CHAPTER 15

SPECIES HYBRIDS

Hybrid plants have long held a fascination for farmers, horticulturists, and foresters. There is good reason for this attitude because some remarkable crop plants are of hybrid origin—they have hybrid vigor.

Although of widespread common usage, the word *hybrid* does not have a very precise meaning. Plant breeders define a hybrid as the product of a cross between genetically unlike plants. Inasmuch as most individual plants are genetically "unlike," even within species, races, and varieties, the definition is broad. Many people like to restrict the meaning of the word *hybrid* to offspring of crosses among species. However, hybrid corn, the most commercially important example of hybrid vigor, is a result of crossing inbred lines of corn. Thus, the practice has developed of designating the kind of hybrid produced.

Hybrid vigor or heterosis may be defined in various ways. Allard (1960, p. 468), in *Principles of Plant Breeding*, defines heterosis as "hybrid vigor such that an F_1 hybrid falls outside the range of the parent with respect to some character or characters." Results of hybrid vigor can be measured in terms of size, rate of growth, or other terms, but explaining the phenomenon is quite another matter. Studies of heterosis date from Koelreuter in 1763, but the two common theories, overdominance and dominance, are still being debated. Obviously, the subject is of great importance in plant breeding, but, in *Introduction to Plant Breeding*, Briggs and Knowles (1967, p. 221) summarize their discussion of heterosis as follows: "The two primary theories explaining heterosis lead to essentially the same result and are not, therefore, mutually exclusive. There is no reason to believe that a phenomenon as complex as this should result from a single type of reaction."

Hybrid vigor was the subject of a conference in 1950 of geneticists and plant breeders. The material presented at the conference was published as *Heterosis*, edited by J. W. Gowen (1952), and covers the subject in great depth.

Early attempts to utilize hybrid vigor in breeding southern pines were largely exploratory, as might be expected when it is realized that hybrid vigor could be neither predicted in advance nor explained so that appropriate breeding plans could be devised. Mating "unlike" trees is only a place to start on a very long journey. It leaves unanswered such important questions as what traits should be "unlike" and how much "unlike" each of the parental species or individual trees should be. Pine species can be so unlike that no fertile seed is produced when crossing is attempted.

Although progeny may be referred to as hybrids of certain species, in reality they are the result of crosses between individual trees of each species. Thus, the hybridizer, when choosing parental stock, draws not only on species but races, varieties, and individual trees within species. Individual parents may have characteristics within the normal range of variation for the species, or they might be mutations or natural hybrids. Therefore, this chapter on hybrids between species properly follows those concerned with variation within species.

The objectives of research with hybrids among southern pine species have been to determine the species that can be crossed, the facility with which they can be crossed, vigor of hybrid progeny in comparison to the parental species, and the inheritance of traits that differ among species.

Hybrid forest trees present problems in taxonomy. The rules currently applicable are those followed by Little and Righter (1965), based on the International Code of Botanical Nomenclature. Current issues of the Code should be referred to for guides in designating hybrid trees. Only information necessary to understand the names used will be given here.

Formulas are used to designate hybrids, with the species separated by a multiplication sign (×). Thus, slash × loblolly indicates a cross of these species with slash pine as the female parent. A reciprocal cross is the repetition of a cross where the sexual function of the parent is reversed. A backcross is a cross of a hybrid plant to one of its parental types. In the formula for a backcross, the hybrid is given in parentheses, thus, (slash × loblolly) × loblolly. Here, the hybrid is designated as the female parent. Binomial names of hybrids are written with the multiplication sign immediately preceding the second word, thus, *Pinus × sondereggeri*. Hybrids introduced into commercial production should be given a cultivar or popular name to designate them as a variety. Cultivars may differ in important traits, although the parental species are the same.

Interest in species hybrids among southern pines has been apparent from the time the first crosses were made by Philip C. Wakeley, of the Southern Forest Experiment Station, New Orleans, Louisiana, in 1929, when he crossed slash pine and longleaf pine, with longleaf pine as the female parent. From seed planted in 1933, 19 progeny trees were grown at the Institute of Forest Genetics, Placerville, California (Little and Righter 1965).

Some of the characteristics of interspecies hybrids in pine were described by Righter and Duffield (1951). Later, Duffield (1952) reviewed relationships among species in the genus *Pinus* from the standpoint of species crossability and terpene analyses based on production of fertile seed. Lists of pine hybrids and summaries of work in progress at the Institute of Forest Genetics in California include crosses made between various southern pines species (Duffield and Righter 1953; Righter 1955; Critchfield 1962). Botanical descriptions of 40 artificial pine hybrids prepared by Little and Righter (1965) included many southern pines produced by the Institute of Forest Genetics in California and research agencies at other locations. Wright (1953), in a summary of tree-breeding experiments by the Northeastern Forest Experiment Station from 1947 to 1950, listed crosses involving Virginia pine, pitch pine, and jack pine. Mergen (1954d) planned to use hybrids to improve longleaf pine. In a summary of forest tree improvement research in the South and Southeast, Dorman (1966) gave a brief description of research and studies underway with various southern pine hybrids. Work at the Institute of Forest Genetics at Gulfport, Mississippi, with southern pine hybrids was summarized by Schmitt (1968) on the basis of height growth, survival, and infection by fusiform rust when the hybrids were planted on wet, well-drained, and dry sites. In Texas, hybrids of southern pines had high survival rates and reasonably good growth (Long 1973). Most combinations did not produce progeny comparable in growth or quality to the parental types, although the slash × longleaf hybrid seemed to be an exception.

HYBRIDITY AMONG TAXONOMIC GROUPS OF PINE

It was brought out in the chapter on taxonomy of southern pines that classification into various groups over the years has been based on characteristics such as cones, needles, wood, crossability, and chemical composition of turpentine. Certain taxonomists have based their groups on combinations of two or more characteristics but with major importance on certain ones.

Tree species in hard pines could be grouped according to certain traits, but this would have little effect on crossability patterns. The situation is somewhat similar to that in species when the species can be subdivided into races, varieties, and individual trees. We will see later that the facility with which hybrids can be made depends not only on the species but on the individual tree of each species, and still further by which species serves as the male or female parent.

In 1931, at the start of the hybridization reconnaissance work in *Pinus* at the Institute of Forest Genetics at Placerville, California, the southern pines were not generally considered to be a closely related group (Critchfield 1962). The most widely accepted taxonomic arrangement of the pines 30 years ago was that of Shaw (1914). His relationship groups provided the Institute with its first operating hypothesis for crossing programs. Shaw placed the major southern pines (longleaf, shortleaf, loblolly, and slash) and spruce pine in the *Australes*, a group consisting of most of the Western Hemisphere hard pines having cones that opened at maturity. The *Australes* also included all of the closed-cone pines (among them sand, pond, and Table-Mountain) and a few related open-cone species (including pitch and Virginia).

Efforts to cross the southern pines with species of other regions have been concentrated primarily on the species of Shaw's *Australes* (Critchfield 1962). More than 50 attempts were made to cross the southern and western members of this group. A few germinable seed obtained all yielded nonhybrid seedlings.

In the taxonomic divisions and subdivisions of the hard pines proposed by Duffield (1952) and Little and Critchfield (1969), sand and Virginia pines are in subsection *Contortae* with jack and lodgepole pines. Only sand pine has been crossed with slash pine of the other major and minor pines now in subsection *Australes*.

Crosses of southern and Caribbean pines with pines of other regions have been reported but must be accepted with some reservations according to Critchfield (1962). The putative hybrid between Scotch (subsection *Sylvestres*) and longleaf pine reported by Schmidt (1956) must be considered very doubtful; also, the report of a hybrid between loblolly and Japanese red pine (*P. densiflora* Sieb. & Zucc.) in subsection *Sylvestres* (Nohara *et al.* 1950). Crosses of jack pine of subsection *Contortae* with Table-Mountain and, also, of Japanese red pine of subsection *Sylvestres* with pitch pine produced seed (Ahn 1963), but hybridity of offspring seems to be unconfirmed. The hybrid between pitch, subsection *Australes*, and Monterey pine, subsection *Oocarpae*, has been made in large numbers in South Korea according to Hyun (1956) and was confirmed later by Hyun *et al.* (1967).

ARTIFICIAL HYBRIDS AMONG SOUTHERN PINES

The southern pines of subsection 11, *Australes* (Little and Critchfield 1969), have proved to be one of the most crossable groups in *Pinus* (Critchfield 1962). The taxonomic relations among southern

Table 6.—*Mean cone survival and seed yields from interspecific controlled pollinations, 1953-62 (Snyder and Squillace 1966)*

Male parent	Station-years [1]	Seed parents	Flowers	Cone survival	Seeds	
					Per flower	Per cone
	Number	*Number*	*Number*	*Percent*	*Number*	*Number*
			SLASH PINE FEMALE			
Longleaf	8	28	356	24	0.3	1.4
Loblolly	7	39	732	37	4.1	11.2
Shortleaf	6	59	3,847	42	1.8	4.3
Sonderegger	5	12	249	26	.4	1.6
Slash (controlled)	11	46	1,544	38	10.8	28.4
			LONGLEAF PINE FEMALE [2]			
Slash	19	83	1,733	32	11.8	37.3
Loblolly	12	41	990	4	.6	14.4
Shortleaf	4	7	88	0	.0	.0
Sonderegger	5	13	220	26	10.0	38.1
Longleaf (controlled)	14	96	4,061	37	17.3	46.9
			LOBLOLLY PINE FEMALE			
Slash	13	47	1,689	20	.5	2.6
Longleaf	10	42	1,461	16	.3	1.8
Shortleaf	3	8	345	9	.2	1.8
Sonderegger	4	20	601	50	7.8	15.6
Loblolly (controlled)	10	105	7,193	36	6.6	18.2
			SHORTLEAF PINE FEMALE [3]			
Slash	14	94	8,075	34	2.9	8.5
Longleaf	5	8	476	25	.1	.2
Loblolly	10	32	1,874	36	5.6	15.8
Sonderegger	2	5	98	28	.1	.2
Shortleaf (controlled)	4	23	912	60	11.5	19.1
			SONDEREGGER PINE FEMALE			
Slash	4	9	182	46	13.9	30.2
Longleaf	6	15	375	51	12.0	23.4
Loblolly	6	17	443	57	19.4	34.0
Shortleaf	3	4	40	30	5.2	17.3
Sonderegger (controlled)	5	16	309	63	23.8	37.5
Wind	1	4	...	[4] 20	...	25.6
Self	4	13	305	60	3.1	5.1

[1] 1955 results excluded since late spring freeze caused nearly total failure throughout the South.

[2] The data are mostly from Ashley County, Ark., Morehouse Parish, La., and Harrison County, Miss. Some crosses with longleaf include results from Rapides and Sabine Parishes, La.

[3] Some crosses with shortleaf are from Clarke County, Ga. Most of the shortleaf × slash crosses were in Sabine Parish, La.

[4] Number of cones.

pine species were reviewed in Chapter 2. Early plans at the Institute of Forest Genetics, Placerville, California, for species crosses were based on Shaw's (1914) classification, but there have been changes since (table 1). There are 28 possible combinations of species among the eight southern pines in the *Australes* subsection. Sixteen of these combinations have been attempted at least once at Placerville, California, with 11 of them successful. Some of the combinations that have failed at Placerville have been successfully crossed elsewhere. Crossability is variable among and within subsections 11, *Australes*, and 14, *Contortae*, in species combinations tried at Placerville. Within *Australes* various investigators have found variation in crossability, as summarized by Critchfield (1962).

The combinations of southern pine species vary greatly in the ease in which they can be crossed, as measured by the production of sound seed per cone (table 6) (Snyder and Squillace 1966). Seed yield reflects interspecific incompatibility—the proportion of pollinated strobili which develops into cones and the total number of seed per cone.

On the basis of seed yield, crosses in which longleaf pine is the female parent produced the largest average number of seed per cone. An exception is a cross of longleaf with shortleaf pine in which the reciprocal also produces low yields.

The female parent is an important factor in yield of sound seed. Slash pine pollen on longleaf pine produced fairly high seed yield, but longleaf pollen on slash did not. Also, loblolly pollen on shortleaf resulted in fair seed yield, but shortleaf on loblolly did not.

For a 10-year period, average yields from interspecific crosses were, with one exception, inferior to those from intraspecies crosses. However, the differentials are sometimes small, e.g., longleaf × slash vs. longleaf × longleaf yielded 12 vs. 17 seeds per flower and 37 vs. 47 seeds per cone. In several individual instances, furthermore, the interspecies crosses were as good as the intraspecies. It should be noted that crosses of Sonderegger pine represent backcrosses or multiple-species crosses rather than F_1 crosses. The results of interspecies crosses as indicated by seed per cone made in the southern United States and Placerville, California, are generally in agreement for loblolly pine crossed with longleaf or slash pines and for shortleaf pine crossed with longleaf or loblolly pines. They are not in agreement for shortleaf pine crossed with slash pine or for slash pine crossed with longleaf pine. For the shortleaf × slash crosses, there were only five attempts at Placerville, and perhaps these were too few to average out variation among individual trees. The low value for the slash × longleaf cross and for other hybrids with slash pine is attributed to deterioration of pollen stored nearly a year.

At the time when seed yields were summarized by Snyder and Squillace (1966), there were insufficient results to be meaningful for crosses among minor southern pines and among the minor species crossed with major species. Certain of the hybrids, such as those involving pitch, pond, and sand, are being tested for commercial use.

Performance of pine hybrids at the Institute of Forest Genetics, Gulfport, Mississippi, has been summarized on the basis of survival, height growth, and incidence of fusiform rust (table 7) (Schmitt 1968). Differences were large among those species which were the controls. The various hybrid progenies differed widely in survival and incidence of fusiform rust but not so widely in height. At the time of measurement, plantations A and B were 8 years old and plantation C was 6 years old. In a separate plantation, 6-year-old pond and pitch × loblolly pine hybrids grew slower than trees of the parent species. On different sites, soil moisture improved survival but slowed height growth, except for shortleaf and pitch pines and their hybrids.

A variety of isolating mechanisms act to keep the southern pine species distinct, although artificial crosses are possible. The mechanisms are of two principal types: those preventing cross-pollination between species and those preventing the production of germinable seed once pollination has occurred (fig. 185) (Critchfield 1962). Spatial isolation acts to prevent cross-pollination between species. Nine combinations of southern pines are unable to exchange pollen because their ranges do not overlap. Table-Mountain and pitch pines, in particular, are effectively isolated from certain other southern pines of *Australes* by geographic separation. Phenological barriers (time of flowering) appear to be the chief factor preventing or limiting cross-pollination between a number of species with overlapping ranges.

Hybrid progenies among certain species contain aberrant individuals. In the nursery hybrids of pitch pine crossed with a pitch × loblolly hybrid, the seedlings with 2n=24 chromosomes had needles that were long and curled, short and curled, or short and stiff. Seedlings with 2n=48 chromosomes had needles that were short, thick, stiff, and uneven (Hyun *et al.* 1967). In Louisiana, shortleaf × slash hybrids included 16 percent dwarfs (Grano and Grigsby 1968). In Mississippi, 3 years after outplanting, 2.5 percent of slash pine seedlings were dwarfs, while 12.5 percent of slash × shortleaf seedlings were dwarfs (Schmitt and Snyder 1971). Cytological examination showed that some of the dwarfs were polyploid or mixoploid.

It is possible to obtain several hybrid combinations among the southern pines. Certain hybrids could be produced rather easily as far as the amount and quality of seed is concerned, if the traits of the hybrid were sufficiently valuable to justify the costs of controlled pollination or some other method of producing seed in volume. Hybrid vigor has not been present in progenies produced to date, and, generally speaking, traits have been intermediate with those of the parents. The most important factors influencing production of hybrid progenies are the species, the species used as female parent, and the individual parent tree selected within each species for crossing. More detailed information of traits of hybrid progenies are given in the section on inheritance of traits in hybrids.

NATURAL HYBRIDS AMONG SOUTHERN PINES

Natural hybrids have been identified among southern pines at various geographic locations.

Table 7.—*Performance data from three plantings of southern pines and pine hybrids in south Mississippi (Schmitt 1968)*

Species or species hybrids	Source	Trees surviving	Survival	Mean height	Incidence of fusiform rust[1]
		No.	*Percent*	*Feet*	*Percent*
PLANTING A					
Species					
Loblolly [2] (4-1)	Local	44	89	29.9	34
Loblolly (2-5)	"	30	88	29.2	60
Loblolly (2-6)	"	42	90	28.1	64
Slash (2-3×1-4)	"	45	92	27.5	60
Slash (1-4)	"	24	80	26.9	62
Slash (2-4)	"	43	75	26.5	58
Slash (1-4×2-3)	"	27	96	27.0	70
Slash (2-3)	"	41	85	26.4	63
Longleaf (5-2)	"	40	81	22.9	0
Longleaf (1-18)	"	25	100	22.7	4
Shortleaf (6-3)	"	45	83	18.4	0
Species Hybrids					
Slash (2-4) × loblolly (6-1)	"	47	46	26.0	100
Longleaf (5-2) × slash	"	21	86	25.7	0
Shortleaf (6-3) × loblolly	"	46	94	25.1	2
Shortleaf (6-3) × slash	"	39	65	24.8	5
Slash (2-3) × loblolly (6-1)	"	47	44	23.7	100
Loblolly (2-5) × Sonderegger (1-17)	"	46	87	28.9	85
Loblolly (2-5) × Sonderegger (2-7)	"	34	60	27.9	53
Loblolly (4-1) × Sonderegger (2-7)	"	43	83	27.1	60
Loblolly (2-6) × Sonderegger (2-7)	"	40	74	25.5	77
Sonderegger (2-7) × loblolly	"	46	52	26.2	35
Loblolly (2-6) × Sonderegger (1-17)	"	35	69	26.1	80
Sonderegger (2-7)	"	46	87	25.8	61
Sonderegger (1-17)	"	18	71	25.1	33
Sonderegger (2-7) × (shortleaf × slash)	Local & Calif.[3]	20	95	25.7	50
Longleaf (5-2) × Sonderegger (2-7)	Local	46	98	25.3	5
Longleaf (1-18) × Sonderegger (2-7)	"	23	96	25.5	30
Shortleaf (6-3) × (shortleaf × slash)	Local & Calif.[3]	31	94	24.5	6
Longleaf (5-2) × Sonderegger (1-17)	Local	34	80	23.5	6
Sonderegger (1-17) × (shortleaf × slash)	Local & Calif.[3]	23	58	20.2	57
PLANTING B					
Species					
Loblolly (4-1)	Local	60	94	22.7	16
Slash (2-4)	"	59	92	19.6	25
Longleaf (5-2×5-1)	"	26	93	17.3	0
Longleaf (5-2×self)	"	12	34	14.9	0
Longleaf (5-1)	"	51	80	13.5	0
Longleaf (5-2)	"	39	61	13.4	0
Longleaf (5-1×self)	"	1	50	3.0	0
Shortleaf (6-3)	"	33	92	13.0	0
Species Hybrids					
Shortleaf (6-3) × slash	"	25	69	20.8	3
Shortleaf (6-3) × loblolly	"	33	92	20.6	0
Sonderegger (2-7)	"	18	50	19.5	23
Sonderegger (2-7) × loblolly	"	14	39	19.2	27
Slash (2-4) × loblolly (6-1)	"	47	74	17.2	63
Loblolly (4-1) × Sonderegger (2-7)	"	39	61	17.0	28
PLANTING C[4]					
Species					
Slash	"	228	84	21.7	17
Longleaf	"	133	78	12.8	0
Species Hybrids					
Slash × shortleaf	"	132	77	24.0	2
Slash × loblolly	"	89	57	23.8	45
Sonderegger × loblolly	"	68	92	22.9	35
Slash × Sonderegger	"	87	61	21.9	31
Longleaf × slash	"	92	58	21.8	3
Longleaf × Sonderegger	"	72	80	20.0	0

[1] On shortleaf and shortleaf hybrids the fungus may be *Cronartium quercuum* rather than *C. fusiforme*.

[2] Hyphenated numbers are tree numbers.

[3] Pollen mix supplied by Institute of Forest Genetics, U. S. Dep. Agr. Forest Service, Placerville, California.

[4] Entries for plantation C are averages for one to four progenies.

	palustris	elliottii	taeda	echinata	serotina	rigida	glabra
elliottii	F g d						
taeda	f G d	F g d					
echinata	F G d	F g d	F g d				
serotina	F - d	F - d	F g d	f - d			
rigida	- - D	- G D	- g d	f g d	- g d		
glabra	f - d	F G d	f G d	F G d	F - d	- - D	
pungens	- - D	- - D	- G D	F G d	- - D	F G d	- - D

LEGEND:

F - difference in flowering time more than two weeks 1/
f - difference in flowering time less than two weeks
D - little or no overlap in distribution
d - distributions overlap
G - strong genetic barrier (few or no hybrids produced artificially) 2/
g - weak genetic barrier (cross readily) 2/
\- no information

1/ Data on flowering time from Dorman and Barber (1956).

2/ Based on results at Placerville.

Figure 185.—Types of isolation barriers between southern pines of Group XI. Difference in flowering time (F) is important in 13 combinations, overlap in distribution (D) is important in 8, and genetic barriers (G) are important in 8. (Critchfield 1962)

There is always variation in time of pollen dissemination and conelet receptivity among individual trees of a species and, also, from year to year because of weather fluctuations. These conditions permit crossing (fig. 185).

Although traits of natural hybrids can be defined, these trees are not good material on which to base precise estimates of inheritance in specific crosses among species. This is true because the parents are unknown and themselves may have been hybrids of some kind.

Natural hybrids are available for selection and possible use as seed orchard clones or in inheritance studies. Probably many of those noted have been chosen because they have a good combination of traits.

Because of the contribution natural hybrids make to variation within and among stands, a description of these unusual trees was also included in Part III on geographic variation.

INHERITANCE IN SPECIES HYBRIDS

At some point or other in creative breeding programs, pollinations or crosses are made among individual trees of particular species. This is true because tree breeding problems usually relate to traits of individual trees and species within definite geographic locations. Thus, in addition to general characteristics of species hybrids among southern pines, the characteristics of individual trees or families or progenies of each species combination are of great importance. In this situation, it is the exception to the rule that may be of great concern to the tree breeder. The importance of the individual tree, either maternal or paternal, in species hybrids was discussed briefly in the introductory chapter on species hybrids. The full extent of the effects of the individual tree, as well as whether it is used as a maternal or paternal parent, is incompletely known at present. However, enough is known to place the tree breeder on guard so that he can expect some variation in characteristics of hybrids according to the individual tree or the race that happens to be used for parents.

In tree breeding, species crosses are usually written with the female parent first. However, in work that has been done to date, both species have been used as the maternal or paternal parent at various times. In the following discussion of characteristics of hybrids, titles for the sections show crosses between species without regard to sex of parents. Many of them contain reciprocal crosses, and this will be indicated in discussion of various progeny groups.

Pinus elliottii × *taeda*
Slash Pine × Loblolly Pine

Characteristics of the hybrid, as given by Keng and Little (1961) and Little and Righter (1965, p. 17-18), are as follows:

> Bark rough, thick, furrowed into scaly plates, blackish gray with brown exposed in deep furrows. Spring shoots multinodal. Twigs glabrous, glaucous when young, light yellow green the first year, becoming brown the second year. Buds reddish brown, the scales whitish fringed. Leaves 3 and 2 in a fascicle, stout, stiff, 10-19 cm. long, acuminate, serrulate, green; stomatal rows of leaves in 3's 7-12 dorsal and 4-8 on each ventral surface, of leaves in 2's 12-14 dorsal and 9-10 ventral. Needle anatomy in cross section: Hypodermis biform, of 2, sometimes 3, layers of cells, the inner border straight; endodermis of thin-walled cells; resin canals medial, internal and medial, or partly subinternal, 2-7, 2 large usually medial at angles and often 1-5 additional smaller.
>
> Cones 1-4 at a node, almost sessile, ovoid conic, symmetrical, 7-11 cm. long, 5-7 cm. across when open at maturity, persistent 1 year or more, apophyses dull nut brown, elevated along a transverse keel, umbo raised and about 3 mm. high including the sharp spine.
>
> The occurrence of leaves partly in 2's is similar to *Pinus elliottii*, as *P. taeda* has needles uniformly 3 in a fascicle. Parents have similar needle anatomy except that resin canals are mostly medial in *P. taeda*, mostly internal in *P. elliottii*, and intermediate in the hybrid. Hybrid cones are intermediate between the small cone with stout spines in *P. taeda* and the large cone with smaller prickles in *P. elliottii*. Cones of *P. taeda* and the hybrid are dull nut brown, while those of *P. elliottii* are shiny reddish brown.
>
> Four trees at the Institute were from pollination in 1931 with *Pinus taeda* as female parent and from seed sown in 1933. Three trees with *P. elliottii* as female parent were from pollination in 1933 and seed sown in 1935. In 1956 these trees were about 30 feet high and 6 inches d.b.h.

Southern fusiform rust is the most serious disease of both slash and loblolly pines. Thus, hybrids between these species are prone to heavy infection (fig. 186).

In Georgia, tracheid length in hybrids of loblolly and slash pines were generally intermediate with tracheid length of parent trees (Jackson and Greene 1958). In three of the hybrid families, tracheid length of the progeny was closer to that of the maternal parent than that of the paternal parent, and in one group it was intermediate. The tracheid length range between all parents varied from 1.09 to 1.55 mm. Wood samples were taken from the first ring from the pith of the branches. Single branches were taken from the topmost whorls of 10 cross-pollinated progeny of each family. Wood samples of parents and their progeny were obtained from the forests and outplantings at the Ida Cason Callaway Foundation, Pine Mountain, Georgia.

Wood specific gravity of control-pollinated progeny of individual loblolly and slash pines and of crosses between trees of both species were intermediate with that of the parents (Jackson and Warren 1962). Of 13 families, 4 were species hybrids. Specific gravity ranged from 0.338 to 0.435 for the female parent and 0.351 to 0.431 for the male parent. Progeny means ranged from 0.356 to 0.429. For both species and the hybrids, the specific gravity of the progeny was closely related to that of the average of both parents, as shown by a highly significant correlation coefficient of $r = +0.903$, and the equation was $Y = 0.078 + 0.814\times$, in which Y represents the progeny. Likewise, the specific gravity of the progeny was closely related to that of the female parents, with a highly significant correlation coefficient of $r = +0.810$. The specific gravity of the progeny was not so closely related to that of the male parents, as shown by a coefficient of $r = +0.573$, which was barely significant at the 5-percent level. In one cross involving loblolly and slash pine parents whose specific gravity was between 0.36 and 0.39, specific gravity of the progeny was between 0.38 and 0.39. For another cross of loblolly × slash where specific gravity of the parents was in the range of 0.42 and 0.43, the specific gravity of the progeny was just under 0.43. Similar relationships occurred in crosses of individual slash pine trees and individual loblolly pine trees that varied widely in wood specific gravity. It is apparent that specific gravity in both slash and loblolly pines can be moved up or down the scale according to parents chosen for breeding purposes.

Fibril angle in wood of loblolly and slash pine hybrids from control pollination within and among species was correlated with that of the parents (Jackson and Morse 1965b). Branch wood was taken from eight offspring of crosses among loblolly pine trees, among slash pine trees, and among species hybrids. For loblolly × slash crosses, a correlation of $r = +0.885$ was obtained for female parents and progeny, a significant correlation of $r = +0.996$ for the parent averages and progeny, and a nonsignificant correlation of $r = +0.189$ for the male parents and progeny. In loblolly and slash pines, the orientation of fibrils with respect to longitudinal axis of tracheids may vary from a small angle of 10° or less to a large angle of 30° or larger. Correlations for fibril angle in crosses among individual slash or loblolly trees were similar to that for crosses between species. For slash × slash crosses with mid-point parent averages, the correlation was $r = +0.869$. For loblolly × loblolly crosses, a significant

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Figure 186.—High incidence of fusiform rust infection in a hybrid of slash and loblolly pines (left center row) in contrast to the low infection in the parent species. This contrast illustrates the effect of combining undesirable traits of certain species.

correlation $r = +0.826$ was obtained for female parents and progeny, and a nonsignificant correlation of $r = +0.401$ was obtained for male parents and progeny. A discussion of the relationship between wood characteristics in branches of upper whorls and the stemwood in upper parts of the tree and the base of the tree was given in chapters 8 and 11 on variation and inheritance within loblolly and slash pine species.

Certain characteristics of the needles of loblolly × slash pine hybrids are intermediate with those of a parent species (Mergen 1958a). Loblolly pines have a much greater number of stomata on their needles than slash pine. The intermediacy of the hybrid in number of stomata was well defined for both sides of the needle when frequency distribution curves were developed. The means in the distribution patterns of slash pine and loblolly pine were separated enough for analysis, and there was only limited overlapping in the distribution of the two species. The standard deviation for the hybrid, based on the individual rows of stomata, was also smaller than that for either of the two parental species. The number of rows of stomata on the hybrid was also intermediate between the parents; the relationship was present for both sides I and II. Needles from the loblolly pine tree had a much greater number of teeth per unit length on the edges of the needles than those from slash pine trees. Those on the loblolly needles, however, exhibited a much greater variation. The number of teeth on the needles from the hybrid were intermediate between both parent species, and the distribution pattern was similar to that of slash pine. The number of teeth along each edge, rather than the average for each needle, was used to compile the frequency distribution data.

Interspecific crosses between loblolly and slash pines were made with difficulty in South Africa, but offspring with marked hybrid vigor were produced (South Africa Department of Forestry 1967).

In Texas, loblolly pines selected for drought resistance and crossed with slash pine produced vigorous progeny (Zobel, Campbell, Cech, and Goddard 1956).

Pinus elliottii × *palustris*
Slash Pine × Longleaf Pine

At Placerville, California, where Wakeley's first longleaf × slash trees were planted, heights were only 10 to 25 feet after 23 years, and snow damage was heavy. Later, the reciprocal cross, slash pine as the female parent, was made at Placerville.

Vegetative characteristics of the species hybrid, with needle characteristics from Keng and Little (1961), are given by Little and Righter (1965, p. 17) as follows:

> Bark rough, thick, furrowed into long scaly, slightly shaggy plates, blackish gray with brown exposed in deep furrows and where scaled off. Spring shoots uninodal. Twigs stout, glabrous, light yellow green the first year, becoming light brown the second year. Buds large, reddish brown and whitish, the scales whitish fringed. Leaf sheaths whitish, light tan toward base, 2–3 cm. long, in age only about 1 cm. long. Leaves 3 and 2 in a fascicle, stout, stiff, straight to curved or drooping, 15–30 cm. long, acute-acuminate, serrulate, green; stomatal rows of leaves in 3's 8–12 dorsal and 3–6 on each ventral surface, of leaves in 2's 10–15 dorsal and 6–10 ventral. Needle anatomy in cross section: Hypodermis biform, of 2–4 layers of cells, the inner border curved or straight; endodermis of thin-walled cells; resin canals internal and medial, or internal, 2, sometimes 3–4.
>
> Parentage of *Pinus palustris* is indicated by the stout twigs, large buds with white-fringed scales, whitish leaf sheaths, very long leaves, and uninodal spring shoots. Leaves partly in 2's suggest *P. elliottii*. In needle anatomy the parents and hybrid are similar and not readily separated, but the hybrid has hypodermis often intermediate in thickness.

The means of the distribution patterns for the number of stomata per millimeter and per row of stomata in the putative natural slash pine hybrids-longleaf pine hybrids were intermediate between those of slash and longleaf pine but with a greater standard deviation than either (Mergen 1958a). Slash pine needle samples were obtained at random from the leaders of 25 seedlings of the local slash pine growing in a racial variation study. The needle samples from the putative natural hybrids between slash and longleaf pines were collected from 4-year-old trees from a natural hybrid swarm growing in an abandoned field on the Osceola National Forest in Florida. The trees surrounding the abandoned field were slash pines with a few longleaf pines on the northern edge. An extensive reconnaissance of the surrounding forests indicated that neither loblolly nor pond pine trees were within pollination distance of the presumed mother trees. The seedlings had the general appearance of slash pines, but their pattern of height growth and shape of terminal bud resembled that of longleaf pines. Three of the seedlings were potted and transferred to a greenhouse. The needles from the putative hybrids were collected just prior to the microscopic analysis, while a composite sample of longleaf pine needles was collected from five longleaf pine trees growing in the vicinity. The frequency distribution of the stomata per millimeter and per row of stomata transgressed outside the upper value for longleaf pine. The average number of rows of stomata and the average number of teeth for the two putative parent species were very similar and therefore could not be used for analysis.

In later work, Mergen (1959a) concluded that the number of stomata per unit length was relatively independent of environmental effects and was under fairly rigid genetic control. The frequency of the stomata was not controlled by a single gene but by a large number, resulting in intermediacy of a hybrid. This was tested on five artificial hybrids growing in test plantations, of which three were crosses among hard pines and two were crosses among soft pines. This confirmed earlier conclusions that number of stomata was a fairly good trait on which to base analysis of species hybrids.

Longleaf × slash pine hybrids at age 7 planted in central Louisiana closely resembled longleaf pine in form and branching habits but started height growth immediately and grew almost as fast as slash pine (Derr 1966). The hybrids appeared less susceptible than their parents to brown-spot needle blight of longleaf or to fusiform rust of slash pine (fig. 187). Families of individual longleaf maternal parents pollinated with the same slash pine pollen mix varied widely in survival, height growth, brown-spot infection, and fusiform rust infection (percent infected trees, stem galls per infected

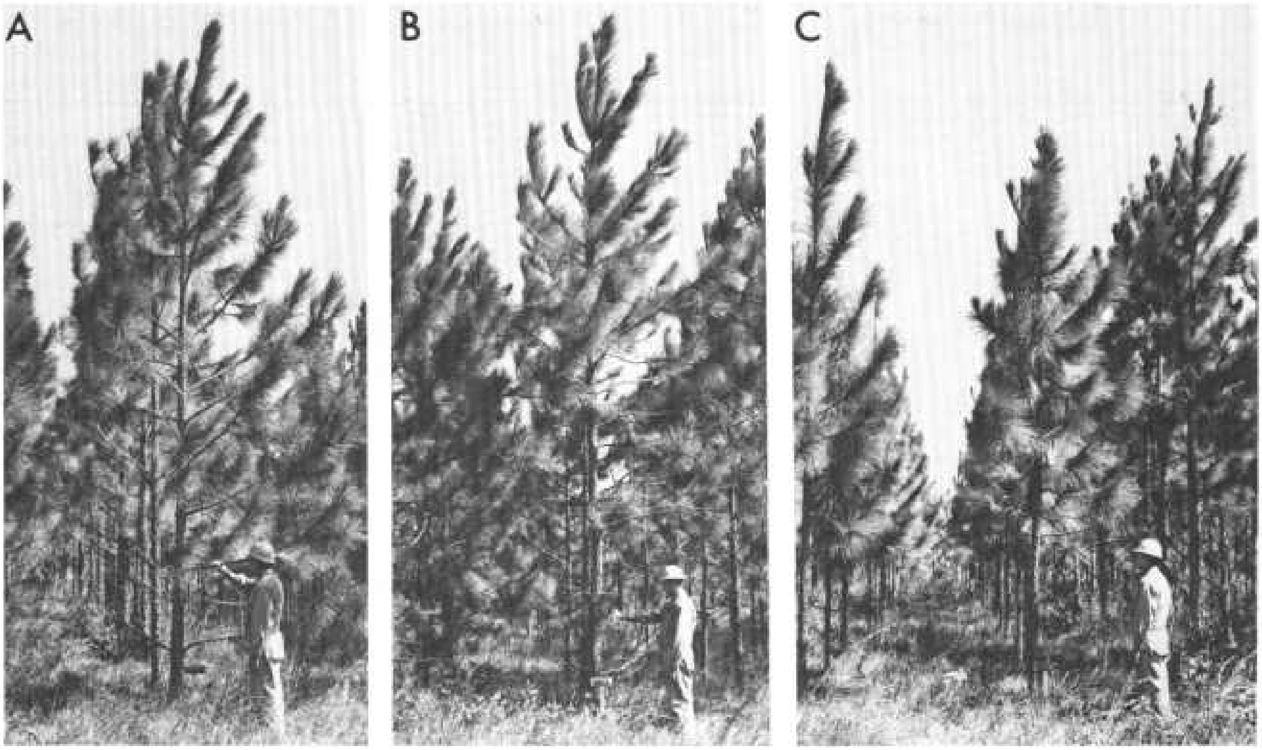

Figure 187.—Stem form and branching habit of the longleaf × slash hybrid (A), wind-pollinated slash (B), and longleaf (C). The low live branches on slash pine persist because they are galled by rust. (Derr 1966)

tree, and branch galls per infected tree). These observations were based on 240 open-pollinated seedlings of slash pine, 160 to 260 seedlings in each of three longleaf-slash pine hybrid families, and 80 seedlings each in three open-pollinated progenies of individual longleaf pine families. Survival among the three hybrid groups varied considerably more than among the three wind-pollinated half sibs. In both the hybrid and wind-pollinated groups, however, the trees with the poorest survival were from the same longleaf parent.

At age 4, the average height of brown-spot-resistant hybrids ranged from 6.8 to 8.1 feet for the three parental groups (Derr 1966). The slash pines were within this range at 7.8 feet, while the longleaf seedlings were just emerging from the grass stage and averaged 2.6 feet. In the following 3 years, slash pine grew 3.7 feet per year, the hybrids 3.5 feet, and the longleaf 3.1 feet. These data exclude seedlings with brown spot that failed to reach 4.5 feet by age 7.

The hybrids appeared to have considerable resistance to brown spot, even though some seedlings within each group were susceptible. Since the seedlings were sprayed, severity of the disease on planted longleaf could not be estimated. However, natural seedlings of the same age adjacent to the study area were all heavily infected by the fourth year, and it is doubtful if position of the hybrids within the plantation influenced exposure to the disease. Infection varied widely among the three groups of hybrids. Those from longleaf tree No. 7 were the most resistant; at age 2 years, 6 percent were either dead from the disease or severely infected, while 25 to 42 percent of those from trees Nos. 5 and 6 had proved highly susceptible. At age 4, brown spot had killed 28 percent of the hybrid seedlings from tree No. 5, 13 percent from tree No. 6, and 3 percent from tree No. 7. While a proportion of susceptible seedlings varied among the three hybrid progenies, each group contained a substantial number that remained completely free of brown spot to age 7. They ranged from 38 percent of the first-year survival for progeny of tree No. 5 to 86 percent for tree No. 7. The hybrids apparently segregate into well-defined classes of individuals susceptible or resistant to brown spot. Those susceptible became heavily infected in the first or second season in the field, whereas the initial infection in longleaf seedlings planted in a typical grass rough is usually restricted to the needle tips. Infected hybrids continued height growth, dying from the disease after they reached 2 to 5 feet. Planted longleaf, by contrast, seldom die within the initial 4 years; if heavily infected, they stay in the grass stage and eventually succumb; or if vigorous enough to reach a height of about 4.5 feet, they become substantially free of the disease. The number of infected hybrids did not increase greatly after the first year, an indication that resistant individuals withstood infection during the period when the amount of inoculum normally builds up. The three hybrid groups differed sharply in susceptibility. As the same slash pine pollen mix was used on all trees, these differences may indicate genetic control of this trait through the female longleaf parent. They also suggest considerable variation in resistance among individual longleaf trees.

The young hybrids appeared to have a certain amount of resistance also to southern fusiform rust. Less than 1 percent had rust galls at age 4, while branch or stem galls were found on 42 percent of the slash pines (Derr 1966). Three years later the incidence of infection had increased to 74 percent in slash pine and to 13 percent for the three groups of hybrids. Longleaf trees had no infection at either age 4 or 7. Multiple infections were common among the slash pines; infected trees averaged 2.6 branch galls each, and half of them had well-defined stem galls. In contrast, the infected hybrids averaged 0.85 branch gall per tree, and about one-third had stem galls. Additional study is required to determine the extent of rust resistance in hybrids, but work in Mississippi also shows it may exist (Schmitt 1968).

During the first 7 years in the field, longleaf × slash pine hybrids displayed good stem form and branching habit (Derr 1966). They appear to have the desirable features of longleaf pine—a straight bole free of sweep or fork. Branch sizes are intermediate between slash and longleaf, and low branches are not persistent. The hybrids in three different parental groups were remarkably uniform in appearance. In Texas, a polymix cross of slash × longleaf had excellent growth rate, form, and limb characteristics (Long 1973).

After an intensive study with longleaf, loblolly, and their natural hybrid Sonderegger, Brown (1964) felt that the genetic information obtained on multiple-gene inheritance would probably apply to longleaf × slash hybrids.

Pinus elliottii × *clausa* Slash Pine × Sand Pine

Slash pine and sand pine were successfully crossed in 1962 and 1963 (Saylor and Koenig 1967). This cross is one of the few successful inter-Group crosses in the genus *Pinus*, and it represents the first well-documented hybrid between a species of *Australes* and species from any other group. Five hybrids were analyzed and compared to open-pollinated seedlings from the parental trees at different times over a 22-month period. The hybrids were intermediate between their parental controls in seven of the nine growth and needle characteristics studied, but they closely resembled the sand pine male parent in the early stages of development. One sand pine as the male parent crossed only with two out of three slash pine trees as the female parent; one other sand pine crossed with only one of the slash pine parents; and the third sand pine would cross with none of the slash pine trees. With slash pine as the female parent, yield of sound seed was very low, and the reciprocal cross produced no sound seed. In the volatile fraction of the cortical oleoresin of slash pine, no myrcene was found, but beta-phellandrene averaged 1.7 percent. In sand pine, oleoresin myrcene averaged 0.7 percent, but there was no beta-phellandrene. In the slash × sand hybrid, myrcene averaged 0.5 percent and was inherited from the male parent, but no beta-phellandrene was inherited from the female parent. In the hybrid, the average percentage of alpha-pinene was higher, beta-pinene lower, and camphene about the same as the average of all parents. Chemical composition of oleoresin varied among individual hybrid trees and each of the parental species; thus, inheritance of these materials is complex and must await additional work. Since both slash and sand pines are used for pulp, by-products of pulping may be important. Survival of the slash × sand pine hybrid in a Florida planting was 83 percent, and height was 3.6 feet after 3 years (Saylor and Zobel 1973).

Pinus elliottii var. *elliottii* × *elliottii* var. *densa* Slash Pine × South Florida Slash Pine

In putative hybrid populations of typical slash pine crossed with South Florida slash pine, the number of stomata per millimeter was intermediate with that of the parent trees (Mergen 1958a). The difference between the means in the distribution pattern for the number of stomata per millimeter in South Florida slash pines and typical slash pines from Baker County, Florida, was relatively small. This difference in distribution was, however, sufficient to illustrate the intermediacy of the trait in hybrid offspring. The seedlings from Polk County in southern Florida were of particular interest. Their distribution based on individual measurements on a needle had a large standard deviation, as a result of which both tails of the distribution curve extended to the extremities of both typical and South Florida slash pines. The number of rows of stomata was more variable, and on side II, it was greater than that of either of the putative parent species. For side I, both of the putative hybrid sources were intermediate between their parents. The distribution pattern of the teeth on the hybrids was similar to that of the typical South Florida slash pine. The intermediacy in the number of stomata per millimeter, along with their intermediate grass-stage growth features, indicate that these seedlings were hybrids between typical slash and South Florida slash pines. It was reported previously (Mergen 1954e) that the Polk County seedlings probably were hybrids on the basis of their height growth, stem characteristics, overall needle growth, and outward signs of frost hardening.

From a study of geographic variation, it was concluded that trees in the transition area between the two varieties of slash pine were not hybrids (Squillace 1966b). This conclusion was reached because diversity among trees within stands was not greatest in the transition area.

Pinus caribaea × *elliottii* Caribbean Pine × Slash Pine

In Australia, the low fertility and seed production already recognized in a slash pine × Caribbean pine hybrid were evident in the reciprocal (Nikles 1964). The seed was sown immediately following extraction. Four trees of Caribbean pine were used as female parents for four trees of slash pine pollen parents. Number of flowers pollinated per cross ranged from three to seven. Crosses on two trees failed to produce cones, and three to seven cones each were produced on the remaining trees. However, four cones from one tree failed to produce seed. Number of seed produced per cone on the remaining trees ranged from 10 to 42, with germination percent from 4 to 33.

In offspring from backcrossing of the F_1 of slash pine × Caribbean pine with pollen from slash pine and from Caribbean pine, there was a gradation between the two pure species through the hybrid stocks in relation to the occurrence of bundles of adult needles, time of flushing, and color of the seedlings (Nikles 1964). The F_1 hybrids showed "halfway" intermediacy, while the backcrosses approximated their recurrent parents. The growth rate of the F_1 hybrids was intermediate, but the backcrosses clearly surpassed slash pine and the F_1 hybrids and had a slight superiority over Caribbean pine at 8 months of age. The fertility of the F_1 hybrid seed was very low (10 percent), while the backcross seed was approximately the same as that of the recurrent parent. Eleven-year-old hybrids were superior in economic yield to both parents in Australia but only when grown on swampy sites (Nikles 1970).

Pinus echinata × *taeda* Shortleaf Pine × Loblolly Pine

Characteristics of the hybrid, with needle characteristics as given by Keng and Little (1961), are given by Little and Righter (1965, p. 19–20) as follows:

> Bark rough, thick, furrowed into long scaly plates, gray. Spring shoots multinodal. Twigs glabrous, glaucous when young, light yellow green and shiny the first year, becoming light reddish brown the second year. Buds acuminate, light reddish brown, resinous. Leaves 3, sometimes mostly 3 and less frequently 2, in a fascicle, slightly stout and stiff, 7–12 cm. long, acute-acuminate, serrulate, green; stomatal rows 9–15 dorsal and 5–7 on each ventral surface or 10–12 on ventral surface of leaves in 2's. Needle anatomy in cross section: Hypodermis usually biform with 2 (rarely 3) layers of cells, sometimes uniform with 1 layer, the inner border straight; endodermis of thin-walled cells; resin canals medial, sometimes medial and internal, 2 large medial at angles and often 1–4 additional, about 0.04–0.08 mm. in diameter.
>
> Male strobili (dry) 10–18 mm. long, 3–5 mm. in diameter, orange brown. Cones single or paired, sometimes in whorls of 3 or 4, almost sessile, ovoid conic, symmetrical, 6–8 cm. long, 4.5–7 cm. across when open, often persistent for several years on old branches; apophyses dull pale fulvous brown, elevated along a transverse keel, the nut-brown umbo forming a sharp stout curved prickle or spine about 3 mm. long. Winged seeds 17–27 mm. long, the detachable wing nut-brown, body ovoid, 5–6 mm. long, blackish.
>
> The hybrid might appear to be a variation of *Pinus taeda* with small cones, having the sharp stout prickles of the cone scales. In needle length and cone size the hybrid is intermediate. The number of needles in a fascicle, 3 and 2, distinguish the hybrid, because *P. taeda* has 3 uniformly, while *P. echinata* has usually 2. In needle anatomy the hybrid is intermediate between the slightly differing parents.
>
> This cross was made at the Institute as early as 1933. The reciprocal backcross with *Pinus taeda* was made in 1948.

As a part of the work at the Institute of Forest Genetics, Gulfport, Mississippi, artificial hybrids were made between shortleaf pine (which is generally considered resistant to fusiform rust) and slash and loblolly pines (both of which are highly susceptible to rust). It was realized that the number of interspecies crosses was small, but it was felt, nevertheless, that crossing slash or loblolly with shortleaf would give variable results in regard to progenies resistant to fusiform rust (Jewell 1961; Schmitt 1968).

Hybrids of shortleaf and loblolly pines from seed produced at the Institute of Forest Genetics, Placerville, California, have been planted at various locations throughout the South. In Washington Parish, Louisiana, hybrids between Oklahoma shortleaf and Louisiana loblolly pine were outplanted in 1950. An examination in 1955 and in 1956 of 31 surviving hybrids revealed no cankers due to fusiform rust, although 65 of 97 slash pines planted nearby had galls (Henry and Bercaw 1956). In northern Mississippi, the hybrids failed to grow as well as the shortleaf or loblolly parental species

(Harrington 1953). In middle Georgia, loblolly × shortleaf pine hybrids of certain geographic origins grew about as fast as parental pine species and at the same time had a very low rate of infection by southern fusiform rust (Sluder 1970). At age 18 years, one hybrid (Oklahoma shortleaf × North Carolina loblolly) was almost as good as local loblolly pine in average tree size and exceeded it in survival and volume production per acre.

In Mississippi, means for most of 20 vegetative characters of young F_1 hybrids between loblolly pine and shortleaf pine were intermediate with those of the interplanted parental checks and the ranges overlapped (fig. 188) (Mergen *et al.* 1965). Separation of hybrids and parents, which minimized much genotype-environmental disturbance, was obtained by combining certain vegetative characters in pictorialized scatter diagrams. The diagrams resulted in good distinction between the parental species in hybrids in two areas in Mississippi where natural hybrids occurred. In the hybrids, dominance was noted for loblolly pine in vegetative characters and flowering phenology, and it was noted for shortleaf in morphologic reproductive characters.

In southern Illinois, planted shortleaf × loblolly pine hybrids—open-pollinated and inter-pollinated, and a hybrid from backcrossing shortleaf × loblolly pine to loblolly pine (with parental seed sources in Virginia and North Carolina)—had survival of 88 and 82 percent, respectively, as compared with loblolly pine from Tennessee with 88 percent and loblolly pine from Maryland with 96 percent. Height growth was 3.1, 3.7, 4.3, and 3.6 feet, respectively (Minckler 1951, 1952). Specific hybrids of northern parents were more resistant to cold damage and ice breakage than trees of the parental species from southern locations in their natural ranges. Height growth of the hybrid was greater than that of loblolly pine except those races from the northern part of the natural range.

The occurrence of natural loblolly × shortleaf pine hybrids in Texas was suggested by Zobel (1953), based on observation of trees with traits intermediate between the two species. Also, it was noted that in certain cases there was overlap in flowering time of these two species. Shortleaf × loblolly pine hybrids in Texas were reported to be "early flowering" (Zobel, Campbell, Cech, and Goddard 1956). Trees with characteristics intermediate with loblolly and shortleaf have been located and are being tested for resistance to fusiform rust (Florence 1973).

Pinus echinata × *elliottii* Shortleaf Pine × Slash Pine

Characteristics of the hybrid, with needle characteristics as given by Keng and Little (1961), are given by Little and Righter (1965, p. 18–19) as follows:

> Bark rough, thick, furrowed into scaly plates, blackish gray. Spring shoots multinodal. Twigs glabrous, glaucous when young, light yellow green and shiny the first year, becoming brown the second year. Leaves 2 or sometimes 3 in a fascicle, stout, stiff, 11–20 cm. long, acute-acuminate, serrulate, green; stomatal rows of leaves in 2's 13–16 dorsal and 10–12 ventral, of leaves in 3's 11–14 dorsal and 5–7 on each ventral surface. Needle anatomy in cross section: Hypodermis biform, of 2 or sometimes 3 (rarely 4) layers of cells; endodermis of thin-walled cells; resin canals medial, or medial and internal, 2 large medial at angles and often 1–4 additional, about 0.03–0.06 mm. in diameter.
>
> Cones 1–4 at a node, almost sessile, ovoid conic, symmetrical, 5–7 cm. long, 3.5 cm. in diameter when closed, 5–6 cm. across when open, persistent 1 or 2 years; apophyses elevated along a transverse keel, the umbo raised and ending in a sharp prickle about 1 mm. long.
>
> In needle length and cone size the hybrid is intermediate, though with smaller organs nearer to *Pinus echinata*. The two species differ but slightly in needle anatomy. The hybrid resembles *P. echinata* in the resin canals mostly medial.
>
> Five trees were planted in 1933 from the cross made in 1931. When 23 years old these trees were 30–35 feet high and 6–9 inches d.b.h., mostly with good form and narrow crowns.

Hybrids of shortleaf and slash pines produced by the Institute of Forest Genetics, Gulfport, Mississippi, show branching characteristics intermediate with that of the parents. Branches are smaller than those of slash pine but somewhat larger than those of shortleaf pine. Generally, the form of the trees is good (fig. 189) (Wakeley *et al.* 1966).

In Texas, shortleaf × slash pine hybrids were reported as "early flowering" (Zobel, Campbell, Cech, and Goddard 1956).

The southern fusiform rust is a very serious gall rust affecting three of the major southern pines. Slash and loblolly pines are the most susceptible, and longleaf is usually considered intermediate. One source of resistance originally thought to be stable was from shortleaf pine (Jewell 1966).

Research in methods of developing pines resistant to the rust was conducted at the Institute of Forest Genetics, Gulfport, Mississippi. The program had two main objectives: find and evaluate resistance in susceptible species, and attempt to incorporate by interspecies crosses the resistance assumed for shortleaf pine. Artificial inoculations have shown resistance to rust in the hybrid, but the amount of resistance is strongly influenced by the characteristics of the parent trees of each species (Jewell 1966). Variation among trees in resistance to rust is summarized in the chapters on variation and inheritance.

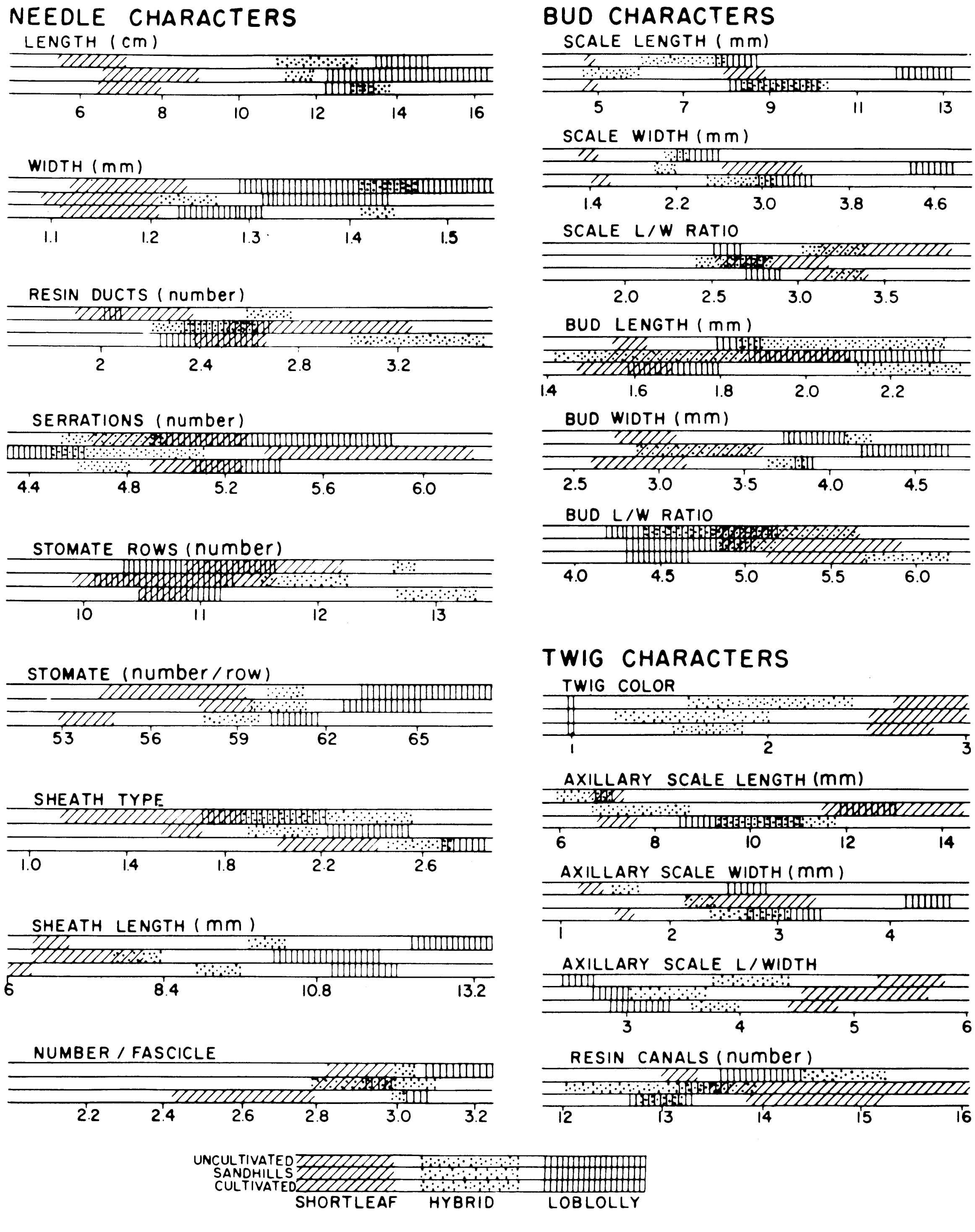

Figure 188.—Comparisons of means ± one standard error for needle, bud, and twig characteristics of parental species and hybrids grown in progeny test plantations on three sites. (Mergen *et al.* 1965)

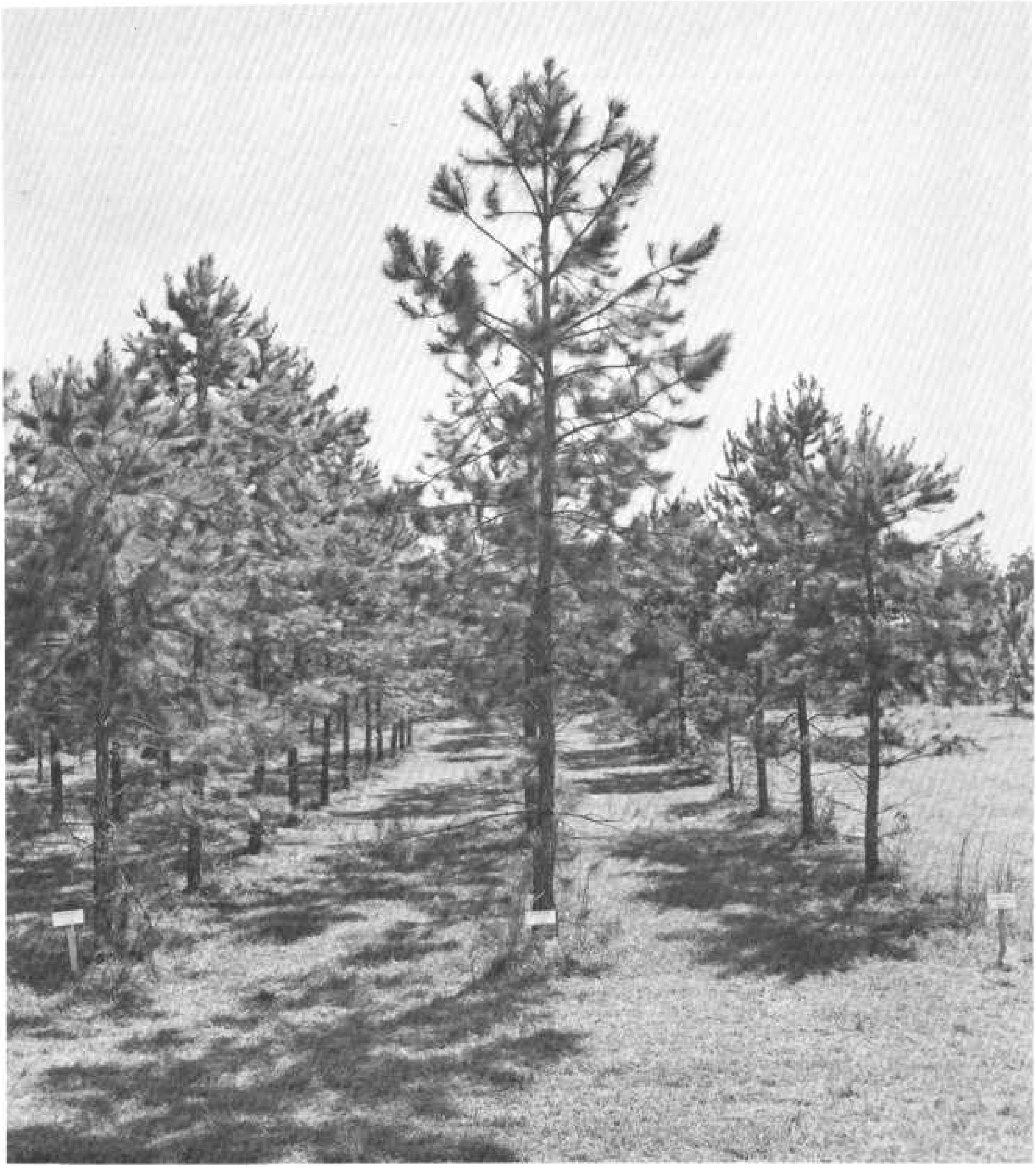

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Figure 189.—Hybrids of shortleaf and slash pines. At left, shortleaf × slash hybrid backcross to shortleaf pine; center, shortleaf × slash hybrids; and right, shortleaf pine.

In connection with the work on breeding southern pines resistant to fusiform rust, attempts were made to mass-produce shortleaf × slash pine hybrids by pollinating unbagged female flowers (Wakeley *et al.* 1966). Mass-pollinated cones yielded an average of 13.2 full seeds, in comparison to a yield of 6.6 seeds from cones that were control-pollinated on shortleaf pine. About 10.7 percent of the mass-pollinated seeds were hybrids, but the range among seeds from 10 mother trees was 1.2 percent to 21.5 percent.

Aberrant seedlings have been observed in hybrids between shortleaf and slash pines. Hybrids in Louisiana contained 16 percent dwarfs (Grano and Grigsby 1968). In Mississippi, seedlings in the nursery beds showed 0.9 percent dwarfs in slash pine and 5.2 percent in slash × shortleaf hybrids (Schmitt 1969). After 4 years, 2.5 percent of slash pine seedlings and 12.5 percent of the hybrids were dwarfs (Schmitt and Snyder 1971). Hybrids between nonselected parents had outstanding fusiform rust resistance, but they did not grow or survive as well as slash pine. However, certain combinations of parents were superior in survival, growth, and rust resistance to the best slash pine progenies. Hybrids were more variable in height after 3 years in the field than open-pollinated slash pine progeny, and the height frequency distribution curve was not normal in shape (fig. 190).

Shortleaf × slash pine hybrids were not particularly resistant to tip moth in Louisiana (Grigsby 1959; Grano and Grigsby 1968). Shortleaf pine is highly susceptible to tip moth, while slash pine is slightly susceptible.

After an evaluation of southern pine hybrids, Schmitt (1968) concluded that site, cultural conditions, and particularly seed and pollen parents affected performance.

Pinus palustris × *taeda*
Longleaf Pine × Loblolly Pine

A natural hybrid among species of southern pines was probably first observed in Louisiana (Chapman 1922). The tree *(Pinus ×sondereggeri* H. H. Chapm.) occurs quite commonly in longleaf pine stands adjacent to a source of loblolly pine pollen. Because of its historical significance, Chapman's (1922, p. 730–732) description is given here:

> 1. The seed appears to originate from longleaf seed trees; so that the male parent is probably the loblolly. . . .
>
> 2. The seed evidently germinates at the time of longleaf seed germination; i.e., in the late fall, and the seedling establishes itself during the winter instead of the spring as does loblolly pine.
>
> 3. The embryonic foliage of the seedling is from 1 to 2 inches long, resembling longleaf seedlings; while that of loblolly is about one-half inch long and much finer.
>
> 4. The seedling by spring of the same season, i.e., in April after the fall of the seed, develops a stalk from 1 up to 2 inches in length. Even the most vigorous longleaf seedlings of this age develop no stalk whatever in the first two years and commonly not for five seasons. . . .
>
> 5. The sapling develops foliage whose needles measure from 9 to 14 inches in length, averaging 10 to 11 inches. . . .
>
> 6. The bud and the annual shoot and the needles are intermediate in size and appearance between longleaf and loblolly pines.
>
> 7. The seedling makes most of its growth in one shoot, but commonly produces a second growth or shoot 3 to 4 inches long in the same season. . . .
>
> 8. The branching habit of the pine distinctly departs from that of longleaf with its characteristics absence of whorls, and develops at least three branches at the end of the main shoot of the previous year, for each season. . . .
>
> 9. The leaf bases on the hybrid are raised, protruding one-tenth inch from stem in the first year after the leaves fall, and are retained for 3 or 4 years after the manner of longleaf. . . .
>
> 10. The growth of the seedling in its second season is about 1 to 2 inches in height. In its third season, it grows from 6 to 18 inches, and from then on height growth is rapid. In this respect it is intermediate between loblolly and longleaf pine.
>
> 11. The hybrid pine grows more rapidly than the longleaf pine. . . .
>
> 12. The cones are intermediate between longleaf and loblolly pine in all respects. . . . This hybrid is said by Sonderegger to possess in a high degree the capacity to yield naval stores, similar to the longleaf parent. It also resembles the latter in being subject, in its juvenile stage,to the attack of a defoliating rust *(Septoria pinus)*, which affects longleaf pine seriously, but apparently does not damage loblolly pine.

The number of clean seeds of Sonderegger pine ranges from 12,730 to 14,138 per pound, averaging 13,400, which is midway between longleaf (5,200) and loblolly (21,300) (Wakeley 1930). Longleaf pine seedlots may have 0.5 to 6.0 percent hybrid seed, according to Wahlenberg (1946), but this might be highly variable over different years and geographic locations.

Seed of Sonderegger pine occur in longleaf pine seedlots and may cause seedlings to be variable in nursery beds. In 1941, Sherry (1947) established in Africa a plot of vigorous individual seedlings from a group of longleaf pine seedlings and another plot of apparently normal seedlings from the same seedbeds. At planting, the vigorous seedlings ranged from 6 to 12 inches in height, while the control seedlings were still in the "grass" stage with a stem length of about 1 inch. No weeding was done in

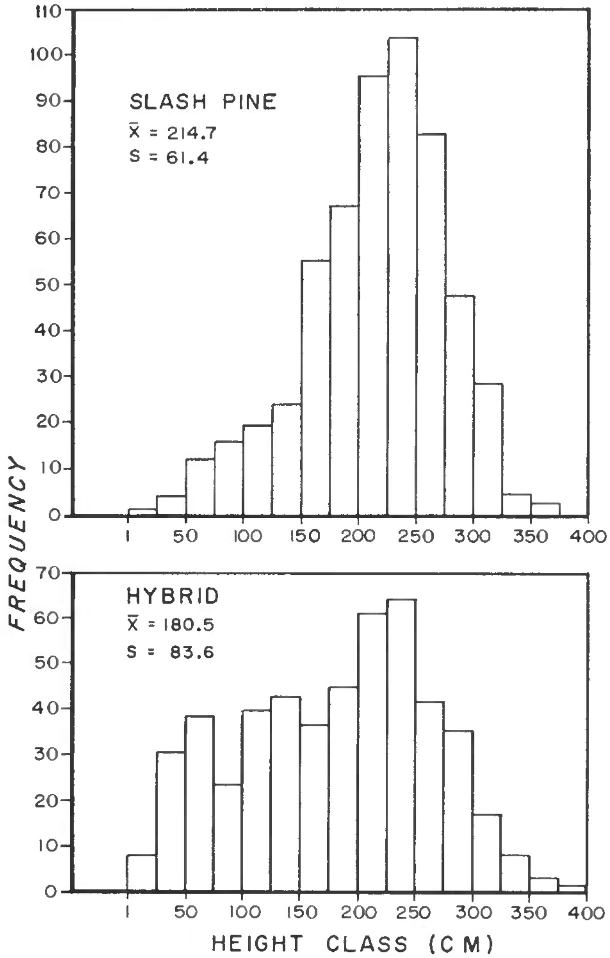

Figure 190.—Height frequency distribution for slash pine seedlings was unimodal, and for hybrids with shortleaf pine nearly bimodal. The range in height among the hybrid trees after 3 years in the field was not greater than in slash pine seedlings. Shortleaf pine normally grows slower in height than slash pine. (Schmitt and Snyder 1971)

either plot, and the normal seedlings did not appear through the grass until the third year, whereas the vigorous seedlings were visible from the beginning and had killed the grass completely by the fifth year. At 5 years of age, nearly 70 percent of the vigorous seedlings were 20 feet or more in height, over 4 inches in diameter, and ready for their first pruning, while none of the normal seedlings had yet reached the height of 20 feet. When the vigorous seedlings were scored for external characters, it was found that about 71 percent were longleaf-loblolly hybrids, since some had intermediate characters and others had combinations of characters of both species. These included 4.3 percent of dwarfs and 9.5 percent of aberrant forms, possibly resulting from some disharmonious genic combination. The remaining 29 percent were apparently normal longleaf pine, of which seven were as vigorous as the best of hybrids.

Many needle characteristics of longleaf × loblolly hybrids were intermediate with those of parental species (Keng and Little 1961). Needle number per fascicle was the same in all three groups.

The form of loblolly pine trees is generally characterized by numerous branches dividing frequently from the stem outward. Longleaf pine has few branches, but these are large in diameter. Many natural hybrids of the two species show a combination of characteristics—branches numerously divide and are much larger in diameter than in longleaf pine (fig. 191).

Wide variation occurred in percent cone set and percent seed germination in a wide variety of crosses among longleaf and loblolly pines in Texas (Brown 1964). Controlled crosses involved intraspecific and interspecific crosses among both longleaf and loblolly pines and selfs of longleaf, loblolly, and Sonderegger pines. Some type of crossing barrier exists between the F_1 Sonderegger hybrids and the longleaf parents, whereas pollen from

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Figure 191.—Longleaf × loblolly pine hybrid (foreground) that appeared among planted longleaf seedlings (background) makes faster height growth than longleaf seedlings, but crown and stem form are not good.

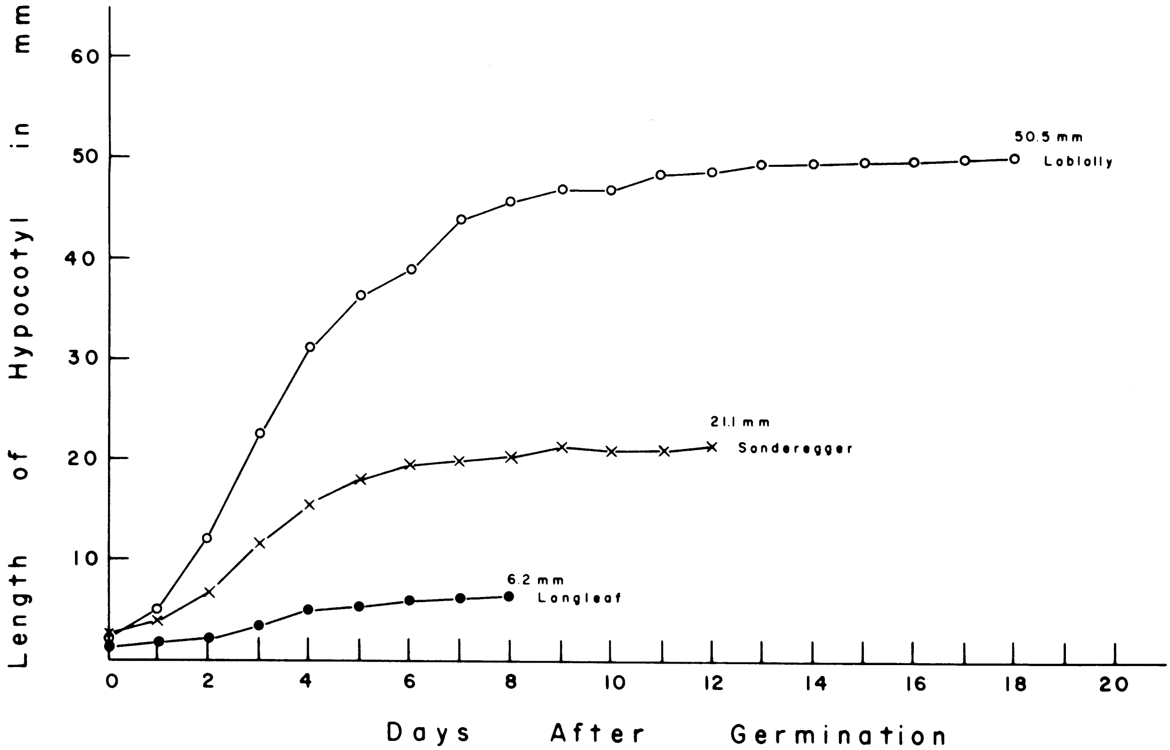

Figure 192.—Hypocotyl growth of longleaf, Sonderegger, and loblolly pines from seed germination to maturity shows that the hybrid is intermediate. (Brown 1964)

the same hybrid is highly fertile on the loblolly parent. The nature of this apparent sterility is unknown, although Brown felt it was unlikely that it was a purely physical phenomenon. It was concluded that, for the population studied, introgression is toward the loblolly parent, which was in contrast to the observation of Namkoong (1966) for an area in Louisiana in which introgression seems to lead toward the longleaf parent. For loblolly pine in which many reciprocal crosses were made by Brown, percent germination of selfed seed as well as the intraspecific and interspecific crosses and backcrosses were fairly high compared to percent germination of seed from other crosses. In general, the percent germination of seed from selfs of all the parent trees, such as longleaf, loblolly, and individual Sonderegger pines, was quite low compared to many of the backcrosses and interspecific crosses. In one selfed Sonderegger seedlot, 2,530 seed were obtained, but germination percent was zero; in another cross, 931 seed were obtained, with germination percent of 30. In a self of loblolly pine, 437 seed had a germination of 37 percent.

In Texas, sapling-sized progenies of Sonderegger pines have had unsatisfactory survival, growth, and form (van Buijtenen 1969c). Many trees have stem forks and heavy branches that break in ice storms and high winds.

In studies in Texas to determine the pattern of inheritance of the grass-stage condition in longleaf pine, and to determine whether seedling hypocotyl length was significantly correlated with subsequent shoot elongation, controlled crosses among longleaf, loblolly, and Sonderegger pines were used (Brown 1964). The rate and duration of hypocotyl extension in the longleaf seedlings was found to be distinctly different from the loblolly pine, while the F_1 progeny tend to be intermediate in both respects (fig. 192).

The pattern of variation of initial shoot growth in longleaf seedlings, as expressed under uniform nutrition and semi-controlled greenhouse conditions, is typically that of quantitative inheritance (Brown 1964). The final observations on primary shoot growth for each progeny group are expressed quantitatively (fig. 193). The general pattern of inheritance is similar to that observed for hypocotyl length, although there are notable differences between certain progeny groups. For example, in the F_2 progenies, the mean shoot growth of the selfed hybrids (hybrid 3 and hybrid 1) is skewed toward the longleaf parent, whereas this is not the case for hypocotyl length in the same progenies.

Pinus palustris × *echinata*
Longleaf Pine × Shortleaf Pine

The longleaf × shortleaf pine is difficult to pro-

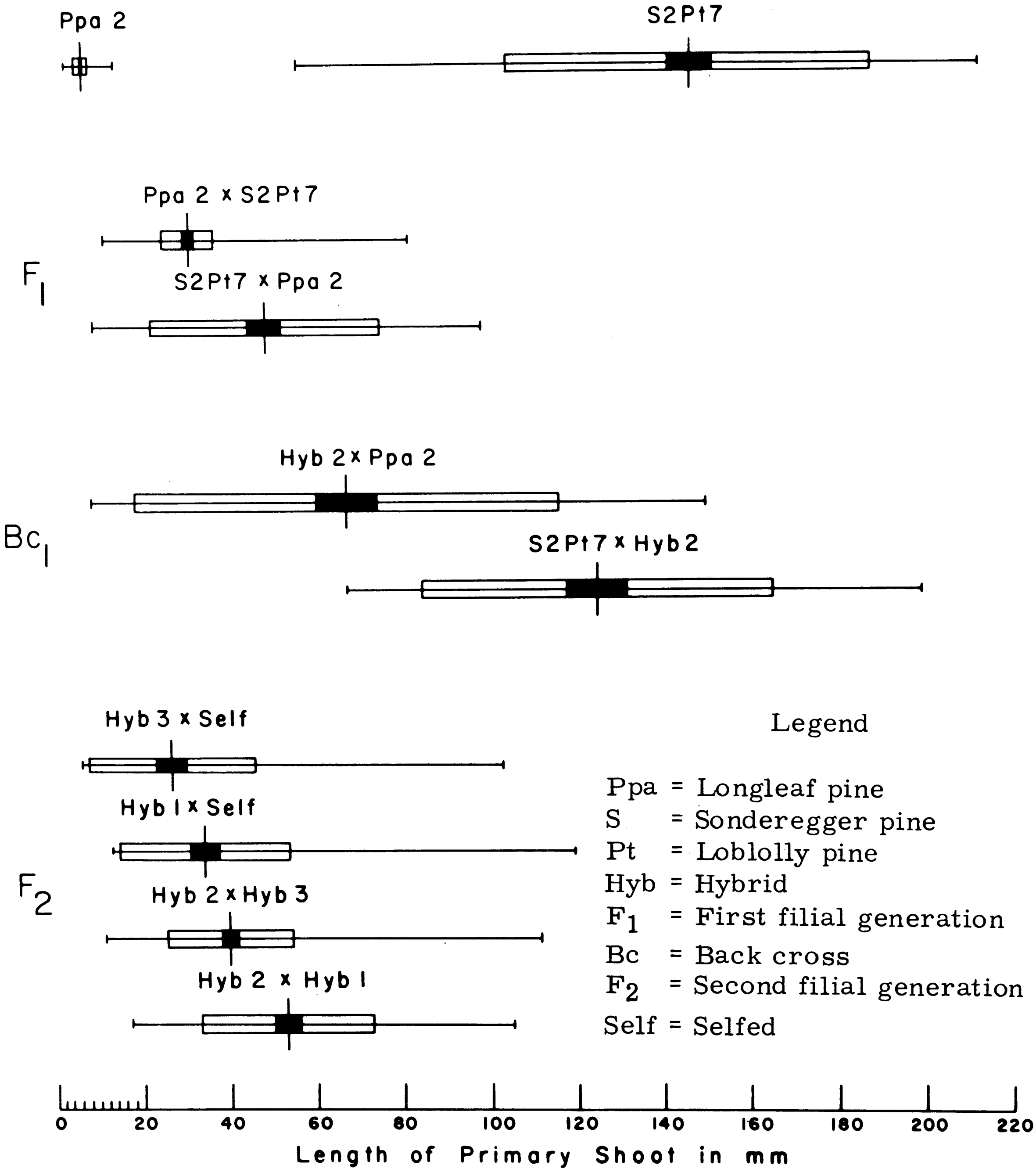

Figure 193.—Length of primary shoots of parents and progenies. Measurements were made from the base of the cotyledons to the base of the first formed terminal bud. Symbols used are: range, represented by the long horizontal line; sample mean, a short vertical line; one standard deviation on each side of the mean, a wide open bar; and two standard errors on each side of the mean, the solid black bar. Numbers refer to the individual tree used. (Brown 1964)

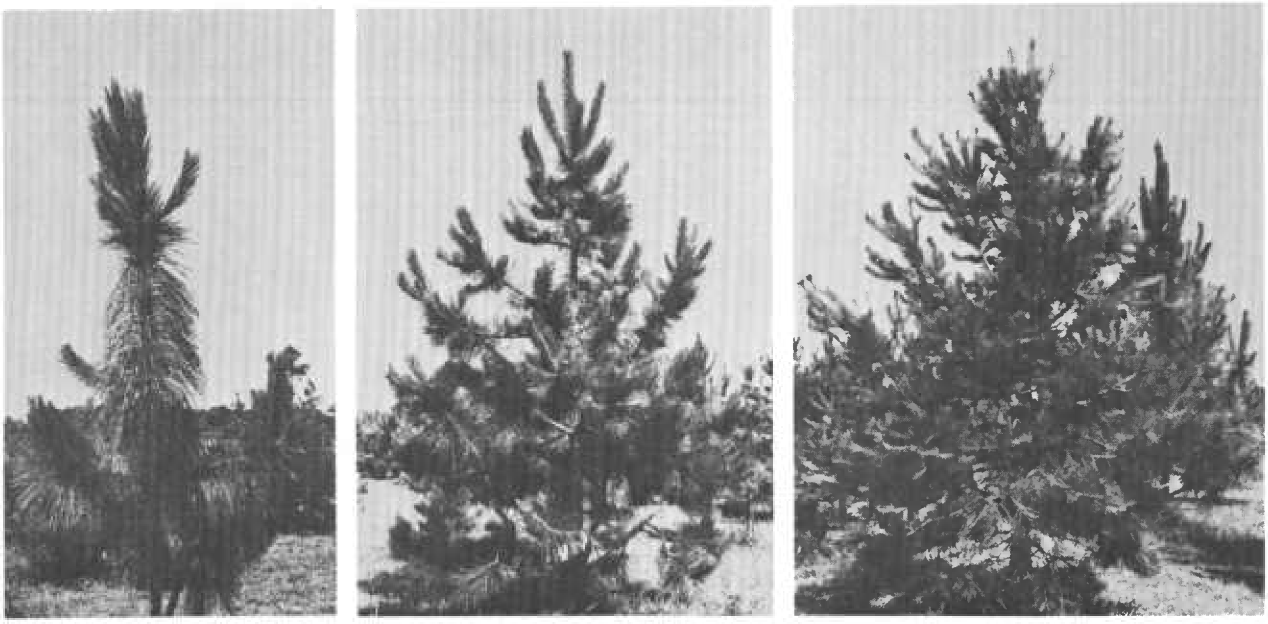

Figure 194.—Longleaf, longleaf × shortleaf, and shortleaf pines, respectively, after six growing seasons. (Campbell *et al.* 1969)

duce. A few hundred crosses resulted in a few seedlings from one longleaf pine seed parent (Campbell *et al.* 1969).

The hybrid (fig. 194) is described by Campbell *et al.* (1969, p. 524) as follows:

> Bark rough with gray plates, brown exposed in furrows. New shoots yellowish-green, glabrous, first-year shoots rust-brown becoming gray with age. Buds 16.1 cm in maximum elongation, cylindrical, acuminate apex. Leaves mostly three per fascicle, 16–24 cm long, flexible, serrulate. Hypodermis biform with one to two, sometimes three, layers of cells, endodermis of thin-walled cells, resin canals chiefly (76%) medial, occasionally internal. Male strobili yellow to straw-colored, approximately 3.4 cm long and 0.6 cm broad at anthesis in late March or early April in south Mississippi. Conelets elliptic, single or in whorls nearly sessile. Mature cones approximately 9.5 cm long and 7 cm wide, apophyses nut-brown and elevated along transverse keel with a raised (0.57 mm) umbo terminating in a short (1.0 mm) prickle.

In the hybrid, features of the buds, needles, and flowers of both sexes were intermediate with those of the parents. One seedling was an albino and another was a dwarf; later both died. Seedling height growth was not delayed, as is normal for longleaf pine seedlings.

Pinus rigida × *taeda* Pitch Pine × Loblolly Pine

Botanical characteristics of the hybrid, with needle characteristics as given by Keng and Little (1961), are given by Little and Righter (1965, p. 23) as follows:

> Bark rough, thick, furrowed into scaly plates, blackish gray, the trunk sometimes bearing short twigs with needles. Spring shoots multinodal. Twigs glabrous, light yellow green and shiny the first year, becoming light brown the second year. Buds acute, reddish brown, resinous. Leaves 3 in a fascicle, stout and stiff, 10–20 cm. long, acute-acuminate, serrulate, green; stomatal rows 10–15 dorsal and 5–8 on each ventral surface. Needle anatomy in cross section: Hypodermis biform, of 2–5 layers of cells, the inner border often angled; endodermis of thin-walled cells; resin canals medial (rarely also internal), 2 (rarely 3), about 0.04–0.08 mm. in diameter; a line of thick-walled cells often outside phloem in transfusion tissue.
>
> Male strobili (old and dry) 17–25 mm. long, 4–5 mm. in diameter, orange brown. Cones 3, 2, or 1 at a node, almost sessile, ovoid-conic, symmetrical, 7–8 cm. long, 4–4.5 cm. in diameter closed, serotinous, opening after 1 or more years, long persistent in quantity for several years; apophyses pale fulvous brown or tawny yellow, dull or slightly shiny, elevated along a transverse keel, the nut-brown umbo forming a sharp stout prickle or spine about 3 mm. long. Winged seeds about 25 mm. long, the detachable wing nut-brown, body ovoid, 5 mm. long, blackish.
>
> In needle anatomy the hybrid and both parents are similar. The hybrid is like *Pinus taeda* in the large resin canals, while *P. rigida* has diameters of about 0.02–0.04 mm. Needle length is intermediate. The intermediate cones have the larger, stout prickles of *P. taeda* and the slightly serotinous habit of *P. rigida* in this variation from southern New Jersey.
>
> This hybrid with *Pinus rigida* as female parent was made at the Institute first in 1933 and was back-crossed with *P. rigida* in 1942. The cross has been repeated in 1941 and later years, and 13 trees are growing here as well as plants from open pollinated

seeds of a hybrid tree. Nine trees from seed sown in 1945 averaged 22.6 feet high and 5.2 inches d.b.h. at 15 years.

Natural reproduction of pitch pine × loblolly pine hybrids around a loblolly pine plantation at Lebanon State Forest, Burlington County, New Jersey, and natural hybrids on the Beltsville Experimental Forest in Maryland, had characteristics similar to the artificial hybrids of the same cross made at the Institute of Forest Genetics, Placerville, California, and growing at the Lebanon State Forest, Burlington County, New Jersey (Little *et al.* 1967).

The largest amount of work on the characteristics of the pitch × loblolly pine hybrid has been done in Korea. This is a result of the widespread interest in that country in reforestation with this particular hybrid. Pitch pine was introduced in Korea by the United States about 1916. It has been used extensively for reforestation because of its hardiness, vigor, and rapid growth. There are many plantations of pitch pine in Korea which prove this tree's superiority in growth and its high resistance to insect damage, as compared to Korean native red pine. Approximately 50 million pitch pine seedlings have been planted in South Korea annually in recent years. The tree is too poor in quality, however, to produce good timber. This forms one example of a successful introduction of an exotic species (Hyun 1956). Loblolly pine was one of the better timber pines in the United States, being endowed with rapid growth and high stem quality. Along the southern coast of Korea, where the winter is mild, planted loblolly pine shows a three times greater volume growth than pitch pine in the same area. The tree has a straight stem, and the physical strength and durability of its timber surpass that of other pines in South Korea; but it is cold-tender and not able to withstand the frigid winter in Korea except in a narrow belt along the southern coast. The hybrid between pitch pine and loblolly pine shows much more rapid growth than pitch pine, to the extent of about two times greater volume growth, and its stem is upright and has far better form than that of pitch pine. Moreover, it is as cold resistant as pitch pine. In an attempt to gradually replace pitch pine with pitch × loblolly hybrid in reforestation in Korea, the mass production of hybrid seed has been undertaken. Controlled pollination and establishment of seed orchards are being employed as a means of mass-producing hybrid seed.

According to Hyun (1958), a 10-year-old pitch pine plantation about 5 hectares in extent was employed as a maternal stand, and approximately 60,000 ovulate strobili were isolated with 30,000 pollination bags. Loblolly pine pollen was transported by air from the Institute of Forest Genetics; pollen from several individuals was mixed before using. Pollination was performed in three stages because the ovulate strobili did not reach the receptive stage simultaneously. On an average, 0.3 cm^3 (0.1 g) of pollen was used for each pollination bag to complete the pollinations. As a result of the pollination, 45,000 matured cones were produced, and from these cones over 2 million seeds were produced. From the average pollination bag, seed was about 58 percent fertile, 43 sound seed were produced, and 25 seedlings were obtained. The hybrid seedlings, through the test at the nursery bed as well as in the field planting up to 4 years old, have proven that the hybrid combines cold resistance of pitch pine with the better form and growth of loblolly pine. Thus, the mass production of hybrid pine seed through hand pollination is feasible, not only technically, but also economically; and on a large scale, control pollination would be a shortcut to the mass production of hybrid seed for reforestation until the seed orchard of parental species comes into production (Hyun 1958).

An investigation of the sequence of fertilization in the cross of pitch × loblolly and pitch × Monterey pine showed that the rate of pollen-tube growth in the nucellus was slow compared with that in wind-pollinated pitch pine for the pitch × loblolly cross; and fertilization occurred in only 50 percent of the ovules observed, which indicated something of a lack of compatibility between the parents. In the pitch × Monterey hybrid, fertilization occurred in only 3 of 40 ovules observed, and the pollen tubes ceased growth at the top of the nucellus in the remainder. In both hybrids, fertilization occurred in mid-June, but development of the zygote was slower in the pitch × Monterey hybrid than in pitch × loblolly pine (Hyun and Yim 1963; Hyun and Lee 1964).

Pine species have 24 (2n) chromosomes; however, the size of chromosomes is different according to the species. Even in the same species, each individual may be different. But relative ratio of the size of the chromosome is the same within the same species (Kim 1963). The means of haploid chromosome length of three plates each for loblolly pine, pitch pine, and the pitch × loblolly hybrid are given by Kim. When chromosomes are arranged in descending order of the length of the short arm, the lengths of the long arms do not form a continuous descending sequence. It is evident, also, that chromosomes in which the long arms are out of order are different in each species. In pitch pine they are the 4th, 6th, and 10th chromosomes, but the 5th, 6th, and 9th in loblolly pine, and the 3rd, 6th, and 9th in the F_1 hybrid. In each species the longest chromosome ranges from 16.5 to 14.32 nm, while the shortest chromosome ranges from 9.61 to 9.00 nm. In mean chromosome length, pitch pine was the longer and the F_1 hybrid was 10 percent shorter. The value of the ratio of length of short arm to the length of total sum of the chromosomes of three species ranged from 4.8 to 2.3. However, the average was found to be high in the F_1 hybrid. The value of the ratio of length of the entire chromosome to the length of the short arm of the smallest chromosome was lower in pitch than in loblolly pine and in all except one chromosome, but it was greater than in the F_1 in all except two chromosomes. In order of the mean value, loblolly pine was first, pitch pine second, and the pitch × loblolly pine hybrid third. The formula of the karyotype was given in full. Many similarities of the chromosomes were observed between loblolly pine and the pitch × loblolly hybrid; these seem to coincide with the similarities of morphological characteristics in the two species.

Most characteristics in the F_1 of pitch × loblolly hybrids, such as germination behavior, morphological characters, cold hardiness, and growth rate in juvenile age, were intermediate between those of the parental species, whereas some other characters, such as thickness of hypodermal layers in leaf cross section, were somewhat strengthened in the hybrid (Hyun and Ahn 1959a, 1959b; Ahn 1963). In nursery-bed tests of seed germination in Korea, pitch pine seed germinated between April 25 and May 17, pitch × loblolly pine seed between April 30 and May 27, and loblolly pine seed between May 12 and June 11. Germination tests in a germinator at 25° C showed a similar order in germination, but the pitch × loblolly hybrid seed followed pitch pine seed germination more closely than that of loblolly pine. Frequency distribution curves for needle length of pitch pine and the pitch × loblolly hybrid were normal in shape; the mean length for pitch pine needles was 7.59 cm and the hybrid 14.51 cm. In pitch pine, needles ranged from 4.5 to 11 cm, whereas in the hybrid they varied from 12 to 19 cm. Frequency distribution curves of the length of the needle sheath and needle width were normal in shape and, like needle length, showed that inheritance was based on multiple factors. Tests of cold resistance of transplants in a refrigerator showed that seedlings of pitch and pitch × loblolly hybrids were hardy at −5° C, −10° C, and −15° C, while loblolly pine seedlings were hardy only after being kept at −5° C. Duration of the cold test was 5 hours. Comparison of growth of the pitch × loblolly pine hybrid in the nursery and arboretum showed in every case greater growth for the hybrid. In some cases, the growth was in the range of 29 to 37 percent greater at the end of 1 year. In every case, the standard deviation of height growth for the hybrid was greater than that of pitch pine seedlings. In three different plantations at age 2, the standard deviations of the pitch pine seedlings and the pitch × loblolly seedlings were in the magnitude of 13.1 and 16.3, 8.9 and 11.2, and 18.7 and 21.0, respectively.

In Korea, an attempt was made to increase cold hardiness and rate of fertile seed production of pitch × loblolly hybrids by backcrossing; pitch × loblolly was used as both pollen tree and seed tree in crosses with parental species, and results were compared with the F_1 pitch × loblolly hybrid. Thus, three types of backcross hybrids were obtained, such as pitch × (pitch × loblolly), (pitch × loblolly) × pitch pine, and (pitch × loblolly) × loblolly pine. All three backcross hybrids produced an average of 2.5 to 2.7 times more fertile seed than the pitch × loblolly hybrid. However, there were no differences in fertile seed production among the three backcross hybrids. In the nursery beds as well as in the field, the backcross of the pitch × loblolly to the loblolly pine outgrew the other two backcross hybrids. There was no difference between growth rate of the pitch pine cross with the hybrid or the reciprocal. In cold hardiness, the crosses between pitch pine and the pitch × loblolly hybrid were distinctly better than either the crosses of the hybrid and loblolly or crosses among pitch × loblolly hybrids. It was concluded that crosses between pitch pine and the pitch × loblolly hybrid could be recommended for use in reforestation in Korea, particularly in those areas where the pitch × loblolly pine hybrid was not readily established because of the winter cold (Hyun and Lee 1964); Hyun *et al.* 1965).

When planted near Suwon, Korea, pitch × loblolly hybrids of parental stock from northern locations (Pennsylvania and New Jersey) had better growth and higher cold resistance than seedlings of loblolly pine pollen of southern origin (fig. 195) (Hyun 1969; Hyun and Hong 1969). Hybrids from loblolly pine pollen of Texas and Florida origin were badly damaged by cold. Selection of the proper race is important, but hybridization between different races to create even better breeding stock was not found promising in a study by Woessner (1972a). Selection of parental trees within race was more important for increasing growth rate than selecting two races to cross.

In the United States, seed of the pitch × loblolly pine hybrids have been planted at various places in the Midwest, East, and South. In southern Illinois at 6 to 8 years of age, the hybrid is comparable with loblolly and shortleaf pine seedlings and with the hybrid between pitch and shortleaf pines. The inherently weak shortleaf × pitch cross was considered worthless under any circumstances for that location, but the pitch × loblolly cross produced a tree of reasonably good form. Its growth rate was less than that of loblolly or even shortleaf pine. The pitch × loblolly cross was noticeably less suscepti-

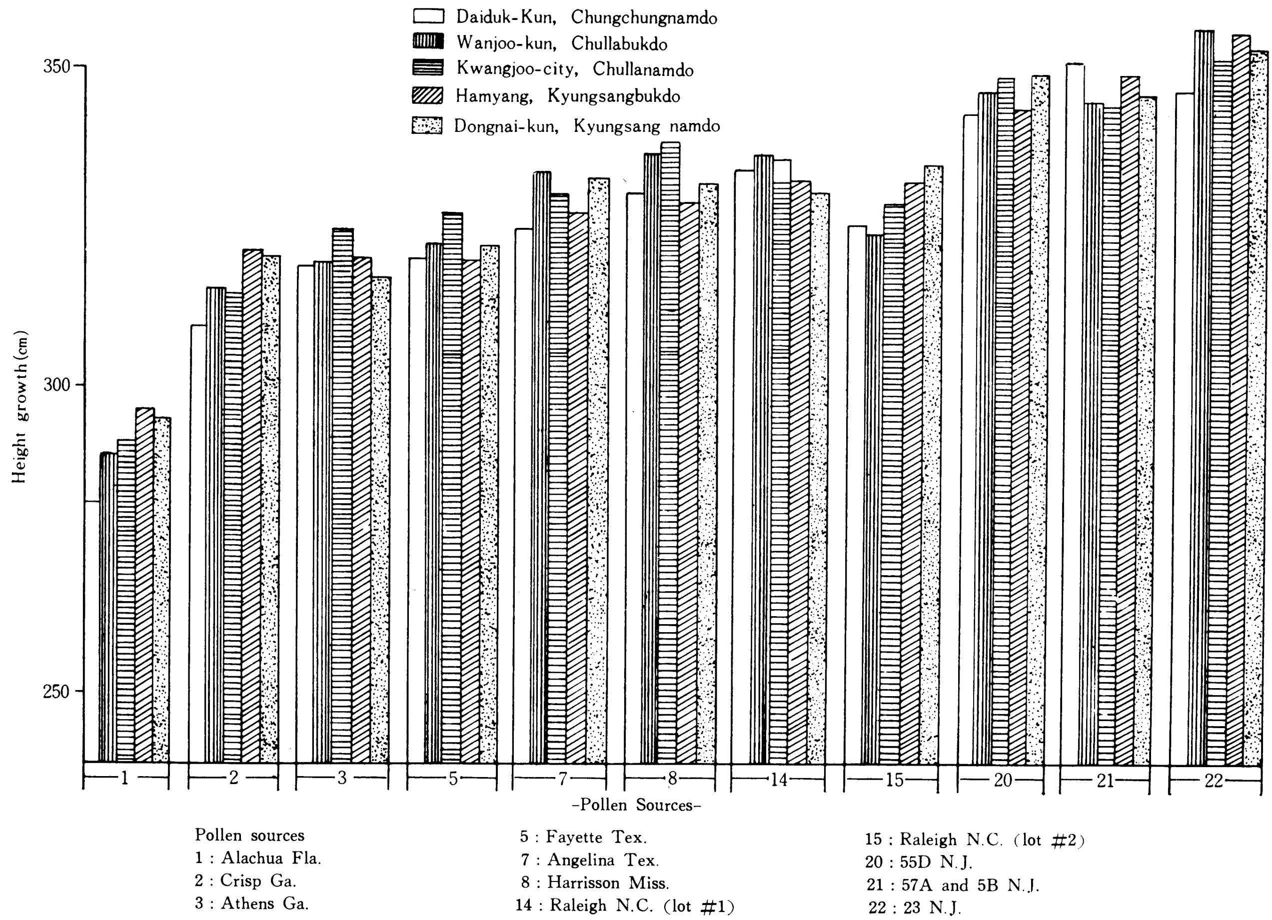

Figure 195.—Four-year height of hybrid pines planted at five locations in Korea. Loblolly pine pollen from 11 locations was used on pitch pine of Pennsylvania origin. Height indicates clinal variation in combined vigor and cold resistance, with hybrids of northern origins, approximately the same latitude as Korea, performing best. (Hyun and Hong 1969)

ble to low-temperature injury than loblolly pine. It was thought that it might have possibilities north of the area to which loblolly pine can be extended. Growing at the northern limit of the natural range of shortleaf pine, the pitch × loblolly cross exhibited a growth rate almost equal to that of shortleaf; in addition, it had fairly good form and was more hardy than either loblolly or shortleaf pine (Lorenz and Spaeth 1953).

In Iowa, Ohio, Illinois, and Indiana, growth of the pitch × loblolly pine hybrid was superior to loblolly and pitch pines north of the 39th parallel, but to the south loblolly pine from Arkansas was superior to the hybrid and pitch pine (Bey and Lorenz 1970). Geographic origin of the hybrid parental trees was unknown.

At the Institute of Forest Genetics in southern Mississippi, pitch × loblolly hybrids of nonlocal parents had slower height growth than hybrids among the major southern pines of local parents (Schmitt 1968).

In western Virginia at 14 years of age, the loblolly × pitch pine cross planted on the Lee Experimental Forest showed a height growth of 33 feet in comparison to loblolly pine of 35 feet from Arkansas. However, neither the Arkansas loblolly nor the hybrid equaled the growth of the North Carolina race of loblolly pine (USDA Forest Service 1962).

In Tennessee, pitch × loblolly hybrids were only lightly infected by Comandra rust, as were Virginia and pitch pines, while loblolly and shortleaf pines were much more susceptible (Powers 1972).

In Maryland and New Jersey, natural and artificial pitch × loblolly pine hybrids were observed to have eight characteristics similar to pitch pine and one like loblolly pine and to be intermediate in seven (Little *et al.* 1967). The hybrids had resinous buds which were similar to pitch pine. Other traits that were similar to the pitch pine parent were the stiffness of the needles, the length of the cones, the shape of the open cone, the persistent nature of the cones, the prickle on the cone scale, the color of the apophysis, and the shape of the body of the seed. The only trait in which the hybrid resembled the loblolly parent was the shape of the closed cone. In pitch pine, the closed cone was narrowly ovoid and in the loblolly it was conic, as it was in the hybrid (Little *et al.* 1967). The traits that were intermediate in the hybrid were the leaves on the short twigs, the length of the needles, the resin canals, the width of the cone when open, the width of the cone scales, length of the seed with the wing, and length of the body of the seed.

Pitch and loblolly pines have almost entirely separate ranges, but both do occur naturally in the upper portion of Maryland's western shore—chiefly in Prince Georges County. It is here that natural hybrids have been observed, and they should also be expected whenever loblolly pines have been successfully planted with the range of pitch pine (Little *et al.* 1967).

Artificially produced pitch × loblolly hybrids have grown more slowly on the Eastern Shore than regular nursery stock of loblolly pine. Dominant loblolly pine trees at a spacing of about 125 per acre at 17 years after planting were 44 or 45 feet tall, and dominant pitch × loblolly hybrids at 17 years were 33 to 37 feet tall. The growth of the hybrids was similar to that of shortleaf pine, a species with a growth rate comparable to pitch pine. The results are similar to those reported for 6-year growth (Little and Somes 1951). Height ranking was essentially unchanged between ages 6 and 17, although average height was given in the first report and largest stems only in the second. Pollen of just one loblolly pine tree was used for crossing with the three pitch pines. Of the three hybrid families, difference in height at 6 years was 2.7 feet and at 17 years 3 feet. Thus, the pitch pine maternal parent had an effect on growth of hybrid progeny. The ease with which loblolly can be crossed with pitch pine suggests that perhaps the hybrid should be given greater consideration for planting north of loblolly's natural range. Some of the hybrids might be expected to be both hardier than loblolly and somewhat faster growing than pitch pine. The only test plantings to date were of crosses made by the Institute of Forest Genetics, Placerville, California. On a deeply leached, sandy (Lakewood) soil in New Jersey, these hybrids have had the best survival—50 percent after 17 years, as compared to 41 percent for regular shortleaf stock and 11 percent for regular loblolly stock. Height and diameter growth of the hybrids have been roughly comparable to both loblolly and shortleaf stocks, probably because the site is so poor that shortleaf's growth approaches loblolly's. On better soils in southern New Jersey, loblolly pines grow faster; in 29-year-old plantations in one field, dominant and codominant loblolly pines were 57 feet tall, shortleaf pines 42 feet tall, and pitch pines 41 feet tall. And in natural reproduction around the older plantations of loblolly pine, some of the natural hybrids with pitch pine are growing nearly as fast, and with nearly as good form, as the loblolly pine seedlings. They seem to offer promise that certain of the hybrids would be at least superior to pitch pine seedlings. Possibly the relatively poor results in existing trials are due to geographic source and genotype of the parent trees. Since both species have wide range and local geographic races apparently exist, future tests of loblolly × pitch pine hybrids in the Northeast will be based on Maryland or Delaware sources of loblolly pine and the best local strains of pitch pine (Little *et al.* 1967).

The pitch and loblolly pine hybrid is believed to have good potential in commercial forestry at various locations in certain Atlantic Coast States. Breeding plans are based on choice of geographic source of parents, traits of parent trees, and potential planting site.

Pinus rigida × *radiata*
Pitch Pine × Monterey Pine

In Korea, interspecific hybridization within Sub-genus 3, *Pinus*, (table 1) was carried out, and crossabilities between different species, production rate of F_1 hybrid seed, morphologic characteristics, and growth rate of F_1 hybrids were determined (Ahn 1963). Also, relationships between crossabilities and taxonomic affinities were investigated. In these experiments, a relatively high taxonomic affinity between pitch pine and Monterey pine was evident from the production of fertile hybrid seed. From pollination of 1,880 pollination bags, 13,600 seed were obtained, with 22 percent sound seed and an average of 6 sound seed per cone. The hybrid nature of trees from the seed was indicated by the form of the cones, seeds, and needles of mature trees (Hyun *et al.* 1967).

The pitch × Monterey pine hybrid is a cross of a species in Subsection 10, *Australes*, with a species in Subsection 15, *Oocarpae*.

Pinus rigida × *serotina*
Pitch Pine × Pond Pine

Botanical characteristics of the hybrid, with needle characteristics as given by Keng and Little (1961), are given by Little and Righter (1965, p. 23–24) as follows:

> Bark of branches and trunk becoming rough and thick, composed of gray brown scaly plates and exposing brown in crevices, the trunk sometimes bearing a few short twigs with needles. Spring shoots multinodal. Twigs slender, glabrous, glaucous, light green when

young, becoming pinkish brown, year-old lateral twigs 6–7 mm. in diameter, purplish brown, the bases of bracts decurrent, rough, and forming narrow rectangular plates long persistent. Buds cylindric, acuminate or acute, often resinous, reddish brown, the scales with white, slightly fringed margins.

Leaves 3 in a fascicle, straight, stiff, erect, 9–12 cm. long, 1.4–1.7 mm. wide, acuminate, serrulate, slightly flattened, dull green; stomatal rows 16–20 dorsal and 6–10 on each ventral surface; basal sheath becoming 7–13 mm. long, gray brown. Needle anatomy in cross section: Stomata slightly sunken; hypodermis biform, of 2 or 3, sometimes 4, layers; resin canals 3–7, usually 3 medial at angles and additional smaller medial and internal, small, bordered by thin- or thick-walled cells; endodermis in outline elliptic or sometimes triangular, of thin-walled cells; transfusion tissue with thick-walled cells outside phloem.

Male strobili (old and dry) cylindric, 8–24 mm. long and 4–5 mm. in diameter, orange brown. New female or ovulate strobili 1–3 in a whorl and sometimes 2 whorls in a year, on stout, scaly, brown, slightly ascending stalk about 1 cm. long, ovoid, shortly after pollination about 8 mm. long, pink purple, turning light green, the scales with soft point 2 mm. long. Year-old conelets ellipsoidal or subglobose, 15–20 mm. long and 12–15 mm. in diameter, pinkish red and green, scales with prickle nearly 2 mm. long. Mature cones sessile or nearly so, ovoid, symmetrical, about 6–6.5 cm. long and 3.5–4.5 cm. broad when closed, tawny yellow but weathering to light gray, persistent and remaining closed; apophyses nearly flat, umbo raised and ending in straight, sharp, weak prickle 1–2 mm. long.

These hybrids are slightly larger than adjacent plants of *Pinus rigida* of the same age. The only significant difference in the two groups is in needle length, 6–10 cm. in *P. rigida* and 9–12 cm. in the hybrid, while the parent plant of *P. serotina* has needles 12–20 cm. long. The parent species and hybrid are indistinguishable in needle anatomy. Cones of the hybrid and adjacent plants of *P. rigida* are similar.

Five plants from pollination in 1952 and seeds sown in 1954 averaged 5.7 feet high at 5 years and were about 11 feet high after 9 growing seasons. The female parent was from Atlantic City, N. J., and the male parent from near Starke, Fla.

Pinus rigida and *P. serotina* are closely related species, or according to a few authors, geographical varieties of the same species. *P. serotina* has longer needles spreading to slightly drooping in age and broader, nearly spherical, closed cones. However, *P. rigida* sometimes has closed cones, for example, in these plants from near the range of *P. serotina.*

Pitch pine and pond pine are closely related and have more characters in common with each other than with loblolly pine (Little *et al.* 1967). Of 23 characteristics of the pitch-pond hybrid, 10 were intermediate with the two parents and 2 were similar to pond pine. The only traits similar to pond pine were the weak keel on the basal scales of the cones and the small prickle on the base of the cones (fig. 196).

Pitch and pond pines have almost entirely separate ranges and meet only in narrow constricted areas in southern New Jersey, especially lower Cape May County, and possibly in central Delaware and the central portion of Maryland's Eastern Shore. This area can be seen on the maps showing natural ranges. Because they are usually separated geographically, pitch and pond pines have relatively few natural hybrids or intergrades. Intergrades can be found in spots in Cape May County, New Jersey, and near Beltsville, in Prince Georges County, Maryland (Little *et al.* 1967; Smouse 1970). In Delaware, there seems to be a tendency to grade from typical pond pine in Sussex County toward pitch pine in the vicinity of Dover. Whether the decreased length of needles observed on some of the latter trees is evidence of some pitch pine ancestry is questionable. Therefore, on the whole, the hybrids or intergrades between pitch and pond pines are chiefly of taxonomic interest. However, certain dominant trees examined by workers in seed orchard projects have proven to be hybrids. In both Delaware and Maryland, pond pine and its hybrids or intergrades are not restricted to wet sites but are found on a wide variety of soils. The differences between loblolly pine and pond pine are important in forestry practice in Delaware and on Maryland's Eastern Shore, mainly because pond pine is slower growing and has less desirable form and clear length than does loblolly. At 50 years, on the usual 80–85 wet sites, a typical pond pine is 13 to 15 feet shorter, with a smaller diameter than nearby typical loblolly pines.

Pinus rigida × *echinata*
Pitch Pine × Shortleaf Pine

Botanical characteristics of the hybrid, with needle characteristics as given by Keng and Little (1961), are given by Little and Righter (1965, p. 21–22) as follows:

Bark of branches and trunk reddish brown, scaly, the trunk sometimes bearing a few short twigs with needles. Spring shoots multinodal. Twigs slender, glabrous, when elongating yellow green and slightly shiny or glaucous and whitish green, becoming purplish brown, year-old lateral twigs 4–6 mm. in diameter, the bases of bracts decurrent and forming narrow, rectangular plates. Buds acuminate, often slightly resinous, reddish brown, the scales with white, slightly fringed margins.

Leaves 3 or sometimes 2 in a fascicle, straight, erect, 6–9 cm. long, 1.1–1.9 mm. wide, acuminate, serrulate, dull yellow green; stomatal rows 10–17 dorsal and 5–9 on each ventral surface (8–10 ventral in paired leaves); basal sheath becoming 5–8 mm. long. Needle anatomy in cross section: Stomata slightly sunken; hypodermis biform, of 2 or 3 layers; resin canals 2–10, usually 2 or 3 medial at angles and additional smaller medial and internal, small or sometimes large, bordered by thin- or thick-walled cells; endodermis in outline elliptic or sometimes triangular, of thin-walled cells; transfusion tissue with tick-walled cells outside phloem or none.

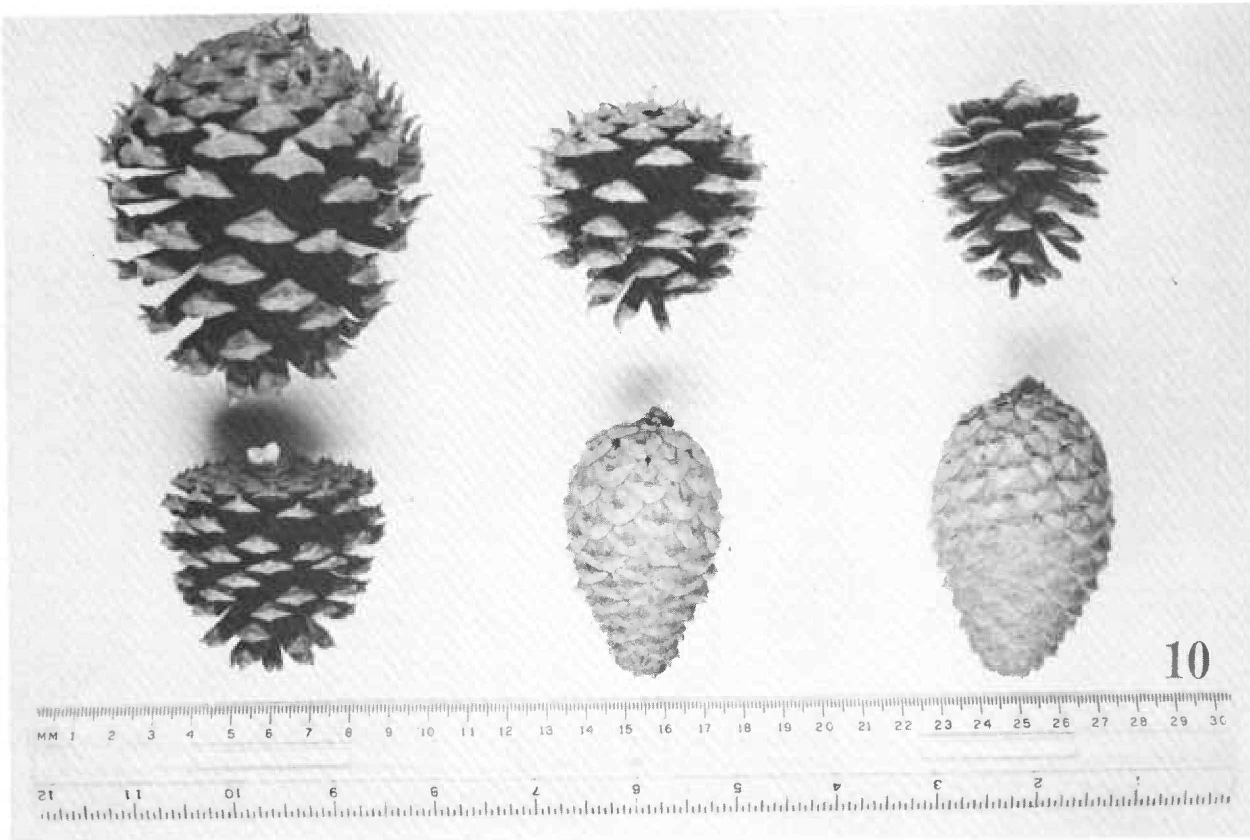

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Figure 196.—Cones, left to right, top row, Table-Mountain, Table-Mountain × shortleaf, and shortleaf; bottom row, pitch, pitch × pond, and pond. One-third natural size. (Little and Righter 1965)

Male strobili (old and dry) cylindric, about 15 mm. long and 4–5 mm. in diameter, orange brown. New female or ovulate strobili on young plants 1–3 in a whorl on stout, scaly, slightly ascending stalk 5–7 mm. long, ovoid, after pollination about 6 mm. long, dark red, turning light green, the scales with soft point more than 1 mm. long. Mature cones sessile, ovoid, about 5–5.5 cm. long and broad when open, 3.5 cm. broad when closed, dark brown weathering to gray, opening at maturity, persistent; scales with weak prickle less than 1 mm. long.

The hybrid plants resemble those of *Pinus rigida*, having often slightly crooked axis and broader crown of fewer, long, coarse, spreading branches and slightly stout twigs of larger diameter. Adjacent plants of *P. echinata* have better form with straight axis and narrower crown and begin growth later. In needle number the hybrid is intermediate in sometimes having 2 in a fascicle, though generally 3. The hybrid has broader needles like *P. rigida*, though the single plant of the reciprocal cross has narrow needles like *P. echinata*. *P. echinata* has needle serrulation of minute teeth close together, while *P. rigida* and the hybrid have slightly larger and fewer teeth. Stomata appear as minute white dots on needles of *P. echinata* and are slightly larger in the other two. In needle anatomy all three are similar. The hybrid is intermediate in having the biform hypodermis of 2 or 3 layers.

Plants of both the hybrid and *Pinus rigida* were producing cones when examined. Conelets and cones were similar except that mature cones of the latter, originating from a closed cone variation in southern New Jersey, remained closed after maturity. Male cones produced by one hybrid plant were similar to those of *P. rigida*.

This cross pollination was made here in 1941, 1954, and 1957. Five plants from seeds sown in 1956 averaged 3.1 feet high at 5 years. Nine others were grown from seeds planted in 1959. One plant of the reciprocal cross, *Pinus echinata* × *rigida*, from pollination in 1954 and seed sown in 1956, was 4.3 feet high at 5 years. This plant of the reciprocal cross was similar to the others; however, it was perhaps of below normal vigor, later in beginning growth, and with the new elongating twigs glaucous whitish green. From the reciprocal cross repeated a year later the single surviving plant was poor.

The natural range of pitch and shortleaf pines overlaps in the Appalachian Mountains and northward for a considerable distance. When pitch and shortleaf pines grow together, natural crossing may occasionally occur. Trees with intermediate characteristics have been seen in southern New Jersey, and similar trees have been reported in southern Pennsylvania (Illick and Aughanbaugh 1930).

Hybrids of shortleaf and pitch pines produced at Placerville, California, were tested with native species in Delaware. None of the hybrids showed exceptional vigor (Little and Somes 1951). The seed from the crosses of these species produced very few seedlings, and they survived and grew poorly. Pollen of one pitch pine was used on two maternal parents of shortleaf pine. Average 6-year growth from one cross was 0.3 foot and the other 5.8 feet. Average 6-year growth of the shortleaf pine in the same plantation was 4.8 feet and the loblolly pine 12.4 feet. Survival of the shortleaf × pitch pine hybrids was lower than that of shortleaf or pitch pine.

In Korea, crosses of pitch × shortleaf hybrids produced a fairly high percentage of sound seed. A total of 11,870 seed had a percentage of sound seed of 68.4, and there were 43.4 sound seed per cone (Ahn 1963).

The shortleaf × pitch pine hybrid was tested in southern Illinois, with several shortleaf pine seed parents and with pollen from one pitch pine. When the plantations were 6 to 8 years old, the shortleaf × pitch cross was observed to be inherently weak and was considered of low value (Lorenz and Spaeth 1953). In contrast, the pitch × loblolly hybrid tested in the same area had reasonably good form, cold hardiness, and growth almost equal to that of shortleaf pine.

Pinus rigida × *elliottii* var. *elliottii* Pitch Pine × Slash Pine

In Korea, crosses involving pitch and slash pines produced a very small amount of seed (Ahn 1963). Seed from 5,612 cones averaged 11.8 percent, and number of sound seed per cone averaged 1.7.

Pinus serotina × *taeda* Pond Pine × Loblolly Pine

Vegetative characteristics of the species hybrids are given by Little *et al.* (1967, p. 13–14) as follows:

> *Pinus serotina* × *taeda*, pond pine × loblolly pine, or pond-loblolly hybrid pine. Natural hybrid tree with leaves and cones intermediate between *Pinus serotina* Michx., . . . pond pine, and *P. taeda* L., . . . loblolly pine. Medium-sized tree 12 m. (40 ft.) or more in height and 20 cm. (8 in.) or more in trunk diameter. Bark dark gray, rough, furrowed into scaly plates. Trunk usually without short twigs and leaves. Buds cylindric, acute, reddish brown, resinous.
>
> Leaves 3 in fascicle, flexible to slightly stiff, 12–21 cm. long, 1.4–1.6 mm. wide, serrulate, green; whitish stomatal rows 11–13 on dorsal surface and 7–9 on each ventral surface. Needle anatomy in cross section: hypodermis biform, of 2–4 layers; endodermis of thin-walled cells; resin canals 4–5, medial or medial and internal, mostly small.
>
> Mature cones sessile or nearly so, 7–9 cm. long, when closed conic or narrowly ovoid and 3.5–4.5 cm. wide, when open ovoid, broadest below middle, flattened at base, 5.5–6 cm. wide, early or late dehiscent, partly persistent. Cone scales spreading, lower ones slightly reflexed, mostly 9–13 mm. wide; apophysis keeled though keel weak on basal scales, tawny yellow, dull; umbo ending in small, slender, sharp, persistent prickle about 2–3 mm. long, smaller on basal scales. Winged seeds about 24–27 mm. long, including detachable brown wing and rhomboid or ovoid body 6–7 mm. long, blackish.

From an analysis of characteristics of the tree trunk, leaves, cones, cone scales, and seed of natural hybrids, the hybrid trees were found to be similar to pond pine in 3 characteristics, intermediate in 15 characteristics, and similar to loblolly in 3 characteristics (Little *et al.* 1967). The buds were usually resinous in the hybrid, which is similar to those of pond pine. The other two characteristics similar to pond pine were the keel, which is weak on basal scales, and the prickles on basal scales of the cones. Of the characteristics similar to those of loblolly pine, the shape of the seed and the length of the seed and the marginal teeth on the needles were constant. All traits investigated were intermediate with the parent species.

Because they are usually geographically separated, pitch and pond pines have relatively few natural hybrids or intergrades. In contrast, natural hybrids that intergrade between loblolly pine and pond pine are more widespread. They can be found quite commonly throughout southern Delaware, from Marydel and Dover south to the Maryland line, as well as along the dunes below Rehoboth Beach. In Maryland, similar hybrids and intergrades are less common, with typical trees of loblolly pine much more prevalent. However, the hybrid intergrades have been observed, especially in the vicinity of Wicomico State Forest and south in the vicinity of Nassawango Creek to the northern portion of the Pocomoke State Forest. This general section has had more wildfires than usual for the Eastern Shore, and the fires have undoubtedly played a major role in favoring pond pine and its hybrids, since these trees are more fire resistant but slower growing than typical loblolly pine. Pitch pine and its hybrids are also closely associated with the recent fire history. In both Delaware and Maryland, pond pine and its hybrids or intergrades are not restricted to wet sites but are found on a wide variety of soils. In much of southern Delaware, hybrids or intergrades between pond pine and loblolly pine seem more common than typical loblolly (Little *et al.* 1967). The prevalence of hybrids and intergrades in Delaware makes the collection of typical loblolly seeds more difficult there than in Maryland. However, few intergrades will be included if seed collections are limited to large cones with stout prickles from trees that have few cones older than 1 year and that have nonresinous buds and relatively long, flexible needles.

Evidence of introgressive hybridization in pond and loblolly pines was found in the North Carolina Piedmont and Coastal Plain by Kang (1966) and Saylor and Kang (1973). The 30 traits studied in natural and artificial hybrids were intermediate with the parents, except for composition of terpenes which resembled those of the loblolly parent. Natural hybrids occurred more frequently in loblolly than pond pine stands. Gene movement was predominantly from pond pine to loblolly pine.

Pinus pungens × *echinata*
Table-Mountain Pine × Shortleaf Pine

Botanical characteristics of the hybrid are given by Little and Righter (1965, p. 20–21) as follows:

> Spring shoots multinodal. Twigs slender, glabrous, glaucous, light yellow green when elongating, becoming whitish purplish brown, year-old lateral twigs 5–7 mm. in diameter, the bases of bracts decurrent and forming narrow rectangular plates. Bark of branches and trunk light gray brown, scaly. Buds acuminate, often resinous, reddish brown, the scales with white, slightly fringed margins.
>
> Leaves in fascicles of both 2 and 3, stout, slightly flattened, stiff, slightly twisted, 7–10 cm. long (as short as 5 cm. on late summer twigs), 1.1–1.8 mm. wide, acuminate and appearing sharp-pointed when touched owing to stiffness, serrulate, dull yellow green; stomatal rows 17–20 dorsal and 9–15 ventral on needles in 2's, 10–14 dorsal and 5–8 on each ventral surface on needles in 3's; basal sheath 4–6 mm. long. Needle anatomy in cross section: Stomata slightly sunken; hypodermis biform, of 2 or 3 layers; resin canals usually 2 dorsal medial at angles, sometimes also 1 ventral internal, small and large, bordered by thin- or thick-walled cells; endodermis in outline elliptic, sometimes constricted elliptic or triangular, of thin-walled cells; transfusion tissue with thick-walled cells outside phloem.
>
> Male strobili (old and dry), cylindric but tapering and slightly curved, 10–16 mm. long, 3–4 mm. in diameter, orange brown. New female or ovulate strobili or conelets 1–5 in a whorl, sometimes in 2 whorls on vigorous shoots, on stout, scaly, slightly ascending stalk 8 mm. long, ovoid, when closed after pollination 12 mm. long, light yellow green, the scales with soft slender tapering point 2–3 mm. long. Year-old conelets with umbo about 4–5 mm. long, light brown, with long prickle 2–3 mm. long and pointed toward apex. Cones sessile, ovoid, conic, symmetrical or nearly so, 5–5.5 cm. long, 5–6 cm. across when open at maturity, persistent 1 or 2 years; apophyses dull fulvous brown, much raised along a transverse keel, the umbo forming a stout, flattened, sharp spine 2–5 mm. long, slightly incurved. Seed with 3-angled blackish body 5 mm. long and membranous, light brown detachable wing 15–18 mm. long. Specimens: *18804*, *19139* (Tree PuE 1, 191/83).
>
> Hybrid plants resemble those of *Pinus pungens* of the same age in branching habit, with broader crown of fewer, long, coarse, spreading branches, in the slightly stout twigs of larger diameter, in the deeper green needle color, and absence of the short twigs and needles along the trunk. The needles of the hybrid are long and 2 or 3 in number as in *P. echinata*, mostly intermediate in width, and twisted as in *P. pungens*. Needles of *P. pungens* are stiff and cause pain when touched, those of *P. echinata* are flexible, while the intermediate needles of the hybrid are stiff and short-pointed but do not produce pain. The needle serrulation consists of minute teeth close together in *P. echinata*, larger teeth farther apart in *P. pungens*, and intermediate teeth nearer the latter in the hybrid. The stomata of the needles appear on the surface as minute white dots in *P. echinata* and are larger in the hybrid and largest in *P. pungens*, being slightly sunken in last two. Needle anatomy is similar in all three, though the hypodermis in the hybrid is intermediate between the weak, uniform or biform hypodermis of 1–3 layers in *P. echinata* and the well-developed, biform hypodermis of 2–4 layers in *P. pungens*. Conelets show the influence of *P. pungens* in the long pointed scales. The cones are small as in *P. echinata* but intermediate and nearer *P. pungens* in keel of apophyses and length of spines.
>
> From pollination made here in 1955 and from seeds sown in 1957, 2 plants were raised. In 1962, after 5 growing seasons, they were about 5 feet high, slightly larger than adjacent plants of *Pinus pungens* of the same age and slightly smaller than average plants of the other parent species. Plants of *P. pungens* and the hybrid began needle elongation before those of the other parent in the growing season of 1962.

Cones of Table-Mountain and shortleaf pines are intermediate in size and form with the parent species (fig. 196) (Little and Righter 1965).

Pinus pungens × *rigida*
Table-Mountain Pine × Pitch Pine

The first indications of hybrids between Table-Mountain and pitch pines were obtained during a study of the ecology of Table-Mountain pine (Zobel 1969). Trees intermediate in certain morphological characteristics between the two species suggested that natural hybridization occurs to a small degree.

Pinus virginiana × *clausa*
Virginia Pine × Sand Pine

Characteristics of the hybrid are given by Little and Righter (1965, p. 38–39) as follows:

> Bark of small trunks gray, rough, with scaly plates. Spring shoots multinodal. Twigs slender, glabrous, glaucous, whitish green when young, becoming purplish brown, smoothish. Buds acuminate, nonresinous, reddish brown, the attenuate scales with white margins becoming fringed.
>
> Leaves 2 (rarely 3) in a fascicle, stout, often slightly flattened, slightly twisted, stiff, spreading at nearly right angle, 4–6 (7) cm. long (as short as 2.5 cm. on late summer twigs), 1.2–1.6 mm. wide, acute, serrulate, dull green to yellow green; stomatal rows 10–17 dorsal

and 8–12 ventral (6–8 ventral on leaves in 3's). Needle anatomy in cross section: Outer epidermal cell walls slightly arched; hypodermis biform, sometimes uniform, of 2 or 1 layer; resin canals 2, medial, dorsal near angles, bordered by thin- or thick-walled cells; endodermis elliptic, of thin-walled cells; vascular bundles separated slightly less than bundle width; thick-walled cells mostly absent in transfusion tissue.

Male stobili (old and dry) cylindric, 7–12 mm. long and 3–4 mm. in diameter, orange brown. New female or ovulate strobili or conelets on horizontal brown scaly stalks 5–8 mm. long, after pollination 1 cm. long, ovoid, scales with weak prickle more than 1 mm. long. Cones sessile, ovoid conic, 4.5–5 cm. long, 4–4.5 cm. across when open at maturity, persistent; apophyses shiny nut-brown, raised along a transverse keel, the umbo forming a prickle about 1 mm. long.

As both parent species are closely related and similar, the hybrid is distinguished from the parents with difficulty by partly variable characters. Study of older plants shows a few changes in needle characters reported on 2-year seedlings by Keng and Little [1961, table 17]. *Pinus virginiana* and the hybrid have the needles often slightly flattened and slightly broader than the semicircular needles of *P. clausa.* The hybrid is intermediate in the outer epidermal cells slightly arched, less than in *P. clausa,* and in the 2 vascular bundles separated by only slightly less than bundle width, less than in *P. virginiana.* It is like *P. virginiana* in the hypodermis usually biform, rather than mostly uniform, and like *P. clausa* in the endodermis elliptic in outline, not constricted. Cones of hybrid and parents are similar. Though *P. clausa* typically is characterized by closed cones, the pollen parent was from Pensacola, within the range of the western open-cone race.

Five plants of this hybrid from cross pollination in 1953 and from seeds sown in 1955 averaged 5.2 feet high after 5 years.

In Maryland, survival of the Virginia × sand pine hybrid was 94 percent after 10 years and the Virginia pine control 84 percent; average height of the hybrid was 17.6 feet and of Virginia pine 15.6 feet (Saylor and Zobel 1973). The hybrid seed was produced by personnel at the Institute of Forest Genetics, Placerville, California.

DISCUSSION

Any review of species hybridization with southern pines shows both the opportunities and limitations of genetic disassortative mating in creative breeding.

Taxonomic classification of the hard pines, the group to which the southern pines belong, has changed since exploratory hybridization began in 1931; thus, crossability between groups on the basis of species is not very meaningful. The trend has been to group species on the basis of several traits rather than a few, and the species that Shaw in 1914 placed in four groups have been divided into six. Of the southern pines, sand and Virginia pines are grouped with jack and lodgepole pines; but, of the major group containing eight southern species, sand pine is the only one that can be crossed with slash pine. The majority of southern pine species form a group with species in the Caribbean Sea and Central America. The southern pine group will not hybridize with pines in the western United States or with those of other countries.

Crossability among southern pines in the same taxonomic group is variable. Among the eight species in the Subsection *Australes*, certain species cross readily, others with great difficulty, and some not at all. In addition to the species, crossability is influenced by the individual parent tree and by the species used as the female parent. Crossability information in detail is incomplete for many species because few studies have been made, and the variables involved are numerous.

Natural hybrids have been identified in several locations throughout the southern pine regions. Hybridization contributes to phenotypic and genotypic geographic variation. Certain outstanding individual trees of hybrid origin have found their way into selection and breeding programs. Natural hybridization is influenced by geographic isolation of the natural range, genetic barriers, and phenological isolation resulting from differences in time of flowering.

Inheritance of traits in hybrid progeny has been studied in more detail for certain species than others, and much remains to be learned. Progeny testing with hybrids is beset with many of the same problems in experimental design, such as estimating growth, survival, tree form, and resistance to pests, that are troublesome in other forest genetic subjects. Thus, results to date are largely preliminary for inheritance of growth rate, wood yield per acre, tree quality, and resistance to minor pests. Botanical characteristics of hybrids have been well recorded; resistance to fusiform rust and brown spot is being carefully studied. Traits in progeny of reciprocal crosses are similar where comparison can be made in studies to date. However, the choice of maternal parent species may affect seed yield.

Hybrid vigor, the major motivating factor in early hybridization research, apparently is lacking in southern pine hybrids. Vigor is difficult to measure in progeny, but outstanding height growth over all the controls has not been evident in tests by any plant breeder at different locations. Variation among individual trees and seed from different geographic locations, combined with the relationship among traits affecting areawise yield, such as growth, survival, and resistance to pests, complicate progeny testing. Appropriate seed for controls has not been available in certain tests. Inheritance of vigor in crosses between inbred lines has not been determined.

Most morphological and physiological traits of hybrids are intermediate with those of the parental species. Needles, buds, seed, cones, and time of flowering have been studied most frequently. Resistance to fusiform rust and brown spot is inherited in hybrid progeny, but the amount of resistance is strongly influenced by the individual parent tree of each species.

Height growth of individual trees in hybrid families has not been studied in depth. In one study of a hybrid of shortleaf and slash pine, the range in heights did not vary between the slash pine and the hybrid progeny, but the frequency distribution curve for slash was unimodal and the hybrid nearly bimodal.

Dwarf seedlings occur more frequently in hybrids than in wind-pollinated progeny of the parental species. The occurrence of malformed trees may be sufficiently high in certain hybrids to lower yield of wood per acre.

Interspecific hybridization has not been an important breeding method with southern pine. This is not because opportunities are lacking but because tree breeders have felt that the greatest gains in relation to effort expended could be obtained by selection within species followed by natural crossing among clones in seed orchards. There have been only isolated attempts to use species hybridization to solve problems in tree breeding based on a preselected geographic location, a special planting site, the ideal type of tree or strain needed, and selection of the appropriate mating scheme, tree species, race, and individual parental trees. In some respects, interspecific hybridization is much more complicated than intraspecific breeding: all the problems of selecting the parental species, race, and individual parental trees, as well as the inheritance of traits, the correlation among traits, and the production of seed in volume, are encountered in two species rather than just one. Species hybridization may provide an opportunity to combine the best traits of two species, but, at the same time, the undesirable or minus traits of two species must be manipulated also.

To be most efficient as a method of breeding, interspecific hybridization should be combined with racial, stand, and single-tree selection to obtain the most promising combination of parental stock. Rigid selection has not always been possible in studies of crossability, and this is one of the reasons for the lack of data about maximum gains possible from the breeding method. Before breeding by hybridization is begun, cost-effectiveness estimates should be compared with those for alternative methods of breeding.

At present, the most promising use for interspecific hybridization is to produce strains with combinations of traits that cannot be obtained by intraspecific selective breeding, strains needed for planting on special sites. Problems of this type in tree breeding are illustrated by the Korean breeding project that combined the cold resistance of pitch pine with the good growth and form of loblolly pine.

The greatest need in hybridization research seems to be for inheritance data. Tree breeders need to learn how to obtain the best combination of the desired traits in the shortest time. Implied here, also, is the need for ways to evaluate the overall performance of hybrid progenies that may have a variety of good as well as bad traits. In addition to the need for methods of creating strains of hybrid trees, we should know how to mass-produce them in seed orchards or by other methods for commercial-scale planting. Also, there is a need for more information about the quality of naturally regenerated stands from hybrid plantations. However, natural regeneration of pine stands may be used less frequently in the future if tree breeders keep producing genetically superior strains that require planting.