; Gansel *et al.* 1971). Seedlings originating in south Florida suffer very heavily from freezing when planted in northerly areas, as might be expected.

Growth rate.—When planted in northern portions of the species range, sources from a band extending from Calhoun County in west-central Florida to Colleton County, S.C., show the best growth (Gansel *et al.* 1971). Seed from around Stone County, which is north of Gulfport, Miss., may do equally well. Fusiform rust infection was found to influence height growth, but percentage of trees infected did not follow a geographic pattern by seed source. When planted in south Florida, seed from the area centered around Alachua County in north-central Florida does best. When planted in areas north of the species range, western and northern sources do best (Synder *et al.* 1967). Reports by Squillace and Kraus (1959), Langdon (1958), Saucier and Dorman (1969) and Squillace (1966b and c) generally agree with these results.

In plantings at Lake City, Fla., sources of slash pine differed in pattern of seasonal height growth (Bengtson, McGregor, and Squillace 1967). Northern sources tended to grow relatively more than southern sources in the early part of the growing season and less in the latter part.

No meaningful genetic differences seem to occur between slash pines growing on wet sites and those on dry sites (Gansel 1967b). Slash pines planted in countries other than the United States show differences attributable to geographic source of seed, as summarized by Burley (1966).

Wood characteristics.—In trees growing in their native habitat, specific gravity of stemwood and percentage of summerwood increase from north to south and from west to east through the species range (Larson 1957; Perry and Wang 1958; USDA Forest Products Laboratory 1965; Goddard and Strickland 1962). However, when trees from different sources of similar latitude were planted in Louisiana, the pattern did not seem to hold (Derr and Enghardt 1960). Tracheid length showed no geographic variation in one test (Strickland and Goddard 1966a). South Florida trees apparently have higher extractives content than north Florida trees (Taras and Saucier 1967; Clark and Taras 1970).

Oleoresin yield and composition.—From reports of commercial producers, Ineson and Rayl (1941) concluded that oleoresin yields are higher in the coastal areas of southeast Georgia and northeast Florida than at other locations. But Bengtson and Schopmeyer (1959) found no differences in oleoresin yields adjusted for stem diameter among 10 comparable stands sampled in south Georgia and north Florida. In south Florida, where trees are generally smaller, oleoresin yield is only slightly more than one-half that of trees in north Florida (Clements 1959). When trees from different sources of similar latitude were planted in a common location, no differences in oleoresin yields (either adjusted or unadjusted for diameter) were apparent among sources (Barrett and Bengtson 1964). However, when sources from throughout the species range were planted in common locations, Gansel *et al.* (1971) found that some sources differed in yield (adjusted for diameter) by as much as 70 percent, although no geographic pattern was apparent.

The composition of the monoterpenes in the cortical oleoresin of slash pine varies continuously, with most of the major chemicals either increasing or decreasing in a north to south direction through the species range.[3] No interactions between seed source and planting site were found; hence, the patterns would apparently hold for trees growing in their native habitats as well as in test plantings of seed sources. Mirov and Iloff (1956) reported that South Florida slash pines have a higher percentage of B–phellandrene in the oleoresin from stem xylem than do typical slash pines.

Other traits.—Geographic patterns have been observed in relatively minor traits such as cone dimensions, seed yield per cone, seed weight, needles per fascicle, needle length, length of fascicle sheath, hypoderm thickness, number of resin ducts in the needles, and frequency of stomata (Mergen, Snyder, and Burley 1966; Squillace 1966b). Such patterns have also been observed in susceptibility to insect attack (Langdon 1958), flowering (Goddard 1964), and hypocotyl color (Snyder, Squillace, and Hamaker 1966).

Tree-to-Tree Variation

Slash pine is an extremely variable species, many of its traits showing wide variation (fig. 2). Variation in many physiological, morphological, and chemical traits is economically important because of their influence on tree growth rate, volume yield per acre, tree quality, wood quality, and resistance to pests.

[3] Squillace, A. E. Racial patterns for monoterpenes in cortical oleoresin of slash pine. (Paper presented at a meeting of the Working Group on Quantitative Genetics, Section 22, IUFRO, Gainesville, Fla., March 18, 1971.)

Table 1.—Reports of inherent individual-tree variation in slash pine

Trait	Literature citations	Range of heritability estimates[1]	
		Broad-sense	Narrow-sense
Survival	Barber 1964, Kraus and Hunt 1971	(2)	(2)
Total height	Barber 1964, Goddard and Cole 1966, Goddard and Smith 1969, Goddard and Vande Linde 1967, Kaufman 1968, LaFarge and Kraus 1967, Nikles 1966, Peters and Goddard 1961, Squillace and Bengtson 1961	—	0.03 to 0.37
Stem diameter	Barber 1964, Goddard and Cole 1966, Kaufman 1968, Squillace and Bengtson 1961	—	−.22 to .58
Stem volume	Goddard and Cole 1966, Schultz 1972, Squillace and Bengtson 1961, Webb and Barber 1966	0.59	.16 to .35
Stem straightness	Barber 1964, Gansel 1966, Mergen 1955c, Nikles 1966	.29 to .47	—
Pruning height	Barber 1964	—	.36 to .64
Branch angle	Strickland and Goddard 1966b	—	.33
Crown width	Barber 1964, Gansel 1966, Squillace 1971, Strickland and Goddard 1966b	.40 to .47	.13 to .48
Branch thickness	Gansel 1964, Strickland and Goddard 1966b	.31 to .38	.18
Bark thickness	Barber 1964, Squillace and Bengtson 1961	—	.33 to .67
Wood specific gravity	Einspahr, Goddard, and Gardner 1964, Goddard and Cole 1966, Squillace, Echols, and Dorman 1962, Zobel, Cole and Stonecypher 1962	.48 to .73	.21 to .56
Extractives content	Einspahr, Goddard, and Gardner 1964, Franklin, Taras, and Volkman 1970, Taras and Saucier 1967	.25	.13
Other wood properties	Einspahr, Goddard, and Gardner 1964, Squillace, Echols, and Dorman 1962, Zobel, Cole, and Stonecypher 1962	(3)	(3)
Oleoresin yield	Franklin, Taras, and Volkman 1970, Goddard and Peters 1965, Mergen, Hoekstra, and Echols 1955, Peters 1971, Squillace and Bengtson 1961, Squillace and Dorman 1961, Squillace and Harrington 1968	.89 to .90	.45 to .90
Other oleoresin traits	Bourdeau and Schopmeyer 1958, Kraus and Squillace 1964a, Mergen, Hoekstra, and Echols 1955, Squillace 1971, Squillace and Fisher 1966, Squillace, Hedrik, and Green 1971	—	—
Resistance to diseases	Arnold and Goddard 1966, Barber 1964, Dinus 1969, Dinus 1971, Jewell 1966, Jewell and Mallett 1967, Kraus and Hunt 1971, LaFarge and Kraus 1967, Schmidt and Goddard 1971, Webb and Barber 1966	—	(4)
Resistance to insects	Merkel 1967, Merkel, Squillace, and Bengtson 1966, Sartor and Neel 1971	—	—
Response to fertilization	Pritchett and Goddard 1967, Schultz 1972, Walker and Hatcher 1965	—	—
Flower production	Barnes and Bengtson 1968, Goddard 1964, Varnell, Squillace, and Bengtson 1967	—	—
Seed traits	Kraus 1967	—	—
Needle, bud, and hypocotyl traits	Kraus and Squillace 1964a, Snyder, Squillace, and Hamaker 1966, Sorenson 1964, Squillace and Kraus 1963	—	—

[1] Heritability estimates are listed in this table only for commercially important traits. Although variation among trees was dealt with in each report listed, some of the reports did not include heritability estimates.

[2] Differences between families were relatively small.

[3] Einspahr, Goddard, and Gardner 1964, reported strong broad-sense heritabilities for a number of wood quality traits.

[4] Narrow-sense heritability of 0.24 was reported for resistance to fusiform rust by Arnold and Goddard 1966.

It is generally assumed that, in slash pines selected for seed orchard clones, there is a straight-line relationship between economic value and variation among trees in traits such as wood volume and oleoresin yield. However, there is a different relationship for other traits because trees that are disease-free, good seed producers, and straight and unforked have high value, whereas diseased, sterile, crooked, or forked trees have little or no value. There may be gradients in traits classified as defects, but such gradients are of little importance when trees can be found that have no defects of any kind.

Heritability estimates (table 1) and the absolute values for differences among families and clones indicate that genetic gain from selection and crossing will be high. The kind and extent of inherent differences among trees have been indicated by studies varying in size, design, and location because of the size and complexity of the subject. However, there is a consistent pattern in the results, although individual estimates may vary.

The importance of selection in improving yields and quality of oleoresin in slash pine can best be illustrated by a few examples. Among economically important traits, oleoresin yields and chemical composition are strongly inherited. Carefully selected phenotypes with twice the average oleoresin yield produced control-pollinated offspring with about twice the average yield (Squillace and Harrington 1968). Two parent trees with low alpha-pinene in cortical gum (12 and 16 percent) and high beta-phellandrene (32 and 13 percent) had offspring with 8 to 36 percent alpha-pinene and 18 to 36 percent beta-phellandrene. Two parental trees with a different combination of chemical components (high alpha-pinene and low beta-phellandrene) had progeny with the same combination as the parents (Squillace and Fisher 1966).

The average gain in wood volume production per unit area from selection has been difficult to estimate because of the differences in methods of study. For example, in Florida plantings, where fusiform rust infection is not an important factor, several control-pollinated families of seed orchard clones averaged 40 percent greater dry weight production than the controls (Goddard and Cole 1966). In Georgia, where rust influences survival, some fast-growing families produced over 100 percent more wood per plot (Webb and Barber 1966). In a test with clonal stock, the stem volume of the smallest clone averaged 4.1 cubic feet and that of the largest averaged 12.8 cubic feet at 12 years. The volume of ortets ranged from about 14 to 28 cubic feet. The ortet-ramet correlation for wood volume of stems was 0.60 (Schultz 1972). The wood volume figures may be higher than average, but they do serve to illustrate some of the possibilities in selection. Amount of volume gain will vary among studies because of the emphasis that may be given to other traits besides volume when selections are made.

Figure 3.—Control-pollinated progeny of highly vigorous parents with good traits show uniformly superior height growth and stem and crown form. Breeding for high wood yield will not reduce tree quality if parent trees are selected for good stem and branch traits along with rapid growth.

No immunity to pests has been found in slash pine, but offspring of certain trees have shown important amounts of resistance to fusiform rust or cone and seed insects (Jewell 1966; Sartor and Neel 1971).

With respect to tree and wood quality, young progeny of outstanding parental trees have shorter branches of smaller diameter, better natural pruning, straighter trunks, fewer forks, and better wood traits than controls (figs. 3 and 4) (Barber 1964; Goddard and Cole 1966).

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Figure 4.—Control-pollinated offspring of parents with slow growth, large limbs, and poor natural pruning have the same combination of undesirable traits as the parents.

Inherent variation is so wide in slash pine that the traits of the individual parent tree strongly influence performance of the hybrid in crosses with other species (Schmitt 1968).

Economically important traits in slash pine generally show continuous rather than discontinuous variation. Performance of a family may be markedly superior to the controls or average, but there will be pronounced differences among trees within the family. Thus, silviculturists can expect differences among trees of improved strains, although there should be far fewer trees of extremely slow growth or poor stem and crown form or other undesirable traits.

Relationship Among Traits

Many notations of the relationships among traits of slash pine occur in the literature. Most of these, however, deal with traits of little commercial importance. Correlations among most of the commercially important traits are summarized below. Relationships among expressions of the same general trait (such as growth in height, diameter, and volume) are omitted.

1. Growth rate does not appear to be correlated with relative crown width (such as the ratio of crown width to total stem height) or with stem straightness to any appreciable degree (Barber and VanHaverbeke 1961; Schultz 1972).

2. The relationship between growth rate and resistance to fusiform rust is complicated and not entirely clear. But the literature suggests that at juvenile ages there is a moderate, positive correlation between growth rate of stands of trees and incidence of rust. This correlation may be due to the fact that rapidly growing trees usually have a larger crown surface and, hence, provide a greater

target area for spores than slow-growing trees. As trees advance in age, the infected ones are likely to slow down in growth rate and could cause a negative correlation between growth rate and severity of rust infection.

Thus, if the breeder selects trees for rapid growth in stands which are only lightly infected, the progeny are likely to contract somewhat more infection than progeny of unselected trees. If the progeny are planted in areas with a low rust hazard, serious problems will probably not occur. If planted in areas with a severe or moderately severe hazard, genetic gains in growth and yield per acre may be appreciably reduced. But, as shown by several authors, much genetic variation occurs among trees in both resistance to rust and rate of growth, and families having superiority in both traits occur. Thus, the breeder can reevaluate and reselect parents on the basis of early performance in progeny tests and either rogue the current orchards or establish new ones. Of course, if the breeder selects his parent trees in areas with a high rust hazard, he can make appreciable gains in rust resistance and growth rate in a single generation, as has also been shown by several authors.

Literature on which the above conclusions were drawn are summarized below:

> Schmidt and Goddard (1971) found that progeny of rust-free parents selected mainly for vigor contracted more infection than controls (24 versus 18 percent), at 3 and 5 years of age.
>
> Goggans (1957) found that, in a survey of 5- to 16-year-old plantations, there was a highly significant increase in number of infestations per tree with rate of growth.
>
> Barber and VanHaverbeke (1961) found that 4-year-old trees selected in nursery beds had more cankers per tree than the controls but that there was no difference in percentage of trees infected.
>
> Balthis and Anderson (1944) found that a 4-year-old cultivated plot of trees grew more rapidly and had higher survival but contained more rust infection than the controls (14.0 versus 8.6 percent).
>
> Barber (1964) found that, in progeny test 102, the correlations between number of cankers at 6 years and height at various ages were as follows: 0.6 at 2 years, 0.12 at 3 years, −0.02 at 6 years, and −0.14 at 8 years. In test 103, the correlations between number of cankers at 5 years and height at various ages were: 0.11 at 1 year, 0.13 at 2 years, −0.03 at 5 years, and −0.13 at 7 years.

3. Growth rate and oleoresin yield tend to be genetically correlated (Squillace 1966a). Progeny of high oleoresin yielders averaged about 12 percent greater in stem volume than progeny of average yielders.

4. At juvenile ages, growth rate appears to be positively correlated with survival (Barber 1964). Families which grew the fastest tended, on the average, to have the greatest percentages of survival.

5. The correlation between stem volume growth and specific gravity is probably small (Goddard and Cole 1966). However, Squillace *et al.* (1962) found that tall, thin-stemmed trees tended to have higher specific gravity than short, thick-stemmed trees.

6. There appears to be no appreciable genetic correlation between oleoresin yield and branch size (Gansel 1966). Many people have assumed that progenies of high oleoresin yielders will have large branches because of observations that large-crowned trees usually yield more oleoresin than small-crowned trees. The latter relationship, however, is apparently environmental: widely spaced trees will grow larger branches and produce more oleoresin than closely spaced trees because competition affects both traits in the same direction. This relationship points up the need for care in interpreting phenotypic correlations.

7. Oleoresin yield has a positive genetic correlation with extractives content and with tall oil yield (Franklin *et al.* 1970).

By way of summary, some favorable correlations among traits occur, and these will enhance the speed with which genetic gains will occur. Some unfavorable correlations also occur, but none seems to be strong enough to prevent genetic gains from being made among several traits simultaneously. Regardless of the broad general relationships among trees and stands, one can usually find individual trees having combinations of several genetically superior traits (figs. 5 and 6), although, in some cases, progeny testing is required to reveal them.

Interspecific Hybrids

Crossing pine species offers an opportunity for creating hybrids with combinations of traits that do not often occur in nature because of some barrier. Slash pine will cross with several major and minor southern pine

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Figure 5.—Slash pine has a high capacity for rapid growth, as illustrated by this 3-year-old tree 14.5 feet tall. In intensive studies of growth genetics and response to intensive culture by irrigation and fertilization, families are first screened by test plantings at close spacing for a few years and only the most promising are planted later in standard plots. Fast growth can be combined with small branches, straight stems, and resistance to pests, all traits that are required for high-quality forest trees.

species (Critchfield 1962); description of offspring has been given by Little and Righter (1965). Seed yield from crosses among species is generally lower than from crosses within species (Snyder and Squillace 1966).

Progeny of crosses between loblolly pine and slash pine are usually susceptible to fusiform rust because both parents are susceptible, but in Texas, where rust is not important, the hybrids are vigorous (Zobel *et al.* 1956). Wood characteristics of the hybrids are intermediate between those of the particular maternal and paternal parents (Jackson and Greene 1958; Jackson and Morse 1965; Jackson and Warren 1962).

In crosses of sand pine (*Pinus clausa* (Chapm.) Vasey) with slash pine, seed yields are low and most traits are intermediate between those of the parental trees (Saylor and Koenig 1967).

Crosses between shortleaf pine (*Pinus echinata* Mill.) and slash pine have been produced in attempts to obtain resistance to fusiform rust, but the degree of resistance is influenced by the individual parent tree of each species (Jewell 1966). Hybrids of shortleaf and slash pines may contain as many as 16 percent dwarfs (Grano and Grigsby 1968); their tree form is good, but they are not resistant to tip moth (Grigsby 1959).

Hybrids of slash pine with longleaf pine (*Pinus palustris* Mill.) have juvenile growth characteristics similar to those of slash pine but resemble longleaf pine in form and branching habit; like slash pine, they are resistant to brownspot (Derr 1966). The hybrids are resistant to fusiform rust, as is the longleaf pine parent (Schmitt 1968).

IMPROVEMENT PROGRAMS

The objectives of a tree improvement program must be related to the management and utilization of the species. An additional requirement is that opportunities exist, such as in the large tree planting programs with slash pine, to use the genetically improved seedlings.

Slash pine breeding has proceeded along various lines because the management objectives and customers for seedlings are diversified. Almost all of the major public and private forestry organizations within the slash pine region breed slash pines for their own special use.

Estimates of cost-benefit ratios in southern pine breeding show that the investment is sound (Marler 1963; Davis 1967). The most common method entails within-species selection, followed by establishment of clonal orchards and progeny testing. Technically, this method combines racial selection, plus-tree selection within race, propagation of plus-tree clones in seed orchards, and, in some programs, progeny testing and roguing of undesirable clones. The theory and methodology of the establishment of seed orchards have been discussed in other publications (Zobel and McElwee 1964).

Methods such as species hybridization, haploid breeding, mutation breeding, and polyploid breeding are still in the experimental stage. Advantages and disadvantages of the

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Figure 6.—This 20-year-old progeny test at Olustee, Fla., was used to demonstrate the inheritance of oleoresin-yielding ability in slash pine. Progenies of parents selected for high yield produced an average of 19.6 pounds of gum during the first year of chipping, whereas progenies of parents with average and low yields produced an average of 8.8 pounds. Possibilities for improvement of other characters such as growth rate and wood specific gravity in combination with oleoresin yield were also demonstrated by the test.

various breeding methods have been discussed (Dorman 1962; Cech 1963), and for slash pine some of the methods have serious limitations.

Selection of Stands

Gansel *et al.* (1971) recommend that, for planting in areas north of central Florida (but within the species range), seed should be collected from a narrow region extending from Colleton County, S.C., to Calhoun County, Fla. Seed from a small area centered at Stone County, Miss., may be equally suitable. For planting in south Florida, the same authors recommend that seed be collected from an area centered at Alachua County, Fla. For planting in areas north of the species range, Snyder *et al.* (1967) recommend that the more northerly or westerly provenances be used.

For breeding work, Gansel *et al.* (1971) recommend that separate strains be developed for the region north of central Florida and the region south of central Florida. They do not feel that a separate strain is required for the western part of the species range. These recommendations may be revised as we learn more about genotype-environment interactions.

Selection of Individual Trees

Regardless of whether individual trees are to be used for clonal seed orchards or for breeding stock, maximum pressure should be exerted in selecting the best individual trees in the best stands of the best race. Selections should be made from several different stands rather than from just a few.

Selection criteria or tree-rating schemes used by tree breeders often vary because of different objectives (Cech 1959). If selected for seed orchard clones, trees with a combination of several good traits are preferred over those with a single good trait. Grading systems for seed orchard clones encompass as many as 10 to 12 characteristics, but the most weight is given to the more important traits.

Growth rate.—Major emphasis in selection should be given to volume growth. This rule applies to growth rate of individual trees as well as to those additional traits such as resistance to pests, resistance to drought, and others that influence wood yield per acre. Only dominant trees in a stand should be considered for selection, and selection is most efficient in regularly spaced, even-aged stands.

Inherent growth rate is highly variable among slash pine trees, and it is usually possible to have growth superiority along with good tree form, resistance to pests, and wood quality. Trees with large volume and an excellent combination of other economically important traits are not common, but they do exist (Squillace 1966a). Selection for volume growth is more effective than selection for wood specific gravity alone in increasing pulp yield (Goddard and Strickland 1962).

Wood specific gravity.—Because weight of wood, as reflected by specific gravity, affects strength, yield of pulp, and other features lumped together under the category of wood quality, selection practices should be based on product requirements. The requirements may be for specific products or products in general, but they must be articulated.

Selection for high specific gravity would increase yield of pulp per unit of wood volume but might affect fiber quality. Thus, the interrelationship of many wood and fiber properties must be evaluated before objectives are established. J. P. van Buijtenen (1964) has discussed these relationships.

Fiber length.—Length of slash pine fibers is under genetic control and could be altered by selection if this proves desirable. This problem should be carefully considered, however, because of the high cost of sampling and the possibility of low economic gain.

Pest resistance.—Selection of slash pine for resistance to fusiform rust is important in order to maintain good stem quality and improve volume production per acre. Variation in resistance to rust is wide, heritability is high, and progress is rapid in breeding to improve resistance. Both racial and plus-tree selection may improve resistance to rust. The economic importance of such resistance is very high in the central and northern part of the slash pine range.

Selection for resistance to cone and seedling insects is difficult in natural stands but might be profitable within seed orchards or progeny tests of seed orchard clones.

Tree form.—Slash pine generally has good but not excellent form. Trees with extremely poor form occur at a low frequency and are easy to avoid by concentrating selection on straight trees with little taper, particularly if lumber or poles are listed among product objectives. Trees with sweep, crook, and spiral are to be avoided.

Forking may be genetically controlled, and trees with this defect should be avoided. Trees with good natural pruning are preferred, but crown efficiency, as indicated by excellent volume growth, should be high. Preference should be given to trees with short, fine branches growing as nearly to a right angle with the trunk as possible.

Oleoresin yield.—Wide variation and high heritability make selection for yield and chemical composition of oleoresin and sulfate naval stores highly effective when these traits are included in breeding and forest management objectives. Selection for high yields of oleoresin should be combined with good volume growth and tree form because trees with these traits occur, even though at low frequency (Squillace 1966a).

Flowering ability.—Stringent selection for heavy flowering, at the expense of selection for traits that have a direct bearing on the final product, is not recommended. Slash pine is generally a good seed producer under seed orchard conditions. Management practices used in orchards may also increase fruitfulness. Roguing of unfruitful clones, or clones whose phenology is out of harmony with others, may be required, however.

Seed Production Areas

As with other pine species, management of carefully selected and treated slash pine stands for seed production may be an improvement over purchasing seed on the open market. Genetic gains in seed production areas are likely to be small—in one study with slash pine only a slight improvement in stem form was obtained (Gansel 1967a). Nevertheless, seed production areas assure a supply of seed of suitable geographic source until genetically improved seed can be developed through other methods. Assurance is also attained that the seed will not be from poor phenotypes, as is often the case when purchasing seed on the open market.

Seed Orchards and Progeny Tests

Slash pine is well suited to the use of seed orchards for mass production of seed from selected trees. Seed orchards may be established with seedlings or grafted stock; there are advantages and disadvantages with either system (Goddard and Brown 1961; Barber and Dorman 1964). In most slash pine orchards, a final spacing of 30 by 30 feet is sought. Some breeders start with a closer spacing to permit roguing of clones or families found to be inferior after progeny testing. A seed orchard is not static and may be modified, expanded, or replaced according to the needs and limitations imposed by the administrative requirements of producing large amounts of high-quality seed each year.

Gains in performance of planting stock of slash pine from seed orchards can be estimated only in general terms because each orchard is a special case. At certain geographic locations or planting areas, use of the proper race or source for selection of clones might result in as much gain as plus-tree selection in local stands for seed orchards at some other location. A trait such as oleoresin yield might show a much higher percentage of increase in seed orchard strains than would some wood quality factors because the range in variation among races and trees is much wider.

Seedlings that have both increased growth rate and resistance to fusiform rust will show a higher percentage of increase in volume growth per acre if planted at a geographic location where losses to rust disease have been high than if they are planted in an area where losses to rust are very low. The inherent genetic quality of seed from an orchard that contains many clones and has been rogued on the basis of progeny tests will be higher than that from orchards that have only a few clones and cannot be rogued. Following are some examples of expected gains from first-generation selection in slash pine, from Franklin (1972):

Trait	*Percent gain*
Volume	20
Specific gravity	6
Straightness	50
Resistance to fusiform rust	35
Oleoresin yield	100
Tall oil yield	25
Sulphate turpentine yield	25

Usable information from progeny tests can be obtained within as little as 10 years. Short-term progeny tests, designed mainly for assessment of oleoresin yield, have been described by Squillace and Franklin (1968) and Squillace and Gansel (1968).

Progeny testing of slash pine has been widely practiced. Such tests permit roguing of undesirable clones in the original orchards and, hence, will increase genetic gain over and above that obtained by mass selection. Some people are also considering establishment of new orchards from clones reselected after information from progeny tests is available. Such use of progeny testing is most worthwhile when the test information can be obtained very early. But, because such information will probably not be available until about 10 years have elapsed, it may be more desirable to begin establishment of new orchards for production of F_2 seed (Franklin and Squillace 1973). Such orchards can be established by selecting superior individuals within the tests and establishing clonal orchards from them or perhaps by converting progeny tests into seedling seed orchards. Various problems, such as avoidance of severe inbreeding, will have to be worked out. But the greatest gains per unit of time will probably come about through breeding and establishing broad-based populations and seed orchards as rapidly as possible.

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