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Inherent Variation Among Slash Pine Progenies at the Ida Cason Callaway Foundation

by

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Reported here in detail is information obtained from two open-pollinated progeny tests of slash pine at the Ida Cason Callaway Foundation, Pine Mountain, Georgia. Because of the small amount of similar data available to tree improvement workers, it was decided to include as much information as possible, even though some of it is too limited for statistical analyses. These limited data are presented only as indications of possible trends, not as proof of definite relationships.

The author wishes to express his sincere appreciation to the many people who have contributed to this undertaking. Foremost is Mr. Keith W. Dorman, who has supervised the Callaway project through the years and has provided endless encouragement to the author. Messrs. James T. Greene, Rufus A. Jordan, and Eitel Bauer on the staff of the Foundation were responsible for the establishment of the tests and for a large portion of the data collection prior to 1956. The Institute of Statistics of the University of Georgia provided unlimited assistance in data handling and processing at their computing center.

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INTRODUCTION

The South has only recently recognized the importance of improving the genetic quality of the tree seed used in its vast nursery and direct seeding programs. In 1960 forest planting and direct seeding amounted to nearly 1.6 million acres in 11 Southeastern and Southern States (U. S. Forest Service 1960). An estimated 300,000 pounds of tree seed were used in this region for that year.

These figures indicate the tremendous importance of the genetic quality of the seed used, and emphasize the opportunity to make immediate use of any seed from genetically improved sources. At present most of the seed are obtained by purchase from individual collectors and as a rule there is no control over the choice of parent trees. Only in recent years has serious consideration been given to the geographic source of seed. The last decade has seen the development of intensive programs of forest genetic and tree improvement research throughout the country, and simultaneously, a degree of recognition of the importance of seed source, both geographically and individually by parent tree. This same concern for the individual parent has also achieved more recognition from the silvicultural standpoint in providing the seed source for natural regeneration. Silvicultural marking rules will be improved and refined as the results of the many studies in forest tree genetics become available and the heritabilities of the more important traits are known.

Early in tree improvement Programs an important basic decision has to be made, The question is whether to proceed along a line of research and trial, withholding any large scale application of genetic principles until proof of their application to forest trees is obtained, or to assume that basic principles of heredity will apply to forest trees as to other studied plants and animals, and to begin an action program simultaneously with research and accept the risk of making wrong decisions. A few have adhered to the first line of thought (Forest Genetics Research Foundation 1958, pp. 24-25), but most workers have taken the latter course and have begun the development of seed orchards, seed production areas, and breeding programs designed to take advantage of any known information and to fill gaps in our knowledge with the best approximations which can be drawn from related work.

The Ida Cason Callaway Foundation, Pine Mountain, Georgia, began a tree improvement project in 1949. This project was planned and established with the cooperation of the Southeastern Forest Experiment Station. The opening paragraphs of the "Statement of Policy for Tree Improvement Project under Ida Cason Callaway Foundation" prepared by Keith W. Dorman, December 20, 1950,1/ outline the purposes of the project.

"The objective of the tree improvement project established in 1949 is to make available in west central Georgia improved types of forest trees for commercial planting. This region is principally forest and, with the development of a much more active market, forest products have become a very important factor in the local economy. People are growing timber as a crop, and they have become interested in improving returns by scientific means. In other fields of agriculture, one method of increasing yields that has been universally successful is to isolate or create plants of better inherent quality and get them into commercial use. This is what the project hopes to accomplish.

"The tree improvement work under the Ida Cason Callaway Foundation will not be a research project except in an applied sense. It will proceed upon the assumption that it is possible to improve forest trees by using standard plant breeding methods. It will be necessary to demonstrate that strains or hybrids are superior to ordinary stock and how much so, and this objective should be paramount in planning progeny tests. Performance of the offspring will be the sole criterion for evaluating genetic quality of the parent stock."

A graduate forester was employed by the Foundation in 1950 and began work under the general supervision of the Southeastern Forest Experiment Station, Initial work involved the selection of superior and aberrant phenotypes of the four major species of southern pine: slash (*Pinus elliottii* Engelm.), loblolly (*Pinus taeda* L.), shortleaf (*Pinus echinata* Mill.), and longleaf (*Pinus palustris* Mill.). Collections of cones were made from these trees and seed obtained for the establishment of open-pollinated progeny tests of each species. Seedlings were grown for 1 year in a small nursery established and operated by the Foundation. In addition to the seedlings for progeny tests, the nursery also grew several hundred thousand seedlings for routine planting on the Foundation property.

A total of 45 plantings involving 1,405 plots was made by the project through 1957. These plantings contained mostly open-pollinated seedlings the first few years, with progenies from inter- and intraspecific crosses becoming a considerable part of the program in 1955, 1956, and 1957.

The project was staffed with a graduate forester through 1955. The general emphasis of the Foundation changed at that time and the data collection and analysis aspects of the tree improvement work were turned over to the Southeastern Forest Experiment Station. The Foundation assists in the program by continued maintenance of the test plantations and selected trees. Other assistance is provided as personnel and facilities permit. The Foundation is con-

1/ On file, Southeastern Forest Experiment Station, Macon, Georgia.

tinuing its development of seed orchards established from seedling progenies of the selected trees which appear to be best, based on the performance of the progenies in the test plantations.

When the Foundation project got underway in 1950, there was little available information on the progeny testing of individual forest trees. There had been few tests established in this country or elsewhere and there were few references in the literature which dealt with them, especially references considering the statistical aspects of design and analysis. Even today there is a noticeable lack of agreement among tree breeders and forest geneticists on methodology and design. The designs chosen were based primarily on the judgment of the individuals involved.

This paper closely examines a portion of the Foundation's progeny tests to determine the performance of several progenies and to decide which information from these tests will help in designing better future tests. Tests of slash pine were selected because they contained more progeny groups than any of the other species, because the parent trees were of more uniform age, and because many had grown in the same plantation. Slash pine is not native in the area of the Foundation properties.

The literature available to the forest geneticist contains a great amount of information on plant breeding, theoretical genetics, and statistical techniques and theory. The crux of the situation is the lack of fundamental information about forest trees. Forest genetics research on a significant scale is rather recent. This fact, coupled with the complex physiological-environmental relationships of tree growth and the long generation time, means that appreciable genetic information and comparisons of breeding methods will not be available for many years. In the meantime, full advantage must be taken of all information as it becomes available.

Work is underway at a number of installations--Federal, State, and private--to answer many of the pressing questions of critical importance to the establishment of well designed breeding programs with forest trees. The normal generation time for trees is much longer than for agronomic plants, and crop maturity may take from 30 to 120 years. Tests of the Callaway Foundation are among the oldest large-scale trials of open-pollinated progenies in the South. They offered an opportunity to study the performance of progeny groups up to 8 years of age, and included parent trees with a range of characteristics. The open-pollinated tests discussed in this paper contribute to the great mass of information needed before adequate breeding programs can be designed.

Material and Methods

In the phenotypic selection of forest trees the most difficult problem is to establish a basis of comparison for different trees. The individual is usually compared with other individuals in the immediate vicinity in the same stand, of comparable age, competitive status, etc. (Cech 1959). There are serious shortcomings in evaluating a selection in relation to its surrounding trees because it is difficult to determine past stand history and the variations in soil, available moisture, and competition of roots and crown. When attempts are made to compare selections from different stands, or even different portions of the same stand, this difficulty is compounded because it is impossible to estimate site quality precisely and also because the assumptions about the genetic constitution of the stand must be accepted with less confidence.

The slash pine tests of the Foundation contain progenies from a number of trees selected in a 15-year-old plantation on the property of the late Mr. Cason J. Callaway (fig. 1). This plantation was made with nursery stock provided by the State of Georgia in 1935-36. The seed source is not known exactly, but the records of the Georgia Forestry Commission show that the seed used in their nurseries to produce seedlings for that planting season came from CCC collections in the state. 2/ This plantation was on abandoned agricultural land at a spacing of approximately 15 by 15 feet.

Figure 1. --Seventy-one percent of the trees in this 15-year-old slash pine plantation were infected with southern fusiform rust when selections were made in 1949 and 1950.

2/ Unpublished information on file with Georgia Forestry Commission, Macon, Georgia.

In 1949, there was little information available to guide the establishment of selection criteria. Trees were selected which appeared desirable for many traits, and others were picked which had only one or two good traits (figures 2 and 3). Selections were made to include a broad range of growth (table 1) and crown and stem form. At the time of the initial selection of individual trees, the stand had not been thinned, but it showed evidence of severe attack by fusiform rust [Cronartium fusiforme (A. & K.) Hedgc. & Hunt]. Dorman reported that 71 percent of the trees in the plantation had stem cankers of the rust, 3/ and mortality from rust left irregular stocking in the plantation, putting it below desirable levels in many spots. The high infection rate made it possible to select trees with a high probability of resistance to the disease, though the fact that infections on the branches of trees might have been undetected because of natural pruning reduced the confidence one might have in such selections. Examination in 1959 revealed that several trees apparently free of rust when selected now have cankers. These infections have occurred in the upper crown and were either small and undetected at the time of selection or have developed since the work began in 1950.

Table 1. --Slash pine parent trees selected for the Callaway Foundation, 1950

Tree number	Age	Total height	D.b.h. 1/
	Years	Feet	Inches
c-4	15	48	13.6
C-6	15	44	14.4
C-l	15	59	10.7
c-10	15	49	13.2
c-37	15	54	12.7
c-50	15	56	8.7
c-51	15	57	10.0
c-54	15	66	10.0
C-56	15	50	10.2
C-58	15	59	11.8
c-59	15	57	10.8
C-60	15	57	11.1
C-61	15	52	9.2
C-62	15	57	10.0
C-63	15	51	11.2
C-65	15	48	10.5
c-134	15	59	11.2

1/ Diameter at breast height.

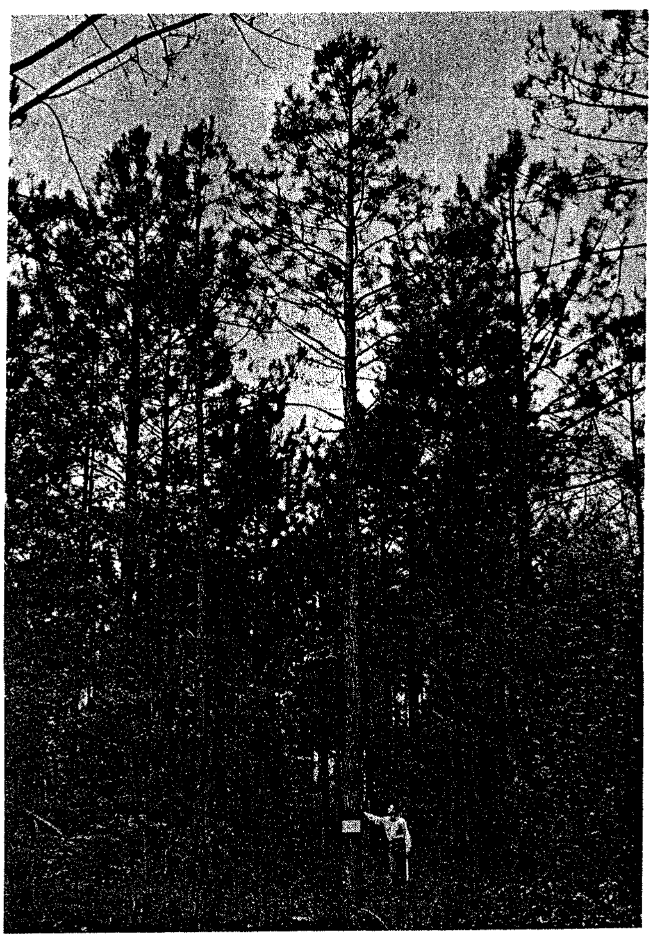

Figure 2. --Parent tree C-37 selected for good form and rapid growth rate. The progeny of this tree are among those most resistant to fusiform rust. (Photo at age 20.)

3/ "Tree Selection and Breeding under Ida Cason Callaway Foundation," November 1950. (Unpublished report on file at Southeastern Forest Experiment Station, Macon, Georgia.)

Figure 3. --A, Parent tree C-50 selected for rapid height growth and small branch diameter. Note the contrast of its branches with the tree on the left. (Photo at age 23.) B, Parent tree C-6 selected for rapid diameter growth, average form, and average height. (Photo at age 20.)

The figures on rust infection reported by Dorman show that most of the trees surrounding any selection were infected with rust; thus, we can safely assume that a large portion of the pollen that fell upon the female strobili of the selected trees came from trees susceptible to rust. Quite possibly the amount of pollen from rust-susceptible trees may have varied according to the location of the selected individual and may have varied from year to year according to variations in climatic factors. The plantation has been thinned twice since 1950, and it is now impossible to determine the original occurrence of rust-infected trees in relation to the selected trees.

Beginning in the spring of 1952, tests of open-pollinated progenies were established in the field. The number of progenies in the individual studies varied according to availability of seedlings and the expressed purpose of the test (table 2). Each year, new collections of open-pollinated seed were made from the selected parents; thus, the different tests may reflect chance differences in pollination associated with a particular season. The primary objectives of these tests were to evaluate the various parent trees for characters of economic importance and for their abilities to transmit these characteristics to their progenies. Some trees with undesirable traits were included to study the heritability of these characteristics along with those which are desirable, and to provide demonstrative proof that they are or are not transmitted from parent to progeny.

Table 2.--Studies established for the progeny testing of slash pine selections (1952-1955) and data collected

Study number	Planted	Lots	Replications	Trees per plot	Height	D.b.h.	Fusiform rust	Crown width	Pruning height	Other defects
	Year	Number			Age in years after planting					
102	1952	19	3	10 - 100	1, 2, 3, 4, 6, 8	6, 8	3, 6	3	8	6
103	1953	21	4	25	1, 2. 3, 4 5, 7	5, 7	2, 5	4, 5	7	5
104	1953	5	3	25	5	5	5	5		5
105	1954	20	4	25	1, 2, 3, 4,	-	4	4		4
106	1954	12	4	25	1, 3, 4	-	4	4		
107	1954	12	4	25	1, 3, 4	-	4	4		
108	1954	12	3	25	1, 3, 4	-	4	4		
109	1955	12	4	25	2, 3		3	3	-	
110	1955	12	4	25	2, 3		3	3	-	
111	1955	12	4	25	2. 3		3	3	-	
112	1955	4	2	25	2, 3					

In addition to the open-pollinated progenies from the selected trees (designated by "C" before the number), most studies included several "control" lots of seedlings. Lots identified as "control seedlings" were obtained from normal public distribution of planting stock. The exact geographic source of the seed is unknown, though we can be reasonably sure that they were collected within the State of Georgia. Lots identified as "control seed" were grown in the Foundation nursery from seed of known geographic origin obtained through commercial channels. Lots identified as "Callaway" or "CJC" were seedlings produced from seed collected by the Callaway Foundation for their routine planting. These seed were collected only from dominant or codominant rust free trees, but the pollen source was uncontrolled. The seed came from planted stands, though not necessarily from those in which the selected trees were located. All "controls" represent different seed lots and parentage each year.

Two mixed lots of seed used the first 2 years were obtained from the U. S. Forest Service, Southern Forest Experiment Station, New Orleans, Louisiana. One of these came from Southern Mississippi, the other, a mixed lot, was from storage in New Orleans and the exact geographic origin was unknown. In co-operation with other research groups, progenies were included in the tests from selected trees in plantations near Auburn, Alabama (designated by "A" before the number), and from Australia (designated by "CA" or "CB" before the number). These progenies were also grown in the Foundation nursery.

The seedlings were grown as 1-O stock, lifted, culled for fusiform rust, small size, or injury, then transferred directly to the field and planted by hand in scalped spots. The progeny groups were not graded for size of seedling other than culling. Average heights for each progeny group were determined in the nursery bed but do not lend themselves to analysis because of the absence of replication.

The planting site was an abandoned field with varying degrees of soil erosion and vegetative cover (fig. 4). Topsoil had been removed from a portion of the area for use in landscaping, and apparently this removal has complicated the analysis of the data. In order to minimize the risk of loss from fire, the block locations of studies established in 1952 and 1953 were widely separated in the field. This separation was easily justifiable in view of the high flammability of the "old-field" type fuels on the area. Fortunately, no fires have occurred. The only serious damage has been attributed to a tornado which struck parts of two studies and caused some windthrow, breakage, and mortality. A few trees were overthrown by snow but their importance is negligible.

Seedlings were planted at 10- by lo-foot spacing. Such spacing permits growth to pulpwood size without thinning and also permits a free expression of crown form for 8 to 10 years. Height measurements were taken soon after planting and were continued annually on all studies until 1955. Since that time height measurements have been taken intermittently. Diameter at breast height measurements were begun when plantings reached their fifth year in the field. Measurements of crown width, pruning height, and tallies of rust infection and other defects were made (table 2).

All studies were established in randomized block designs with two, three, or four replications. Study 102 contains plots of varying sizes. The other studies, with occasional exceptions, contain 25 trees per plot. The number of trees available for analysis at each age varies according to initial mortality after planting and according to losses in subsequent growing seasons. These latter losses are primarily from fusiform rust, with only minor losses to other miscellaneous causes.

Analyses of variance were used for examining data, such as height, d.b.h., crown width, pruning height, rust infection, and other defects. Multiple range tests were used to test differences among individual lots (Duncan 1955). Percent data were transformed before analysis. Simple correlations were determined for certain characteristics of the progenies, and regression was used for the relationships of progenies to parents and the relationships among different progeny groups from the same parent trees. Although the data were limited in quantity and range, heritability values were computed for growth characteristics and analyses were attempted in the hope of throwing some 'light on the existing relationships.

Initially, data were collected during January and February 1958. At that time the studies ranged from 3 to 6 years in the field. Examination of these data indicated that only the 5- and 6-year material would provide appreciable information. These studies, numbers 103 and 102, also had the most data collected at earlier ages. Subsequently the decision was made to examine these two studies in November and December 1959 to obtain 7- and 8-year data, respectively. Studies 102 and 103 provide the data presented in this paper.

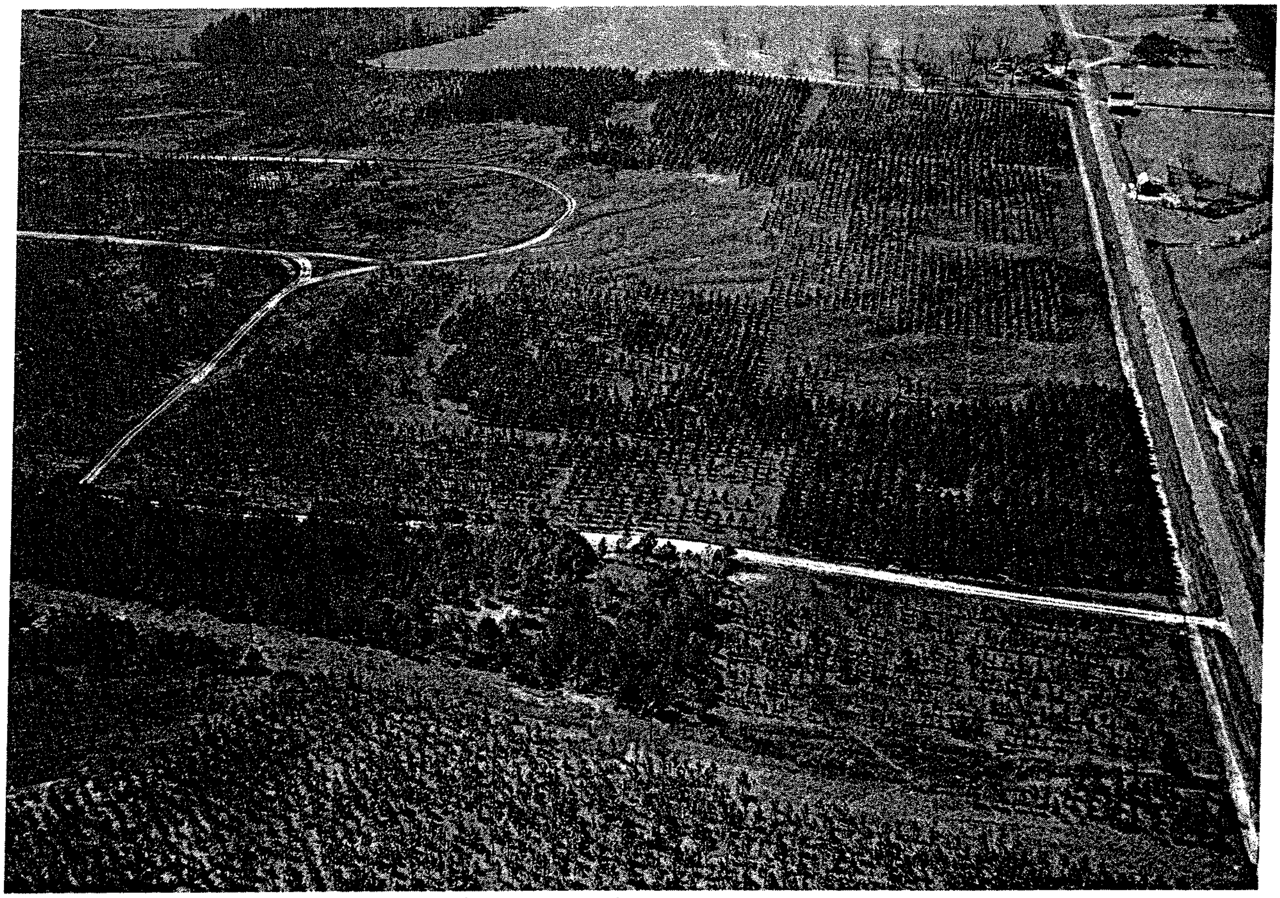

Figure 4. --An aerial view of a portion of the Callaway Foundation progeny testing area. Four species (and hybrids) in six age classes are under test in this field.

GROWTH CHARACTERISTICS

Survival

The initial survival, as measured by number of trees living after 1 year in the field, has been good at the Callaway Foundation (table 3). In study 102 highly significant differences [4/] were obtained among blocks and significance at the 5 percent level among lots. Inspection of the data indicates that the lots from Southern Mississippi and New Orleans contributed the major portion of the variance among lots. Lots C-59 and C-7 also showed very poor performance in block I because of damage by chemicals used to control kudzu (Pueraria thunbergiana) growing on these plots. In contrast to study 102, the survival of the Southern Mississippi and New Orleans lots in study 103 exceeded 90 percent, indicating good inherent ability to survive. These were the only two lots of seedlings grown from the same seed lots for both studies. In study 103 the control seedlings apparently contributed a major portion of the variation in the analysis. Most of the discrepancies in planting survival can be attributed to the handling of the stock, the actual planting operation, or, in one instance,

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4/ Throughout this paper the term "highly significant" (**) will refer to statistical significance at the 1 percent probability level. "Significant" (*) will refer to statistical significance at the 5 percent probability level.

Table 3. --First year survival, studies 102 and 103

Lot	Trees planted per plot	Study 102 Block: I	Block: II	Block: III	Average	Study 103[1/] Block: I	Block: II	Block: III	Block: IV	Average
	Number	- - - - - - - - - - - - - - -				Percent - - - - - - - - - - - - - - -				
c-4	25	92	88	84	88	96	88	68	68	80
C-6	35	63	49	94	69	96	84	76	76	83
c-7	30	47	93	97	79	80	72	76	44	68
c-10	100	86	95	74	85	100	96	100	100	99
c-37	80	90	96	84	so	92	84	88	72	84
c-50	80	82	98	81	87	100	92	88	100	95
c-51	80	82	95	80	86	96	88	92	88	91
c-54	20	so	80	90	87					
C-56	25	92	96	96	95					
C-58						96	92	88	96	93
c-59	20	15	95	so	67					
c-60	10	70	90	100	87					
C-61	70	80	91	83	85					
C-62	35	74	89	77	80					
C-63	20	100	100	95	98	88	92	88	100	92
C-65	100	66	93	92	84	96	92	96	72	89
c-134						96	72	72	100	85
sou. Miss.	40	20	55	48	41	92	84	100	100	94
New Orleans	20	20	72	85	59	96	96	72	96	90
Control Seedlings[2/]	30	80	68	65	71	52	20	36	24	33
Control Seed[2/]	45	76	91	98	88	76	88	84	92	85
A-l						76	80	56	28	60
A-2						92	84	60	84	80
CA-82						80	100	72	92	86
CB-23						96	80	96	80	88
CB-74						92	92	96	LOO	95
Callaway						92	96	36	96	80

1/ All plots contained 25 trees
2/ Control lots have no relationship between years

Analysis of Variance (102)[3/]

Source	d.f.	s.s.	"F"
Blocks	2	1,649	[4/] 6.49**
Lots	18	5.537	[5/] 2.42*
B X L (error)	36	4,673	
Total	56	11,759	

Analysis of Variance (103)[3/]

Source	d.f.	s.s.	"F"
Blocks	3	792	[6/] 2.54NS
Lots	20	10,192	[4/] 4.90**
B X L (error)	60	6,245	
Total	83	17,228	

3/ Date transformed to arcsin $\sqrt{\text{percent}}$
4/ ** denotes significance at the 1 percent level of probability
5/ * denotes significance at the 5 percent level of probability
6/ Not significant at the 5 percent level of probability

chemical damage. The amount of ground vegetation was variable and in some plots with lower survival it is quite probable that competition from herbaceous vegetation was critical during the first year. Figure 5 shows the comparison of survival in study 103 with the survival in study 102 for the 11 common parents, Figure 5 also shows the comparison of survival in 1959 with survival in 1953 for study 103. Much of the mortality can probably be attributed to fusiform rust.

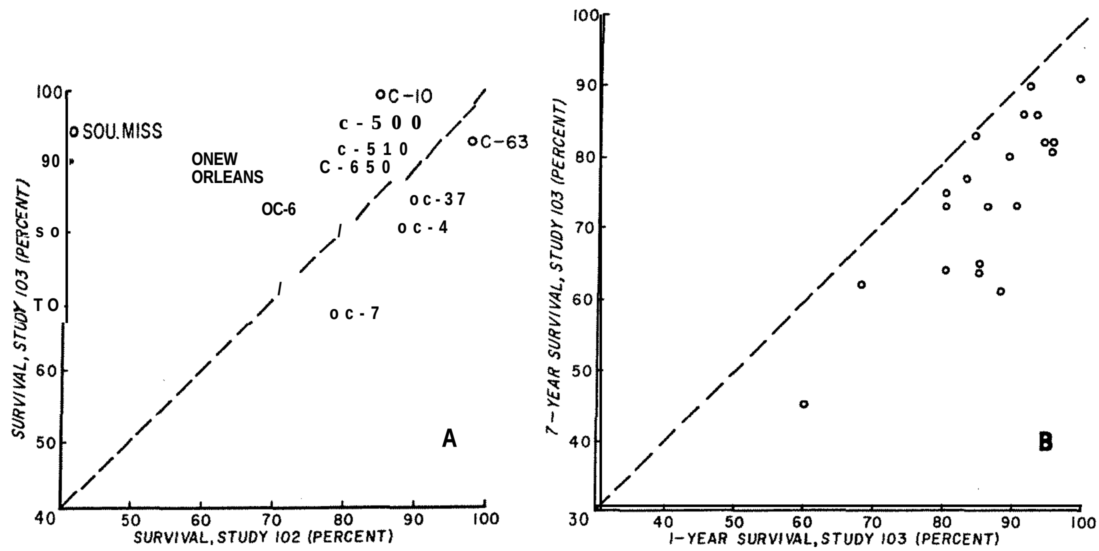

Figure 5.--A, The relationship of first-year survival of lots with common maternal parentage for studies 102 and 103. B, The relationship of survival at 1 year and 7 years after planting for study 103.

The data show that initial survival was not a critical factor in the establishment of these progeny tests. Though survival may have been low on individual plots, all of the progeny groups tested have the ability to survive under planting conditions present at the Callaway Foundation in 1952 and 1953. Probably in a year of critical drought, such as 1954 in the Southeast, differences between progenies might occur in survival which would truly measure the difference in the ability to obtain moisture from the soil and endure severe conditions of desiccation. If drought resistance were not of concern in a test, control of competing vegetation and watering would be justified to insure high initial survival. In any instance, special care should be given in handling and planting the stock.

Seed Weight

The weights per thousand open-pollinated seed for several consecutive years at the Callaway Foundation were analyzed by Snyder.[5] His analysis showed highly significant differences in seed weight among the different Callaway slash pine selections.

The relationship of growth of seedlings to seed size has been examined by several workers. Righter (1945) found in working with several species and hybrids of *Pinus* that initial seedling size was related to seed size but that differences diminished each year until they had disappeared by the third year. Fowells (1953) in his work with ponderosa and Jeffrey pines found that seed size affected the rate of germination and initial seedling size but had no effect on first-year survival. Seed size effect on growth was evident up to 5 years but was not detectable beyond this age.

5/ Unpublished data contained in memorandum RS-SS Genetics, General, October 31, 1956, on file at Southeastern Forest Experiment Station, Macon, Georgia.

In order to examine the possibility of seed weight influencing height of the progeny or reflecting inherent vigor in the Callaway tests, regression analyses were computed. For study 102 the regression of average height at age 8 years for trees free of stem cankers in relation to weight per thousand seed in grams was found to be not significant. Twelve lots were involved in this analysis. A similar analysis for the 10 lots in study 103, where complete data were available, also yielded a nonsignificant regression (fig. 6). The absence of any determinable relationship is in agreement with literature previously cited.

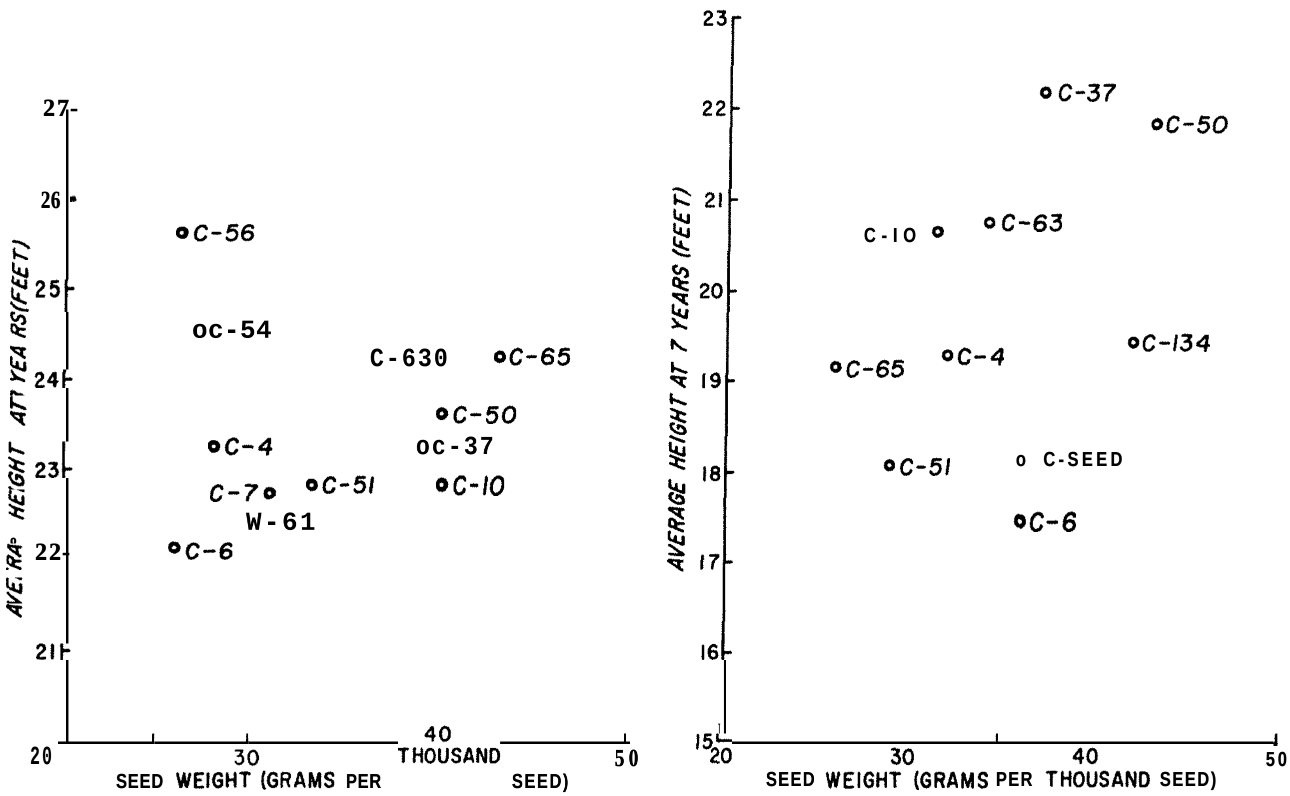

Figure 6. --The relationship of average heights of trees without stem cankers of fusiform rust to seed weight. Study 102, 8 years after planting (left), and study 103, 7 years after planting (right).

Height

The literature of forest tree improvement contains many contributions on the subject of growth. Basically, an increase in forest productivity is the goal of most work, and the first step is to increase the volume of wood produced per unit area of land. Volume growth is a complex relationship of height, diameter, and stem form. Our primary concern is to discover trees that will yield more wood per acre in less time. We are concerned with many other characteristics in addition to the dimensions which determine volume growth, but they will be discussed later.

Most of the early reports in the literature on height growth were concerned with provenance tests where mixed lots of seed from a number of trees represented each source. Many of the early workers recognized that individual tree differences were important (Bates 1927; Hartley 1927; Coville 1928) and some gave observational data about them (Tourney 1914; Roeser 1926).

Lubjako (1941) in his examination of 11 -year progenies found that first quality stands produced trees which were *more* than double those from third quality stands in diameter and 1.8 times as great in height. He detected "hereditary" differences in the third and fourth years but considered that still too early for selection. Hough (1952b) correlated IO-year growth of red pine seedlings with the green weight of 2-l stock in a provenance test. He found that the heaviest seedlings gave a faster growth rate than lighter ones and that this growth rate differential increased at a faster rate during the second 5 years after planting than during the first 5 years. Rohmeder (1956) in his discussion of racial tests of Douglas-fir reported that the order of growth rate had not changed from the second to the forty-fourth year except for unimportant displacement in the middle of the ranking. Most of the shifting was between the ages of 15 and 25 years. This was a period in which disease appeared in the plantation and may have accounted for some of the shift. Schröck and Stern (1952) plotted annual growth data of Populus sp. and concluded that extrapolations could be made to permit selection for final growth capacity after 4 to 5 years of measurements for fast growing trees and 8 to 10 years for slower growing ones.

Schmidt and Stern (1955) developed a growth quotient for Scotch pine where variety "A" is expressed as a percent of variety "B". They showed a "rhythm" of growth for a 20-year period and in their opinion early tests would be possible based on their growth quotient. Their data were based on racial tests. Fischer (1949) in a summary of provenance trials with spruce found that the maximum differences in height occurred between ages 10 and 25 years.

Height data for study 102 were recorded at ages 1, 2, 3, 4, 6, and 8 years after outplanting in the field (fig. 7), and analyses of variance showed that during the first 3 years highly significant differences were evident among progeny groups. At the end of the fourth year the significance level had dropped to 5 percent and at the end of the sixth year, the test failed to reach the 5 percent level. At age 8, significant differences were not obtainable in study 102 (table 4). In every case, block differences were highly significant. Using an approximate method by Snedecor (1956, pp. 385-386) the block-lot interaction was examined. The examination of the block-lot interaction, which is the error term in the usual analysis of variance, indicated a highly significant interaction. This is interpreted to mean that the different progeny groups react differently to the varying sites upon which the blocks are located. As was pointed out previously, the blocks were not contiguous and were scattered over the field in order to reduce the risk of fire. In study 102, plot size varied from 10 to 100 seedlings; thus, the area occupied by the individual plots was quite variable.

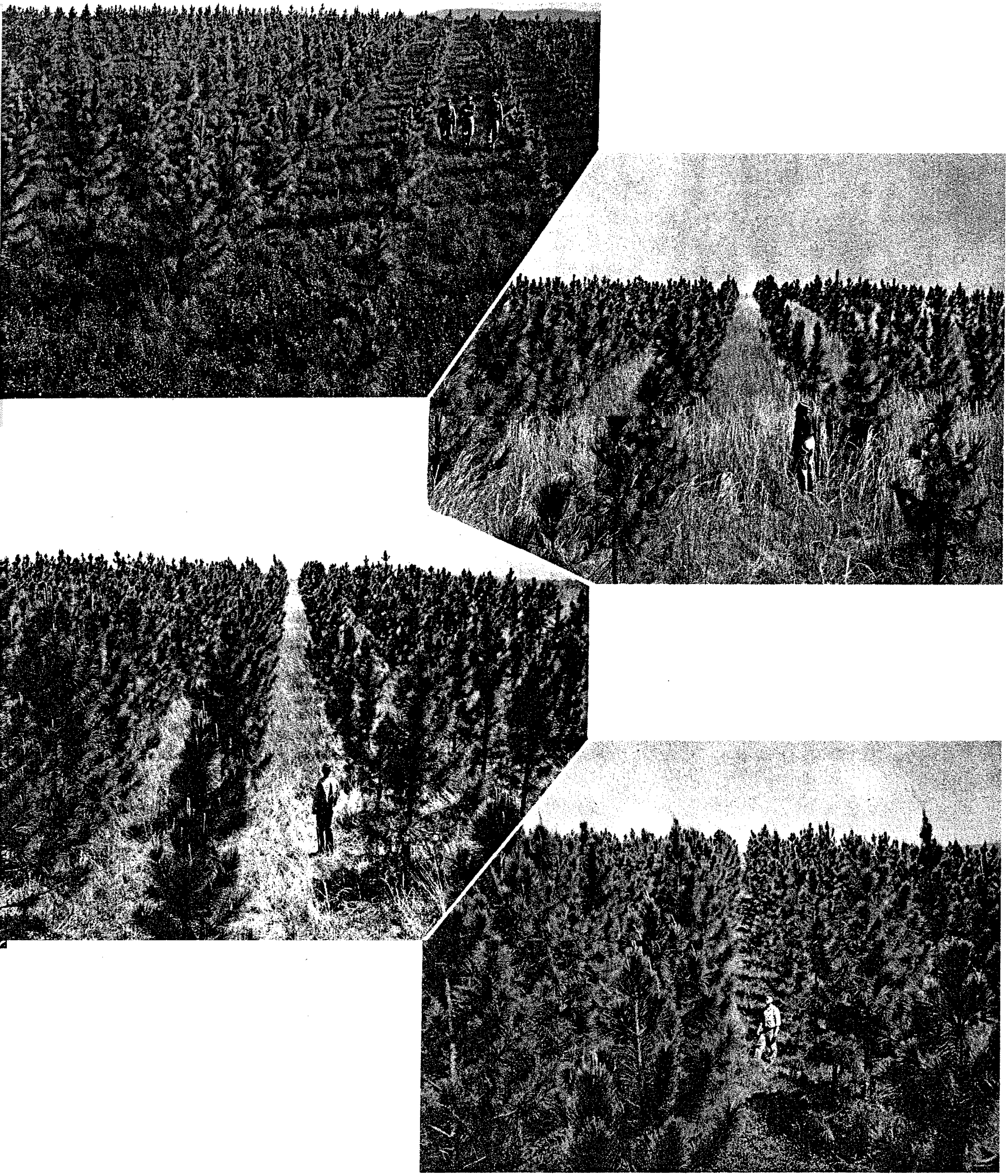

Figure 7.--The rapid height growth of the progenies is shown in this series of photographs taken at 3, 4, 5, and 6 years after planting. (Block II, study 102.)

Table 4. --Height data, study 102, 8 years after planting

Lot	All trees				Trees without stem cankers of fusiform rust			
	Block I	Block If	Block III	Average	Block I	Block II	Block III	Average
	---------	-Feet-	---------		---------	-Feet-	---------	
C-4	24.24	22.34	20.61	22.40	25.61	23.29	20.96	23.29
C-6	21.45	22.05	20.81	21.44	22.66	22.56	21.24	22.15
c-7	19.73	24.01	20.77	21.50	22.25	24.99	21.04	22.76
c-10	24.87	24.59	17.13	22.20	25.67	25.35	17.60	22.88
c-37	23.42	23.30	21.48	22.73	24.15	23.60	22.09	23.28
c-50	26.40	23.63	17.61	22.55	27.66	24.74	18.52	23.64
c-51	24.29	19.55	22.51	22.12	24.67	20.32	23.47	22.82
c-54	25.95	26.79	20.29	24.34	26.13	27.34	20.29	24.59
C-56	25.59	25.23	24.15	24.99	26.49	25.56	24.85	25.63
c-59	19.00	20.86	22.82	20.89	19.00	21.07	22.82	20.96
C-60	22.57	22.56	21.17	22.10	24.68	22.73	21.17	22.86
C-61	22.59	23.18	19.18	21.65	23.69	23.57	20.11	22.46
C-62	24.64	23.24	18.20	22.03	25.73	23.67	18.66	22.69
C-63	23.69	23.57	24.62	23.96	24.79	23.20	24.86	24.28
C-65	24.66	23.13	23.96	23.92	25.03	23.41	24.38	24.27
Sou. Miss.	19.18	22.25	17.95	19.79	23.50	24.13	21.20	22.94
New Orleans	23.03	20.60	14.65	19.43	22.47	21.43	17.33	20.41
Control Seedlings	22.55	21.48	19.66	21.23	22.90	22.71	19.77	21.79
Control Seed	23.01	23.51	22.70	23.07	23.71	24.13	23.12	23.65

Analysis of Variance

Source	d.f.	s.s.	"F"
Blocks	2	81.8177	9.90**
Lots	18	111.4884	1.50NS
B X L (error)	36	148.6884	
Total	56	341.9945	

Analysis of Variance

Source	d.f.	s.s.	"F"
Blocks	2	95.0428	13.14**
Lots	18	81.7855	1.26NS
B X L (error)	36	130.2141	
Total	56	307.0424	

The occurrence of this significant interaction was not anticipated. Analyses of height data from each of the other Callaway slash pine studies revealed highly significant interactions with one exception. This high frequency of significance of the interaction minimizes the possibility that it could be chance; therefore, it must be attributed to the sensitivity of the progeny groups to varying sites. This reflection of micro-site in growth responses is disturbing because from a practical standpoint any improved strain must be well adapted to a given site in the broad sense. It is impractical to attempt to develop or use individual progenies or strains adapted to the normal patterns of micro-site variation in the Piedmont.

The interaction also increases variation and reduces the sensitivity of the test. The attainment of a more sensitive test will require the use of very uniform sites or a much better sample of micro-sites than these studies represent. This problem of sensitivity immediately poses the question of what design must be used for future tests to insure adequate samples of micro- and macro-sites. How do we test a progeny for performance in the lower Piedmont? Do we have to test on each phase of each soil series ? Can we test for general adaptability? Only the analyses of similar studies established on other sites can furnish the answers. Fortunately, many of the needed studies are already established and we await the lapse of time until data can be collected and analyzed.

On-the-ground observations indicate that the different progenies are quite sensitive to minor variations in site. Within a single plot, on what appears to be a uniform soil as judged by slope, aspect, and ground vegetation, there is considerable variation. In some of the plots where there has been erosion of the surface soil, usually reflected by differences in ground vegetation, there are frequently very striking contrasts between the heights of trees on the eroded portion of the plot and those in the next row of trees on the non-eroded portion. These trees seemed to be much more sensitive to what has been previously thought minor site variations than was expected.

Study 103 shows significant differences among lots at all ages. In the early years tests were significant at the 1 percent level; however, at ages 5 and 7, differences were significant only at the 5 percent level (table 5). Once again examination of the block-lot interaction shows it to be highly significant, and there is a highly significant difference between blocks. Two factors may contribute to the retention of significance in study 103 at various ages in contrast with 102. First of all, study 103 has 4 blocks instead of the 3 in 102, and secondly, all plots are the same size and originally contained 25 trees. Survival has been more consistent in study 103, which would tend to give less variable estimates of the progeny means, There is considerable variation in the performance of individual progenies among the different blocks for both study 102 and 103 (tables 4 and 5). The effect of fusiform rust stem cankers on growth also becomes evident. In general, the mean height for each plot shows an increase when stem-cankered trees are removed. Only relatively large differences are significant (table 6).

Table 5. --Height data, study 103, 7 years after planting

Lot	All trees: Block I	Block II	Block III	Block IV	Average	Trees without stem cankers of fusiform rust: Block I	Block II	Block III	Block IV	Average
	Feet					Feet				
C-4	21.06	17.72	14.63	20.44	18.46	21.95	18.20	15.26	21.78	19.30
C-6	20.60	14.23	11.88	20.56	16.82	21.16	14.87	13.14	20.75	17.48
C-7	21.64	18.78	19.21	19.81	19.66	21.95	20.90	20.73	20.39	20.99
C-10	24.30	19.96	16.22	19.04	19.88	24.59	20.28	17.35	20.51	20.68
C-37	23.37	21.54	21.51	19.97	21.60	23.78	22.52	22.28	20.31	22.22
C-50	22.73	21.43	17.65	21.45	20.82	24.04	22.38	19.24	21.76	21.86
C-51	20.47	15.61	15.57	18.01	17.42	20.47	16.31	16.53	18.98	18.07
C-58	22.33	21.51	20.54	19.42	20.95	23.12	22.88	21.41	20.97	22.10
C-63	20.65	21.33	17.78	20.64	20.10	21.06	22.18	18.65	21.23	20.78
C-65	22.55	17.55	19.46	16.41	18.99	22.84	17.48	19.95	16.47	19.18
C-134	19.59	23.22	12.32	17.52	18.16	20.54	23.88	14.28	19.07	19.44
Sou. Miss.	19.90	16.26	11.19	18.94	16.57	20.86	19.97	15.65	21.69	19.54
New Orleans	20.32	16.68	13.09	20.93	17.76	21.32	18.51	15.03	21.26	19.03
CA-82	21.18	18.58	16.50	19.08	18.84	23.11	20.33	17.50	19.62	20.14
CB-23	20.82	17.31	14.19	17.79	17.53	22.2s	18.74	16.14	19.82	19.20
CB-74	18.88	12.12	14.39	19.27	16.16	19.25	14.11	16.17	21.40	17.73
A-1	17.01	19.58	14.40	19.43	17.60	19.10	20.85	15.85	20.90	19.18
A-2	18.39	19.62	12.96	18.82	17.45	20.23	20.36	15.30	20.93	19.20
Control Seedlings	17.18	16.82	18.74	11.28	16.00	17.30	16.30	20.83	14.55	17.74
Control Seed	20.09	15.79	14.13	20.62	17.66	20.93	15.80	14.13	21.87	18.18
Callaway	22.77	18.70	13.06	18.54	18.27	22.95	19.55	13.49	19.14	18.78

Analysis of variance

Source	d.f.	s.s.	"F"
Blocks	3	277.49	19.17**
Lots	20	204.76	2.12*
B X L (error)	60	289.46	
Total	83	771.71	

Analysis of variance

Source	d.f.	s.s.	"F"
Blocks	3	219.97	16.84**
Lots	20	182.02	1.850*
B X L (error)	60	262.66	
Total	83	644.65	

A regression was computed of the average tree height for each lot on the average number of trees surviving per plot in study 103. Nelson (1952) reported no differences in height for thinned and unthinned slash pine plantations, but contrary to his findings, a positive regression was found with its coefficient highly significant (fig. 8).

$$Y = 14.34 + 0.224\ X$$

where Y = average progeny height in feet
X = average progeny survival in number of trees per plot

The explanation is not clear. Chance occurrence of site differences might explain it, but more likely is the possibility of a true relationship between inherent vigor and survival; more vigorous progenies survive better and grow taller,

Though the tests of differences among lots seem to indicate that studies 102 and 103 are relatively insensitive from a statistical viewpoint, the general pattern of growth seems fairly well defined (table 7 and fig. 9). Generally those progenies which performed well the first 2 or 3 years in the field have continued to maintain their positions of leadership. The initially slow growing progenies tend to remain so. There is considerable shifting of position among progenies near the center of the distribution where differences are small.

Table 6. --Multiple range test of differences in average total height among progenies of study 103, 7 years after planting

All trees: Lot	Average height (Feet)	Trees without stem cankers of fusiform rust: Lot	Average height (Feet)
c-37	21.60	c-37	22.22
C-58	20.95	C-58	22.10
c-50	20.82	c-50	21.86
C-63	29.10	c-7	20.99
c-10	19.88	C-63	29.78
c-7	19.86	c-10	20.68
C-65	18.99	CA-82	20.14
CA-82	18.84	sou. Miss.	19.54
c-4	18.46	c-134	19.44
Callaway	18.27	c-4	19.30
c-134	18.16	CB-23	19.20
New Orleans	17.76	A-2	19.20
Control Seed	17.66	C-65	19.18
A-l	17.60	A-l	19.18
CB-23	17.53	New Orleans	19.03
A-2	17.45	**Callaway**	18.78
c-51	17.42	Control Seed	18.18
C-6	16.82	c-51	18.07
sou. Miss.	16.57	Control Seedlings	17.74
CB-74	16.16	CB-74	17.73
Control Seedlings	16.00	C-6	17.48

s_m = 1.098 (All trees); s_m = 1.046 (Trees without stem cankers)

1/ Values not included in the same bracket are significantly different at the indicated 5 percent level.

Analysis of Variance (All)

Source	d.f.	s.s.	"F"
Blocks	3	277.49	19.17**
Lots	20	204.76	2.12*
B X L (error)	60	289.46	
Total	83	771.71	

Analysis of Variance (Without stem rust)

Source	d.f.	s.s.	"F"
Blocks	3	219.97	16.84**
Lots	20	162.02	1.85*
B X L (error)	60	262.66	
Total	83	644.65	

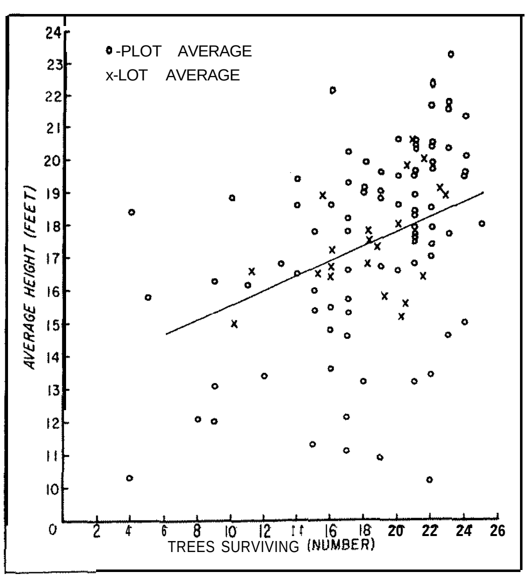

Figure 8.--The relationship of average height to number of trees surviving, study 103, 7 years after planting. Each plot contained 25 trees.

Table 7. --Average annual heights, studies 102 and 103

Lot	Study 102: Nursery height	Study 102: Age in field (Years) 1	2	3	4	6	8	Study 103: Height after planting	Study 103: Age in field (Years) 1	2	3	4 1/	5	7
	- - - - -	- - - - -	- - -	Feet	- - -	- - -	- - -	- - - - -	- - -	- - -	Feet	- - -	- - -	- - -
C-4	0.83	1.22	3.26	6.00	7.93	14.95	22.40	0.95	1.48	2.88	4.36	7.91	11.49	18.46
C-6	.72	.95	2.37	4.81	7.07	14.58	21.44	.93	1.34	2.47	4.04	7.46	10.87	16.82
C-7	.81	1.04	2.66	5.08	7.12	14.43	21.50	.88	1.42	2.83	4.63	8.52	12 41	19.86
C-10	.88	1.14	2.79	5.33	7.49	15.05	22.20	1.02	1.62	3.11	5.03	8.50	12.38	19 88
C-37	.93	1.13	2.86	5.45	7.35	15.15	22.73	.93	1.56	3.39	5.49	9.26	13.78	21 60
C-50	.87	1.13	2.83	5.20	7.70	15.07	22.55	1.12	1.67	3.15	5 44	9.65	13.24	20.82
C-51	1.18	1.23	2.85	5.70	7.20	14.85	22.12	.93	1.47	2.79	4.44	7.73	10.98	17 42
C-54	.83	1.13	2.93	5.68	8.17	16.58	24.34							
C-56	.86	1.17	3.14	6.20	8.38	17.34	24.99							
C-58								1.00	1.59	3.15	5.22	9.23	13.15	20.85
C-59	.78	.83	2.25	4.72	6.83	13.42	20.89							
C-60	.75	.96	2.55	5.21	7.83	14.88	22.10							
C-61	.77	1.01	2.72	5.22	7.30	14.77	21.65							
C-62	.68	.89	2.56	4.94	7.01	14.86	22.03							
C-63	.83	1.18	3.35	6.39	8.70	16.71	23.96	1.02	1.55	2.96	4.86	8.68	12.40	20.10
C-65	1.08	1.16	2.90	5.62	7.92	16.07	23.92	1.01	1.38	2.52	4.12	7.21	11 37	18.99
C-134								1.03	1.50	2.71	4.31	8 23	11.16	18.16
Sou. Miss.	.82	.95	2.65	5.18	7.30	13.85	15.25	1.00	1.51	2.84	4.25	7 42	10.42	16.57
New Orleans	.76	.90	2.47	4.76	6.61	13.41	19.43	1.00	1.53	2.89	4.42	8.05	10.99	17.76
Control Seedlings		.97	2.15	4.97	6.90	14.29	21.23	.46	.79	1.67	2.74	5.36	9.20	16.00
Control Seed	.82	1.09	2.99	5.60	7.70	15.43	23.07	.94	1.31	2.59	4.33	7.56	10.67	17 66
A-1								1.02	1.47	2.50	3.87	6.99	10.58	17.60
A-2								1.07	1.47	2.41	3.95	7.54	10.71	17.45
CA-82								.80	1.34	2 88	4.98	8.47	12 15	18.84
CB-23								.95	1.37	2.69	4.17	7.45	10.60	17 53
CB-74								.92	1.39	2.56	4.13	7.35	10.24	16.18
Callaway								.99	1.46	2.62	4.23	8.25	11.36	18 27

1/ Block IV was not measured at the end of the fourth growing season in the field.

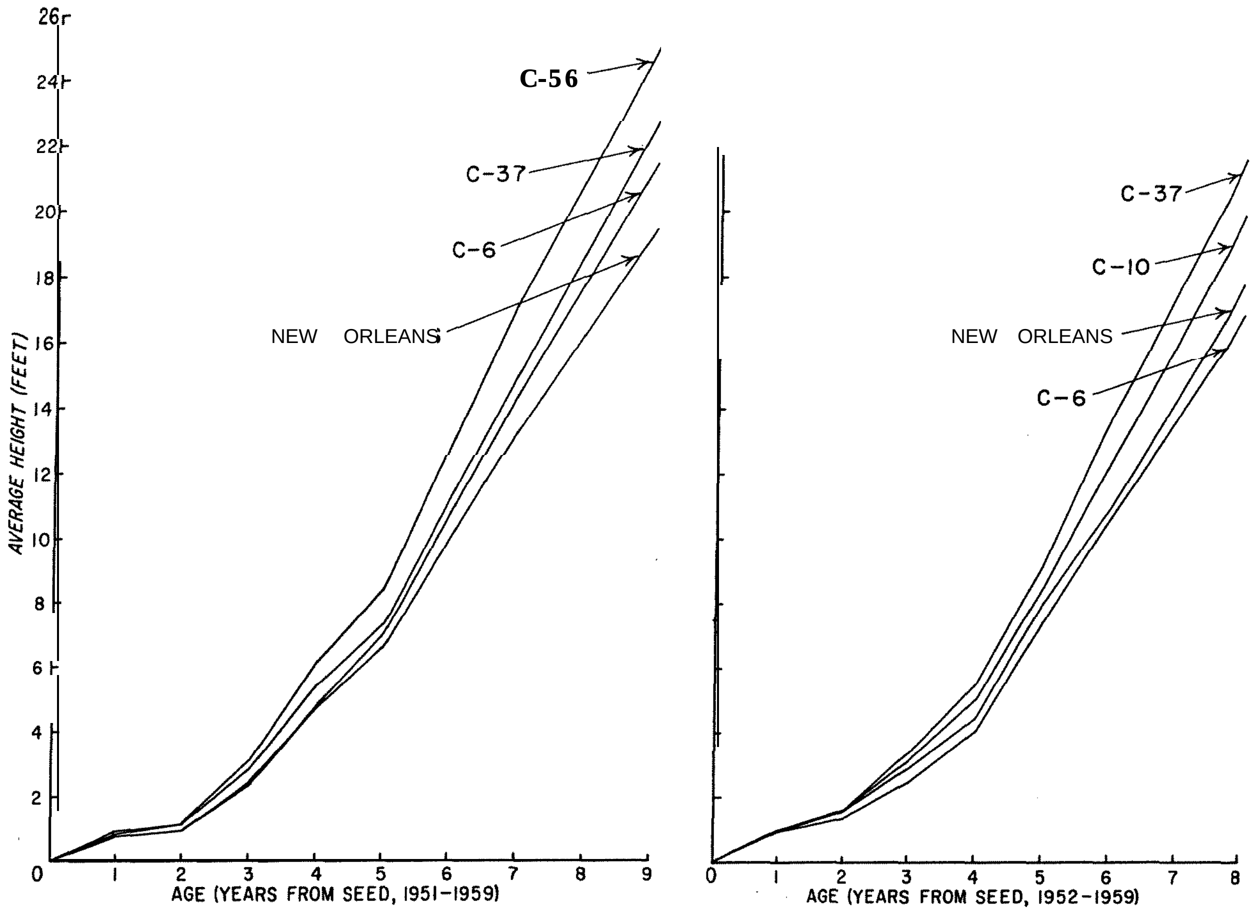

Figure 9. --The patterns of height growth for several progenies of study 102 (left) and study 103 (right) are sfmilar.

If minor site and competitive differences within the plots were important as contributors to variation in the analyses, it would seem that the most likely cause of variation would be erosion, compaction, *or* severe herbaceous competition, any of which would have a detrimental effect on height growth. Were this the case, the use of sample data from each plot might avoid some of the problem. To test this, the five tallest trees in each plot of study 103 were selected as a sample. This immediately is recognized as a disproportionate sample, but the small numbers of trees on some of the plots did not lend themselves to proportionate sampling. The analysis of variance of these data yielded results similar to those of the complete analyses. The rankings changed little with the exception of lots "Sou. Miss." and "Control Seed" (table 8).

The trial indicated that a purposively selected subsample of the tallest trees was no more sensitive than the entire sample population.

Table 8. --Average heights of tallest five trees on each plot, study 103, 7 years after plantings

Lot	Block I	Block II	Block III	Block IV	Lot average
	Feet	Feet	Feet	Feet	Feet
c-4	25.14	19.98	17.24	22.76	21.28
C-6	23.24	17.62	15.76	23.88	20.12
c-7	24.96	21.92	22.24	21.90	22.76
c-10	27.20	21.88	19.98	22.64	22.92
c-37	26.12	24.82	23.98	21.62	24.14
c-50	25.46	24.22	22.02	23.60	23.82
c-51	22.50	17.92	20.32	20.50	20.31
C-58	25.90	23.88	24.08	22.60	24.12
C-63	23.40	24.06	21.34	23.84	23.16
C-65	24.44	19.60	22.94	18.72	21.42
c-134	23.36	25.86	16.42	20.18	21.46
Sou. Miss.	23.22	20.56	17.20	22.74	20.93
New Orleans	23.98	19.98	17.24	23.76	21.24
CA-82	24.82	22.76	19.20	22.36	22.28
CB-23	24.20	19.68	18.68	20.36	20.73
CB-74	23.04	16.30	18.68	22.78	20.20
A-1	22.04	22.42	17.50	1/19.42	20.34
A-2	22.08	22.08	15.70	22.40	20.56
Control Seedlings	19.74	16.82	22.74	1/11.28	17.64
Control Seed	23.16	17.34	16.30	23.78	20.14
Callaway	24.68	21.84	15.02	20.52	20.52

1/ Four trees per plot.

Analysis of Variance

Source	d. f.	S. s.	"F"
Blocks	3	233.92	14.25**
Lots	20	207.94	1.90NS
B X L (error)	60	328.12	
Total	83	769.98	

Diameter

Measurements of d.b.h. were first taken in studies 102 and 103 in 1957 at 6 and 5 years, respectively. Repeat measurements were taken in 1959. Both sets of data were examined by analyses of variance; first, including all trees in each plot, and second, removing those trees which had stem cankers of fusiform rust and analyzing the remaining data. In no case were significant differences shown between lots for study 102. In study 103, highly significant differences were obtained when all trees were considered and differences significant at the 5 percent level were obtained when only trees free of stem cankers of rust were considered (table 9). Very high correlations were obtained between d.b.h. and total height of individual trees, 0.83 and 0.88 for all trees in studies 102 and 103, respectively. At these young ages d.b.h. seems to be closely associated with the total height of the individual trees (fig. 10).

Table 9. --Multiple range test of differences in average d.b.h. among progenies in study 103, 7 years after planting

Lot	Average d.b.h. (Inches)	Lot	Average d.b.h. (Inches)
C-37	4.92	C-37	5.16
C-10	4.40	C-58	4.65
C-58	4.31	C-10	4.63
C-7	4.30	C-7	4.57
C-50	4.30	C-50	4.54
C-63	4.26	C-63	4.46
C-4	4.12	C-4	4.39
C-65	4.04	CA-82	4.31
Callaway	4.02	Sou. Miss.	4.29
C-51	3.96	**Callaway**	4.24
CA-82	3.95	C-6	4.17
C-6	3.92	C-51	4.17
Control Seed	3.84	C-134	4.14
C-134	3.81	New Orleans	4.11
New Orleans	3.79	C-65	4.08
A-1	3.56	A-2	4.05
CB-23	3.53	A-1	4.04
A-2	3.52	CB-23	4.01
Sou. Miss.	3.44	Control Seed	3.99
CB-74	3.30	CB-74	3.80
Control Seedlings	3.24	Control Seedlings	3.80
s_m = 0.261		s_m = 0.241	

Column groups: All trees (Average d.b.h.; 5[1] percent level; 1[1] percent level) and Trees without stem cankers of fusiform rust (Average d.b.h.; 5[1] percent level). Significance is shown by brackets in the level columns.

1/ Mean values not included in the same bracket are significantly different at the probability level indicated.

Analysis of Variance (All)

Source	d.f.	s.s.	"F"
Blocks	3	15.76	19.26**
Lots	20	13.54	2.49**
BXL (error)	60	16.37	
Total	83	45.67	

Analysis of Variance (Without stem rust)

Source	d.f.	s.s.	"F"
Blocks	3	11.86	16.98**
Lots	20	8.25	1.78*
BXL (error)	60	13.97	
Total	83	34.08	

Under forest conditions in an even-aged stand, one normally expects the average diameter to be inversely related to the number of stems per unit area. The effect of competition in reducing diameter growth in young slash pine plantations was reported by Nelson (1952). Using the data of study 103, a regression was computed for d.b.h. on the number of trees surviving per plot (fig. 11). The regression coefficient was highly significant.

$$Y = 2.67 + 0.069 X$$

where Y = average progeny d.b.h. in inches
X = average progeny survival in number of trees per plot

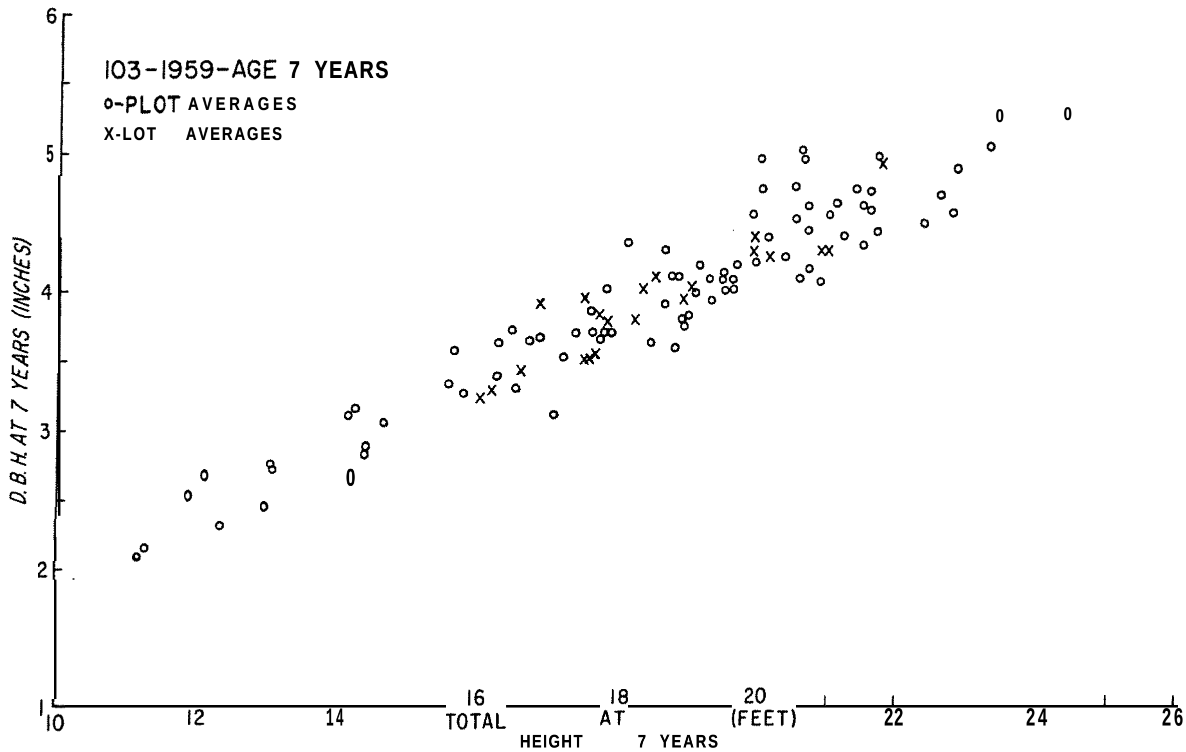

Figure 10. --The relationship of d.b.h. to total height at 7 years in study 103.

Contrary to expectation and to Nelson's report, the regression is positive, indicating that the lots with the best survival have the largest average diameters. If we assume that site has been sampled uniformly, and this may be questioned, the explanation may lie in part in the fact that the most vigorous progenies have the highest survival, and even under increased competition are more productive than the less vigorous lots. Of course, the true explanation may be a combination of this and chance site occurrence and may be related to the interaction which was apparent between lots and blocks. Additional studies that have been installed at other locations on more uniform sites will eventually shed light upon this unusual situation. For the purpose of analysis, it was assumed that the plot means were the best available estimates of the true progeny means.

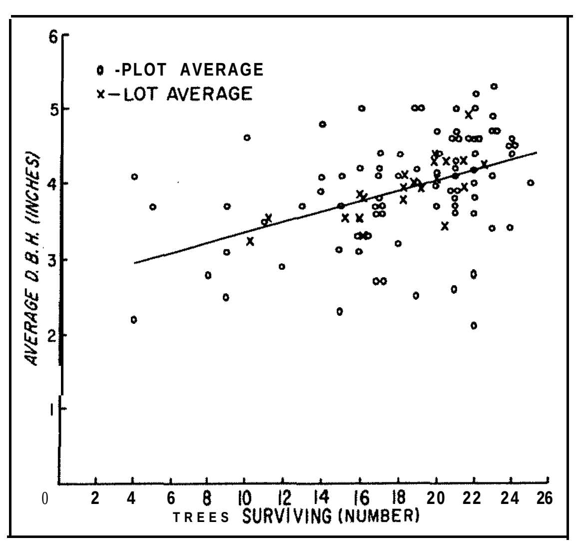

Figure 11. --The relationship of average d. b. h. to number of trees surviving, study 103, 7 years after planting. Each plot contained 25 trees.

Natural Pruning

Observations at about 5 years of age indicated that natural pruning among progenies was not closely related to the amount of crown competition, and that it took place before crowns began to compete for space (fig. 12). In 1959, studies 102 and 103 were measured and a pruning height record was taken. This height was the distance from the ground to the first whorl having two or more live branches, excluding branches having basal fusiform rust cankers.

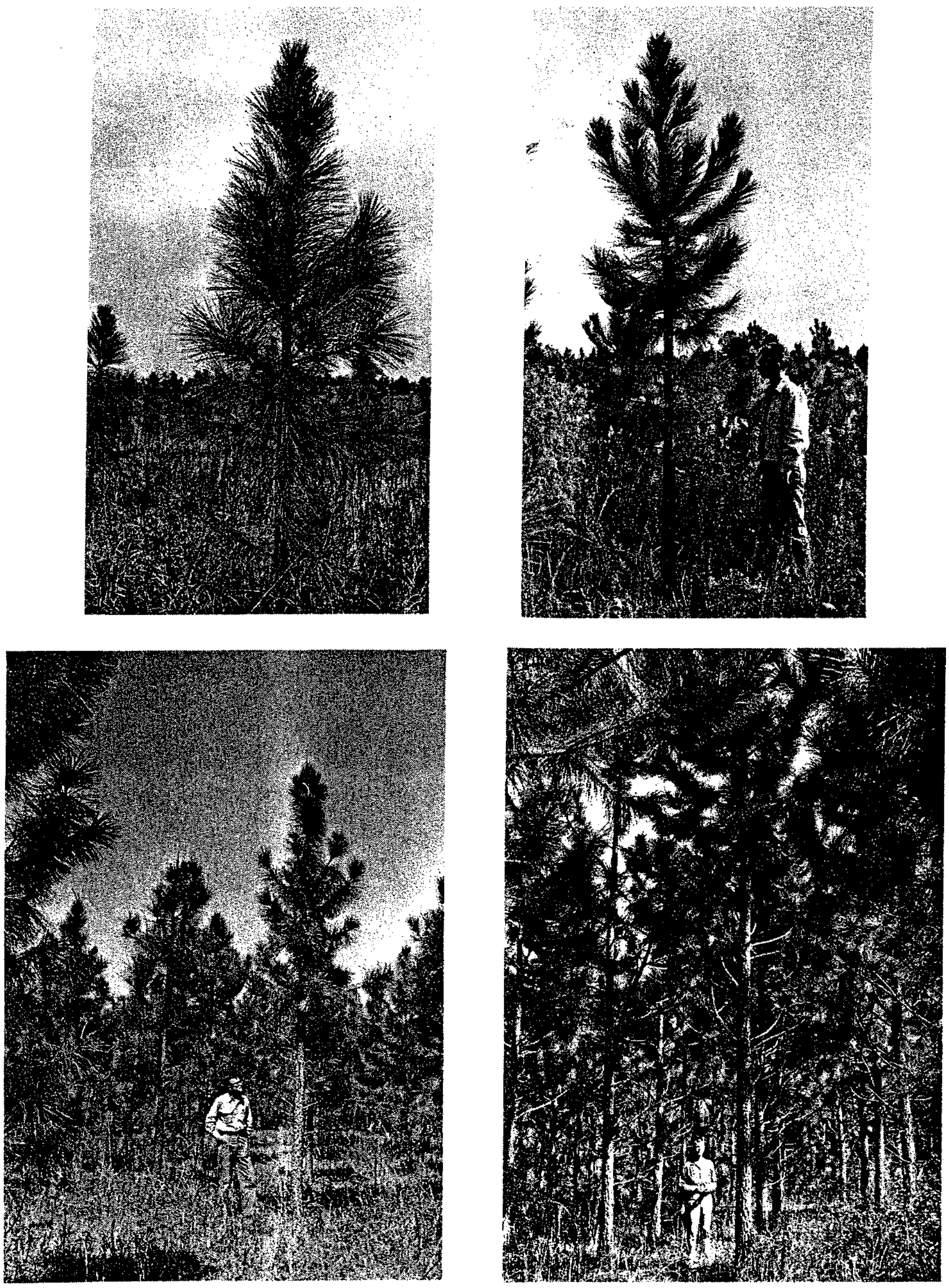

Figure 12. --This well-formed fast-growing offspring of C-37 shows the tendency for good form and rapid natural pruning at an early age. These photos were made at 3, 5, 6, and 9 years after planting.

These branches were excluded because of their tendency to remain alive and become more vigorous than uncankered limbs. Analysis of study 102 data revealed significant differences among progenies when all trees were included and highly significant differences when only trees free of stem cankers were considered (table 10). For study 103 (table 11), highly significant differences among progenies were obtained for similar analyses. Figure 13 shows the relationship of pruning height in study 103 to pruning height in study 102 for the 11 common lots based on trees free of stem cankers. Two lots, Southern Mississippi and New Orleans, had low survivals in study 102. Although there is an apparently strong relationship between pruning height and total height of the trees, there is a wider range of values among lots in study 102 than in 103, which reflects the age, variable plot size, and greater total height. The height of natural pruning at 8 years (study 102), when analyzed on an individual tree basis, has low, though significant, correlation with the second- (0.18), and third-year (0.16) height growth. Correlations with second- (0.33) and third-year (0.36) total height are nearly as good as 8-year total height (0.40).

Table 10. --Multiple range test of differences in average pruning height among progenies in study 102, 8 years after planting

Lot	All trees: Average pruning height	All trees: 5 percent level1/	Trees without stem cankers of fusiform rust: Lot	Average pruning height	5 percent level1/	1 percent level1/
	Feet			Feet		
C-56	7.26		c-54	7.28		
c-54	7.17		C-56	7.20		
c-37	6.81		c-37	6.98		
C-65	6.74		C-65	6.78		
C-63	6.57		C-63	6.52		
c-7	6.28		c-7	6.16		
Control Seed	6.02		Control Seed	6.02		
c-60	5.56		C-60	5.68		
c-10	5.49		c-10	5.52		
c-51	5.49		c-51	5.40		
C-61	5.46		C-61	5.37		
c-50	5.33		c-50	5.31		
C-6	5.18		C-6	5.28		
C-62	5.12		C-62	4.96		
Control Seedlings	4.70		Control Seedlings	4.53		
c-4	4.61		c-59	4.47		
C-59	4.50		c-4	4.27		
sou. Miss.	4.45		sou. Miss.	4.27		
New Orleans	3.79		New Orleans	3.64		

$s_m = 0.647$ $s_m = 0.609$

1/ Mean values not included in the same bracket are significantly different at the probability level Indicated.

Analysis of Variance (All)

Source	d.f.	s.s.	"F"
Blocks	2	14.08	5.60**
Lots	18	53.06	2.34*
B X L (error)	36	45.24	
Total	56	112.38	

Analysis of Variance (Without stem rust)

Source	d.f.	s.s.	"F"
Blocks	2	28.44	12.77**
Lots	18	60.99	3.04**
B X L (error)	36	40.08	
Total	56	129.51	

Table 11. --Multiple range test of differences in average pruning height among progenies in study 103, 7 years after planting

All trees

Lot	Average pruning height	5[1/] percent level	1[1/] percent level
	Feet		
c-37	6.06		
C-58	5.54		
c-7	4.96		
C-63	4.92		
CA-82	4.70		
c-50	4.43		
Sou. Miss.	4.33		
c-10	4.26		
CB-74	4.18		
CB-23	4.14		
c-51	4.10		
A-2	4.01		
C-65	3.96		
Callaway	3.96		
A-l	3.94		
New Orleans	3.93		
c-134	3.80		
C-6	3.62		
Control Seedlings	3.39		
Control Seed	3.36		
c-4	3.14		

s_m = 0.376

Trees without stem cankers of fusiform rust

Lot	Average pruning height	5[1/] percent level	1[1/] percent level
	Feet		
c-37	6.16		
C-58	5.55		
c-7	5.10		
CA-82	4.77		
C-63	4.71		
c-50	4.49		
sou. Miss.	4.4s		
c-10	4.21		
CB-74	4.18		
c-51	4.08		
New Orleans	3.99		
CB-23	3.9s		
C-65	3.95		
A-2	3.89		
Callaway	3.87		
C-6	3.65		
A-l	3.64		
c-134	3.58		
Control Seed	3.40		
Control Seedlings	3.14		
c-4	2.97		

s_m = 0.388

1/ Mean values not included in the same bracket are significantly different at the probability level indicated.

Analysis of Variance (All)

Source	d.f.	s.s.	"F"
Blocks	3	45.11	26.65**
Lots	20	39.82	3.53**
BXL (error)	60	33.86	
Total	83	118.79	

Analysis of Variance (Without stem rust)

Source	d.f.	s.s.	"F"
Blocks	3	52.00	28. SO**
Lots	20	46.45	3.86**
BXL (error)	60	36.11	
Total	83	134.56	

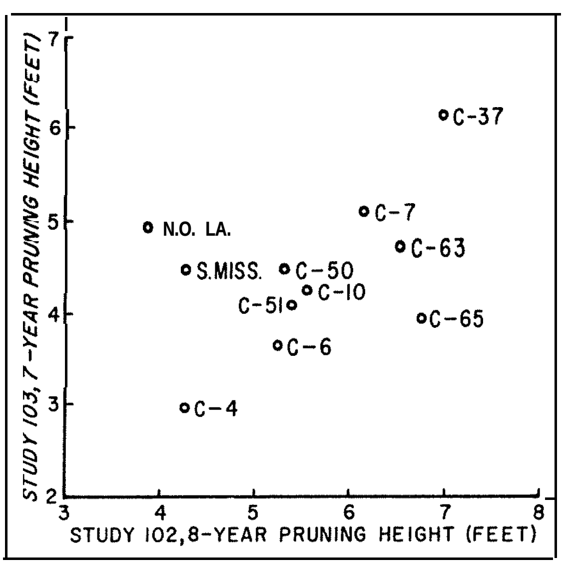

Figure 13.--The relationship of pruning height in studies 102 and 103 for lots with common maternal parentage.

Field observations show that some trees have inherent ability to prune early (fig. 12). The characteristic of early pruning is valuable because it reduces the amount of knots produced; knots in general degrade and weaken lumber and provide poor quality raw material for pulping. The reduced cost of limb removal in the logging operation is also of importance.

Bark Thickness

Preliminary examination of table 12 seemed to indicate little relationship between bark thickness and diameter inside bark for individual trees in study 102. Investigating further, three progeny groups that had individual measurements taken on the largest numbers of stems were analyzed individually by regression techniques. The three progenies examined were C-37 (n = 35), C-50 (n = 22), and C-65 (n = 33). Interestingly, the average bark thickness of the progenies of C-50 and C-65 were nearly identical, but the average diameter inside bark was different by greater than one-half inch.

Individual regressions of bark thickness on diameter inside bark were computed for each progeny group (table 12). Both C-50 and C-65 had low non-significant regression coefficients. C-37 had a regression coefficient much stronger than the other two groups and it was highly significant.

Table 12. --Bark thickness and d.i.b. relationships for some progeny groups in block I, study 102, 8 years after planting

Lot	Trees	D.i.b. 1/	Bark thickness	Regression coefficient	"t" value
	Number	Inches	Inch		
c-4	10	4.84	0.654	--	--
C-6	4	4.26	.662	--	--
c-37	35	4.24	.551	0.082	3.900**
c-50	22	4.66	.588	.011	.402
c-54	11	4.56	.593	--	--
C-65	33	4.07	.586	.033	1.357

1/ Diameter inside bark.

$$Y = 0.202 + 0.082 X$$

where Y = average progeny bark thickness in inches (C-37)
X = average progeny d.i.b. in inches (C-37)

Figure 14 shows the wide dispersion of the individual values for each progeny group and the regression line for C-37.

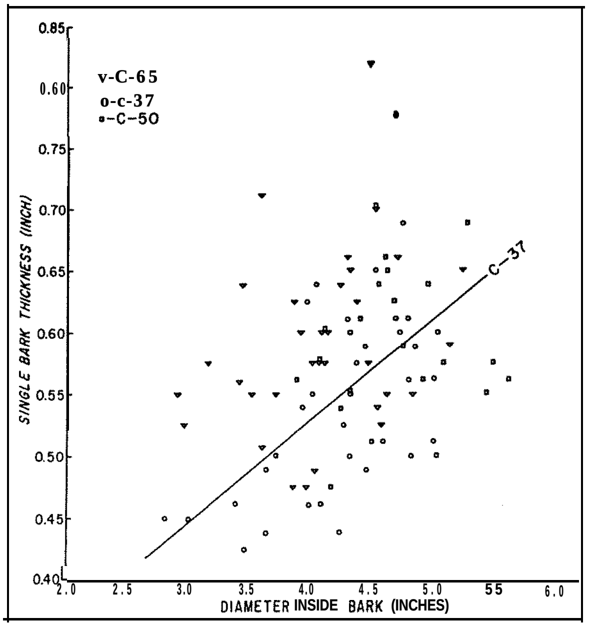

Figure 14. --The relationship of bark thickness to diameter inside bark, study 102, 8 years after planting.

Each bark thickness value was an average of 4 measurements taken on the individual tree. The measurements were taken to the nearest 0.05 inch, estimated to 0.01; they showed a considerable uniformity on the individual trees. Some of the extreme values that occur on figure 14 are striking, such as the individual of C-65 which has a bark thickness of 0.82 inch though only 4.45 inches diameter inside bark. A similar individual of C-37 shows a bark thickness of about 0.78 inch though only 4.65 inches d.i.b. In contrast, of course, are other trees, such as the individual of C-50 with a bark thickness of about 0.50 inch and a d.i.b. of 5.00 inches. Similarly, an individual of C-37 with a bark thickness of 0.50, one-third less than the previously cited individual of C-37, had a d.i.b. of 4.80 inches. These figures indicate strikingly different rates of bark growth as compared with wood growth (d.i.b.) for any given diameter. The lack of a wide range of bark thickness for progeny of C-37, with diameters from 3 to 4 inches, is somewhat in contrast with the wide variation that occurs above 4 inches d.i.b.

The individual parent trees showed considerable differences in bark thickness. The relationship existing between parent and progeny for this characteristic is not well defined (fig. 15), but a positive relationship is indicated.

The relationship of bark thicknesses among progenies of the two studies is defined more clearly in figure 15. In study 103, trees C-4, C -6, and C-65 had approximately the same average d.b.h., but differed in average bark thickness.

It is probably too early to tell how much of the evident variation in bark thickness might be attributed to heredity and how much to environment. At this young age, the bark has not begun to break into large blocks and show appreciable sloughing. It will require 5 to 10 more years before true progeny differences in bark thickness can be safely established.

The range of variation in bark thickness would seem to indicate inherent differences in the relative rates of growth of bark and wood. If this is a true relationship, and these data support that view, it will then be possible to include bark thickness as one of the selection criteria for trees used in breeding programs and in seed orchard establishment. Relatively small differences in bark thickness can mean large differences in the amount of bark in relation to the wood contained in the log. At the present time, the only appreciable use for pine bark *is* fuel for the boilers *in* large sawmills and *in* pulp mills. When logs are transported great distances, the cost of hauling the bark is substantial and more than the fuel value it returns. Thus, it would seem desirable, from an economic viewpoint, to breed for trees with thin bark.

Considering an opposite viewpoint, if bark thickness is related to fire resistance of the individual trees, it might be desirable to breed trees for thick bark to provide more resistance to fire. This would be desirable not only from resistance to wildfire, but also to provide more latitude in the silvical application of fire for the control of hazardous fuels and understory vegetation. If bark thickness proves highly heritable, it is quite probable that breeding will take both directions, depending upon the needs of the particular landowner.

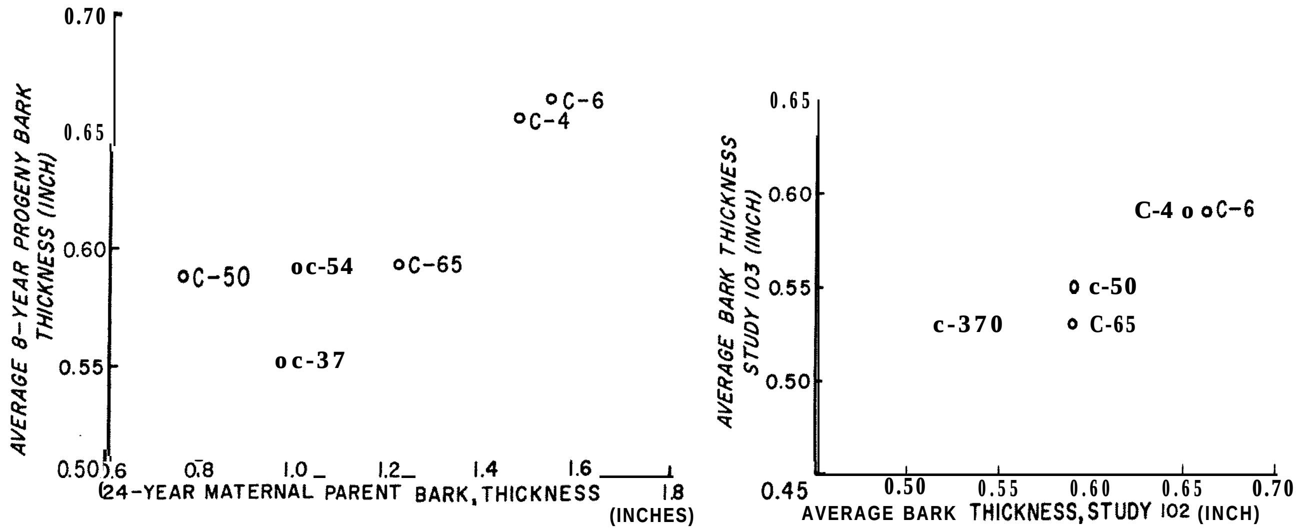

Figure 15.--The relationship of progeny bark thickness to maternal parent bark thickness, study 102 (left). The relationship of progeny bark thickness for lots with common maternal parentage in studies 102 and 103 (right).

Correlations

All basic measurements taken in studies 102 and 103 were assembled for a correlation analysis among the characteristics of individual trees. In an effort to determine what might be the best measurements to take on very young progenies for estimates of later relative values, correlations were attempted between early measurements and height, diameter, and pruning height at age 8 in study 102 and age 7 in study 103 (tables 13, 14). The degree of rust infection on each tree was also examined in relation to the growth characteristics at earlier ages. In summary, for study 102:

1. Height at 8 years correlates well with height at 2 or 3 years.
2. The removal of stem-cankered trees from the data before analysis usually increases the correlation coefficients. Stem cankers usually reduce the growth of trees and increase variation.
3. The rust correlations are low with all growth and height values for ages 2 and 3 years. The correlations of rust with height and diameter at age 8 are generally negative, indicating that rust infections have had a detrimental effect on growth.
4. Height and d.b.h. are highly correlated.
5. Early growth and height values are correlated with d.b.h. almost as well as with total height.
6. Height of natural pruning has a low correlation with second- and third-year height growth.
7. Total height after 2 years in the field compares favorably with the same value in study 103 for correlation with total height at ages 7 and 8, respectively.

Table 13. --Correlation values between Various characteristics of slash pine trees, study 102

	All trees (n = 1927)										Trees without stem cankers of fusiform rust (n = 1433)									
Variable:	X2	X3	X4	X5	X6	X_7	X_8	X_9	Xl0	X11	Variable:	X_2	X_3	X_4	X5	X_6	X_7	XS	X_9	Xl0	Xl1
Xl	0.92	0.71	0.70	0.61	0.62	0.33	0.16	0.45	0.79	0.67	Xl	0.93	0.73	0.74	0.67	0.67	0.38	-	0.41	0.73	0.61
X2		.83	.82	.73	.72	.36	.12	.61	.71	.72	X2		.84	.84	.78	.76	.43	-	.52	.66	.64
X3			.88	.92	.82	.40	-.02	.53	.53	.58	X_3			.88	.92	.82	.45	-	.44	.48	.50
X4				.83	.94	.30	-.08	.52	.53	.57	X_4				.83	.94	.35	-	.43	.49	.50
X5					.83	.40	-.14	.46	.45	.50	X_5					.82	.47	-	.39	.44	.45
X_6						.23	-.14	.47	.47	.51	X6						.28	-	.40	.45	.46
X7							.02	.16	.18	.18	X_7							-	.16	.19	.19
X_8								.03	.15	.10	X_8							-	-		
X_9									.66	.92	X_9									.68	.93
X10										.90	X_{10}										.91

VARIABLE	All trees Mean	Std. Dev.	C.V.	Trees without stem cankers Mean	Std. Dev.	C.V.
Xl = 2-year total height - Inches	34.76	10.32	0.30	34.26	10.42	0.30
X2 = 3-year total height - Feet	5.52	1.43	.26	5.47	1.46	.27
X3 = 6-year total height - Feet	15.58	2.72	.17	15.70	2.69	.17
X4 = 6-year d.b.h. - Inches	3.49	.72	.21	3.55	.69	.19
X_5 = 8-year total height - Feet	32.88	3.59	.16	23.32	3.33	.14
X6 = 8-year d.b.h. - Inches	4.90	.90	.18	5.01	.83	.17
X7 = 8-year height of pruning - Feet	5.79	2.29	.40	5.86	2.28	.39
X_8 = B-year fusiform rust cankers - Number	.92	1.37	1.49			
X_9 = Third year height growth - Feet	2.61	.72	.28	2.61	.73	.28
X10 = Second year height growth - Feet	1.80	.65	.36	1.76	.65	.37
X11 = Second and third year height growth - Feet	4.41	1.25	.28	4.36	1.26	.29

Table 14. --Correlation values between various characteristics of slash pine trees, study 103

All trees (n = 1391)

Variable:	X_2	X3	X_4	X_5	X_6	X_7	X_8	XQ	X_{10}	X_{11}
Xl	0.80	0.54	0.54	0.46	0.47	0.34	0.11	0.38	0.52	0.51
X2		.75	.75	.65	.66	.48	.13	.53	.93	.a2
X3			.91	.91	.86	.52	-.03	.76	.74	.86
X4				.89	.94	.47	-.11	.74	.73	.85
X_5					.88	.51	-.13	.70	.64	.77
X6						.37	-.20	.65	.65	.75
X_7							.17	.44	.47	.52
X_8								.02	.12	.oa
X_9									.52	.89
X10										.a5

Trees without stem cankers of fusiform rust (n = 1058)

Variable:	X_2	X_3	X_4	X_5	X_6	X_7	X_8	X_9	X_{10}	X_{11}
Xl	0.83	0.58	0.61	0.53	0.56	0.35	-	0.42	0.58	0.55
x2		.79	.81	.72	.75	.50	-	.60	.93	.84
x3			.91	.92	.a7	.55	-	.76	.78	.86
X_4				.88	.94	.52	-	.76	.80	.87
X_5					.86	.55	-	.72	.72	.80
X6						.44	-	.69	.74	.80
X_7							-	.46	.50	.54
xa										
X_9									.60	.91
X_{10}										.aa

VARIABLE	All trees: Mean	Std. Dev.	C.V.	Trees without stem cankers: Mean	Std. Dev.	C.V.
Xl = l-year total height - Inches	17.97	4.44	0.25	17.92	4.44	0.25
X2 = 2-year total height - Feet	2.91	.85	.29	2.90	.85	.29
X3 = 5-year total height - Feet	12.23	2.59	.21	12.48	2.53	.20
X4 = 5-year d.b.h. - Inches	2.63	.73	.28	2.73	.69	.25
X_5 = 7-year total height - Feet	19.43	3.68	.19	20.03	3.40	.17
X_6 = 7-year d.b.h. - Inches	4.21	.94	.22	4.39	.85	.19
X_7 = 7-year pruning height - Feet	4.40	1.80	.41	4.36	1.81	.42
X_8 = 5-year fusiform rust cankers - Number	.73	1.28	1.75			
X_9 = Third year height growth - Feet	1.86	.68	.37	1.89	.65	.34
X_{10} = Second year height growth - Feet	1.42	.59	.42	1.42	.58	.41
X_{11} = Second and third year height growth - Feet	3.28	1.11	.34	3.31	1.10	.33

The correlation values for study 103 may be summarized as follows:

1. Total height at 2 years in the field and either second- or third-year height growth are equally good in terms of correlation with total height, age 7. The growth values are much higher in terms of correlation for study 103 than 102.
2. Removing trees having stem cankers improves the correlations.
3. Rust infection has a low correlation value with all early growth and height values. The correlation with height and d.b.h. at age 7 is negative for rust infection, indicating that rust infection apparently reduces growth.
4. Height and d.b.h. are highly correlated.
5. D.b.h. is correlated with early growth and height values equally well.
6. Pruning height, age 7, is correlated only moderately with growth and height values.
7. Total height after 2 years in the field compares favorably with study 102 in terms of correlation values.

Regressions for prediction equations were not computed because of the limited number of lots of seedlings contained in these studies. Examination of the correlation values obtained would indicate that progenies that perform well at young ages can be expected to perform well at older ages. How long this high correlation will remain is, of course, a moot question. The greater the number of years between values correlated, the lower the correlation. However, the change in the correlation value is relatively small after several years.

Callaham and Hasel (1961) obtained much better correlation values for ponderosa pine when using height growth than when using total height of young seedlings with total height at age 15 years. With the data in study 102 the opposite was true, and growth values were no better than total height values in study 103. In considering the Callaham-Hasel (1961) data, it should be noted that they were dealing with transplanted seedlings, whereas the slash pine reported in this study were field planted as 1-O stock. The growth rates of ponderosa seedlings are also much slower than those of slash pine.

A plotting of the values of mean height for different progeny groups in studies 102 and 103 at increasing ages shows that those progenies which become well established and have the greater heights at young ages tend to maintain themselves. As the trees get older, the differences between the means of the progenies generally increase (fig. 9). These curves are based upon all trees in the plot. As has been noted earlier, there are minor changes between progeny lots in these groups. Of course, we do not know whether the relative positions of the different progeny groups in terms of total height will change in future years, but we can expect minor changes and shifts back and forth where the differences are small. Whether or not progenies that are slow growing during the first 7 or 8 years will suddenly change their growth pattern and grow more rapidly than those which have been fast growing is a subject for further study.

Studies 102 and 103 will be continued until a thinning becomes necessary, probably at 15 to 18 years of age. Beyond this point growth values will become uninterpretable because plots of varying densities and competitive levels cannot be systematically thinned to retain the same relative competitive status. In normal forest management practice, the timber marker determines which trees will be retained for future growth; therefore, trees not exhibiting good growth at early ages will be removed and never have the opportunity to show any changed pattern of growth in later years, if such potential exists.

In all of the characteristics considered in the foregoing presentation, there is evident the variation within and among progenies. The agreement between the data of the two studies is good except for height and diameter measurements. These are probably the characteristics most sensitive to site variation. The agreement in other measured characters is encouraging.

CROWN RELATIONSHIPS

Toumey (1914), in reviewing early work done by Zederbauer in Austria and Engler in Switzerland, pointed out that seedlings produced from poor mother trees are mostly of poor form. Engler also recognized that if the mother tree was poor because of weather, man, or beast, its poor form would not be transmitted to the progeny. Bannister (1959) has discussed the complexities involved in selecting for characteristics, such as branching, where at present the genetics are unknown, the interrelationships are unknown, and the physical properties of the products are unknown, as well as the economics. Using 7-year-old open-pollinated progenies of Pinus radiata, he found that they were significantly different in branching characteristics, and that branching characteristics were not correlated with tree height. Fielding (1953) pointed out the importance of branch angle in terms of the formation of knots. The more acutely angled branches cause worse knots than horizontal branches and also may give bark inclusions. He reported that branch angle in some clonal material increased with age. Fielding found differences in crown width between clones, and that the number of whorls per year varied widely. Breeding done with exotic pines in Queensland (Queensland Forest Service 1950) showed that 7-year-old selfed progenies had branch characteristics, such as size, angle, and number of whorls per unit length of trunk, that could be correlated with the parent. Johnson (1954) considered crown-width relationships "perhaps safely established," and branch angle and relative degree of apical dominance important. Kleinschmit (1959) has reported a Mendelian segregation of growth and branch forms in progenies of European larch.

Péter-Contesse (1941) reported that poor beech trees gave excessively branched seedlings which did not respond to silvicultural manipulations in terms of branching characteristics. Work with Pinus radiata in South Africa (Union of South Africa, Department of Forestry 1948) showed a high percent of progeny that reproduced the morphology of the mother tree. The data indicate that certain morphological characteristics, such as slender branches and short internodes are probably dominant. It was also found that defects in crown and leading shoot were heritable. Toda (1956) considered the crown slenderness in clones and seedlings. He tried to use a formula to express crown slenderness in Larix decidua but found it unsatisfactory; neither was a "spacing value" acceptable. He found that site quality in the usual meaning did not affect crown slenderness very much. In considering the practical application of breeding for narrow-crowned trees, Toda determined that if the number of stems per acre was proportional to crown slenderness, then one might increase the number of stems per acre 50 percent by a 17 percent decrease in crown diameter. He recognized that individually the trees may be slow growing, but the total yield would be greater; however, crown slenderness did not seem to be related to the vigor of growth.

Schmidt (1952) compared the timber producing capacities of wide-crowned and narrow-crowned types of Norway spruce (Picea abies). He found that isolated trees with the wide type yielded higher, but in close stands the yields were about equal. From this he also cautioned one to use care in applying single tree results to stands. Kiellander (1957) also considered inheritance of branching type in spruce. He examined two racial plantings; one planted at 1.5 meters spacing produced finely branched trees and yielded wood of good quality; the other plantation was planted at 1.2 meters and the trees were coarsely branched and poor in quality. This demonstrated that the characters of branching could not be controlled entirely by close planting.

Squillace and Bingham (1954) measured crown characteristics in a number of western white pine and used the 9th, 10th, and 11th whorls from the top of the tree; they measured the length and diameters of the branches and found that average branch length was significantly correlated with the average periodic elongation of the stem during the last 10 years. Their value was 0.61, significant at the 1 percent level. Spahlinger (1957), working with grafted offspring of finely branched trees, suggested early testing of branching characteristics by measuring branching at a height of 1 meter. He assumed that branch diameter at this height would be closely related to branch diameter at a greater height on the tree. Kleinschmit (1955) reported on a-year-old open-pollinated progenies of larch from six stands. He found that branch angle differed from 25 to 55 degrees at the extremes and that crown spread depended on branch angle, not branch length. He found that individual parent trees and provenances could be distinguished. Arnborg and Hadders (1957)found significant differences between branch angles among clones. They also found that branch angle generally increased in the first three whorls. The variation in their clonal material was very small. They found that the angle of branches in clones changed less with acute angles than with those angles nearer horizontal. Their tests of normally branched parents gave mostly normally branched progenies from open-pollination, and acutely angled parents gave progenies with 75 percent having acute angles. When clones were planted at different locations, branch angle did not seem to be modified to the same extent as height and diameter growth. They also found an inverse relationship of branch length and angle in some clones, the acutely angled branches being longer. They obtained significant differences in branch length, and observed a tendency for the branch angle of the ramets to agree with the ocular estimate of the angle of the ortet.

Johnson, Robinson, and Comstock (1955) in their discussions of estimates of genetic and environmental variability in soybeans, pointed out the importance of watching for a negative correlation of yield with other characteristics. These slash pine data are insufficient to test whether certain desirable branching characteristics might be negatively correlated with growth and yield. An interesting point brought out by Fielding's work with Monterey pine (1953) was that trees with approximately equal total volumes of wood may vary greatly in the amount of merchantable stem volume. He gave data on two trees of similar volumes, 9.59 cubic feet and 9.75 cubic feet, with 48.9 and 62.6 percent of the total volume of wood in the trunks, respectively. This reflects a considerable difference in the amount of wood contained in the branches of the two trees. The tree with the smaller total volume had approximately 4.90 cubic feet in branches, the other tree 3.65 cubic feet.

Goddard et al. (1959) compared branching characteristics of 5-year open-pollinated progenies from several selected loblolly pines with those of nearby check trees. They found that the limb diameter-bole diameter ratio was significantly lower for three of the select trees than their controls, and limb length-total height ratios were also significantly lower for three select trees.

Barber, Dorman, and Jordan (1955) reported differences in crown width of several progeny groups in the slash pine tests of the Ida Cason Callaway Foundation. Their presentation was brief and did not include any detailed analyses. The data were based on measurements of the maximum crown width of individual trees in the progeny tests at 1/3 and 2/3 of the total tree height. For discussion purposes, a ratio was determined for the relationship of the crown width at one-third height to total tree height. Preliminary trials using an average crown width of the two measurements or the measurement at two-thirds of the total tree height were not as good as the ratio which they used. An analysis of variance of the crown width ratios determined for the nine progeny groups, measured in study 102 at 3 years of age, indicated a highly significant difference among progenies (fig. 16). The data in table 15 show good agreement between the crown width ratios in blocks I and II of study 102. These were the only blocks measured at that time.

Crown Width

In 1956 crown width measurements were recorded on all progenies of study 103 in blocks I, II, and IV. Block III was omitted because of the considerable variation in site. The data analyzed were the ratios determined by taking the mean height and the mean crown width at one-third height for the plot, and then computing an average plot ratio. Ratios for individual trees were not computed. Once again, the data in the various blocks are in fairly good agreement and the analysis shows highly significant differences among lots (table 16). These data are for trees 4 years of age, in contrast to trees 3 years of age for study 102, and although the ratios are slightly smaller for the 4-year data, the range is approximately the same in both studies. The lots used in the initial measurements of study 102 were selected to give a full range of the data. The number of common parents in the two studies was insufficient to make comparisons.

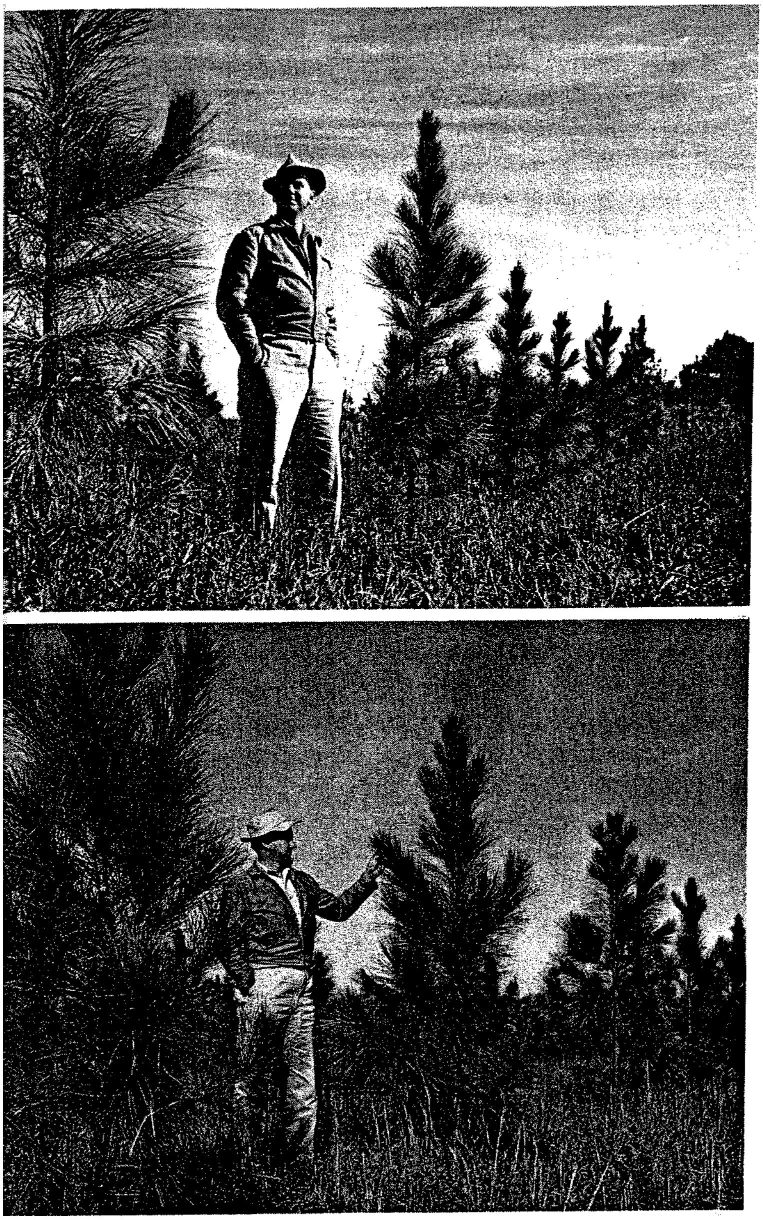

Figure 16. --These plots represent typical narrow-crowned and wide-crowned types after 3 years in the field. Progeny of C-50 (top) and C-10 (bottom).

Table 15. --Ratios of crown width at one-third tree height to total tree height for S-year-old progenies, study 102

Lot	Block I	Block II	Average
c-4	0.53	0.56	0.55
c-10	.52	.56	.54
c-37	.43	.44	.44
c-50	.36	.41	.39
c-54	.41	.43	.42
C-56	.46	.42	.44
C-63	.35	.44	.40
Control Seedlings	.50	.53	.52
Control Seed	.52	.54	.53

Analysis of Variance

Source	d.f.	s.s.	"F"
Blocks	1	0.0035	5.83*
Lots	6	.0671	14.00**
B X L (error)	6	.0048	
Total	17	.0754	

Crown width measurements at one-half the height of the tree were taken at 5 years in study 103 and significant differences were found. However, because crown width and height are correlated, it was felt that some of the true differences in crown width might be masked by differences in mean height of the various progeny groups. Ratios of crown-width to height were determined for the different progenies in study 103 and analyzed (table 16). Once again highly significant lot differences were obtained.

Table 16. --Ratios of crown width to total height for study 103 at ages 4 and 5 years

Lot	Ratio of crown width at 1/3-height to total height at 4 years				Ratio of crown width at l/a-height to total height at 5 years				
	Block I	Block II	Block IV	Average	Block I	Block II	Block III	Block IV	Average
	Ratio								
C-4	0.42	0.53	0.45	0.47	0.45	0.49	0.54	0.48	0.49
C-6	.36	.43	.40	.40	.44	.49	.54	.44	.48
C-7	.34	.35	.35	.35	.38	.42	.44	.39	.41
C-10	.40	.54	.48	.47	.42	.45	.50	.50	.47
C-37	.33	.36	.37	.35	.36	.42	.38	.39	.39
C-50	.34	.35	.33	.34	.37	.40	.41	.40	.40
C-51	.31	.44	.35	.37	.38	.45	.43	.39	.41
C-58	.36	.36	.36	.36	.40	.39	.43	.44	.42
C-63	.33	.33	.37	.34	.40	.37	.46	.41	.41
C-65	.30	.44	.36	.37	.38	.43	.44	.42	.42
C-134	.30	.34	.35	.33	.39	.38	.49	.38	.41
Sou. Miss.	.31	.48	.39	.39	.42	.45	.52	.41	.45
New Orleans	.40	.47	.39	.42	.45	.46	.49	.41	.45
CA-82	.38	.34	.34	.35	.39	.42	.42	.46	.42
CB-23	.38	.40	.38	.39	.41	.47	.48	.54	.48
CB-74	.35	.44	.37	.39	.40	.46	.44	.41	.43
A-l	.38	.35	.33	.35	.43	.43	.55	.43	.46
A-2	.38	.42	.43	.41	.47	.48	.55	.53	.51
Control Seedlings	.35	.44	.36	.38	.39	.52	.46	.51	.47
Control Seed	.41	.42	.41	.41	.46	.46	.48	.41	.45
Callaway	.34	.40	.46	.40	.39	.45	.47	.49	.45

Analysis of Variance (4 years)

Source	d.f.	s.s.	"F"
Blocks	2	0.0321	13.37**
Lots	20	.0901	3.76**
B X L (error)	40	.0479	
Total	62	.1701	

Analysis of Variance (5 years)

Source	d.f.	s.s.	"F"
Blocks	3	0.0428	15.33**
Lots	20	.0889	4.77**
B X L (error)	60	.0559	
Total	83	.1876	

Within-Crown Measurements

At the end of the 1959 growing season, detailed measurements were made of the tree crowns of certain progeny groups in block I of studies 102 and 103; similar measurements were made on their parent trees (fig. 17). Initially, six parent trees were selected.

Detailed measurements were made of five parent trees. The sixth had a rust canker in the upper portion of the crown and it was too dangerous to climb for collecting data. This tree, C-51, was subsequently dropped and an additional parent tree substituted in each study. Trees C-10 and C-63 had been lost and were no longer available. Tree C-7 occurred in a different plantation and was not included for that reason. As mentioned earlier, the various parent trees, though grown in the same plantation, probably were growing on sites of different degrees of fertility and they had differing competition because of initial mortality after planting and subsequent losses from fusiform rust. For these reasons, it is difficult to compare the measurement data on the individual parent trees presented in table 17.

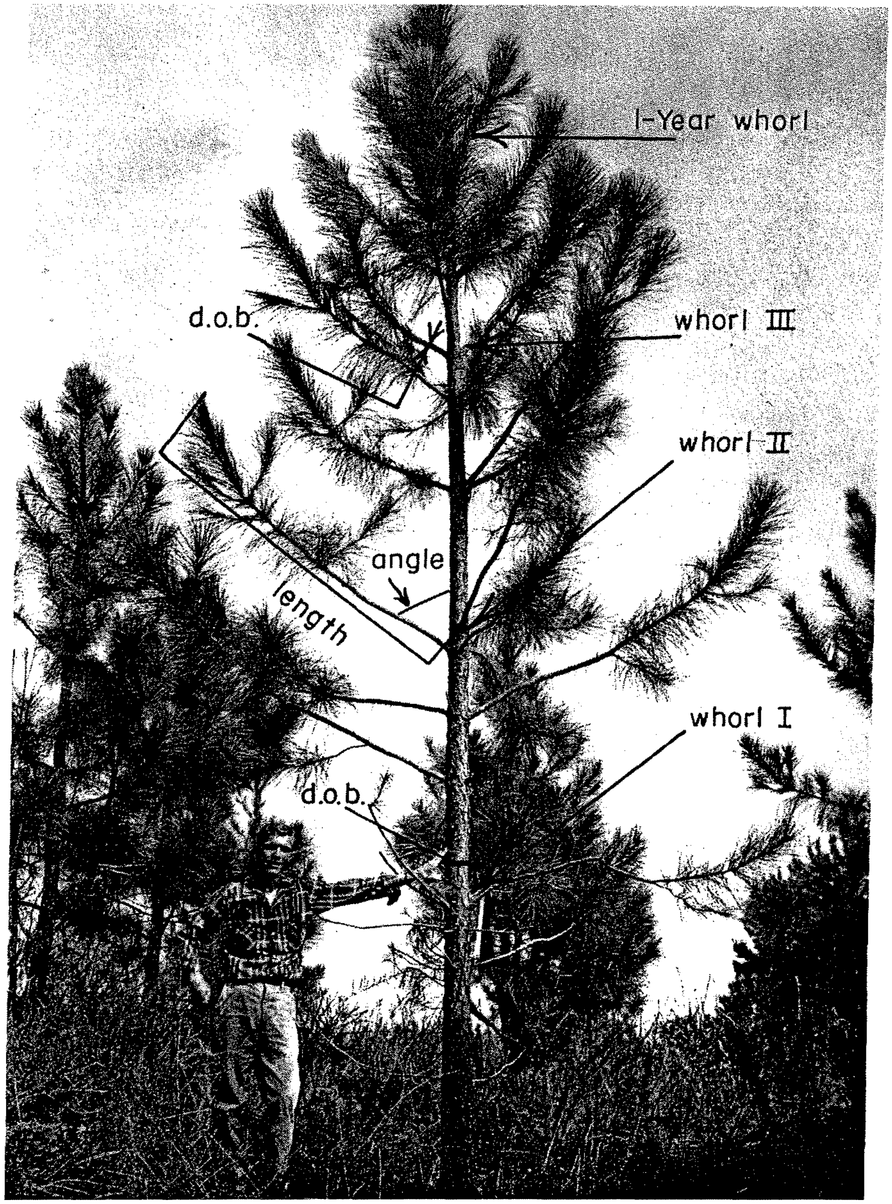

Figure 17.--This (i-year-old tree is typical of young slash pine. The locations of crown measurements are shown. Ages of whorls were determined from previous height measurements.

Table 17. --Measurements of slash pine parent trees at age 25 years

Parent tree	Total height	Diameter outside bark at --			Bark thickness at--			65 to 80 percent crown zone				
		Breast height	17.3 feet	1/2 height	Breast height	17.3 feet	1/2 height	Average branch length	Average branch diameter	Average branch angle	Total whorls measured	Total branches measured
	Feet	- - - Inches - - -			- - - Inches - - -			Feet	Inches	Degrees	Number	Number
c-4	68	17.4	13.9	10.9	1.47	0.84	0.68	11.72	2.05	56.6	7	17
C-6	66	18.2	16.2	12.7	1.54	1.10	.79	12.95	2.57	52.5	5	17
c-37	67	15.4	13.4	10.5	.97	.75	.59	10.19	2.01	55.0	4	15
c-50	68	11.8	10.8	8.9	.76	.69	.51	10.55	1.77	54.5	7	18
c-54	68	13.2	12.4	9.2	1.00	.88	.69	10.74	1.94	53.7	7	17
C-65	63	13.7	12.0	9.9	1.22	.88	.82	10.06	2.00	51.1	6	18
c-134	70	15.2	14.2	10.6	1.45	1.11	.72	10.30	2.08	54.1	8	20

In recording data on the individual parent trees, the treetop was rigged with spars and guy ropes to prevent breakage; measurements were begun at the tree's terminal bud and continued to its base. Detailed measurements were made of the last 3-years' growth, including diameter and length of the internodes, diameter and length of the branches, and growth of the branches for each of the years. Below that point in the crown, measurements *were* taken of the length of the internodes between what appeared to be primary whorls, and a diameter of the stem was taken at a distance of 0.5 foot above the whorl. Each branch in the whorl had its diameter determined 0.5 foot from the stem and its length and angle from vertical recorded. These measurements were made to a point in the crown where lateral competition was evident or where natural pruning began to take place.

The measurements, along with bark thickness, stem diameter at several heights, d.b.h., and total height measurements, made it possible to reconstruct the crown and branching characteristics of each of the parent trees.

Measurements of branching characteristics of the individual progenies were confined to trees with no stem cankers of fusiform rust. Measurements of total height, d.b.h., bark thickness at breast height, and diameter at one-half height were taken, along with detailed measurements of three whorls (table 18). These whorls contained branches with 4-, 3-, and 2-years' growth, respectively. They were primary whorls for the particular years concerned; their exact positions were determined from previous height measurements of the trees. Height from the ground to the lower whorl was determined and the length of the internodes between the whorls was measured. The diameter of the stem at 6 inches above the whorl was recorded and the length, diameter, and angle of each branch in the whorl was also tallied. In determining the average branch length, diameter, and angle for each whorl in the progenies, ramicorns were excluded from the averages, as were obviously damaged branches, or occasionally branches that had not developed normally and were suppressed. For marginal branches in this latter category, length or diameter had to be at least one-half the mean value of the other branches in the whorl for inclusion; in only a few instances was the application of this rule necessary. A total of 26 measurements and combinations of measurements was determined for each individual tree in the progenies for analysis purposes.

The parent trees showed little difference in average branch angle, and several of the trees were grouped closely for branch length and angle (table 1'7). Using average branch length in the portion of the crown, between 65 and 80 percent of total height seemed to give the least variable estimate in each parent. The progeny branch lengths of whorl II appear to agree with the parent trees in both studies 102 and 103 (fig. 18), except for the relationship of C -6. The two progenies are in close agreement, however, leading one to suspect that the crown of parent C-6 has been unusually influenced by environment.

Regression equations and individual progeny correlations were not computed because of the limited numbers involved. Whorl II branch lengths agree well for progenies in both studies (fig. 19). Crown diameters at whorl II were converted into diameter-total height ratios for comparisons with earlier values computed.

Table 18.--Average progeny values for stem and crown characteristics

STUDY 102 (8 YEARS)

Lot	Trees measured	Total height	D.b.h.	Bark thickness	Whorl I branches: Diameter	Whorl I branches: Length	Whorl I branches: Angle	Whorl II branches: Diameter	Whorl II branches: Length	Whorl II branches: Angle	Whorl III branches: Diameter	Whorl III branches: Length	Whorl III branches: Angle
	Number	Feet	Inches	Inch	Inches	Feet	Degrees	Inches	Feet	Degrees	Inches	Feet	Degrees
c-4	10	25.97	6.15	0.654	1.26	7.14	56.5	1.28	7.04	54.7	1.15	5.49	46.4
C-6	4	23.55	5.58	.662	1.07	5.57	63.2	1.18	5.41	57.1	1.06	4.58	58.6
c-37	35	24.53	5.34	.551	1/ .91	1/5.38	1/58.6	.96	5.41	58.8	.94	4.56	53.1
c-50	22	28.32	5.84	.588	.95	5.52	61.3	1.06	5.78	62.2	.94	4.52	53.7
c-54	11	26.60	5.75	.593	1.07	6.48	55.0	1.12	6.26	58.0	1.06	5.15	47.0
C-65	33	24.92	5.24	.586	1/ .82	1/4.91	1/59.4	.88	4.79	59.3	.93	4.38	51.3

STUDY 103 (7 YEARS)

Lot	Trees measured	Total height	D.b.h.	Bark thickness	Whorl I branches: Diameter	Whorl I branches: Length	Whorl I branches: Angle	Whorl II branches: Diameter	Whorl II branches: Length	Whorl II branches: Angle	Whorl III branches: Diameter	Whorl III branches: Length	Whorl III branches: Angle
c-4	11	22.81	5.22	0.591	0.96	5.68	64.6	1.14	6.12	61.7	0.98	4.51	56.6
C-6	13	20.86	5.08	.589	2/ .86	2/5.12	2/65.3	1.03	5.30	66.7	3/ .96	3/4.30	3/58.1
c-37	10	24.85	5.50	.546	4/ .91	4/5.65	4/59.2	.98	5.46	61.0	.95	4.66	55.1
c-50	10	24.79	5.05	.554	5/ .82	5/4.81	5/66.8	.99	5.39	65.4	.92	4.46	59.1
C-65	15	22.55	4.60	.532	6/ .60	6/3.86	6/63.2	.80	4.39	65.1	.82	3.78	57.3
c-134	11	19.96	4.15	.497	2/ .66	2/3.86	2/65.3	.78	4.11	66.4	.79	3.69	59.3

1/ n = 27   2/ n = 10   3/ n = 12   4/ n = 7   5/ n = 9   6/ n = 13

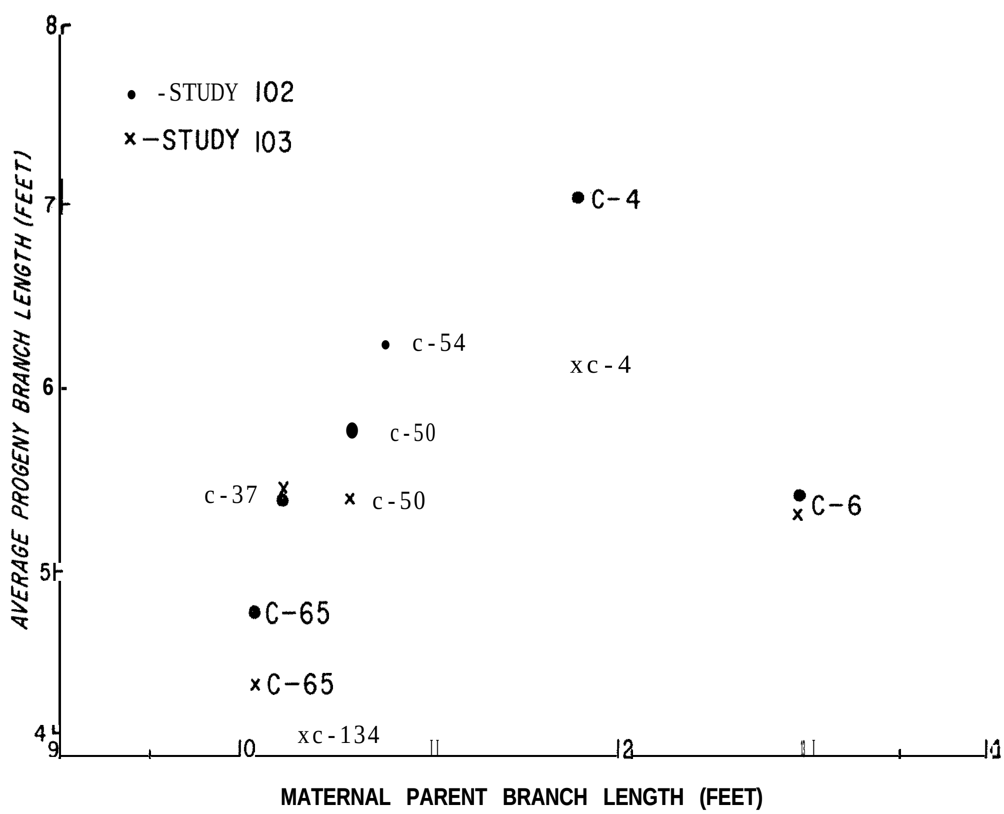

Figure 18.--The relationship of average progeny branch length in whorl II (3 years old) to average branch length of maternal parent measured in a zone between 65 percent and 80 percent of total height.

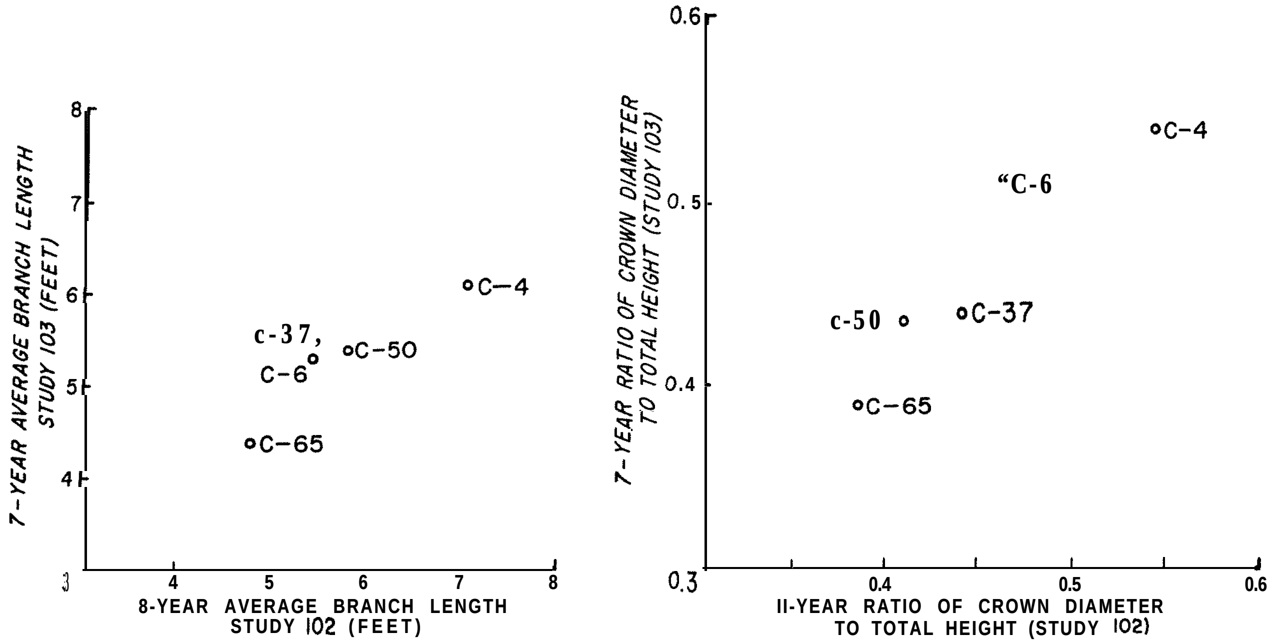

Figure 19.--The relationship of average branch lengths in whorl II(3 years old) for lots with common maternal parentage in studies 102 and 103 (left). The relationship of ratios of crown diameter at whorl II to total height for lots with common maternal parentage in studies 102 and 103 (right).

The limited progenies available show that they are maintaining crown width relations in close agreement with the determinations made at earlier ages (fig. 20). This is very encouraging, for it may mean that estimates of crown characteristics can be made reliably at young ages (fig. 21).

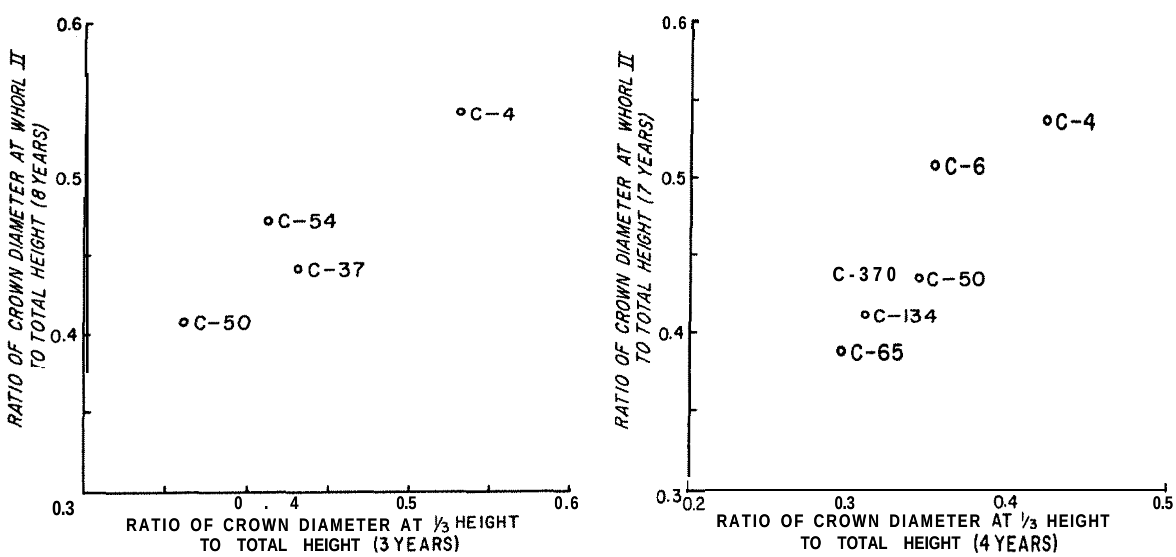

Figure 20.--The relationship of the ratios of crown diameter to total height at different ages in studies 102 and 103. The relationship of 8-year to J-year ratios in 102 (left), and ?-year to 4-year ratios in 103 (right).

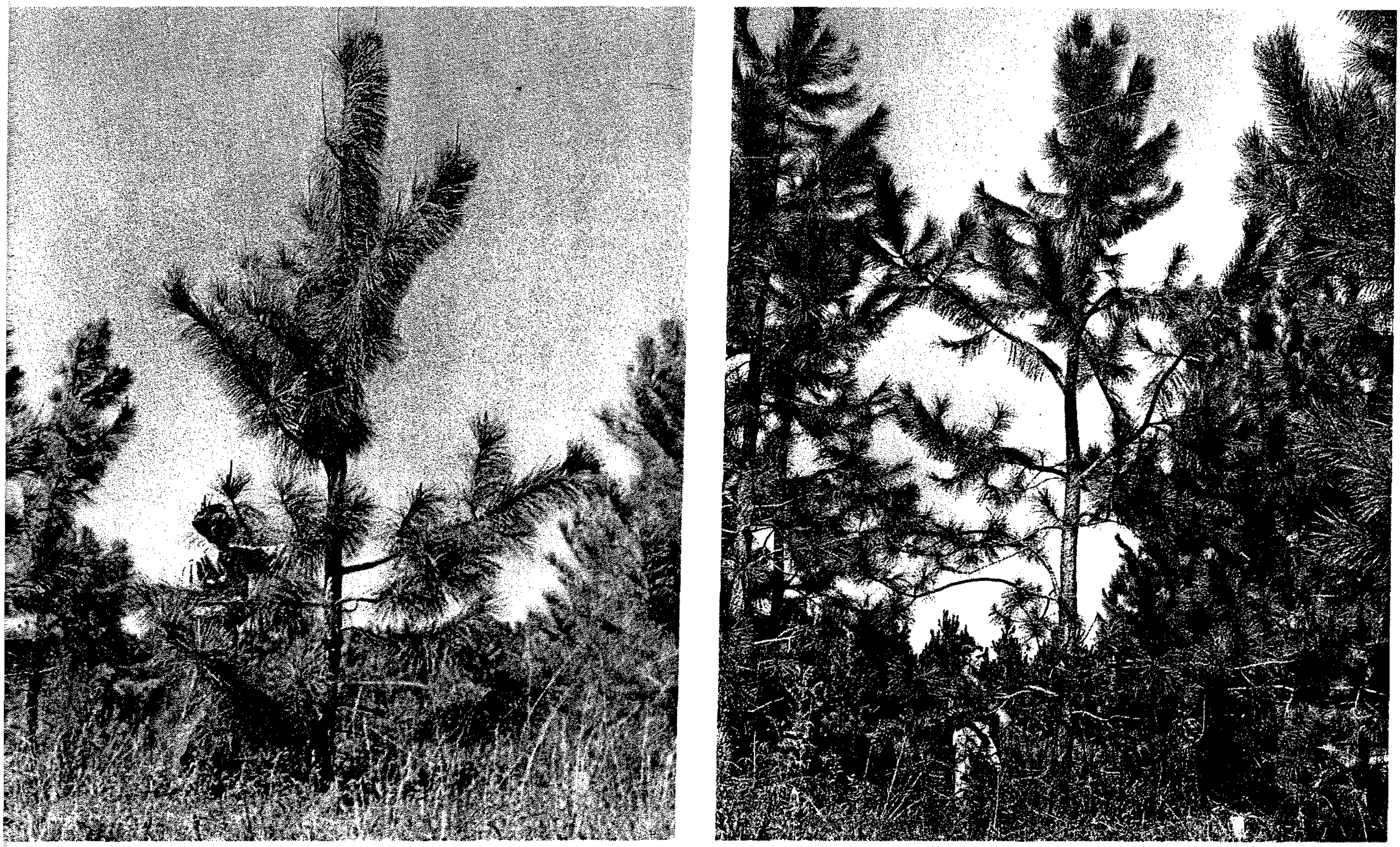

Figure 21. --This crooked and poorly branched offspring of C-4 demonstrates some of the undesirable traits typical of the progeny of this parent. These pictures were taken at 5 and 8 years after planting. Large branches in the earlier photo are still identifiable at 8 years of age.

In addition to these values based on lengths of branches, the ratio of branch diameter in whorl II to d.b.h. was determined for the progenies; once again studies 102 and 103 agree well (fig. 22).

Using the IBM 650 electronic computer, simple correlations were computed for all possible combinations of the 26 characteristics. Highlights of these correlations for studies 102 and 103 are presented in table 19, the complete set of values for all the combinations in table 20. The design of the experiment was such that small correlations are highly significant.

The correlation values obtained when branch length in whorl II was compared with height growth of stem above the whorl are low. Values for study 102 are not significant and just make the 5 percent level for 103. This is somewhat in disagreement with the data presented by Squillace and Bingham (1954) in which they obtained a correlation of 0.61 between branch length and height growth of the stem above the whorl; however, they were working with a species which produces a single whorl of branches each year and were also able to use lo-year growth data in older trees. In contrast, the correlations of branch length with total height of the *tree* and of branch diameter with d.b.h. of the tree are significant at the 1 percent level. It is also interesting that branch diameter is correlated approximately as well with total height of the tree as it is with diameter, and is correlated only slightly less with total height of the tree than is branch length.

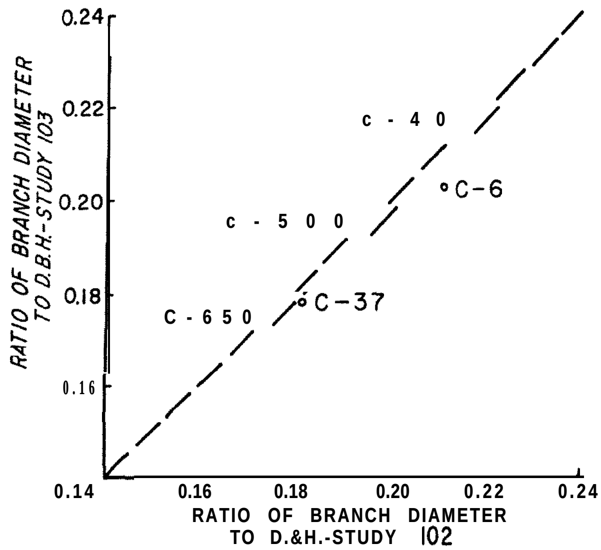

Figure 22.--The relationship of the ratio of branch diameter in whorl II (3 years old) to d. b. h. in study 103 (7 years old) to the same ratio in study 102 (8 years old).

Table 19. --Correlation coefficients for characteristics of individual open-pollinated progeny

STUDY 102 1/

Characteristic	Whorl II		
	Branch diameter	Branch length	Branch angle
Branch diameter whorl II	--	0.947**	-0.430**
Branch length whorl II	0.947**	--	-.481**
Height of stem growth above whorl II	--	.178NS	--
Total height	--	.351**	--
D.b.h.	.529**	--	--
STUDY 103 2/			
Branch diameter whorl II	--	0.951**	-0.458**
Branch length whorl II	.951**	--	-.467**
Height of stem growth above whorl II	--	.285*	--
Total height	--	.534**	--
D.b.h.	.753**	--	--

1/ n = 100

2/ n = 59

Table 20. --Correlation coefficients among characteristics of individual slash pine trees

a. --Description of variables and mean values

Variable	Study 102[1]			Study 103[2]		
	Mean	Standard deviation	C.V.	Mean	Standard deviation	C.V.
			Percent			Percent
X_1 = Total tree height - feet	25.73	2.60	9	22.64	2.41	11
X_2 = D.b.h. - inches	5.58	.62	9	4.96	.70	14
X_3 = Bark thickness at d.b.h. - inches	.59	.07	8	.55	.06	11
X_4 = D.i.b. at breast height - inches	4.39	.57	8	3.66	.62	16
X_5 = Stem diameter, o.b., 0.5 feet above whorl - inches	4.76	.43	9	4.67	.53	11
X_6 = Total number of branches in whorl	3.50	1.02	29	3.90	1.00	26
X_7 = Number of branches in whorl used in average	2.89	1.17	42	2.69	1.15	44
X_8 = Average branch diameter - inches	.95	.21	22	.79	.21	26
X_9 = Average branch length - feet	5.57	1.19	21	4.75	1.18	25
X_{10} = Average angle of branching from vertical - degrees	59.00	6.06	14	64.50	6.50	13
X_{11} = Total height of stem above whorl - feet	17.37	1.61	9	17.14	1.76	10
X_{12} = Stem diameter o.b., 0.5 feet above whorl - inches	3.92	---	9	3.94	.40	10
X_{13} = Total number of branches in whorl	3.70	1.12	30	3.80	1.14	30
X_{14} = Number of branches in whorl used in average	3.10	1.05	34	3.39	.98	30
X_{15} = Average branch diameter - inches	1.02	.20	20	.97	.23	24
X_{16} = Average branch length - feet	6.63	1.12	20	5.19	1.20	23
X_{17} = Average angle of branching from vertical - degrees	59.00	8.96	15	64.40	9.82	15
X_{18} = Total height of stem above whorl - feet	13.35	1.23	9	13.35	1.33	10
X_{19} = Stem diameter, o.b., 0.5 feet above whorl - inches	2.64	.27	10	2.72	.28	10
X_{20} = Total number of branches in whorl	3.80	1.20	32	4.30	1.18	27
X_{21} = Number of branches used in average	3.20	.98	31	3.70	1.09	29
X_{22} = Average branch diameter - inches	.99	.15	15	.90	.16	17
X_{23} = Average branch length - feet	4.73	.79	17	4.20	.78	19
X_{24} = Average angle of branching from vertical - degrees	52.00	10.58	20	58.00	.93	14
X_{25} = Total height of stem above whorl - feet	8.66	1.03	12	8.56	1.93	12
X_{26} = Diameter, o.b., at 1/2 total stem height - inches	4.01	.48	12	3.69	.45	12

1/ n = 100

2/ n = 59

Table 20. --Correlation coefficients among characteristics of individual slash pine trees

b. --Study 102, 9 years from seed

Variable	X_2	X_3	X_4	X_5	X_6	X_7	X_8	X_9	X_{10}	X_{11}	X_{12}	X_{13}	X_{14}	X_{15}	X_{16}	X_{17}	X_{18}	X_{19}	X_{20}	X_{21}	X_{22}	X_{23}	X_{24}	X_{25}	X_{26}
X_1	3/ 0.60	0.11	0.63	0.56	0.11	0.14	0.21	0.27	0.10	0.86	0.47	-0.03	0.03	0.31	0.36	0.08	0.76	0.54	-0.13	-0.21	0.30	0.39	-0.08	0.66	0.56
X_2		.49	.98	.87	.06	.23	.58	.55	.10	.35	.76	-.03	.03	.53	.50	.18	.27	.57	.02	-.12	.56	.55	-.02	.20	.83
X_3			.28	.34	-.02	.12	.37	.30	-.13	-.05	.28	-.11	-.06	.29	.22	-.07	-.12	.14	-.01	-.04	.26	.24	-.09	-.13	.37
X_4				.87	.07	.22	.54	.53	.14	.40	.77	.00	.05	.51	.49	.21	.33	.59	.02	-.12	.54	.54	.00	.25	.82
X_5					.13	.23	.52	.52	.16	.43	.89	.00	.06	.49	.46	.17	.34	.59	.11	-.06	.44	.43	.06	.20	.86
X_6						.62	-.08	-.13	.25	.00	.13	.15	.21	-.05	-.09	.12	.00	.02	.10	.06	-.09	-.13	.22	-.05	.17
X_7							.01	-.04	.32	-.04	.23	-.05	.05	.17	.11	.07	-.06	.10	.10	.08	.10	.07	.18	-.08	.29
X_8								.95	-.29	-.02	.43	-.09	-.10	.68	.66	-.19	-.02	.26	-.15	-.18	.47	.45	-.15	.01	.52
X_9									-.31	.07	.40	-.05	-.07	.66	.70	-.24	.07	.25	-.15	-.16	.47	.50	-.22	.08	.49
X_{10}										.09	.17	-.02	.04	-.08	-.14	.41	.04	.05	.27	.22	-.20	-.29	.48	-.08	.18
X_{11}											.39	.02	.03	.12	.17	.10	.93	.52	-.08	-.15	.08	.18	-.02	.80	.27
X_{12}												-.06	.04	.36	.33	.22	.40	.69	.13	-.03	.40	.38	.17	.24	.78
X_{13}													.72	-.17	-.12	.06	-.01	-.04	.10	.03	-.13	-.10	-.01	.01	.01
X_{14}														-.19	-.17	.14	-.01	.04	.08	.06	-.13	-.09	.07	.01	.09
X_{15}															.95	-.43	.12	.26	-.13	-.19	.44	.49	-.13	.11	.44
X_{16}																-.48	.18	.25	-.19	-.19	.44	.56	-.18	.18	.41
X_{17}																	.02	.14	.31	.21	-.16	-.27	.45	-.04	.13
X_{18}																		.56	-.11	-.15	.07	.21	-.02	.88	.16
X_{19}																			.05	-.10	.19	.25	.22	.60	.54
X_{20}																				.72	-.26	-.26	.44	-.09	.02
X_{21}																					-.32	-.26	.38	-.09	-.16
X_{22}																						.91	-.59	.01	.42
X_{23}																							-.59	.21	.40
X_{24}																								.01	.06
X_{25}																									.05
X_{26}																									

3/ Values which exceed 0.254 are significant at the 1-percent level. Values which exceed 0.195 are significant at the 5-percent level.

Table 20. --Correlation coefficients among characteristics of individual slash pine trees

c. --Study 103. 8 years from seed

Variable	X_2	X_3	X_4	X_5	X_6	X_7	X_8	X_9	X_{10}	X_{11}	X_{12}	X_{13}	X_{14}	X_{15}	X_{16}	X_{17}	X_{18}	X_{19}	X_{20}	X_{21}	X_{22}	X_{23}	X_{24}	X_{25}	X_{26}
X_1	4/ 0.72	0.38	0.73	0.66	-0.01	0.05	0.43	0.43	-0.03	0.93	0.59	0.04	0.01	0.49	0.53	-0.34	0.83	0.51	0.09	0.07	0.42	0.47	-0.17	0.73	0.65
X_2		.68	.99	.93	.11	.21	.77	.75	-.02	.59	.80	.04	-.01	.75	.75	-.35	.46	.51	-.07	.01	.64	.59	-.29	.29	.79
X_3			.56	.66	.01	.23	.53	.46	.08	.29	.55	.06	-.08	.59	.50	-.18	.25	.40	-.12	.03	.53	.36	-.27	.11	.44
X_4				.91	.13	.19	.76	.75	-.03	.60	.79	.03	.00	.73	.75	-.36	.46	.50	-.05	.00	.61	.59	-.27	.31	.80
X_5					.05	.18	.72	.71	-.02	.56	.91	.05	.10	.72	.69	-.27	.41	.57	-.12	-.01	.60	.54	-.18	.21	.85
X_6						.38	-.09	-.11	-.03	-.05	.08	.45	.29	-.04	-.07	-.12	-.06	.05	.14	.01	-.08	-.14	-.16	-.12	.08
X_7							.29	.22	.17	-.05	.11	-.08	-.10	.34	.24	.04	-.10	.19	-.12	-.25	.19	.10	-.01	-.13	.12
X_8								.94	-.12	.26	.58	-.14	-.15	.77	.74	-.32	.18	.41	-.26	-.11	.53	.49	-.13	.09	.56
X_9									-.12	.28	.55	-.11	-.08	.77	.81	-.32	.18	.36	-.22	-.07	.50	.53	-.11	.08	.56
X_{10}										.01	.03	-.05	-.21	.10	.06	.27	.03	.13	.03	.08	.14	.15	.20	.05	.01
X_{11}											.56	.04	.07	.35	.41	-.18	.93	.46	.13	.10	.31	.39	-.10	.79	.54
X_{12}												.10	.11	.55	.52	-.12	.49	.63	-.13	-.04	.52	.46	-.02	.22	.83
X_{13}													.76	-.05	-.05	-.05	.01	.05	.21	.14	-.12	-.15	.09	-.06	.09
X_{14}														-.07	-.08	-.08	-.02	.00	.15	.11	-.26	-.26	.18	-.12	.10
X_{15}															.95	-.46	.22	.39	-.28	-.07	.60	.58	-.17	.11	.55
X_{16}																.47	.28	.35	-.21	-.05	.61	.67	-.19	.18	.54
X_{17}																	-.07	-.22	-.04	-.05	-.13	-.16	.24	-.20	-.22
X_{18}																		.44	.15	.11	.22	.29	-.05	.84	.38
X_{19}																			.01	-.05	.32	.28	.10	.56	.50
X_{20}																				.79	-.26	-.18	.09	.26	-.09
X_{21}																					-.24	-.19	.16	.15	-.01
X_{22}																						.93	-.52	.13	.46
X_{23}																							-.49	.22	.42
X_{24}																								-.05	-.05
X_{25}																									.19
X_{26}																									

4/ Values which exceed 0.328 are significant at the 1-percent level. Values which exceed 0.253 are significant at the 5-percent level.

The correlations of branch length with diameter are very high and positive. Both characters are negatively correlated with branch angle (length slightly stronger than diameter) and all correlations are highly significant.

The parent trees considered for detailed measurements in these studies had a relatively narrow range of branch angle. C-65 had the most acute angle, with an average of 51.1 degrees, and C-4 had the greatest angle (56.6 degrees). There was considerable variation within the crowns of the individual trees. In the progenies, the branch angles of whorls I and II (ages 4 and 3, respectively) are in fairly close agreement in studies 102 and 103. The average branch angle for whorl III (2 years old) is somewhat more acute. This is in agreement with clonal measurements made by Arnborg and Hadders (1957). They found that in the majority of clones, the mean branch angle of the third whorl from the top was 25 to 30 degrees greater than the top whorl. These slash pine data do not include angular measurements in the youngest whorl.

An interesting aspect of the data is the greater branch angle recorded in study 103 for the different progeny groups. In every case the branch angle recorded in 103 is greater than the angle recorded in 102 for progenies from the same mother tree. Table 18 shows differences from 2.2 to 9.6 degrees in whorl II. This consistent trend toward greater branch angle in study 103 has no explanation. At the moment, these data can lead only to speculation until we know more about the physiological relationships of branch growth.

The data and the correlation values obtained indicate that certain definite relationships occur in the branching habit of slash pine. Branch length and diameter are very closely related and are negatively correlated with branch angle. Though we are concerned with individual trees in selection programs, this general tendency is desirable because it can be expected that trees with horizontal branches will tend to have short branches. Both characteristics are desirable.

The data also demonstrate that it would be profitable to select for crown characteristics when developing a breeding program in slash pine. As pointed out by Bannister (1959), we do not know the economic worth of different branching characteristics; however, it would be reasonable to assume that they do have a measurable economic value. If we consider veneer and sawtimber, with the exception of specialty products, such as knotty pine for paneling, any reduction of number and size of knots has an economic value. For the pulp industry, knot wood is more difficult to cook. In most papermills a large part of the material which is screened after cooking and is sent back for a second cook consists of knot material because of the high resin content and high density. It has also been reported by Zobel and Haught (1962) that the volume of compression wood surrounding a knot is approximately equal to the volume of the knot. This means that in addition to having a knot itself, there is wood surrounding it which is undesirable in terms of quality.

One might also consider the economic worth of fewer and smaller branches to the logger who has the task of removing branches from the tree after it is felled in the woods. Some silviculturists argue that branching characteristics, especially diameter and length, can be controlled by spacing in the forest. To a certain extent this is true, but the work of Kiellander (1957) and Schmidt (1952) are in agreement with these data; branching characteristics are inherited. These Callaway progeny tests are all planted at a uniform spacing of 10 by 10 feet. Crown closure is just beginning to take place in study 102 and to some extent in study 103. However, these data, taken under conditions of relatively free growth, indicate that there are measurable differences in crown width between progenies from different mother trees. As was seen in figure 18, there appears to be a favorable relationship between the branch length of the parent and that of its progeny.

The agreement between data taken in study 102 and 103 on progenies from the same mother trees, grown from seed in different seed years, demonstrates that open-pollinated progenies can be relied upon for estimates of the genotype of the parent for crown characteristics.

SOUTHERN FUSIFORM RUST

A considerable portion of growth loss and mortality in the forests of the world is usually attributed to forest diseases. One of the more serious diseases in southern forests is southern fusiform rust, Cronartium fusiforme (A. & K.) Hedgc. & Hunt. This disease infects several species of pine, but is most important on loblolly and slash pines. Goggans (1949, 1957) conducted surveys of plantations in the Piedmont and coastal plain of Alabama to determine the degree of infection and damage by fusiform rust. In his survey of coastal plain slash pine plantations, he found that 43.7 percent of all trees were infected with rust.

In recent years, interest has been stimulated in the possibilities of developing trees resistant to their more important diseases, Clapper (1952) pointed out that control measures for forest tree diseases were generally impractical and stressed the importance of establishing projects to develop disease-resistant trees. He reviewed much of the work up to that time and presented an outline showing methods which might be used for developing such resistance. Riker (1954) also discussed the opportunities for control of disease through forest genetics. Lutz et al. (1958), Boyce (1958), and Schreiner (1958) discussed the various possibilities and limitations of selection and breeding for control of disease and also the relative position of importance which it should take in over-all programs of disease control.

Schütt (1959), reviewing the literature on Pinus, discussed the possibilities of various breeding techniques for use in developing resistance to fungi and other unfavorable factors. Suneson (1960), in his discussion of the problems of diseases and insects in crops, stressed the importance of developing varieties with a broad genetic base in order to maintain diversity of resistance to strains of disease. His discussion was concerned mainly with annual agronomic crops, but the points that he made are of great importance to foresters because of the length of a generation for trees and the inability to use short-term breeding methods to develop new lines of resistance. When.working on resistance of a tree species to a disease, it is best to remember that the causal organism also has a genetic constitution which may change through hybridization or mutation.

A considerable effort has been devoted to the development of white pine species resistant to the blister rust disease (Cronartium ribicola A. Fisch.). Riker and Kouba (1940) reported a number of selections of eastern white pine (Pinus strobus L.) made in blister rust areas in their plans to test open-pollinated progeny and grafts with both natural and artificial inoculation. Riker and his associates have since reported several times on the progress of this work (Riker et al. 1943; Riker, Kouba, and Brener 1949). They were able to demonstrate that some of the parent trees they had selected were highly resistant to the rust. Many of them were not resistant, and in general, the open-pollinated progenies indicated a low degree of resistance; however, they were better than commercial seedlings. Riker, Kouba, and Brener (1949) showed that resistance might manifest itself in one of several ways. In some cases, the fungus failed to establish itself, or established itself in reduced amount. In other cases, the fungus became established but died before forming a canker. Ahlgren (1955) worked with selections of eastern white pine in the Lake States in cooperation with Riker and achieved similar results.

Blister rust has also achieved considerable attention in the West where it attacks western white pine (Pinus monticola Dougl.). Childs and Bedwell (1948) discussed susceptibility of some white pine species to blister rust and reported evidence of resistant trees in sugar pine (Pinus lambertiana Dougl.). Bingham, Squillace, and Duffield (1953) discussed the breeding of blister-rust-resistant white pine and the development of a program to achieve this goal. Bingham, Squillace, and Patton (1956), reporting on the performance of hybrids between eastern and western white pines and their resistance to blister rust, found that second-year seedling height was directly and significantly associated with the number of needle spots in a foliage sample of a given size. Thus, infection was related to vigor.

In a more recent work, Bingham, Squillace, and Wright (1960) reported some of the results of their tests with western white pine and gave estimates of heritability and rate of improvement. They worked with 61 control-pollinated and 50 open-pollinated progenies of resistant trees and 5 open-pollinated progenies of ordinary susceptible trees. Their seedlings were grown 2 years in a nursery under artificial inoculative conditions and then outplanted in areas where blister rust was present. These progenies were scored at 6 years from seed. Using techniques developed by plant and animal breeders, they determined that heritability of resistance in their material was 68 percent in the narrow sense and 8'7 percent in the broad sense. They further calculated that the genetic gain should be 18 to 24 percent per generation using the narrow-sense heritability figure.

European foresters have also been concerned with this disease on eastern white pine which has been extensively planted in Europe. Meyer (1954) discussed selections in hybrids of the white pines in relation to development of resistant strains of trees. He reported that a cross between Pinus strobus L. and Pinus griffithii McClelland gave "fully resistant hybrids with vigorous growth." Based on his experience with 32 selections in white pine, he stressed the importance of using a wide range of material and not working with too limited a number of clones. Mülder (1955) reported that no environmental effects were found which influenced the degree of infection in white pine. Based on his stand samples, the infection increased with age so that, according to his estimate, all trees in a stand would be infected by age 65.

In contrast with Mülder, Van Arsdel et al. (196 1) have shown that local variation in temperature and moisture distribution have a pronounced effect upon the occurrence of white pine blister rust. Patton (196 1) has shown that susceptibility of white pine to blister rust infection decreases with the increasing age of the tree.

Liese (1936) reported that some of his crossings proved the heritable character of resistance to the needle cast Peridermium pini. Schütt (1957) discussed the possibilities for developing resistance to another needle disease, Lophodermium pinastri (Schrad. ex Fr.) Chev. He selected and tested a number of healthy trees from infected areas and after propagating them for 2 to 3 years under infected conditions, he had obtained 11 highly resistant trees and 174 with moderate resistance. He also stressed the possibilities of biotypes of the pathogen and races of pine. Bolland (1957a) was of the opinion that resistance in Scotch pine to both Peridermium pini and Lophodermium pinastri (Schrad. ex Fr.) Chev. was determined by several genes and that breeding for resistance to those diseases was complicated by the fact that several physiological races of both pathogens might occur. He has been successful in selecting elite trees resistant to both pathogens.

Resistance to many diseases has been reported for forest and horticultural trees. Brown(1959) reported some of the more advanced work with horticultural crops in his discussion of mildew resistance in apple. His data were based on incomplete diallel crosses from which he calculated the contribution of each parent to progeny resistance. Rohmeder (1956) reported racial differences in disease resistance for Douglas-fir. Zak(1957) found resistance to the littleleaf disease (Phytophthora cinnamomi Rands) in shortleaf pine. He selected a number of parents and tested them by artificial inoculation techniques, and as a result of these tests, a breeding area of several acres was established for the development of shortleaf pine resistant to the littleleaf disease.

Loblolly pine (Pinus taeda L.) is normally a species highly susceptible to southern fusiform rust; shortleaf pine (Pinus echinata Mill,) is immune to the fungus. Henry and Bercaw (1956) reported that the hybrid between these two species was free of fusiform rust after 5 years' exposure. Similar observations were made on hybrid material near Macon, Georgia.[6] Genetic resistance to the rust apparently is transmitted to the hybrid from the shortleaf parent. In his review of the literature, Goggans (1957) assembled information which indicated that cultivation or other measures to increase growth in slash pine would increase susceptibility to fusiform rust. Contrary to this, Bethune and Roth (1960) found in a loblolly pine seed source planting "apparently little correlation between rate of height growth and incidence of fusiform rust, a relationship often suggested by others." Barber and VanHaverbeke (1961) found that the infection rate in selected slash pine seedlings after 4 years was no greater than in control material, even though the growth rate was 20 percent greater. Barber, Dorman, and Bauer (1957) presented data that indicated a genetic variation in resistance to fusiform rust among slash pines.

Siggers (1955) expressed the opinion that loblolly pine is more susceptible to southern fusiform rust. than slash pine, but once infected, slash pine is more susceptible to invasion of the living bark by the rust (fig. 23). Fusiform rust

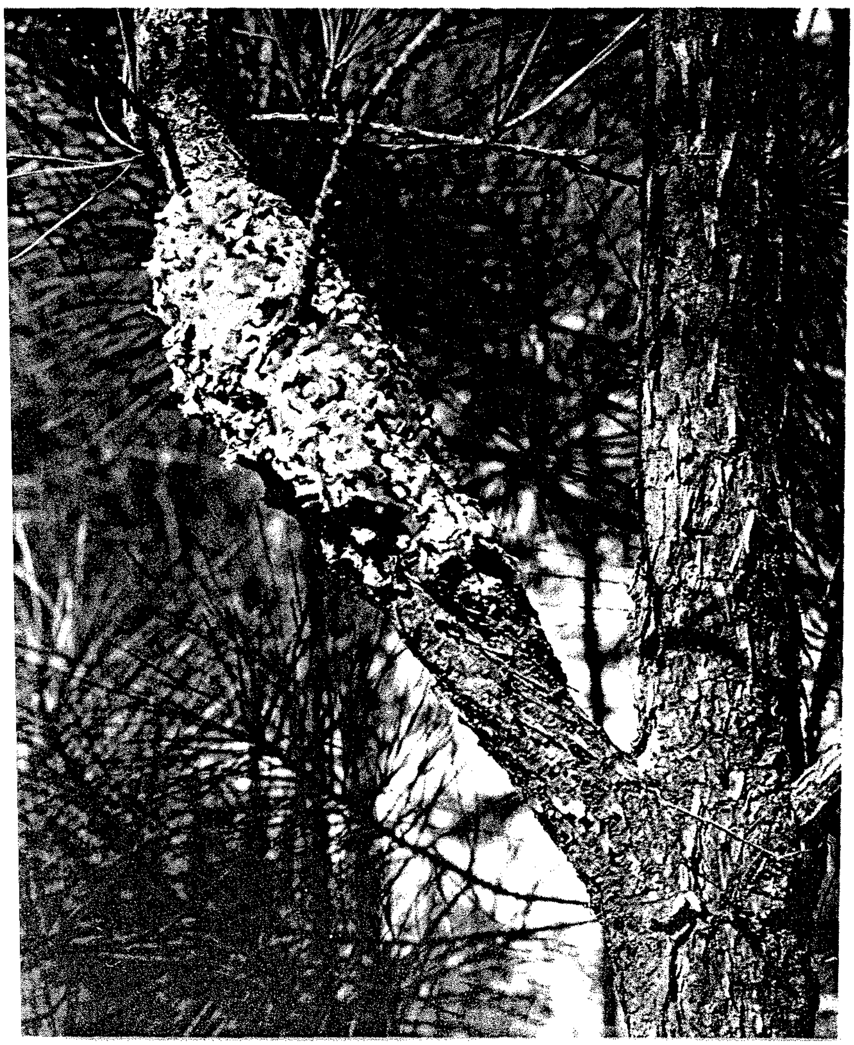

Figure 23. --This is a typical **branch canker of southern fusiform rust in the aecial stage.**

[6] Unpublished data on file with Southeastern Forest Experiment Station at Macon, Georgia.

is most serious at young ages. It has caused tremendous losses in nursery planting stock in the past by infection of newly germinated seedlings. Siggers (1955) cited losses of 50 percent in two nurseries *in* 1947. At *present,* chemical sprays used in nurseries are adequate to minimize infection.

After trees become established in the field, loss can be encountered in two ways. At young ages, mortality can be expected from stem cankers. In dense stands this may be of minor importance because there are excess trees. On the other hand, appreciable mortality in widely spaced plantations may leave irregular stands with openings of considerable size that will not be fully utilized in growing a timber crop. Damage may be serious at all ages (fig. 24).

Figure 24.--Fusiform rust *may* kill or damage a tree when the infection occurs in the stem. The tree at left has a canker near the butt and will probably die or break before producing merchantable material. The tree at right may reach merchantable size, but the canker near the butt will result in the culling of 2 or more feet of the butt log. Both trees are 9 years of age.

When stands reach merchantable size, the presence of cankers on the stems of trees becomes of great economic importance. Siggers (1955) gave some examples of cull in saw logs from fusiform rust cankers, Citing a particular loblolly stand he stated ". . .the average cull due to 30 stem cankers of branch origin was 76 board feet." Cankered wood is also undesirable for paper manufacture because of the problem of debarking the cankered portion of the stem and inclusions of overgrown bark. Fiber quality may also be lowered. As mentioned earlier, the plantation from which most of the slash parent trees were selected had 71 percent of the trees infected with stem cankers of fusiform rust,

The infection period of pines by fusiform rust is closely related to climatic conditions; thus, the amount of infection in any given year may vary widely, according to the particular climatic situation that season. Preliminary examination of the Callaway data on slash pine indicates that heavy rust infection took place in the plantations made in 1952 and 1953. Plantations made in 1954 and 1955 had relatively light infections of fusiform rust, when examined in 1957. The analysis of rust infection data was confined to studies 102 and 103 because of their age and because of the relatively light infection in the other studies.

A count of rust-infected trees was made in study 102 after 3 years. The percent of trees free of rust infection ranged from 38 to 91. The rust data collected in 1957 at age 6 years included a tally of the number of branch cankers and the number of stem cankers for each individual tree (table 21). The data were tabulated in such a way that the various combinations of rust infection could be examined. The percent of trees free of rust in each plot was determined and an analysis of variance was completed using the arcsin $\sqrt{\text{percent}}$ transformation (table 22 and fig. 25). It was found that there were differences in rust infection among lots significant at the 1 percent level.

Table 21. --Fusiform rust infection after 6 years in the field, study 102

Lot	Total trees	Trees free of rust	Trees with branch cankers only	Trees with branch and/or stem cankers
	Number	Percent		
c-4	60	58	13	28
C-6	72	51	18	31
c-7	68	47	21	32
c-10	245	51	26	24
c-37	216	69	11	20
c-50	193	40	16	44
c-51	198	51	22	27
c-54	51	88	6	6
C-56	68	49	19	32
c-59	37	84	11	5
C-60	26	50	35	15
C-61	177	60	12	27
C-62	82	37	27	37
C-63	56	75	4	21
C-65	243	60	21	18
Sou. Miss.	53	25	17	58
New Orleans	31	26	23	52
Control Seedlings	76	34	17	49
Control Seed	118	39	28	33

Table 22. --Percent of trees without fusiform rust infections after 6 years, study 102, and 5 years, study 103 1/

Study 102

Lot	Total trees	Trees without rust	Multiple range test (level of significance) 2/: 5 percent	Multiple range test (level of significance) 2/: 1 percent
	Number	Percent		
c-54	51	88		
C-63	56	76		
c-59	37	73		
c-37	216	70		
C-65	243	61		
C-61	177	61		
c-4	60	59		
c-10	245	52		
c-51	198	51		
C-56	68	49		
C-60	26	48		
C-6	72	47		
c-7	68	41		
c-50	193	41		
Control Seedlings	76	37		
C-62	82	37		
Control Seed	118	35		
New Orleans	31	26		
Sou. Miss.	53	19		

Study 103

Lot	Total trees	Trees without rust	Multiple range test (level of significance) 2/: 5 percent	Multiple range test (level of significance) 2/: 1 percent
	Number	Percent		
C-51	87	78		
c-37	84	73		
C-65	81	71		
c-4	76	69		
Callaway	76	69		
Control Seed	67	67		
C-6	77	66		
C-63	91	60		
c-10	97	59		
A-2	67	57		
C-58	92	57		
c-134	69	53		
c-7	67	51		
A-l	49	48		
New Orleans	82	48		
C-SO	89	48		
Control Seedlings	43	45		
sou. Miss.	a7	38		
CB-23	71	32		
CB-74	88	36		
CA-82	82	32		

1/ Percent data were transformed to arcsin $\sqrt{\text{percent}}$ for analyses. Discrepancies between values in tables 21 and 22 are due to mathematical procedures used.

2/ Values not included in the same bracket are significantly different at the indicated probability level.

Analysis of Variance 102

Source	d.f.	s.s.	"F"
Blocks	2	1,705	10.78**
Lots	18	6,323	4.44**
B X L (error)	36	2,848	
Total	56	10,878	

Analysis of Variance 103

Source	d.f.	s.s.	"F"
Blocks	3	811	4.41*
Lots	20	5,231	4.27**
B X L (error)	60	3,678	
Total	83	9,720	

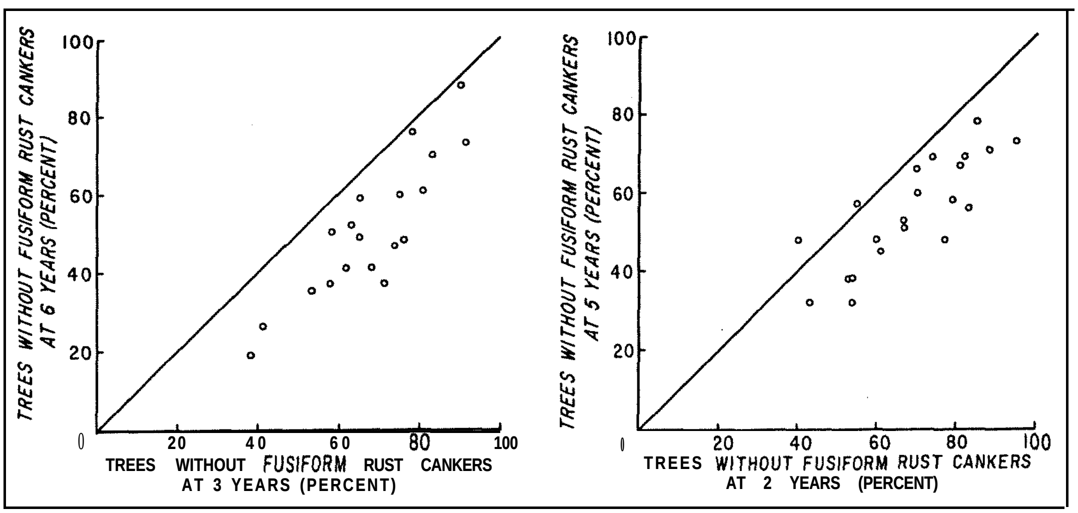

Figure 25. --The relationship of percentage of trees without fusiform rust for each progeny group at different ages. Study 102 was examined at 3 and 6 years (left), and study 103 was examined at 2 and 5 years (right).

An analysis of variance of the average number of cankers per tree indicated that there were no significant differences among lots, although there was a highly significant difference between blocks (table 23); block III was apparently lower in number of cankers per tree than the other two. The great amount of variation within lots and also within blocks is of interest. For instance, one might examine the number of cankers per tree for lots C-60 and C-63. There seems to be no simple explanation for the erratic behavior of lots in the different blocks.

Similar data have been collected for study 103 and identical analyses were performed. The percentage of trees free of rust after 2 years in the field varied from 40 to 95 among lots. After 5 years in the field the percentage of trees free of rust varied from 32 to 78. The analysis of variance of the transformed percentage values again indicated highly significant differences (table 22). Once again the degree of rust infection in the various blocks within lots was quite variable. An analysis of the number of cankers per infected tree again showed nonsignificant differences among lots, but significant differences were encountered among blocks. Blocks I and II had a higher infection per tree; however, the degree of infection in terms of percent of trees infected was little different between blocks I and III, or between blocks II and IV.

Table 23. --Number of cankers per rust infected tree, study 102, age 6 years

Lot	Block I	Block II	Block III	Average
	- - Number - -			
c-4	3.4	2.9	1.2	2.50
C-6	2.2	2.1	1.1	1.80
C-7	3.0	1.4	1.2	1.87
C-10	2.0	2.2	1.8	2.00
c-37	2.7	1.6	1.4	1.90
c-50	2.0	2.3	1.5	1.93
c-51	2.2	2.1	1.4	1.90
c-54	1.0	2.0	1.5	1.50
C-56	2.8	1.4	1.8	2.00
c-59	1.0	2.7	1.0	1.57
C-60	3.5	1.8	1.0	2.10
C-61	2.2	1.5	1.1	1.60
C-62	2.8	2.9	1.4	2.37
C-63	2.4	2.9	4.5	3.27
C-65	1.7	2.0	1.5	1.73
Sou. Miss.	2.3	2.2	2.5	2.33
New Orleans	2.7	2.9	1.4	2.33
Control Seedlings	2.4	2.2	1.7	2.10
Control Seed	2.7	2.4	2.2	2.43

Analysis of Variance

Source	d. f.	s. s.	"F"
Blocks	2	5.417	6.60**
Lots	18	9.270	1.26NS
B X L (error)	36	14.743	
Total	56	29.430	

There were two lots which showed an increase in the percent of trees free of rust from 2 to 5 years (fig. 25). In both instances, there was appreciable mortality during the 3-year period. In the case of lot A-2, there was a loss of seven trees and in the case of A-l, a loss of eight trees. Though no records are available, this mortality was probably attributable to rust infection. The loss of these trees was sufficient to change the percentage value appreciably.

Records of the cause of mortality in the various plots during the second and later years have not been maintained so that it is impossible to determine what proportion of the mortality can be attributed to fusiform rust. However, mortality attributable to rust is probably in excess of 95 percent. Mortality from other causes has been rare. Because it is important to know the amount attributable to rust, future records will be kept on cause of death. Similar records should be kept on all progeny tests of susceptible species.

Where fusiform rust cankers occurred only on branches, natural pruning has sometimes removed them from the trees so that a tree may have been recorded at one age with rust infection and later be recorded as free of rust. If the infection is within 18 inches of the stem, there is a good possibility that it will enter the stem within 3 years and become a serious stem defect (Harms 1961). This occurrence of natural pruning, which might remove branch infections from trees, is a complicating factor in the selection of individual trees for resistance to fusiform rust. Unless detailed records were maintained throughout the life history of the individual tree, it would be impossible to know whether an infection had occurred at an early age and the canker lost because of death and natural pruning of the branch.

Our progeny tests indicate that there *are* wide differences *in* susceptibility among progenies of different mother trees. Conceivably, some of the mother trees may themselves be susceptible, but have lost their cankers by natural pruning. Some of the mother trees have become infected since the original selections *were* made for these progeny tests. We also have no measure of the amount of pollen which might have come from susceptible male parents. However, the range of susceptibility of the different progeny groups leads one to believe that selection for resistance to rust would be profitable. Control lots generally had high infection rates. Within a few years, control-pollinated material from a number of these parents should tell us a great deal more about the amount of resistance and give us some figures which can be translated into heritability values for resistance to southern fusiform rust.

Progenies from 11 parent trees are common between studies 102 and 103. Data for these 11 progenies were extracted and analyzed separately for each study and then put into a combined analysis of variance (fig. 26). For each individual study, highly significant differences were found among progenies. In the combined analysis, the Lot X Year interaction was tested and found to be not significant. Year and lots were both found to be significant at the 5 percent level. The "F" value for lots with combined error is only slightly below that needed for a 1 percent test of significance.

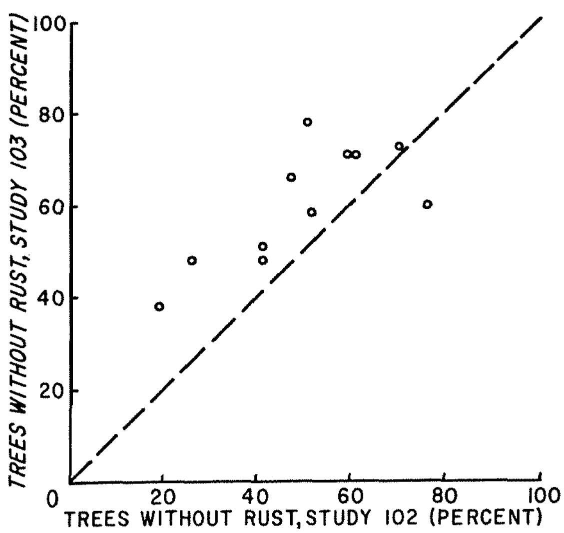

Figure 26. --The relationship of the percent of trees without fusiform rust in studies 103 (5 years old) and 102 (6 years old).

The correlation of rust infection with growth characteristics and the effect of the rust on growth rates of individual trees was discussed in the section on Growth Characteristics. The relatively low correlations between number of cankers per tree and total height at ages 2 and 3, and between number of cankers and height growth during the second and the third growing seasons for studies 102 and 103 seem adequate evidence that resistance to rust has a genetic basis, and rate of growth <u>per se</u> is not an important factor in determining the susceptibility of an individual tree to infection. This supports the findings of Bethune and Roth (1960) and Barber and VanHaverbeke (1961). It is also a very encouraging possibility, for in a practical sense, it means that we can expect to find trees which grow rapidly and have an inherent resistance to fusiform rust. If rust infection is not highly correlated with growth, we can hope to include rust resistance in multiple factor selection with a great deal of success.

The relatively high rate of fusiform rust infection in the two lots of seed from the Gulf Coast is of interest (table 22). All individual parent trees common to studies 102 and 103 represent two lots of seed collected in different years. The seed source "Sou. Miss." and the one labeled "New Orleans" are the same lots of seed planted in both years. The fact that these two lots were heavily infected in both years and maintained their relative position indicates that the field trials are probably valid measures of the natural incidence of fusiform rust. Another point of interest is the very heavy incidence of fusiform rust in lots CB-74, CB-23, and CA-82. These three lots of seed represent individual parent selections made from slash pine plantations in Australia. The seed were sent to the Callaway Foundation for inclusion in their tests. Of course, this is probably a chance occurrence that all three lots performed so poorly, but fusiform rust does not exist in Australia and thus there was no opportunity for natural infection of the parent trees either in the nursery or in the field. Consequently, there was no opportunity for the Australian foresters to select trees which might be resistant to rust. The Australians do not know the original source of the seed for the plantations from which these trees were selected. The seed might have been collected from stands of slash pine which have a low inherent resistance to the disease, such as indicated by the lot of seed from Southern Mississippi. The high amount of fusiform rust in studies 102 and 103 at the Callaway Foundation offers the opportunity for selection of trees resistant to fusiform rust and desirable for other characteristics. With the high degree of infection which has occurred, it is unlikely that a very large portion of the rust-free trees can be considered true escapes. Undoubtedly, a large population of fusiform rust spores has existed throughout the testing area during periods which were optimum for infection to occur.

A considerable amount of control-pollinated material involving a number of parent trees, including C-37 and C-65 which appear to be among those more resistant to rust in this test, has been established in the Callaway progeny test area and also in an area of high rust hazard in Bleckley County, Georgia. This material was outplanted in 1957. The choice of these parents for developing rust resistance was made on the basis of early field observations of the open-pollinated progeny groups. Only time can tell whether the choice of parents was a sound one and whether the development of resistant strains of slash pine might be amenable to a relatively simple solution. Immunity is not absolutely necessary from a practical viewpoint, only a high degree of resistance.

OTHER DEFECTS

In earlier sections the undesirable effects of poor crown characteristics, slow natural pruning, and disease have been pointed out. In addition to these characteristics, stem straightness and forking tendencies are also important factors of form and quality. Recent research at North Carolina State College (1958) indicates that compression wood is associated with even minor stem crook or sweep. This compression wood yields pulp of low strength and causes warp and other drying defects in lumber. Forks and ramicorns 7/ cause cull in the logging operation and also produce large knots and irregular grain in lumber.

Each tree in studies 102 and 103 was evaluated for fork, crook, and sweep in 1957. The studies were 6 and 5 years old, respectively. Any attempt at evaluation of this sort may be premature; however, many of these trees exceeded 17 feet in height, which represents the butt log of a saw-timber tree, or three pulpwood bolts. Defects in this portion of the trunk will affect a large portion of the merchantable volume of the tree when harvested.

Unquestionably, a number of the trees tallied as showing crook or sweep may not show it when they reach a merchantable size for sawtimber because the growth of the stem will mask these now observable minor features. But even if these slight crooks are masked when the tree reaches a larger diameter, it does not correct the poor quality wood now being produced. The compression wood formed at young ages remains compression wood and it causes degrade in lumber and reduces the strength of pulps.

Mergen (1955) reported on the inheritance of deformities in slash pine based on data from progeny tests at Lake City, Florida. Working with both open- and control-pollinated material, Mergen found that crooked parent trees produced a significantly greater number of crooked offspring than straight trees. Ehrenberg (1958) described the occurrence of some deformities in Scotch pine based on crosses carried out between good and poor phenotypes. The progenies of crosses between plus trees were best and progenies where one or both of the parents were minus trees had a high frequency of abnormal development. Ehrenberg attributed much of this effect to the genetic constitution of the tested minus trees. It has been reported from South Africa (Union of South Africa, Department of Forestry 1948) that poor stem form in slash pine appears to be correlated with vigor; that is, the more vigorous trees have the poorer form. This does not appear to be the case in the Callaway Plantations. It was also reported from South Africa that in Pinus radiata D. Don a high percentage of the progeny reproduced the morphology of the mother. It was concluded that defects in the crown and leading shoot are inheritable. Peter-Contesse (1941) in his discussion of heredity and selection stated that tall, upright beech gave erect seedlings and that poor trees gave excessively branched seedlings that produced inferior trees.

7/ A ramicorn is a branch of abnormally large size which occurs at a very acute angle. Ramicorns create large knots and are slow to self-prune and heal.

In addition to reports attributing forking and other defects to heredity, there are others that indicate some types of forking and other poor form may be attributed to environment. A relationship between forking and site quality has been confirmed in Australia (Commonwealth of Australia, Forestry and Timber Bureau 1954); forking decreased as site quality index increased from I to VII. Børset (1951) carried out a progeny test of trees selected at varying distances from an ocean shore. He found no correlation of the growth or form of the open-pollinated progeny with the parent. Shrubby trees along the shore gave progenies as good as others further from the ocean. In this instance, the phenotypes of the parent trees were probably affected by the severe climatic situation in proximity to the shore.

In the past many people have thought that forking was closely related to amount of injury. In some circumstances, as will be seen in some of the Callaway data, this may be true. However, in general, forking does not normally occur in slash pine after injury unless the tree has an inherent tendency for that defect. Following injury to the terminal shoot, one or more buds or branches develop into vigorously growing terminals. Usually within a few weeks, one of these begins to achieve dominance and soon replaces the original leader; the other branches assume their positions as laterals. Sometimes if only two or three branches are competing, the lesser branches may develop into ramicorns. If forking were the normal occurrence after injury in the southern pines, it would be almost impossible in some species, such as loblolly and shortleaf pine, to find an unforked tree, for it is characteristic of these species when young to have their terminal buds destroyed two or more times each growing season by tip moth (Rhyacionia frustrana Comst.). Slash pine is also occasionally attacked by various species of tip moth.

The general form and branching characteristics of the parent trees involved in these studies have been discussed earlier. However, I would like to point out again the degree of crook occurrence in parent tree C-4 (fig. 27). The stem had many small crooks and most of the branches also were crooked. Parent tree C-65 apparently had a tendency for the formation of ramicorns, five were evident on the parent tree.

At the end of the third growing season, a tally was made of all trees in study 102 recording the occurrence of forks and ramicorns. These data (table 24) were converted to percentages and an analysis of variance was performed using the arcsin $\sqrt{\text{percent}}$ transformation of the data. The analysis showed highly significant differences among lots, and no significant difference among blocks. The progeny of tree C-65 was not particularly poor in terms of number of forks and ramicorns occurring, though the parent contained five ramicorns.

In 1957 additional data were taken on the occurrence of defects in studies 102 and 103, ages 6 and 5 years, respectively. Each tree in the progeny tests was examined and the occurrence of forks and ramicorns tabulated. These data were recorded in separate categories by the occurrence of single or multiple forks and/or ramicorns. However, tabulation and inspection of the data indicated that it would be desirable to pool the classifications for analytic purposes. In addition, a visual estimate of the straightness of the individual trees

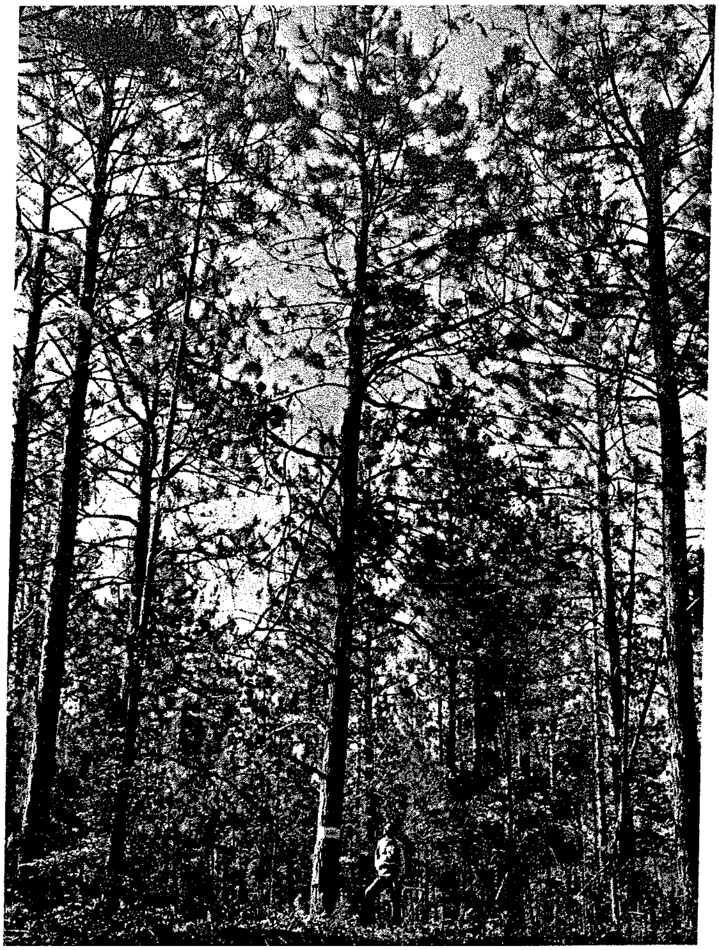

Figure 27. --Parent tree C-4 selected for poor form and crook, but with rapid diameter growth. The breakage in the crown resulted from a severe wind storm. (Photo at age 20.1

was also recorded. These data were recorded as crook, sweep, or spiral, but again inspection of data suggested that it would be best to pool the data for analysis. For both sets of data, percentages of occurrence were computed and the arcsin $\sqrt{\text{percent}}$ transformation was used for analyses of variance.

The analyses for study 102 at age 6 years indicated that the only significant differences among the progeny groups were in the percent of trees having crook defect (table 24). The significant differences for the percent of trees with fork-type defects in 1954 were not obtained in the 1957 analysis. Although exact data are unavailable, there is one factor that probably contributed to this. In late March 1955, a severe freeze occurred in the Southeast, and temperatures in the area of the Callaway Foundation dropped below 20” F. Many of the trees in these progeny test plantations had commenced vigorous spring growth prior to that time. A considerable amount of freeze injury was observed on the new shoot growth. This occurrence of injury was much more noticeable in some progeny groups than others. Those that apparently flushed earlier seemed to be damaged most severely. The progeny of tree C-37 were especially noticeable. It was observed later in the growing season that competition among the new shoots formed after the freeze damage was more uniform than under normal conditions of injury, such as broken tips or insect damage. It appeared that in many cases a single shoot did not express dominance immediately, as is usually the characteristic of slash pine; frequently this dominance was not expressed until the following growing season, Although some injury was noticed in study 103, more occurred in the older, more vigorous trees of study 102.

Table 24. --The occurrence of stem defects, study 102[1]

Lot	Forks and/or ramicorns (3 years): Average	Lot	Crook (6 years): Average	Lot	Trees with no defect (6 years)[3]: Average
	Percent		Percent		Percent
c-54	22	C-61	39	c-4	3
C-60	22	C-62	41	C-6	9
C-61	22	c-10	51	c-7	17
C-62	24	Control Seedlings	54	c-10	15
c-37	25	C-56	61	c-37	18
C-65	28	C-51	62	C-50	16
c-59	28	c-54	63	c-51	14
C-6	39	C-65	63	c-54	22
C-63	30	c-37	63	C-56	9
C-JO	31	C-63	67	C-59	13
c-10	31	sou. Miss.	67	C-60	17
c-7	32	c-so	68	C-61	23
c-51	32	Control Seed	70	C-62	23
c-4	35	c-7	70	C-63	28
Control Seedlings	41	New Orleans	72	C-65	15
Control Seed	42	c-59	74	Control Seed	11
C-56	45	C-6	74	Control Seedlings	23
New Orleans	45	C-4	s o	Sou. Miss.	9
Sou. Miss.	60	C-60	91	New Orleans	15
	s_m = 3.399		s_m = 6.097		

Multiple range test[2] (level of significance): Forks — 5 percent, 1 percent; Crook — 5 percent.

1/ Percent data were transformed to arcsin $\sqrt{\text{percent}}$ for analyses.

2/ Lots not included in the same bracket are significantly different at the indicated level of probability

3/ No significant differences occurred.

Analysis of Variance (Forks)

Source	d.f.	s.s.	"F"
Blocks	2	191.25	2.75NS
Lots	18	2269.75	3.64**
B X L (error)	35[4]	1212.83	
Total	55	3673.83	

Analysis of Variance (Crook)

Source	d.f.	s.s.	"F"
Blocks	2	205.46	0.92NS
Lots	18	3985.98	1.99*
B X L (error)	36	4014.98	
Total	56	8206.44	

Analysis of Variance (No defect)

Source	d.f.	s.s.	"F"
Blocks	2	176.32	0.94NS
Lots	18	2335.33	1.32NS
B X L (error)	36	3396.92	
Total	56	5808.57	

4/ Reduced for missing plot data

The analysis of the B-year data for study 103 indicates highly significant differences among progenies for percent with forks, percent with crooks (table 25a), percent with both forks and crooks, and percent free of defect (table 25b). Parent tree CB-74, one of the Australian selections, seems to be superior to any of the Callaway selections in the occurrence of these defects. The low percentage of forking among this progeny is especially striking. The progeny of tree C-4 is again very low in the ratings. A plotting of the percent trees with fork over percent trees with crook shows no strong relationship (fig. 28).

The relationship of the percent of trees free of defect in study 103 to the percent of trees free of defect in study 102 for the same parent is fairly strong with the exception of parents C-65 and C-51. These two fall somewhat out -of - line. A similar plotting of the percent of trees with crook defect (fig. 29) also shows a fair relationship, with the exception of one or two progeny groups. The graphic comparison of fork-type defect between progeny of common parentage in the two studies shows a somewhat weaker relationship. This weaker relationship is possibly explained on the basis of the freeze injury in 1955.

Table 25a. --The occurrence of stem defects after 5 years, study 103[1/]

Lot	Forks and/or ramicorns: Average	Multiple range test (level of significance)[2/]: 5 percent	1 percent	Lot	Crook: Average	Multiple range test (level of significance)[2/]: 5 percent	1 percent
	Percent				Percent		
CB-74	10			CB-74	30		
C-134	20			C-51	38		
c-7	23			c-10	50		
C-63	27			C-65	54		
Control Seed	28			Control Seedlings	54		
CB-23	29			CB-23	55		
C-65	29			c-7	59		
CA-82	31			Control Seed	60		
c-50	32			c-37	60		
A-2	32			Sou. Miss.	66		
C-58	32			C-63	66		
Control Seedlings	33			CA-82	68		
A-I	35			New Orleans	70		
C-51	38			C-W	72		
Callaway	40			A-2	72		
New Orleans	41			c-134	73		
c-4	43			C-6	74		
Sou. Miss.	46			C-68	77		
C-6	52			c-4	78		
c-10	52			A-I	86		
C-37	56			Callaway	89		

$s_m = 4.136$ (Forks and/or ramicorns); $s_m = 5.651$ (Crook)

1/ Percent data were transformed to arcsin $\sqrt{\text{percent}}$ for analyses.

2/ Values not included in the same bracket are Significantly different at the indicated probability level.

Analysis Of variance (Forks and/or ramicorns)

source	d.f.	s.s.	"F"
Blocks	3	980.60	4.78**
Lots	20	4068.95	2.97**
B X L (error)	60	4105.00	
Total	83	9154.55	

Analysis of Variance (Crook)

Source	d.f.	s.s.	"F"
Blocks	3	583.08	1.52NS
Lots	20	6558.93	2.57**
B X L (error)	60	7664.66	
Total	83	14806.67	

Table 25b. --The occurrence of stem defects after 5 years, study 103[1/]

Lot	Fork and crook: Average	Multiple range test (level of significance)[2/]: 6 percent	1 percent	Lot	No stem defects: Average	Multiple range test (level of significance)[2/]: 5 percent	1 percent
	Percent				Percent		
m-74	1			CB-74	59		
C-7	7			C-51	38		
Control Seed	10			C-65	36		
C-51	13			Control Seedlings	34		
C-134	15			CB-23	30		
CB-23	15			c-7	28		
C-58	19			C-G3	28		
C-G5	19			Control Seed	26		
Control Seedlings	19			CA-82	23		
C-50	21			c-10	22		
C-63	21			New Orleans	21		
CA-82	23			A-Z	20		
A-2	23			C-134	20		
c-10	24			c-50	19		
Sou. Miss.	27			c-37	17		
New Orleans	32			A-I	13		
c-4	32			C-58	13		
A-I	33			Sou. Miss.	12		
C-37	23			C-6	11		
Callaway	35			c-4	8		
C-G	36			Callaway	7		

$s_m = 4.676$ (Fork and crook); $s_m = 6.047$ (No stem defects)

1/ Percent data were transformed to arcsin $\sqrt{\text{percent}}$ for analyses.

2/ Values not included in the same bracket are significantly different at the indicated probability level.

Analysis of variance (Fork and crook)

source	d.f.	s.s.	"F"
Blocks	3	430.63	1.61NS
Lots	20	4654.21	2.45**
B X L (error)	60	5705.44	
Total	83	10820.18	

Analysis Of Variance (No stem defects)

Source	d.f.	s.s.	"F"
Blocks	3	182.19	0.59NS
Lots	20	5300.86	2.56**
B X L (error)	60	6201.63	
Total	83	11684.87	

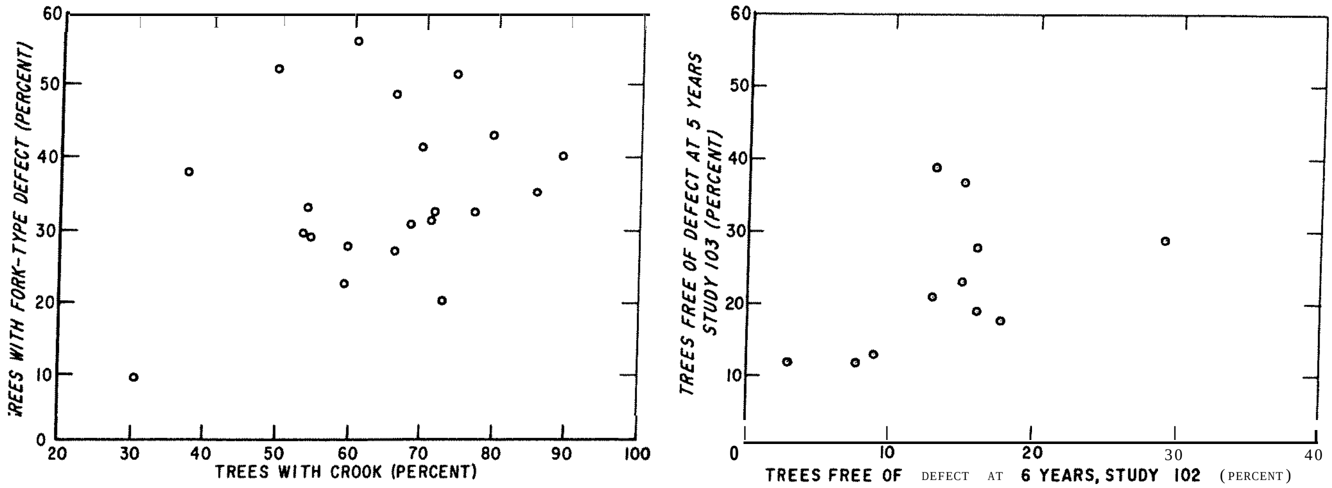

Figure 28. --The relationship of fork-type defect to crook in study 103 at 5 years (left). The relationship of trees free of stem defect in studies 102 and 103 (right).

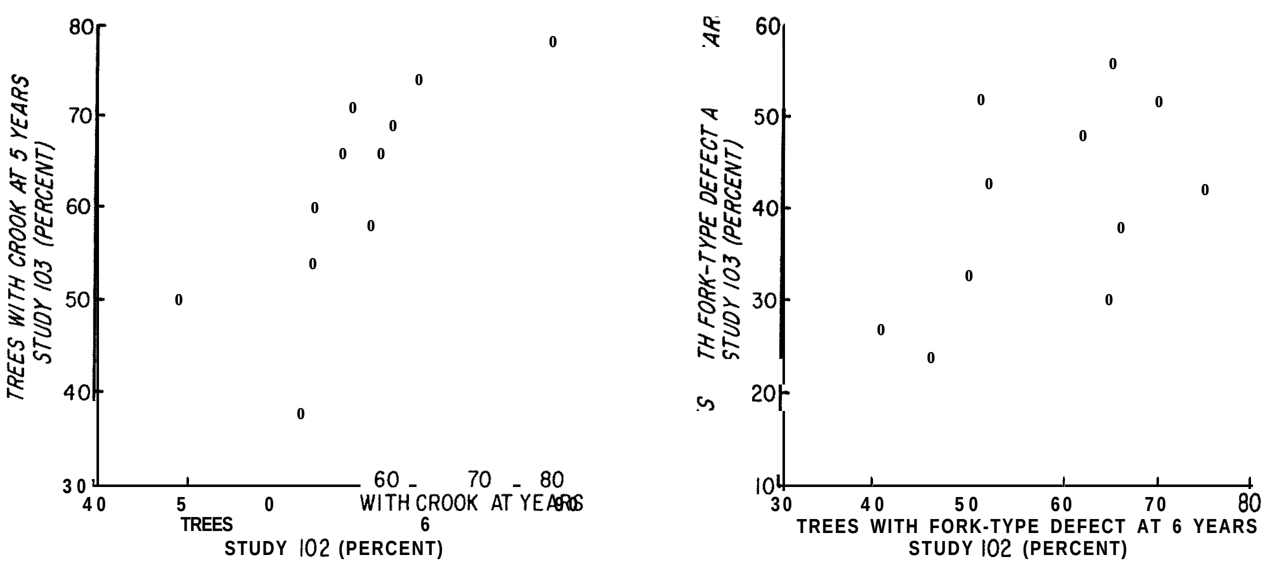

Figure 29. --The relationship of crook (left) and fork-type defect (right) between studies 102 and 103.

Considerable difficulty was encountered in the field in applying the criteria for the types of defects discussed here. Forks, of course, are not a problem to classify nor are the large ramicorns (fig. 30). However, as the ramicorns become less and less conspicuous, it is more and more difficult to classify them. This is especially true in the case of 1 -year-old branches. It is also quite true of older branches so positioned that upper branches tend to suppress them. Many of the ramicorns present as 1 -, 2 -, and g-year-old branches will become suppressed, die, and prune off quickly, and will not cause a major defect. However, for field application, there seems to be no established basis for determining which of these branches might prune and which might maintain themselves to form major defects. The best time to evaluate ramicorns may be after trees have reached an age when all normal branches in the whorl containing the ramicorns and possibly for one or two whorls above it have died naturally and pruned. At that time, it will be much easier to determine whether or not the ramicorn will form a major defect.

Forking also should come under this close scrutiny. It has been observed that trees producing apparently equal forks may grow that way for 1 or 2 years, then one side of the fork will gradually lose vigor until it takes the position of a ramicorn; and of course, in a young tree, it may prune naturally before it becomes a major defect.

Field evaluation of crook was extremely difficult. Young trees which are absolutely straight are relatively rare; therefore, the problem becomes one of determining when a crook or sweep will be recorded as such. The limitations of time and manpower prevented the use of detailed measurement techniques whereby the actual horizontal displacement of the stem at various heights could be plotted on a vertical scale for exact determination. In working with young

Figure 30. --This El-year-old slash pine exhibits two typical ramicorns. These limbs will probably persist several years after other adjacent branches have died and pruned, and will leave large knots.

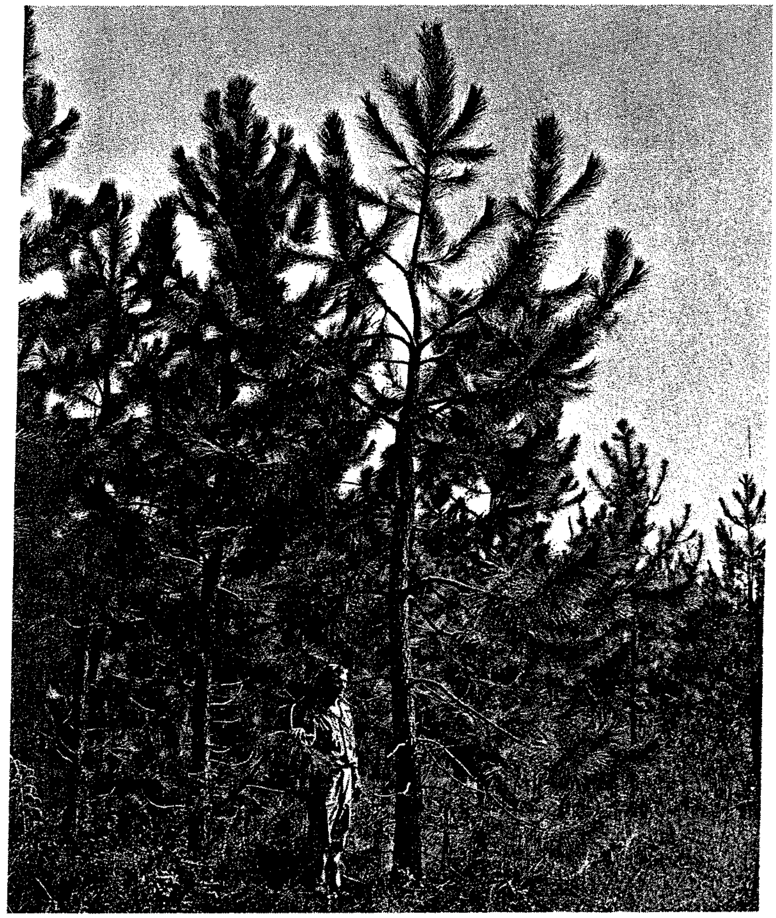

Figure 31.--This 8-year-old slash pine offspring of C-6 displays repeated crook. *Trees* such as this are common in some progeny groups, such as *C-4* and C-6.

trees that have crowns nearly to the ground, it would have been extremely difficult to establish some form of vertical axis without interference from the branches (fig. 31). It is questionable whether or not the observers recording data by visually classifying the trees into categories of straight, sweep, crook, and spiral, can be unbiased. Variation in the number of branches at a whorl on a tree, the density of foliage, and the distance between whorls can create somewhat different mental images of the straightness of a stem. When evaluating trees with many branches, short internodes, and dense foliage, one is inclined to overlook minor sweep and crook which would be very striking in a sparsely branched tree with long internodes. The percentages of stems in the various progeny groups tallied as having a crook-type defect are evidence that the observers were very critical. In spite of these problems, the agreement of the percentages recorded in the progenies of the common parent trees in study 102 and 103 is encouraging. A regression was computed of the percent of trees with crook-type defect in study 103 on similar values in study 102 for the 11 common parents (fig. 29). A highly significant regression was obtained, the equation being:

$$Y = 0.92\ x$$

where Y = the percent of trees having crook-type defects in study 103
X = the percent of trees having crook-type defects in study 102

These data tend to support the conclusions of others that parents of poor quality tend to produce more progeny of poor quality than do phenotypically good parents.

HERITABILITY

The degree of inheritance of different traits of economic worth must be known before a selection and breeding program can be properly designed to take advantage of the genetic constitution of the individuals concerned. At this relatively early point in the history of the breeding of forest trees, little is known of the degree of inheritance of various traits and relatively little is known about the economic values of these traits. Heritability has been defined generally in two senses (Bingham, Squillace, and Wright 1960):

$$\text{Heritability (narrow -sense)} = \frac{\text{Additive genetic variance}}{\text{Total variance}}$$

$$\text{Heritability (broad-sense)} = \frac{\text{Total genetic variance}}{\text{Total variance}}$$

Narrow-sense heritability is the one applicable to the Callaway data.

The subject of inheritance has had considerable discussion in the literature of plant breeders. Panse (1940) reviewed and discussed the literature available on the inheritance of quantitative characters and plant breeding. Smith (1944) assembled literature on the inheritance of quantitative characters in plants. In general, plant breeders are working with more complex methods of determining heritability than can be used by forest *tree* breeders at the present. This is primarily because forest tree breeders do not have the great mass of material with known pedigree that is available to the agronomists. A recent article by Matzinger, Sprague, and Cockerham (1959) discussed results of diallel crosses in maize repeated at several locations and in several years. They found that the genetic components of variance defined over environment indicated little variance of general combining ability (additive), but considerable variance of specific combining ability (deviation from additive). Their data indicated that estimates in a single environment were subject to large biases from interactions of general effects with year and location. The Block X Lot interaction discussed previously in the growth data may indicate that estimates of genetic variances from open-pollinated progeny tests such as these of the Callaway Foundation will be of little value until we have sufficient data to get the average of a number of estimates.

Smith (1944) stated that quantitative characters usually related to measurable differences in degree rather than in kind and that their inheritances usually exhibited continuous ranges. He also considered that quantitative characters were particularly susceptible to environmental influence and that *it* was manner of reaction under a particular set of conditions that was inherited. This pointed to the possibility of any estimate of heritability based on a small sample being in error. He further concluded that typical quantitative characters were under the control of a large number of similar genes, relatively small in effect, nondominant in expression, and which acted in a cumulative manner. Estimates ran from 10 to 200 genes for a single character.

Bannister (1959) pointed out the importance of the range in variation of the characters of importance and estimated that, "There are in New Zealand perhaps 300,000,000 genotypes of Pinus radiata and these are direct descendents of a comparatively small number of ancestral genotypes." Brown (1959), in his discussion of the inheritance of mildew resistance in apple, determined that this resistance was inherited quantitatively and that the parents varied in their contribution to progenies. He found that resistance in progenies was correlated with the reaction of the parent. His statistical analyses, based on incomplete diallel cross data, enabled him to estimate the contribution of the parent to resistance of its progeny, and he extended this to the estimation of the mean resistance of progenies of variety crosses in the absence of complete observational data. It is expected that most characters of economic importance in forest trees are inherited quantitatively.

Pawsey (1960) examined four disorders and defects in clones of Pinus radiata (D. Don) and concluded that heredity was important in the occurrence of each one. He attributed 28 to 53 percent of forking (including ramicorns) to heredity, but pointed out that these figures might be high. Other characteristics examined by him were top dieback, fused-needle, and dead-topping, all of which were probably related to soil, nutrient, and water conditions.

In an effort to determine the variation in heritability of some quantitative characters in Cryptomeria, Toda (1958) compared trees from a 42-year-old seedling stand with those of a 39-year-old clonally propagated stand. In each case he used 49 trees and grouped the material as if he had 7 replications in order to sort out environmental variance. For most of the characters he considered, the coefficients in the clonally propagated material were somewhat less than in the seedling stand. Table 26 contains data from his paper. The broad-sense heritability values he gave are applicable only for clonal propagation.

Toda, Nakamura, and Satoo (1959) made determinations of the heritability of tree height and stem girth based on open-pollinated progenies of Cryptomeria. They found that narrow-sense heritability for tree height was 0.265 and for girth 0.260. These values are, respectively, 39 and 45 percent of the broad- sense heritability previously discussed for this species. Coefficients of variation were 23.2 percent for height and 32.8 percent for girth.

Table 26. --Heritability and expected effect of selection in seedling Cryptomeria--data from Toda (1958)

Character	Broad-sense heritability	Effect of selection: Top 5 percent	Effect of selection: Top 1 percent
	Percent	- - Percent of mean	- -
Height	68	13	17
Girth	58	22	28
Taper	72	48	62
Crown diameter	61	18	24
Bark thickness	68	26	34
Branch angle	72	17	22

Effect of selection (percent of mean) = $\frac{\text{Standard deviation x heritability x selection differential}}{\text{Mean}}$

Recently, Bingham, Squillace, and Wright (1960) presented a rather complete discussion of heritability of blister rust resistance in western white pine (Pinus monticola Dougl.), and gave estimates of heritability and rate of improvement based on progeny tests of a number of controlled crosses. For this characteristic, they arrived at a broad-sense heritability value of 0.869 and a narrow-sense heritability of 0.688. They also developed estimates of progress per generation which ranged from 18 to 24 percent. They commented on the possible value of. using open-pollinated progenies for estimates of heritability and, based on their data, they have estimated that wind-pollinated progenies may have to be 3 to 4 times as many trees as control-pollinated progenies for estimating heritability of resistance to blister rust. They attributed part of this need to the greater variability in wind-pollinated material but also possibly to accidents of pollination in a given year. They further state "... also because of the possibility of selfing, especially in isolated and/or self-compatible trees, wind-pollinated progenies may never give a reliable test." This point was developed in the discussion of resistance to white pine blister rust.

, Squillace and Bingham (1960) presented a discussion of heritability estimates. with special reference to growth rate in western white pine. They discussed the meaning of heritability and also a number of different methods for computing these values. Their analyses were based on height growth during the fourth year from seed. They had available to them parental data consisting of height growth rate per year during the last 10 years and both open- and control-pollinated progenies. Using cross -pollinated progenies, they arrived at a heritability value of 14 percent, and one of 6.4 percent for open-pollinated progenies. Using correlation methods with parents, the heritability value for height growth among cross -pollinated progenies varied from 11 to 2 1 percent, depending upon the method used. Based on these data, estimates of genetic gain per generation were computed and varied from 3.5 to 7 percent, depending upon the level of selection.

Using a method described by Squillace and Bingham, we computed heritability values for several characteristics for studies 102 and 103 (tables 27, 28).

In every case the heritability values for study 103 are somewhat greater than those computed for study 102. The greater variation in 102 which reduces "heritability" is probably attributable to the fact that there were only three replications and also to the great differences in plot size in study 102. The effect of removing trees containing stem cankers on the analyses has been a reduced value for within-plot variances. The effect on the among-plots variances has not been consistent. The diameter values for study 102 may reflect complexities because of differences in plot size and the wide range of survival on existing plots.

These estimates of heritability are based on limited data from studies at one location. It would be presumptuous to attempt to use them for any estimates- of genetic gain or future improvement in breeding work in slash pine. However, one cannot examine them without finding encouragement that selection and breeding in slash pine will be profitable. For most of the characters considered in this paper, it would be possible to select parents which exceed the mean of these studies by 20 percent. If we use this as our selection differential, and apply that with the heritability values from these data, we can expect to achieve gains as high as 10 to 12 percent for some characteristics, such as natural pruning, which have a high heritability. Reliable estimates of heritability and gain can be determined only when we have accumulated similar values from a number of studies planted over a wide range of conditions throughout the South.

One other question for consideration at this point is whether estimates of variances computed on material at this young age are reliable for predicting values at later ages. This we do not know. However, it would seem that those trees and progenies that achieve dominance at young ages will probably maintain themselves until a point when the first thinning operation takes place in a forest stand. Beyond that point, the trees remaining for further production will depend upon the man with the marking gun. Depending upon his methods and his ideas, any combination of trees with various traits can be left so that the final yield in value and products will reflect to a great extent the ability and desires of the timber manager.

Table 27. --Analysis of variance and sample computation of heritability value 1/ for total height, study 102, 8 years of age

Source	Analysis of variance (all trees)			
	d. f.	s. s.	m. s.	"F"
Blocks	2	61.7454	30.8727	3.591*
Lots	18	236.6605	13.1479	1.53
B X L (error)	36	309.5256	8.5979	
Within plots	1982	43.109.1140	21.7503	

1/ k_o = Harmonic mean of trees per plot $= 57\left(\frac{1}{3.0375}\right) = 18.77$

E_p = Environmental variance between plots $= 8.5979 - \frac{21.7503}{18.77} = 7.4391$

F = Additional variance among random progeny due to female differences $= \left(\frac{13.1479 - 8.5979}{3}\right) = 1.5167$

H = Heritability (narrow-sense)

$$H = \frac{4F}{(\text{w/in m. s.}) + E_p + F}$$

$$H = \frac{4\ (1.5167)}{21.7503 + 7.4391 + 1.5167} = \frac{6.0668}{30.7061} = 0.198$$

Table 28. --Narrow-sense heritability values for open-pollinated slash pine progenies

ALL TREES

Study	Age	Height	D.b.h.	Natural pruning	Crown width
	Years	Percent			
102	6	25	16	--	--
102	8	20	6	36	--
103	5	35	37	--	19
103	7	34	34	52	--
TREES WITHOUT STEM CANKERS OF FUSIFORM RUST					
102	6	13	2	--	--
102	8	3	-22	50	--
103	5	36	34	--	16
103	7	37	27	64	--

SUMMARY AND DISCUSSION

The open-pollinated progeny tests of slash pine (Pinus elliottii Engelm.) established by the Ida Cason Callaway Foundation since 1950 are some of the older, large-scale progeny trials in the Southeast. They were established to determine the values of selected trees as parents, based on the performance of their offspring. The Foundation properties lie outside the natural range of slash pine, and all the selected parents are from plantations on old-field Piedmont sites. Progenies from these selected parents were also planted on an old-field Piedmont site north of the natural range of slash pine. The various parents were selected for different reasons, some with one or more desirable characteristics, others with one or more undesirable characteristics, and some with combinations of good and poor characteristics. When these selections were made in 1950, there was little data on variation and heritability available to guide the formulation of selection indices.

Twelve studies involving progenies of slash pine were established in the outplanting area from 1952 through 1955. Preliminary analyses were run on data collected from all 12 studies in 1957. The ages after planting ranged from 6 to 3 years. Analyses of data collected each year in the two older studies, ages 6 and 5, respectively, indicated that analyses of total height would be unreliable during the first several years. Because of this, complete analyses of all data were performed only on studies 102 (established 1952) and 103 (established 1953). Additional data were collected on these two studies in 1959.

Tables 29 and 30 give summaries of the data and show the mean values for each lot of progeny for all characteristics measured, at the oldest age the data were taken. The numerical ranking is in the order from most desirable to least desirable. Care should be exercised in comparing the rank values because they show only a numerical sequence and give no indication of the actual differences among lots.

Table 29. --Values and ranking for various characteristics of open-pollinated progenies, study 102

Lot	Average height 1/	Rank	Average d.b.h. 1/	Rank	Pruning height 1/	Rank	Rust free 2/	Rank	Crook 2/	Rank	Fork 2/	Rank	Crown Width 3/	Rank	1-year survival	Rank
	Feet		Inches		Feet		Percent		Percent		Percent		Ratio		Percent	
c-4	22.40	8	5.02	4	4.61	16	59	7	so	18	75	19	0.54	8	88	4
C-6	21.44	15	4.99	5	5.16	13	47	12	74	16	52	8	-		69	16
C-7	21.50	14	4.54	17	6.28	6	41	13	70	14	43	3	-		79	14
c-10	22.20	9	4.82	10	5.49	9	52	8	51	3	70	17	.54	8	85	10
c-37	22.73	6	4.84	8	6.81	3	70	4	63	8	65	13	.44	4	90	3
c-so	22.55	7	4.60	16	5.33	12	41	13	68	12	50	6	.38	1	87	6
C-51	22.12	10	4.76	12	5.49	9	50	9	62	6	66	15	-		86	9
c-54	24.34	2	5.15	3	7.17	2	88	1	63	7	45	4	.42	3	87	6
C-36	24.99	1	5.16	2	7.26	1	49	10	61	5	70	17	.44	4	95	2
c-59	20.89	17	4.23	16	4.50	17	73	3	74	16	34	1	-		87	17
C-60	22.10	11	4.83	9	5.56	8	46	11	90	18	47	5	-		87	8
C-61	21.65	13	4.61	11	5.46	11	60	6	39	1	60	10	-		85	10
C-62	22.03	12	4.74	14	5.12	14	37	15	40	2	64	12	-		80	13
C-63	23.96	3	5.35	1	6.57	5	76	2	66	10	40	2	.40	2	98	1
C-65	23.92	4	4.95	6	6.74	4	61	5	63	8	67	16	-		84	12
sou. Miss.	19.79	18	4.61	15	4.45	18	19	19	67	11	65	13	-		41	19
New Orleans	19.43	19	4.44	18	3.79	19	26	18	72	15	51	7	-		59	18
Control Seedlings	21.23	16	4.75	13	4.70	15	37	15	54	4	59	9	.52	6	71	15
Control Seed	23.07	5	4.87	7	6.02	7	35	17	70	13	62	11	.53	7	88	4

1/ Data recorded after 8 years in the field.
2/ Data recorded after 6 years in the field.
3/ Data recorded after 3 years in the field.
Only blocks one and two of indicated progenies were measured

Table 30. --Values and ranking for various characteristics of open-pollinated progenies, study 103

Lot	Average height1/	Rank	Average d.b.h.1/	Rank	Pruning height1/	Rank	Rust free2/	Rank	Crook2/	Rank	Crown width2/	Rank	Fork2/	Rank	1-year survival	Rank
	Feet		Inches		Feet		Percent		Percent		Ratio		Percent		Percent	
c-4	16.46	9	4.12	7	3.14	21	69	4	79	19	0.49	20	43	17	60	16
C-6	16.62	18	3.92	12	3.62	19	66	7	74	17	.48	18	52	19	83	15
c-7	19.66	6	4.30	4	4.96	3	51	13	59	7	.41	3	23	3	68	19
c-10	19.66	5	4.40	2	4.26	6	56	9	50	3	.47	16	62	19	94	1
c-37	21.60	1	4.92	1	6.06	1	73	2	60	6	.39	1	66	21	84	14
c-50	20.62	3	4.30	4	4.43	6	46	14	72	14	.40	2	32	9	95	2
C-61	17.42	17	3.96	10	4.10	11	79	1	38	2	.41	3	36	14	91	7
C-58	20.85	2	4.31	3	5.54	2	56	11	77	19	.42	7	32	9	93	5
C-63	20.10	4	4.26	6	4.92	4	60	6	66	10	.41	3	27	4	92	6
C-66	16.99	7	4.04	6	3.96	13	71	3	54	4	.42	7	29	6	69	9
c-134	18.16	11	3.61	14	3.60	17	53	12	73	16	.41	3	20	2	65	12
Sou. Miss.	16.67	19	3.44	19	4.33	7	36	16	66	10	.45	11	49	16	94	4
New Orleans	17.76	12	3.79	15	3.93	16	48	14	70	13	.45	11	41	16	90	8
CA-62	16.64	6	3.95	11	4.70	5	22	20	69	12	.42	7	31	6	66	11
CB-23	17.53	15	3.53	17	4.14	10	32	20	55	6	.48	18	29	6	66	10
CB-74	16.16	20	3.36	20	4.16	9	36	16	30	1	.43	10	10	1	96	2
A-l	17.60	14	3.56	16	3.94	15	48	14	66	20	.46	15	35	13	60	20
A-2	17.45	16	3.52	18	4.01	12	57	10	72	15	.51	21	32	9	60	16
Control Seedlings	16.00	21	3.24	21	3.39	19	45	17	54	5	.47	16	33	12	33	21
Control Seed	17.66	13	3.64	13	3.36	20	67	6	60	6	.45	11	26	6	85	12
Callaway	18.27	10	4.02	9	3.96	13	69	4	89	21	.45	11	40	15	80	lb

1/ Data recorded after 7 years in the field.

2/ Data recorded after 5 years in the field.

The survival in the Callaway progeny test plantations has been acceptable in most cases, though significant differences in survival are indicated in studies 102 and 103. These differences can probably be attributed to the condition of the nursery stock and handling before and during the planting operation. Evidence to support this explanation of survival differences is the performance of two lots of seed from Southern Mississippi and New Orleans, Louisiana, which produced seedlings with poor survival ability in study 102 but seedlings of high survival ability in study 103. All these seedlings were grown from the same lots of seed. With the exception of extreme drought years or other similar extreme climatic conditions, the problem of survival in the establishment of slash pine progeny tests in this area of Georgia is not a serious one. Good site preparation to remove competitive herbaeeous vegetation and proper handling and planting of good nursery stock can achieve excellent survival. In order to provide maximum soil moisture and remove as much competitive vegetation as possible, it would be desirable to use a light disking during the first year after planting to insure early, vigorous growth.

Repeated seed collections from a number of individual parent trees show that weight per 1,000 seed varies among trees and that for the same tree, weight varies from year to year. Analyses of 8- and 7-year heights in relation to weight per 1,000 seed showed that there was no significant relationship. If seed size had any effect on initial seedling size, it has been masked by the growth of the seedlings and need not be of concern in long-range tests.

Height data were collected in studies 102 and 103 each year after planting. Analyses of variance of the height data for each year indicated that significant differences occur among progenies at ages 2 to 4 years. In study 102 these differences gradually disappeared and were nonsignificant at the 5 percent level at ages 6 and 8. In study 103 a similar pattern was followed but differences were significant at the 5 percent level at ages 5 and 7. The difference in the performance of the two studies is probably related to differences in initial plot size and in numbers of replications used. Study 102 had three replications of plots varying from 10 to 100 trees each, whereas study 103 had four replications of 25-tree plots. In study 102 at age 8 years, the difference in height between the tallest and shortest progenies is 5.2 feet, more than 20 percent of the larger mean. For both studies highly significant differences were obtained among blocks.

An examination of the height data showed the Block X Lot interaction to be highly significant in both studies 102 and 103. This is normally the error term in the analysis of variance of these data. The significant interaction indicates that the different progeny groups react differently to the site variability from block to block. This differential reaction increases the variation among the data and contributes to the lack of sensitivity of these tests. It should be pointed out that slash pine is native to the Coastal Plain where sandy soils predominate. These tests were established on a rolling Piedmont area of heavy clay soils where some topsoil removal had taken place for landscaping purposes and much of the area showed evidences of erosion in the past. The micro-site variability within the blocks was probably relatively large.

The relationship of total height to number of trees per plot (in effect, survival) for study 103 showed that progenies with the best survival tended to be tallest; the regression was highly significant. This trend may indicate that more vigorous progenies survive better or that micro-site conditions favorable for survival are favorable for more rapid growth.

An analysis of total height was also computed using a sample of the five tallest trees on each plot of study 103. This was not a proportional sample, but represented “crop trees” from the silvicultural viewpoint. The analysis of these data produced results nearly identical to the analysis of the complete data.

When examined on an individual tree basis among pooled progenies, the total height of seedlings after 2 years in the field was strongly correlated with total height at ages 8 and 7 for the two studies. The values were 0.61 for study 102 and 0.65 for study 103. Correlation of second-year height growth was only 0.45 with 8-year total height in study 102, but was 0.64 in study 103 for second-year height growth with 7-year total height. Correlations of total height with other growth characteristics gave similar values in both studies 102 and 103.

Measurements of d.b.h. were taken at ages 6 and 8 years in study 102 and 5 and 7 years in study 103. Analyses of variance of the data from study 102 showed no significant differences. In contrast, highly significant differences were obtained for 7-year data in study 103 when all trees were considered in the analysis. In an analysis considering only trees free of stem cankers of fusiform rust, the significant difference dropped to the 5 percent level. D.b.h. measurements on an individual tree basis were highly correlated with total height. The oldest data for studies 102 and 103 showed correlation coefficients of 0.94 for this relationship. Similar high correlation values were obtained for the younger data.

A highly significant regression was found between average progeny d.b.h. and the average number of surviving trees per plot in study 103 where plot size was uniform. The "normal" relationship expected in this situation is for the average d.b.h. to decrease as the number of trees per plot increases. The relationship found in the regression of d.b.h. on number of trees per plot (study 103) was contrary to the expected "normal" relationship; average d.b.h. increased as the number of trees per plot increased. One interpretation is that progenies which are inherently more vigorous survive better and grow faster, even under the greater competitive levels. Another explanation may be that variations in micro-site sufficient to affect initial survival also affect growth. The correct interpretation may lie in a combination of these two possibilities.

Differences in pruning height at the older ages were observed in both studies. This measurement was based on the height from the ground to the first whorl having two or more live limbs free of basal cankers of fusiform rust. The variation within progenies was quite large; however, the differences among progenies were great enough to be statistically significant. Observations indicate that some progenies and individual trees within progenies have very definite tendencies toward early natural pruning; analyses of the data support these observations. Correlations of pruning height with total heights at young ages were very low, and only moderate correlations of 0.40 and 0.51 were obtained for the relationship of pruning height to total height at ages 8 and 7, respectively, in studies 102 and 103.

A limited sample of bark thickness taken on several parent trees and their progenies in studies 102 and 103 indicated differences in the relationship of bark thickness to d.i.b. The data were insufficient for a complete analysis. For 3 progeny groups where 20 or more individual trees had been measured, regression analyses of the relationship of bark thickness to d.i.b. were run. For two of the progenies, the regression was not significant. For the third progeny, it was highly significant. Additional sampling of other progenies and parents will be necessary before any conclusions can be drawn from such data; however, inherent differences in bark thickness are strongly indicated. These progenies are relatively young and meaningful bark thickness relationships may not yet be established.

Crown relationships among the progenies were examined. The widths of the crowns were measured at various ages in studies 102 and 103. Using ratios determined from total height and the crown width values, analyses indicated that there were significant differences among progenies in both studies. The planting spacing was 10 by 10 feet and the trees had several years in which they could exhibit free crown growth with no competition from adjacent trees. Lateral competition among crowns does not become evident until about 5 or 6 years after establishment in the field at this spacing. These crown width differences were detectable at ages as young as 3 years.

On several of the parent trees, beginning at the terminal bud, each branch in each primary whorl was measured, moving down the tree until a point was reached where lateral branch competition was taking place from adjacent trees or to the base of the live crown. Examination of these parent tree data indicated that a crown zone from approximately 65 to 80 percent of the total height of the tree was the area of most uniform branching characteristics. Measurements were taken on a sample of progenies from these parent trees, and three whorls of branches were considered. The whorls were 2, 3, and 4 years of age. Branch length, diameter, and angle were taken for each branch of each whorl and stem measurements above the whorls were also recorded; Average branch length of the progenies appears closely related to the average branch length of the parent trees. Progenies from the same parentage in studies 102 and 103 seem to be in close agreement for all characteristics, with the exception that average branch angle was slightly larger in study 103 than in study 102. There is no apparent explanation for this phenomenon.

Correlations of various characteristics of the crowns of the progenies were computed, and it was found that branch length and branch diameter were very highly correlated. Branch length and branch diameter showed negative correlations with branch angle; that is, the greater the angle of the branch from vertical, the shorter and smaller the branch. This relationship is very desirable. The correlation of branch length with the height growth of the stem above the whorl was low, but a high correlation was obtained for the relationship of d.b.h. and average branch diameter. This sample of progenies also indicated that the data on crown-width taken at early ages was a good indication of crown characteristics in later years.

One of the most interesting results of these progeny tests was the difference in susceptibility of the different progenies to infection by southern fusiform rust. Differences had been noted at ages 3 and 4 years, and detailed data on trees infected and the number and position of cankers on each tree were collected in 1957. Highly significant differences among progenies were obtained in both studies for the percent of trees infected with fusiform rust. The number of cankers per infected tree was also examined but there seemed to be no differences among progenies.

The correlation of rust infection with second- and third-year height and height growth indicated that the relationship of rust infection to vigor was very weak. The literature (Goggans 1957) contains reports of a strong relationship between rust infection and rate of growth. Recent reports (Bethune and Roth 1960; Barber and VanHaverbeke 1961) refute this point as do these data. It is encouraging that vigor and rust infection are not strongly related because it increases the likelihood of obtaining extremely vigorous trees resistant to rust.

Three progenies from seed collected in Australia were included in study 103. These were selections of slash pine made in Australian plantations for various desirable growth characteristics. Fusiform rust is not present in Australia and therefore there was no opportunity to select for resistance to this disease. All three of the progeny groups show very high susceptibility. The fact that all three are uniformly high is probably coincidence. However, they are in contrast to the Callaway selections which were made in a plantation heavily infected with the disease.

The problem of selecting parent trees resistant to rust is not a simple one. There is always a possibility that a tree may be an escape and even more likely is the possibility that a tree might have branch infections which kill the branches and the cankers are subsequently lost. It would be impossible to detect such past infections on pole-sized and larger trees in a stand. In examining the rust infection among the Callaway progeny groups, it should be remembered that a large number of remaining trees in the parent stand were susceptible to fusiform rust, as indicated by cankers, and they probably supplied the majority of the pollen which fell upon these rust-free selections. Controlled pollinations will be required to determine more exactly the transmission of rust resistance from parent to progeny. The possibilities of races of the rust will also have to be considered in determining resistance. The very poor performance of the Southern Mississippi seedlings may reflect differences in susceptibility associated with races of trees or races of rust.

Other defects, namely crook and forking, were recorded at ages 6 and 5 years in studies 102 and 103, respectively. Significant differences were obtained among progenies for the occurrence of crook. The data support the fact that the criteria for crook were very rigid, though they may not have been applied without bias. It is extremely difficult to make an unbiased rating of crook in trees having different numbers of whorls, varying numbers of branches per whorl, and varying foliage density. Dense crowns tend to mask stem irregularities.

As the age of the trees increases, some stem irregularities called crook at age 5 and 6 years may be no longer detectable. Even though slight crooks occurring in these juvenile stages might be masked by later diameter growth, they still will represent lower quality wood because of the production of compression wood along the stem.

The occurrence-of forks and ramicorns seemed to be more variable than crook among progenies. A considerable amount of this defect was probably attributable to a very late spring freeze in 1955. An appreciable amount of damage was done to new shoot growth and the injury was more severe on some progenies than others. For those severely damaged trees, the pattern of recovery was somewhat abnormal in that several branches competed nearly equally for leadership; whereas, under normal circumstances of terminal bud injury, one branch soon takes over. It was interesting that there were no significant block differences among the analyses of crook data and only one significant block difference showed in the several analyses of fork data.

The major defect caused by forks and ramicorns is usually the failure of the branch to prune quickly. The large stub may remain on the tree for a number of years and form an irregular knot, sometimes with bark inclusions. For the evaluation of this characteristic, it would seem best to wait until natural pruning takes place in the whorl containing the branch. Observations indicate that forks at young ages frequently become unbalanced and one side takes over as leader, forcing the other into the position of a ramicorn. This ramicorn may then die and prune off naturally so that the defect is minor, or it may remain competitive. These data from open-pollinated progenies strongly support the contention that parents of poor crown form will produce progenies of poor crown form.

Certain data from these open-pollinated progeny tests were suitable for the computation of narrow-sense heritability values. The heritability values obtained for study 103 are consistently greater than those for study 102. The data of study 102 seem to be much more variable than those of 103. Study 103 heritability values for height and diameter were from 0.27 to 0.37, varying with age and whether trees containing stem cankers of rust were included in the analyses. Pruning height showed narrow-sense heritabilities in excess of 0.5 and narrow-sense heritability values in excess of 0.16 were obtained for crown width.

These heritability values represent only two studies in a single situation. As such, we can place little confidence in them as true estimates of the heritability of these characteristics. Only after the completion of analyses from a number of studies will it be possible to develop an average heritability value which might be applied for the prediction of genetic gains.

The equation for the computation of heritability from open-pollinated progeny data assumes that the pollen for each progeny is a sample of the same parental population. In this case most of the progenies came from parents in the same plantation and this is probably a valid assumption, though not necessarily so. If the pollen parents for the different progenies cannot be assumed to be equal, then the heritability values shown here are probably over-estimates. As an extreme, if we assumed that the pollen for each lot was completely different, these heritability values would be reduced by one-half. It is most likely that the pollen source for each of the lots is quite comparable; therefore, the estimates of narrow-sense heritability as presented are probably the best for these data.

The Ida Cason Callaway slash pine progeny tests have pointed up a number of problems deserving serious attention by those interested in progeny-testing forest trees. The Block X Lot interactions found in the height analyses brought out at once the problem of sampling site. From the foresters' viewpoint, site must be considered in a broad sense. The practicing forester cannot be concerned with running soil or other surveys of his planting situations to determine which strain of trees might be best adapted to very small areas. He will want trees adapted to a broad-site situation involving many micro-sites. The problem for the researcher is to determine how to establish his progeny tests so that he can sample the broad-site spectrum and evaluate each progeny for performance over a range of micro-sites.

First of all, a great deal of consideration should be given to the location of very uniform sites for the establishment of progeny tests. The uniformity required is in soil structure, texture, fertility, and moisture relationships. Problems of differences in ground cover can be handled by site preparation techniques. If very uniform sites can be found, then the question arises as to how many of these uniform site classifications must be sampled in order to determine general adaptability to a physiographic region, such as the Coastal Plain.

Secondly, if areas of very uniform site cannot be located, then the problem becomes one of increasing the sample in the progeny-test design so that the micro-site variation is accounted for in the analysis of the data. If the interaction of progeny with site persists under these conditions, then there will be no best progeny or best several progenies for all sites. Under this situation, the best progenies will have to be determined for each of the various site situations and then those parents can be combined in an orchard to produce a synthetic 'variety. This "variety" will then contain some trees of each parentage and when planted on a broad-site area, those progenies best adapted to the various micro-sites will assume dominance and become crop trees; the remaining trees can be taken out in early thinnings. By this technique the best crop trees can be insured on all sites.

The construction of a synthetic variety by selection of the several best parents for each site classification is desirable from a more basic viewpoint: the maintenance of genetic diversity in the population. The broad base of genetic diversity will help maintain resistance to disease and insect attack, and to extreme climatic occurrences.

As mentioned earlier, southern fusiform rust has important silvicultural and economic consequences. In addition, it is a complicating factor in tree improvement programs. The development of rust-resistant strains of trees is a goal in itself and certainly any improved strain of slash and loblolly pine which can be recommended for widespread planting in the South and Southeast must have some degree of resistance to fusiform rust.

If a progeny test is designed to study the yield of products at some age beyond that needed for first merchantability, it is evident that the plot should be of a size sufficient to measure the impact of fusiform rust on the production of that crop. As pointed out by Siggers (1955) and Goggans (1957), there are important fluctuations and local variations in the degree of rust infection. Goggans' tables show that there is considerable variation in over-all infection of plantations at different ages. This variation probably reflects differences in rust infection years during the critical period after planting. The choice of a plantation site in terms of the areas of high and low susceptibilities, and also the chance occurrence of particularly good or bad infection years during the early ages, may result in an evaluation of the tests in such a way that an erroneous interpretation could be made. In tests for yield, one way to circumvent this problem might be to run a two-stage test whereby artificial inoculation or some similar technique would be used as a first step to determine the relative degree of susceptibility to rust of the different lots and then larger field plantings made to determine yield. Final yield figures might then be adjusted with the results of the initial rust susceptibility tests.

If the study to be established is designed to measure some other characteristics, such as wood quality or growth of individual trees, consideration might be given to using smaller plots with more replications. Where there is heavy fusiform rust, it would seem undesirable to use extremely small plots, such as the single tree plots suggested by Wright and Freeland (1959). As an example, let us consider how these progeny tests might have performed if they had been established in single tree plots. As we saw in the discussion of growth, the presence of stem cankers on trees affects the rate of growth; therefore, if we wish to consider a characteristic, such as height or diameter growth, it would be necessary to eliminate from the analysis all trees having stem cankers of fusiform rust. The percent of trees with stem cankers varies from 5 to 58 among the progenies (table 21). The presence of 71 percent of the trees in the parent plantation infected with rust is further evidence along this line. Three-year-old.racial tests of loblolly pine show that some sources have approximately 50 percent of the trees infected with stem cankers at this young age. 8/ The consequences of encountering such infection in a progeny test plantation involving small plots would be the loss of the validity of any statistical analysis. It would be impossible to analyze the data, for such an analysis would require a substitution for missing data in one-third to one-half of the plots. This cannot be done satisfactorily.

Initial survival is another factor contributing to the problem of progeny-test design. Here in the South, we are unable to replant after the first season, and any dead trees cannot be satisfactorily replaced. In other parts of the country, initial mortality may not be serious because transplanted stock can be held for 1 or 2 years for replacement planting.

The length of time a progeny test will run must also be considered in its establishment. If we are concerned with such characteristics as resistance to disease or broad differences in crown form, a test may be designed which would run only 3 to 5 years. However, if we are interested in inherent growth and yield, then the test must run at least beyond the point of first commercial thinning. For slash pine it seems desirable to run these tests a minimum of 20 years. The use of a moderate spacing is desirable in the establishment of tests in order to avoid severe competition and in order to avoid the requirement of thinning before this minimum age.

The problem of thinning a progeny test seems insurmountable at present. If the progenies grow at different rates, and all evidence indicates that they will, at any given point in time the competitive level within a plot will vary from progeny to progeny. When the most rapidly growing progenies reach a density where thinning is required, the slower growing progenies will be much below that level. The question is how to thin. Should all plots be thinned to a uniform density? Should they be thinned to the same relative densities? Should thinning be by a mechanical system? Should thinning be by random selection? Should thinning be by silvicultural marking rules? At present there are no suitable answers to these questions. From the standpoint of the timber manager, once a stand reaches the age for thinning, the timber marker minimizes the genetic variation for the remainder of the rotation. The marking rules followed in thinning a stand will determine from that point onward the genetic constitution of that stand. Because of this, progeny tests for growth and yield characteristics might well be given a final evaluation at about 20 years of age. This would represent a point in the normal rotation where a second thinning would be recommended. There would have been no thinning, of course, prior to the final evaluation.

When working with long-lived plants, such as forest trees, it will be necessary to make judgments as quickly as possible in order to increase the number of generations which can be used in a breeding program. The minimum generation time for the southern pines has not been determined from a

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8/ Unpublished data on file at the Southeastern Forest Experiment Station, Macon, Georgia.

practical viewpoint, and will vary considerably among species. Ten years will probably be the minimum time for a single generation of slash pine. Two growing seasons are required for the production of pine seed after pollination. This period, plus the time for a seedling to develop sufficiently to be evaluated and to produce male or female flowers for breeding purposes, extends at present even beyond the IO-year estimate. The long generation time is in sharp contrast to the rather rapid progress possible in most agricultural crops where one to three generations might be completed in a single calendar year.

At present, no short cuts are known that we can use to reduce the generation time of pine trees appreciably. For this reason, it will be imperative that we use the earliest measurements possible for the evaluation of the genotype. For various characteristics, this period of time may be quite different. Some traits, such as stem straightness and branching habit may be best evaluated at relatively young ages. Minor fluctuations in stem straightness are ***easily*** discerned in trees 10 to 20 feet tall; as these ***trees*** increase in diameter, many of the variations will be hidden by eccentric diameter growth and its resulting compression wood, thus hiding the defect. Similarly, undesirable branching characteristics may be masked by crown competition after crown closure, but would have been easily detectable before competition became serious. An evaluation for rust resistance may be made on l-year-old or at most 2 -year -old seedlings, whereas the evaluation for volume growth or any of the characteristics which determine volume, such as height and diameter, might require ten or more years. In selecting and breeding toward a goal of increased volume production, a number of individual traits will be involved and they may be independent of each other or complexly related.

Similarly, resistance to diseases may be obtained through several different characteristics or combinations of them. The tree breeder must not overlook the complexity of the situation and the confounding by the time element. A broad base must be established and work begun toward the goal, but necessarily, many lines will have to be carried for the eventual development of improved trees to fit specific needs of forest managers.

At this point it is inevitable that the question will be raised about which parents are best, based on the Callaway progeny tests. For this question, there is no direct answer. First of all, one must establish criteria to evaluate the parent. Secondly, ***one*** must then decide the relative values of the different characteristics. For instance, how much difference in height would be needed to offset a 10 percent difference in fusiform rust infection, or how much difference in fusiform rust infection would be needed to offset a 10 percent difference in the occurrence of crook? A valid index cannot yet be established because the relative economic values for the different characteristics are at present unknown, and reliable heritability values are not available for many of them.

It would ***seem*** that if one intended to plant trees in an area where fusiform rust infection was relatively severe, he would do well to choose parent trees such as C-37, C-10, C-63, and C-65. If he were producing sawtimber, he would do well to consider the trees that had a minimum of crooked progeny and also to take into consideration the pruning height. For most products, of course, height and diameter growth would be of major consideration. Considering the trees that occur in both tests, the progenies of C-37 and C-63 seem to be good all-round performers.

Within the next few years some of these progenies will begin to produce flowers. As soon as they do, it will be desirable to make selections among them, where we will know the complete history of each tree, and to establish a breeding program. All of the progeny groups offer possibilities for selecting individual trees having a combination of desirable characteristics. Some progenies, of course, offer greater opportunities than others and have many more trees in certain categories. In addition to the selections among progenies for breeding purposes, of course, we now have an estimate of the performance of open-pollinated progenies from the various parents and these parents can be introduced into a breeding program. In fact, a number of controlled crosses have been made among certain parent trees based on early evidence in the progeny tests. For instance, crosses have been made between C-65 and C-37, in the hope of increasing resistance to fusiform rust.

These data have been in general agreement with reports in the literature for other species, frequently based on less extensive tests. The very good agreement between progenies in study 102 and progenies from the same parents in study 103 is quite encouraging because it must be interpreted that these open-pollinated progeny tests are reliable and that they give sound estimates of the parent trees. The amount of variation in these tests was relatively high and, therefore, many of the analyses indicated insensitive tests. This low sensitivity can be improved by increasing the number of replications in future progeny tests designs. In view of these data, the sensitivity can also be increased by using more uniform sites. Finally, there is the possibility that variability will decrease with age as the trees approach maturity and slow down in rate of growth and rate of change in other characteristics.

CONCLUSIONS

The Ida Cason Callaway Foundation progeny tests of slash pine have been satisfactory. While their sensitivity has not been as great as many had hoped, they will contribute an appreciable amount of information on the genetics of slash pine before maturity. Studies younger than those included in this evaluation have many other parent trees involved and also have controlled crosses among some of these parent trees. The Callaway tests will also be used to examine variation in morphological and anatomical characteristics of the progenies; they will lend themselves well to studies of wood quality. A great opportunity lies in more intensive examination of the younger progeny tests and thorough statistical analyses of data collected in the future.

What does this mean to the silviculturist and forest manager? It means that he should closely examine his present marking rules and silvicultural procedures. It means that each of his rules should be re-evaluated in terms of genetic as well as present economic values because we have a better estimate of traits that are hereditary. There has been very little data heretofore on this subject.

The data here are very limited on survival, but they do indicate that on old-field Piedmont sites, survival is probably much more a function of handling and planting than the inherent ability of the seedlings to survive. This may not hold true for severe sites in the Southeast. It was also shown that seed weight was not important in terms of subsequent growth of the tree; therefore, any sizing of seed should be considered purely from the aspects of nursery procedures, not with the expectation of sorting out fast- and slow-growing trees.

Differences in height growth mean dollars. The faster growing progenies averaged several feet taller than others and this may mean an extra stick or two of pulpwood or half log when the tree is harvested. It also may mean those few extra feet needed for higher value poles and piling. The diameter differences do not appear as distinct as height differences. It was found that diameters are closely correlated with heights in the range examined. Diameter is probably the most sensitive growth characteristic we have in response to management practices, but one should not sacrifice potential diameter growth by ignoring it in marking rules and selections.

Though the trees were planted at a fairly wide spacing and were young, distinct differences among progenies were evident in natural pruning. It can be expected that in dense stands, much of the difference may be masked, but the tendency for lower limbs to die at an early age means faster pruning to a higher, clear length, a smaller core of knots, and fewer rust-infected limbs. Where widely spaced trees are grown, this tendency for early natural pruning will be desired.

There appear to be differences among progenies in the relationship of bark thickness to diameter inside bark. Progeny bark thickness also seems to be related to the bark thickness of the parent tree. These trees are still young and fast growing and the bark differences which appear here may not necessarily be indicative of bark differences at an older age or when larger merchantable sizes are reached.

The examination of crown characteristics showed that some progenies have a more favorable crown-width-to-height ratio than others. It was also found that branch length and diameter were negatively correlated with angle of the branch from vertical, meaning that narrow-crowned trees tend to have a larger branch angle which is more desirable. These branching characteristics not only affect the quality of the material produced from the tree, but they also have an influence on the cost of producing pulpwood or logs from these trees. The timber marker should learn quickly to identify the trees with more favorable crown characteristics.

Striking differences in susceptibility to fusiform rust were found among progenies. These broad differences would have an important influence on the quality of the stand and would give the timber marker a great deal of latitude in selecting his keep trees for other characteristics. These data indicate that all trees having fusiform rust should be removed from the stand before the stand reaches an age when natural regeneration begins or before seed collections. Diseased trees should not be used as parents.

Stem straightness appears to be a characteristic very important to the timber manager. There were big differences in the amount of crook recorded among different progenies. Straight trees mean not only high quality lumber, but high quality pulp as well. The data on forking were not as clear cut and strong as those on crook; however, these tests included no progenies from forked trees. There were differences in forking among progenies, but the data were complicated by freeze injury and by the problems of evaluating subsequent response after injury. The data are valuable enough to indicate that we should consider forked trees as undesirables in our silvicultural procedures.

Where adequate data were available, heritability values were computed for these open-pollinated slash pine progenies. Height, d.b.h., pruning height, and crown width were considered, and the heritability values showed that these characteristics were inherited strongly enough to be important to the silviculturist and forest manager. The data here, of course, are limited to a single set of studies, but the consistently high values for many of the heritabilities computed indicate real potential in terms of improvement of slash pine through selection, whether at the level of superior trees for seed orchards, or by the timber marker and his choice of which trees to cut and leave.

The timber manager must now reconsider his marking rules for slash pine in terms of these data and the data of other researchers which are becoming available. He must now consider the economic maturity values for his trees, the risk classes for disease-infected trees, and stocking and spacing values in terms of a balance with the genetic aspects of silviculture. Where natural reproduction will be used and where reproduction may become established well in advance of the final harvest cut, the forest manager may have to revise his marking rules to have his stand in final regenerative condition 10 to 15 years before the final harvest cut. Trees in those stands should be only the most desirable. which can be left to maintain acceptable growth and stand conditions, and each tree must be considered a potential male as well as female parent.

We now have greater knowledge of the variation in many traits of slash pine and also some indication of the importance of environmental factors such as soil variability. Using this knowledge of variation and the heritability values which we have developed, selections can be made for combinations of good traits, and those trees developed into synthetic varieties of slash pine. These tests show that an opportunity exists to make appreciable improvement by selection. Silvicultural marking rules based on individual phenotypes can be effective in improving the average genotypes of future forests. The results reported in this paper show that present activities in the establishment of seed production areas and seed orchards are on a sound basis.

In applying the information from this paper, first and foremost must be the consideration that tree improvement and genetics are not a panacea for the problems besetting the silviculturist. They must be viewed as working tools, just as other information on soils, pathology, entomology, ecology, etc. This paper is but one of many now being published about the genetics of southern pines. Although only one part of the story, it does point the way to more profitable forest management practices for slash pine in the South.

SELECTED BIBLIOGRAPHY

AHLGREN, C. E.
1955. Grafted selections of eastern white pine tested for resistance to blister rust. Jour. Forestry 53: 727-729.

ARNBORG, T.
1946. Pinus sylvestris f. condensata - kvasttallen. Pinus sylvestris var. condensata, 'the broom pine '. Svenska SkogsvForen Tidskr. 44: 329-343. Forestry Abs. 8: 359, 1638 (1947).

________ and HADDERS, G.
1957. Studies of some forestry qualities in clones of Pinus sylvestris. Acta Horti Gotoburgensis 21: 125-157.

AVERELL, J. L.
1927. The Swedish "better sires" campaign of 1904. Jour. Forestry 25: 742.

BANNISTER, M. H.
1959. Artificial selection and Pinus radiata. New Zeal. Jour. Forestry 8: 69-90.

BARBER, J. C., DORMAN, K. W., and BAUER, E.
1957. Slash pine progeny tests indicate genetic variation in resistance to rust. South. Forest Tree Impr. Conf. Proc. 4: 44-46.

________ DORMAN, K. W., and JORDAN, R. A.
1955. Slash pine crown width differences appear at early age in 1 -parent progeny tests. U. S. Forest Serv. Southeast. Forest Expt. Sta. Res. Notes 86, 2 pp.

________ and VANHAVERBEKE, D. F.
1961. Growth of outstanding nursery seedlings of Pinus elliottii Engelm. and Pinus taeda L. U. S. Forest Serv. Southeast. Forest Expt. Sta. Paper 126, 12 pp., illus.

BARNES, H. F.
1930. On the resistance of basket willows to button gall formation. Arm. Appl. Biol. 17: 638-640.

BATES, C. G.
1927. Better seeds, better trees. Jour. Forestry 25: 130-144.

________ 1928. Tree seed farms. Jour. Forestry 26: 969-976.

BETHUNE, J. E., and ROTH, E. R.
1960. Fifth year results of loblolly pine seed source planting in Georgia. U. S. Forest Serv. Southeast. Forest Expt. Sta. Res. Notes 145, 2 pp.

BINGHAM, R. T., SQUILLACE, A. E., and DUFFIELD, J. W.
1953. Breeding blister-rust-resistant western white pine. Jour. Forestry 51: 163-168.

________ SQUILLACE, A. E., and PATTON, R. F.
1956. Vigour, disease resistance, and field performance in juvenile progenies of the hybrid Pinus monticola Dougl. X P. strobus L. Ztschr. f. Forstgenetik u. Forstpflanzenzücht. 5: 104-112.

________ SQUILLACE, A. E., and WRIGHT, J. W.
1960. Breeding blister-rust-resistant western white pine. II. First results of progeny tests including preliminary estimates of heritability and rate of improvement. Silvae Genetica 9: 33-40.

BOLLAND, G.
1957a. Resistenzuntersuchungsn vor allem über Kienzopf und Schütte an der Kiefer. [Resistance of Scotch pine to Peridermium pini and Lophodermium pinastri.] Züchter 27: 38-47.

_____ 1957b. Untersuchungen über den Drehwuchs an Kiefernmutterbäumen und *ihren* Nachkommenschaften. [Investigations on spiral growth in mother trees of pine and their progeny.] Silvae Genetica 6: 150-151.

BØRSET, O.
1951. [Studies on progenies from single *trees* of Scots pine (P. sylvestris L.) from a coastal forest in Southern Norway.] Meddelelser fra Det Norske Skogforsøksvesen 38.

BOYCE, J. S.
1958. Limitations of forest disease control by breeding and selection. Soc. Amer. Foresters Proc. 1957: 54-55.

BROWN, A. G.
1959. The inheritance of mildew-resistance in progenies of the cultivated apple. Euphytica 8: 81-88.

BUNDY, O.
1945. Avkommekontroll å tall. [Progeny control applied to pine.] Skogen 32: 171-173. [Plant Breeding Abs. 19: 650, 2135 (1949).]

CALLAHAM, R. Z., and HASEL, A. A.
1961. Pinus ponderosa--height growth of wind-pollinated proganies. Silvae Genetica 10: 33-42.

CECH, F. C.
1959. Superior tree selection, slash pine. South. Forest Tree Impr. Conf. Proc. 5: 49-52.

CHILDS, T. W., and BEDWELL, J. L.
1948. Susceptibility of some white pine species to Cronartium ribicola in the Pacific Northwest. Jour. Forestry 46: 595-599.

CLAPPER, R. B.
1952. Breeding and establishing new trees resistant to disease. Econ. Bot. 7: 2'71-293.

COMMONWEALTH OF AUSTRALIA, FORESTRY AND TIMBER BUREAU
1954. Relation between forking and site quality. In Report Forest and Timber Bur. Australia (23), 1953-1954.

COVILLE, P. J.
1928. Some aspects of forest genetics. Jour. Forestry 26: 977-993.

CUMMINGS, W. H.
1947. Progeny test with black locust seed from mother trees of varied age and height growth. Jour. Forestry 45: 793-798.

DIJKMAN, M. J.
1951. Hevea: thirty years of research in the Far East. 329 pp., illus. Coral Gables, Fla. : Univ. Miami Press.

DORMAN, K. W.
1952. Hereditary variation as the basis for selecting superior forest trees. U. S. Forest Serv. Southeast. Forest Expt. Sta. Paper 15, 88 pp., illus.

DUFFIELD, J. W.
1957. What forest genetics offers the Douglas-fir industrial forester. Timberman LVIII (3): 46-48.

DUNCAN, D. B.
1955. Multiple range and multiple "F" tests. Biometrics 11: l-7.

ECHOLS, R. M.
1955. Linear relation of fibrillar angle to tracheid length, and genetic control of tracheid length in slash pine. Tropical Woods 102: 11-22.

ECKBO, N. B.
1916. Importance of source of seed in forestation. Soc. Amer. Foresters Proc. 11: 240-243.

EDWARDS, M. V.
1956. The design, layout, and control of provenance experiments. Ztschr. f. Forstgenetik u. Forstpflanzenziicht. 5: 169-180.

EHRENBERG, C. E.
1958. Uber Entwicklungsanomalien in Kreuzungsnachkommenschaften bei Pinus silvestris L. [On annomalous development of progeny from crossing in Scots pine.] Meddel. Statens Skogsforskn. Inst. 48 (2): 1-14.

EHRENBERG, C., GUSTAFSSON, Å., FORSHELL, C. P., and SIMAK, M.
1955. Seed quality and the principles of forest genetics. Hereditas 41: 291-366.

ENGLER, A.
1913. Einfluss der provenienz des Samens auf die Eigenschaften der forstlichen Holzgewachse. [Influence of provenance of seed on the characters of forest growth.] Mitterlungen der Schweizerischen Centralanstalt fur das forstliche Versuchwesen, Zurich 10 (3): l-386. (Reviewed by Tourney, J. W., Soc. Amer. Foresters Proc. 9: 107-113. 1914.)

FIELDING, J. M.
1953. Variations in Monterey pine. Forest Timber Bur. Austral. Bul. 31, 43 pp., illus.

FINNEY, D. J.
1958. Statistical problems of plant selection. Inst. Internatl. de Statis. (Biometric) 36 (3): 242-268.

FISCHER, F.
1949. Ergebnisse von Anbauversuchen mit verschiedenen Fichtenherkunften [Picea abies (L.) Karst.] [The results of provenance trials with spruce of different origins.] Mitt. Schweiz. Anst. forstl. Versuchsw. 26 (1): 153-200. [Forestry Abs. 13: 40, 219 (1952). I

FOREST GENETICS RESEARCH FOUNDATION
1958. Forest genetics research in the Rocky Mountain and Pacific coast states and British Columbia. 31 pp. November.

FOWELLS, H. A.
1953. The effect of seed and stock sizes on survival and early growth of ponderosa and Jeffrey pine. Jour. Forestry 51: 504-507.

GODDARD, R. E., BROWN, C. L., and CAMPBELL, T. E.
1959. An evaluation of growth and form in 5-year-old open-pollinated progeny from selected loblolly pine. South. Forest Tree Impr. Conf. Proc. 5: 35-43.

GOGGANS, J. F.
1949. Cronartium fusiforme on slash and loblolly pine in the Piedmont region of Alabama. Jour. Forestry 47: 973-980.

______ 1957. Southern fusiform rust. Agr. Expt. Sta., Ala. Polytech. Inst. Bul. 304, 19 pp., illus.

GRAVES, A. H.
1948. Forest tree breeding. Econ. Bot. 2: 284-305.

HARMS, WILLIAM R.
1961. Growth of fusiform cankers on young slash pine. U. S. Forest Serv. Southeast. Forest Expt. Sta. Res. Notes 159, 2 pp.

HARTLEY, C.
1927. Forest genetics with particular reference to disease resistance. Jour. Forestry 25: 667-686.

HAZEL, L. N., and LUSH, J. L.
1943. The efficiency of three methods of selection. Jour. Hered. 33: 393-399.

HELBACK, H.
1959. Domestication of food plants in the old world. Science 130 (3372): 365-372.

HENRY, B. W., and BERCAW, T. E.
1956. Shortleaf-loblolly hybrid pines free of fusiform rust after 4 years exposure. Jour. Forestry 54: 779.

HITT, R. G.
1952. Forest tree breeding in Sweden and other European countries. Jour. Forestry 50: 924-928.

HOUGH, A. F.
1952a. Preliminary results of red pine seed source tests in northwest Pennsylvania. U. S. Forest Serv. Northeast. Forest Expt. Sta. Paper 49, 28 pp., illus.

———— 1952b. Relationships of red pine as to seed source, seed weight, seedling weight, and height growth. U. S. Forest Serv. Northeast. Forest Expt. Sta. Paper 50, 14 pp., illus.

HOUTZAGERS, G.
1952. Forest genetics and poplar breeding in the Netherlands. I. The difference between breeding work in forestry and agriculture and horticulture. II. Poplar, etc. Euphytica 1: 10-14, 161-174.

INMAN, L. L.
1959. The divergent points of view of forest geneticists and of agronomic and horticultural crop breeders. Jour. Forestry 57: 375-377.

IRGENS-MOLLER, H.
1955. Forest-tree genetics research: Quercus L. Econ. Bot. 9: 53-71.

JEFFERS, J. N. R.
1954. Statistical methods in forest research. Internatl. Union Forest Res. Organ. Cong. Proc. 11: 593-600.

JOHNSON, A. G.
1954. Juvenile selection criteria. Northeast. Forest Tree Impr. Conf. Proc. 1: 75-77.

JOHNSON, H. W., ROBINSON, H. F., and COMSTOCK, R. E.
1955. Estimates of genetic and environmental variability in soybeans. Agron. Jour. 47:314-318.

JOHNSSON, H.
1951. Avkommor av masurbjörk. [Progeny of curley birch.] Svenska SkogavFören. Tidskr. 49 (1): 34-45. [Forestry Abs. 13: 158, 1123 (1952).]

KIELLANDER, C. L.
1956. Über eine söttreibende Rasse von Picea abies in Schweden und eine Schwierigkeit bei der Plusbaumwahl. [On a late-flushing provenance of cultivated Picea abies in Sweden and a difficulty in plus tree selection of the same species.]] Ztschr. f. Forstgenetik u. Forstpflanzenziicht. 5: 181-185.

——— 1957. Förbandet och rasen. [Planting distance and race.] Skogen. 44: 5'78-581. [Plant Breeding Abs. 28: 154, 966 (1958).]

KLEINSCHMIT, R.
1955. Einzelstammabsasten von Plusvarianten der europäischen Lärche (Larix decidua Miller) aus frei abgeblühtem Saatgut als Hilfsmittel zur Beurteilung der Erbanlagen. [The use of single-tree progenies of plus variants of L. decidua raised from free-pollinated seed, as a means of assessing inherited characteristics.] Ztschr. f. Forstgenetik u. Forstpflanzenziicht. 4: 1-15.

——— 1959. Eine mendelspaltung bei der europäischen Lärche. [A Mendelian segregation in European larch.] (Abs.) Silvae Genetica 8: 124.

KOEHLER, A.
1939. Heredity versus environment in improving wood in forest trees. Jour. Forestry 37: 683-687.

LARSEN, C. S.
1947. Estimation of the genotype in forest trees. Aarsskr. Vet. Landbohojsk. 1947, pp. 87-128.

——— 1956. Genetics in silviculture. [Translated by Mark L. Anderson.] 224 pp., illus. Edinburgh: Oliver and Boyd.

LAURIE, M. V., and GRIFFITH, A. L.
1941. The problem of the pure teak plantation. Indian Forest Res. (N. S.) Silviculture 5: 13-121.

LIESE, J.
1936. Zur Frage der Vererbbarkeit der rindenbewohnenden Blasenrostkrankheiten bei Kiefer. [Crossing proved heritable character resistance to Peridermium pini or Cronartium asclepeadeum. I Z. Forst-u. Jagdw. 68: 602-609.

LINDQUIST, B.
1948. Genetics in Swedish forestry practice. 173 pp., illus. Waltham, Mass.

LINES, R.
1955. Variation in branch form in the progeny of individual Japanese larch trees. Jour. Forestry Comm. 24: 48-50.

LUBJAKO, M. N.
1941. [Selection of quick-growing forms among local forest species.] Lesnoe Khozjaistvo (Forestry) 1941 (5): 28-32. [Plant Breeding Abs. 12: 168, 599 (1942).]

LUTZ, H. J., SCHREINER, E. J., BEAL, J. A., and others
1958. The place of tree improvement in forest pest control; panel discussion. Soc. Amer. Foresters Proc. 1957: 50-60.

McWILLIAM, J. R., and FLORENCE, R. G.
1955. The improvement in quality of slash pine plantations by means of selection and cross breeding. Austral. Forestry XIX (1): 8-12.

MATZINGER, D. F., SPRAGUE, G. F., and COCKERHAM, C. C.
1959. Diallel crosses of maize in experiments repeated over locations and years. Agron. Jour. 51: 346-350.

MERGEN, F.
1953. Gum yields in longleaf pine are inherited. U. S. Forest Serv. Southeast. Forest Expt. Sta. Res. Notes 29, 2 pp.

______ 1955. Inheritance of deformities in slash pine. South. Lumberman 190 (2370): 30-32.

MEYER, H.
1954. Zur blasenrost-resistenzziichtung mit Pinus strobus. [Blister-rust-resistance breed-ing with Pinus strobus.] Ztschr. f. Forstgenetik u. Forstpflanzenziicht. 3: 101-104.

MINCKLER, L. S.
1939. Genetics in forestry. Jour. Forestry 37: 559-564.

______ 1942. One-parent heredity tests with loblolly pine. Jour. Forestry 40: 505-506.

MITCHELL, H. L.
1956. Breeding for high-quality wood. U. S. Forest Serv. Forest Prod. Lab. Rpt. 2050, 9 pp.

MÜLDER, D.
1955. Beitrag zur Individualauslese bei der Blasenrost -Resistenzzüchtung mit Pinus strobus. [Contribution to individual selection of blister rust resistance of Pinus strobus.] Ztschr. f. Forstgenetik u. Forstpflanzenziicht. 4: 89-99.

NELSON, T. C.
1952. Early competition in slash pine plantations. U. S. Forest Serv. Southeast. Forest Expt. Sta. Res. Notes 10, 2 pp.

NORTH CAROLINA STATE COLLEGE, SCHOOL OF FORESTRY
1958. Second annual report, N. C. State-industry cooperative forest tree improvement program. 18 pp., illus.

PANSE, V. G.
1940. Application of genetics to plant breeding. II. The inheritance of quantitative characters and plant breeding. Jour. Genet. 40: 282-302.

PATTON, R. F.
1961. The effect of age upon susceptibility of eastern white pine to infection by Cronartium ribicola. Phytopathology 51: 429-434.

PAULEY, S. S.
1951. Increasing solar energy conversion efficiency in forest trees by the application of genetics. Amer. Acad. Arts and Sci. Proc. 79: 221-22'7.

PAWSEY, C. K.
1960. Heredity in relation to some disorders and defects of Pinus radiata (D. Don) in South Australia. Austral. Forestry XXIV (1): 4-7.

PEARSON, G. A.
1944. Applied genetics in forestry. Science 58 (6): 444-453.

PETER-CONTESSE, J.
1941. Hérédité et sélection. Jour. Forestry Suisse 92: 121-126.

QUEENSLAND FOREST SERVICE
1950. Breeding exotic pines in South Queensland. Rep. 1949-50 (7). [Forestry Abs. 12: 425, 2683 (1951).]

RICHENS, R. H.
1945. Forest trees breeding and genetics. Commonwealth Bur. Plant Breeding and Genet. , Cambridge, Pub. 8, 79 pp.

RIGHTER, F. I.
1945. Pinus: the relationship of seed size and seedling size to inherent vigor. Jour. Forestry 43: 131-137.

RIKER, A. J.
1954. Opportunities in disease and insect control through genetics. Jour. Forestry 52: 651-652.

_____ and KOUBA, T. F.
1940. White pine selected in blister-rust areas. Phytopathology 30: 20.

_____ KOUBA, T. F. , and BRENER, W. H.
1949. Selecting white pine for resistance to blister rust. Phytopathology 39: 20.

_____ KOUBA, T. F. , BRENER, W. H., and BYAM, L. E.
1943. White pine selections tested for resistance to blister rust. Jour. Forestry 41: 753-760.

ROESER, J., Jr.
1926. The importance of seed source and the possibilities of forest tree breeding. Jour. Forestry 24: 38-51.

ROHMEDER, E.
1956. Professor Münchs Anbauversuch mit Douglasien verschiedener Herkunft und anderen Nadelbaumarten im Formstamt Kaiserslautern - ost 1912 bis 1954. [Experimental plantations of Douglas-fir of different provenances and of other conifers established by Prof. Münch at the Forest District of Kaiserlautern - East between 1912-1954.] Ztschr. f. Forstgenetik u. Forstpflanzenziicht. 5: 142-155.

RUDOLPH, T. D., SCHOENIKE, R. E., and SCHANTZ -HANSEN, T.
1959. Results of one-parent progeny tests relating to the inheritance of open and closed cones in jack pine. Univ. Minn. School of Forestry Note 78, 2 pp.

SCHMIDT, H.
1952. Die Verzweigungstypen der Fichte (Picea abies L.) und ihre Bedeutung für die forstliche Pflanzenziichtung. [The branching types of spruce (Picea abies L.) and their importance for forest-tree-breeding.] Ztscbr. f. Forstgenetik u. Forstpflanzenzücht. 1: 81-91.

SCHMIDT, W., and STERN, K.
1955. Methodik und Ergebnis eines Wachstumsvergleichs an vier zwanzigjährigen Kiefernversuchsflächen. [Methods and results of a comparison of growth in four 20-year-old pine trial plots.] Ztschr. f. Forstgenetik u. Forstpflanzenzilcht. 4: 38-58.

SCHREINER, E. J.
1938. Improvement of forest trees. U. S. Dept. Agr. Yearbook 1937, pp. 1242-1279.

_____
1939. Some ecological aspects of forest genetics. Jour. Forestry 37: 462-465.

_____
1958. The possibilities and limitations of selection and breeding for pest resistance in forest trees. Soc. Amer. Foresters Proc. 1957: 50-52.

SCHRÖCK, O.
1951: Beitrag zur Methodik der Leistungsprüfungen in der Forstpflanzenziichtung (Vorläufige Mitteilung). [A contribution to the technique of performance tests in forest tree breeding.] Züchter 21: 368-370. [Plant Breeding Abs. 2.2: 451, 2264 (1952).]

______ 1956. Problematik bei der Anwendung von Frühtesten in der Forstpflanzenziichtung. [Problems in the application of juvenile tests in forest-tree breeding.] Züchter 26: 270-276. [Plant Breeding Abs. 27: 363-364, 2256 (1957).]

______ and STERN, K.
1952. Untersuchungen zur Frühbeurteilung der Wuchleistung unserer Waldbäume, zugleich ein Beitrag zur Pappelzüchtung. [Investigations on early determination of growth capacity in our forest trees, also a contribution to poplar breeding.] Ziichter 22: 134-143. [Plant Breeding Abs. 22: 610, 3014 (1952).]

SCHÜTT, P.
1952. Über Aussichten und erste Massnahmen einer züchterischen Bekämpfung der Kiefernschiitte. [Prospects and initial measures for controlling Lophodermium pinastri on pine by breeding.] Allg. Forstzeitschr. 12 (2): 13-15. [Plant Breeding Abs. 29: 875-876, 4518 (1959).]

______ 1958. Ziichtung mit Kiefern. I. Individualunterscheide und Provenienzversuche. [Pine breeding. I. Individual differences and provenance trials.] Mitt. Bundesforschanst. f. Forst-u. Holzw. No. 40, 65 pp.

______ 1959. Ziichtung mit Kiefern. II. Kreuzungen, Resistenzzilchtung und Zytologie. [Pine breeding. II. Crossing, resistance breeding and cytology.] Mitt. Bundesforschanst. f. Forst-u. Holzw. No. 42, 40 pp.

SHIUE, C-J. , and PAULEY, S. S.
1961. Some considerations on the statistical design for provenance and progeny tests in tree improvement programs. Forest Sci. 7: 116-122.

SIGGERS, P. V.
1955. Control of the fusiform rust of southern pines. Jour. Forestry 53: 442-446.

SMITH, II. H.
1944. Recent studies on inheritance of quantitative characters in plants. Bot. Rev. 10: 349-382.

SNEDECOR. G. W.
1956. Statistical methods. Ed. 5. 534 pp. , illus. Ames, Iowa: The Iowa State Col. Press.

SNYDER, E. B.
1959. Comments on "The divergent points of view of forest geneticists and of agronomic and horticultural crop breeders." Jour. Forestry 57: 666-668.

SPAHLINGER, D.
1957. Zur Frage der erblichen Feinastigkeit der Kiefer. [Fineness of branches as a hereditary character in pine.] Forst-u. Holzw. 12 (14): 233-237. [Forestry Abs. 19: 24, 108 (1958).]

SQUILLACE, A. E., and BINGHAM, R. T.
1954. Breeding for improved growth rate and timber quality in western white pine. Jour. Forestry 52: 656-661.

______ and BINGHAM, R. T.
1960. Heritability of juvenile growth rate in western white pine. (Abs.) Soc. Amer. Foresters Proc. 1959: 40.

STERN, K.
1952. Möglichkeiten zur Kennzeichnung von Differenzen in der Verteilung der Höhen bei Kiefernselektionsversuchen v. Wettsteins. [Possibilities of detecting differences in the height distribution in v. Wettstein's pine selection experiments.] Ziichter 22: 180-189. [Plant Breeding Abs. 23: 137, 693 (1953).]

STRAND, L.
1952. Progeny tests with forest trees. Hereditas 38: 152-162.

______ 1955. Plot sizes in field trials. Ztschr. f. Forstgenetik u. Forstpflanzenzücht. 4: 157-162.

STUBBE, H., and SCHMIDT, W., Editors
1957. Die Fri.&diagnose in der Ziichtung und Ziichtungsforschung; Beiträge zur Methodik der Ziichtung langlebiger Pflanzen. [Early diagnosis in breeding and breeding research: Contributions to the methodology of the breeding of longliving plants.] Ziichter Sonderheft 4: l-100. (Special issue.)

SUNESON, C. A.
1960. Genetic diversity - A protection against plant diseases and insects.+ Agron. Jour. 52: 319-321.

THÜMMLER, K.
1958. Beobachtungen an 6 jährigen Nachkommenschaften freiabgeblühter Einzelstämme von Pinus contorta Douglas (Pinus murrayana Balfour) verschiedener Herkunfte. [Observations on 6-year-old progeny of open-pollinated trees of Pinus contorta Douglas (Pinus murrayana Balfour) from various origins.] Arch. f. Forstw. 7 (10/11): 862-873.

TODA, R.
1956. On the crown slenderness in clones and seedlings. Ztschr. f. Forstgenetik u. Forstpflanzenzücht. 5: l-5.

______ 1958. Variation and heritability of some quantitative characters in Cryptomeria. Silvae Genetica 7: 87 -93.

______ NAKAMURA, K., and SATOO, T.
1959. The heritability of tree height and stem girth in Cryptomeria through sexual reproduction. Silvae Genetica 8: 43-49.

TOUMEY, J. W.
1914. Influence of the source of seed upon the character of forest growth. Soc. Amer. Foresters Proc. 9: 107-113.

UNION OF SOUTH AFRICA, DEPARTMENT OF FORESTRY
1948. Pine genetics. Rep. Dept. Forestry South Africa, 1946-7, 1947 (6). [Forestry Abs. 10: 466, 2455 (1948-1949).]

U. S. FOREST SERVICE
1960. Report of forest and windbarrier planting in the United States 1960. Tree Planters' Notes 44, 14 pp.

VAN ARSDEL, E. P., RIKER, A. J., KOUBA, T. F., and others
1961. The climatic distribution of blister rust on white pine in Wisconsin, U. S. Forest Serv. Lake States Forest Expt. Sta. Paper 87, 34 pp., illus.

WETTSTEIN, W.
1949. Selektion von Kiefern nach 4 Jahren. [Selection of pine within 4 years.] Ziichter 19: 205-206. [Forestry Abs. 12 (3): 284, 1765 (1951).]

WRIGHT, J. W., and FREELAND, F. D.
1959. Plot size in forest genetics research. Mich. Acad. Sci., Arts, and Letters Papers 44 (1): 177-182.

ZAK, B.
1957. Resistance to littleleaf in shortleaf pine. South. Forest Tree Impr. Conf. Proc. 4: 41-43.

ZOBEL, BRUCE J., and HAUGHT, ALDIN E., Jr.
1962. Effect of bole straightness on compression wood of loblolly pine. N. C. State Col. School Forestry Tech. Rpt. 15, 13 pp., illus.