THE GENETIC AND ENVIRONMENTAL BASIS OF
FRUITFULNESS AND GROWTH IN LOBLOLLY PINES

By

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Genetic and environmental variation in fruitfulness in loblolly pines (Pinus taeda L.) were examined in clones and seedlings.

In a young loblolly pine seed orchard in south Mississippi clonal variation was substantial. Over 50% of the variation in female flowering, cone production, and seed production, and about 40% of the variation in male flowering was attributable to genetic effects. The broad-sense heritability for female flowering varied over time, however, increasing at first to about 0.6 at 8 years of age and declining thereafter. The decrease in heritability was mainly due to a large increase in environmental variation after the 8th year.

Although the more fruitful clones tended to be fruitful every year, significant year x clone interactions were found. The top 20% of seed producing clones was not the same every year. Year x clone interactions in male flowering also indicated that the genetic makeup of seeds collected from year to year may vary considerably, even if collected separately by clone.

Flowering was inversely related to height and diameter growth, as flowering was best on soils where growth was poorest. Yearly variation in flowering also could be related to moisture stress, as a drought during the strobilus initiation period seemed to favor abundant flowering the following year. This was true of male as well as female flowering, but the response to drought differed with respect to timing. Male flowering was favored by an early summer drought (May-June) and female flowering was favored by a late summer drought (July-August). It was proposed that moisture stress exerts its effect by causing a cessation of vegetative growth coinciding with the time of flower induction, thus allowing floral initials to form.

Genetic variation in average amount of flowering was very strong among families in a diallel, and most of the variation was additive. Diallel analysis and parent-progeny regressions yielded narrow-sense heritability estimates of 0.61 and 0.52, respectively. The inheritance in flowering at age 2, or precocity, was not as strong as that of average flowering, being only 0.13 on an individual basis and 0.47 on a family basis. Flowering traits were negatively correlated with growth traits, indicating that selection for average flowering or precocity alone would result in some growth loss. The results of a half-sib progeny test incorporating precocious individuals, however, indicated that selection for both precocity and growth could be profitable.

SECTION I

GENETIC AND ENVIRONMENTAL VARIATION IN FRUITFULNESS IN A LOBLOLLY PINE SEED ORCHARD

Introduction

The goal of any tree improvement program is the production of genetically superior trees. At present, southern pine plantations are established with seedlings (rather than vegetative propagules); and the tree improvement method commonly used is to establish clonal seed orchards by grafting scions from phenotypically superior trees onto seedling rootstocks. Traits such as growth, form, and quality of the parent trees selected for the production of seed in either type of orchard, clonal or seedlings, are of prime importance. However, fruitfulness also is important because the selections or their progeny need to produce seed in sufficient quantities for the tree improvement program to be successful.

A related factor influencing seed quality is pollen production of the orchard trees. Breeders assume that most of the pollen effecting fertilization in orchards will originate within the orchard. If not, the realized genetic gain will be greatly reduced. Very little is known about pollen production, for a major part of genetics research has been done on female flowering and seed production. Although it has been assumed that pollen from within the orchard will be adequate for good pollination, this has not been so in many cases, perhaps because conditions which were optimum for seed production may not have

been optimum for pollen production. Very small amounts of pollen are required for controlled crosses in progeny tests. Often even these small quantities are unavailable from some clones, making completion of progeny tests very difficult.

Thus a major problem in tree improvement programs is the development of an understanding of the inherent and environmental conditions contributing to variation in flowering, pollination, and seed production in southern pine orchards.

Flowering and seed yield data collected from a loblolly pine (Pinus taeda L.) seed orchard over a period of several years were examined in this report. The objectives of the study were to:

1. determine the extent of genetic control of male and female flowering and their intercorrelations;
2. determine the year-to-year consistency of clonal differences in flowering to evaluate the importance of yearly variation in genetic worth of the seed produced and to examine the predictive value of early flowering data;
3. examine environmental variation in flowering and its relationship to growth, to provide information on suitable conditions for optimizing orchard output.

Literature Review

The emphasis of this review is on genetic and environmental effects on flowering in conifers from an applied point of view. The role of growth regulators, especially gibberellins (Pharis 1976), is surely important, because they probably play a central role in floral initiation, but is not directly pertinent to this research report.

Genotypic Variation

It is generally recognized that large differences exist in fruitfulness between southern pine clones. This is considered a serious problem in seed production since often only a few clones in an orchard produce most of the seed. Bergman (1968) estimated that 2 of 15 clones produced over half of the seed in a loblolly pine orchard. Others estimated that 20% of the clones produced 80% of the seed (N.C. State University 1976). A less pessimistic estimate was provided by Beers (1974) who found that the top 20% of clones in seed production produced 56% of the seed in a slash pine (P. elliotii Engelm.) orchard. Danbury (1971) estimated that seed production could be increased by 50% and seed cost reduced by one-third if only the most productive half of the clones available in a radiata pine (P. radiata D. Don) seed orchard in Australia were retained. He assumed that growth and fruitfulness were weakly, if at all, correlated genetically. Inherent fruitfulness can be especially important, since as a general rule trees which are inherently unfruitful do not respond as well to treatments as do fruitful trees (Bergman 1968).

The inherent ability of the individual tree to flower is probably the most important factor influencing fruitfulness (Schmidtling 1974, Shoulders 1967). It is important to consider this variation in the design of experiments. In several fertilizer experiments, from 33% (Schmidtling 1974) to 56% (Schmidtling 1975) of the total variation in fruitfulness was attributable to clonal effects, even though the treatment effects were large and significant. Broad-sense heritability

estimates for fruitfulness of 0.50 for slash pine (Varnell et al. 1967) and 0.4 to 0.7 for loblolly pine (Schmidtling 1974) reinforced this observation.

There is a general consensus that inherent variation in male flowering is also large, but the effects seldom are quantified. Male strobilus production is more difficult to measure than female, because pollen catkins do not persist after pollen is shed and counts must be timely. They are also relatively numerous, and thus costly to count. Barnes and Bengtson (1968) and Schultz (1971) found strong clonal effects on male flowering in a slash pine fertilization and irrigation study. Webster (1974) also observed strong clonal effects on male flowering in a loblolly pine orchard.

Most studies have shown that male and female flowering were not closely related. Stern and Gregarius (1972) found that the correlation between male and female flowering was very weak. Schultz (1971) found a slightly negative genetic correlation between male and female flowering in slash pine. This weak relationship between male and female flowering is an important consideration in seed orchard management. If we follow Danbury's (1971) suggestion and rogue 50% of the clones on the basis of seed production, we might very well eliminate some of the best pollen producers in the orchard, subsequently narrowing the genetic base and perhaps eliminating some of the better genotypes.

The physiological basis for genetic differences has not been determined, though Smith and Stanley (1967) showed that high cone producing trees had higher N concentrations in needles than low cone

producers in response to N fertilizers. Considering all the observed genotype x treatment interactions, a simple explanation does not seem warranted. In general, the better flowering trees responded well to fertilizers and the poorer trees responded poorly or not at all (Bergman 1968, Schmidtling 1974, 1975). Deviations from this have been noted. In addition to the kinds of response noted above, it has been observed that some relatively unfruitful trees responded well to fertilizers and some very fruitful trees did not (Schmidtling 1974, 1975). Beers (1974) noted large differences among clones in response to level of fertilizer, which lead him to suggest that individual clones should be fertilized on a "prescription" basis. It appears that the limiting physiological factor for flowering might differ considerably by genotype.

Environmental Variation

A large volume of literature exists that relates fruitfulness in conifers to environmental variables (primarily those induced by experimental means). Reviews by Jackson and Sweet (1972) and Puritch (1972) give comprehensive coverage of the literature up to 1972.

The complex nature of the relationship between environmental variation, either natural or induced, and flowering is clearly evident in these reviews and in subsequent work. Many conditions or treatments which promote flowering in conifers are those which promote the overall growth and vigor of the tree, such as fertilization, thinning, and increased insolation. On the other hand, treatments such as girdling, moisture stress, root pruning or restriction, and poor mineral nutrition which are detrimental to growth and vigor also promote flowering.

The greatest amount of research deals with fertilization and mineral nutrition and their relationships to flowering. Management plans for all southern pine seed orchards now include fertilization, especially with N, as it is assumed that this will be necessary to induce and maintain high levels of seed production. This assumption has a sound basis in past research.

Puritch (1972) tabulated 25 references in which fertilizers were applied to conifers. In all but three, fertilizers stimulated female strobilus production. All 22 of the successful experiments included N in the fertilizer. Nitrogen appeared to be the key fertilizer component. An impressive number of studies showed a positive response to N alone (Smith et al. 1968, Holst 1959, Barnes and Bengston 1968, Cayford and Jarvis 1967, Stephens 1961, Giertych and Forward 1966, Schultz 1971, Ebell 1967, 1972, Morris and Beers 1969, Stoate et al. 1961, Barnes 1969, Goddard and Strickland 1966, Kraus 1925, Beers 1974).

Relatively few experiments distinguished the effects of each component in fertilizer combinations of N, P, and K; and research on nutrients other than these three has been lacking. In an NPK factorial experiment with slash pine, Morris and Beers (1969) found that only N stimulated flowering. Similarly, Goddard and Strickland (1966) reported that N was of great importance, but that P and K also had some effect when combined with N. Phosphorous and K applied without N, however, depressed flowering. In an N-P factorial test conducted in a loblolly pine seed orchard, ammonium nitrate tripled female strobilus production, P had no effect, and the N + P treatment produced the same number of female strobili as N alone (Schmidtling 1975). On the other hand,

Giertych (1973) observed that only K, in an NPK factorial, stimulated female strobilus production in Scots pine (P. sylvestris L.). In 1968, van Buijtenen reported that P increased flowering in loblolly pines and that N alone or in combination with P actually depressed flowering. Although fertilization research has strongly supported a positive role for N, under some conditions other nutrients may be important.

Analyses of tissue N in conifers also has demonstrated a positive role for N in flowering. Smith and Stanley (1967) and Smith et al. (1968) found that good cone producers had a higher proportion of N in their foliage than poor cone producers. Barnes and Bengston (1968) showed that fertilizing with ammonium nitrate, which doubled female flowering, increased N content, free arginine, and total amino acids in twigs. However, N content per se may not be important. Ebell and McMullan (1970) found that nitrate N and ammonium N increased foliar N content and shoot growth in Douglas-fir (Pseudotsuga menziesii [Mirb.] Franco) by similar amounts, but only nitrate-N increased female flower production. Free arginine content was greater in nitrate-treated trees than in the others and appeared to be quantitatively associated with increased flower production.

In contrast to the voluminous research that showed increased flowering related to fertilization and nitrogen content, several reports have related nutrient deficiencies to enhanced flowering. Lyr and Hoffman (1964) were able to induce flowering in Cryptomeria japonica D. Don seedlings by inducing nitrogen deficiency. Kuo (1973) and Kamienska et al. (1973) observed precocious flowering in N deficient Cupressus arizonica Greene seedlings. Sweet and Will (1965) found that precocious

male flowering in radiata pine was associated with low nutrient status. Giertych (1975) examined the mineral distribution in crowns of Scots pine and concluded that female flowers were initiated under conditions of mineral deficiency. Thus, it seems uncertain that mineral nutrition is truly a limiting factor.

Thinning has been an established silvicultural procedure to increase growth, and also has been one of the principal methods to increase cone production. The effects of thinning on fruitfulness have been well documented and were assumed to be associated with increased light, moisture, and minerals. The initial response to thinning may have been due to some kind of stress induced by an abrupt change in environment. Change has not always been necessary, however, as spacing trials in red pine (P. resinosa Ait.) showed that cone production was inversely related to competition (Stiell 1971). The increased light intensity and temperature have been the most likely candidates for thinning effects; but it has been difficult to separate the two, since increasing insolation nearly always increases temperature. The positive role of light and temperature has been supported by climatic associations with cone crops in conifers. Warm, sunny weather during flower induction favored good flower crops (Eis 1973, 1976, Zasada et al. 1976, La Bastide and Van Vredenburch 1970). Also, the distribution of cones within the crowns of slash pines was strongly related to insolation (Smith and Stanley 1969). Increasing temperature without increasing light was effective in experiments involving transfer of Picea sitchensis (Bong.) Carr. to greenhouses (Tompsett and Fletcher 1977) or covering field-grown P. abies L. Karst. with polyethylene (Chalupka and Giertych 1977).

Giertych (1976) surmised that high air temperature favored both male and female flowering whereas high light intensity favored only female flowering.

In addition to the experimental association between vigor-increasing treatments and flowering, increased flowering has been associated with various other manifestations of vigor in conifers, such as tree size (Andersson and Hattemer 1975, Schmidtling 1969), crown size (Grano 1957, Cappelli 1958), shoot size (Varnell 1970, K. J. Lee 1978), and branch order (Thorbjornsen 1960, Rim and Shidei 1974). Treatments which had an obvious deleterious effect on growth and vigor also were associated with increased flowering. For example, girdling, strangulation, and binding were used to effect flowering. These treatments were undoubtedly stressful, as girdled shoots or trees often died. The immediate effects were not much different from increased insolation, however, as carbohydrate accumulated above the girdle (Ebell 1971, Hashizume 1970).

Root pruning or root restrictions and moisture stress have also increased flowering, but linking these treatments to carbohydrate accumulation was difficult. Root pruning (subsoiling) done in June reduced the current year's diameter growth, but increased both male and female flowering in Virginia pines (P. virginiana Mill.) (Greenwood and Schmidtling 1980). Similarly, transplanting red pines into pots and continued confinement greatly increased male and female flowering (Quirk 1973). Confinement in pots has a well-known negative effect on growth, even if water and nutrients are optimum.

Drought, although obviously deleterious to growth, has been shown to promote fruitfulness, especially if it occurs approximately at the time of floral initiation. Matthews (1963) listed a number of references to climatic studies which have shown this to be true in many woody plant species, and experimental evidence in loblolly pines was provided by Dewers and Moehring (1970).

Shoulders (1973) found that abundant rainfall early in the year followed by a drought increased flowering in slash pines. He proposed that the early rains favored luxuriant vegetative growth, thereby increasing photosynthetic capacity. Mild moisture stress in summer curtailed further vegetative growth, allowing the accumulation of carbohydrate necessary for floral initiation. This is an attractive hypothesis, as it can be used to explain how treatments which increase vigor and those which decrease vigor can both have promotive effects on flowering.

Greenwood (1978) believed that the presence of a "quiescent" bud is necessary for an extended period of time during the growing season to form strobilus initials, and that one of the reasons seedlings do not flower is that growth is continuous and a quiescent bud does not exist. He induced bud quiescence by shortening photoperiod and lowering temperature in early spring in very young loblolly pines. A large number of strobili were subsequently produced, when none would otherwise have been expected. Rudolph (1979) noted female strobili but little additional shoot elongation on 12-month-old jack pine (P. banksiana Lamb.) which had been grown under optimum conditions for

10 weeks in the greenhouse, and subsequently transplanted to nursery beds in July. In this case, "quiescence" was induced by transplant shock.

In the studies relating mineral deficiencies to increased flowering (Lyr and Hoffman 1964, Kuo 1973, Kamienska et al. 1973, Sweet and Will 1965, Giertych 1975), nutrient deficiencies observed may not have been the cause. The treatments probably caused an early cessation of growth, allowing a "resting" bud during the growing season on which initials were able to form. Thus, many of the conflicting results relating both growth-promoting and growth-retarding conditions to increased flowering can be resolved.

Materials and Methods

The study area was a seed orchard, maintained by Region 8 of the U.S. Forest Service, located in south Mississippi about 25 miles (40 km) southeast of Hattiesburg. The orchard consisted of ramets from 50 superior loblolly pine selections located on the National Forests in south Mississippi. There were about 4,000 ramets of these clones planted at 15 x 30 foot (4.6 x 9.1 m) spacing.

The ortets ranged from 31 to 67 years of age as determined by increment cores. More than half were between 43 and 54 years of age. All were reproductively mature, as one criterion for selection was "some evidence of cone production," when selected or after release and fertilization. The orchard site was cleared of second growth long-leaf pine (P. palustris Mill.) in 1961. The area was hilly, as the

elevation varied a maximum of 65 feet (19.8 meters). Loamy sands of five different series made up the soils in this planting, ranging from an Iuka loamy sand at lower elevations near a spring-fed stream to a McLaurin sandy loam on the somewhat droughty ridges. A preliminary soil analysis indicated that the soils were all rather low in NPK. The soils at lower elevations were generally lower in available P, higher in total N and organic matter, more acid and generally wetter than those at higher elevations (Table 1-1).

The orchard was established from 1963 to 1972 using potted grafts on nursery-run rootstock. Only a few of the clones were represented among the ramets established the first 3 years, but in 1966 and 1967 more than 1,000 ramets, well distributed over the 50 clones, were planted each year. Grafts were planted in 1968 through 1972 to fill in vacant spots and were also well distributed over the 50 clones, but with very few ramets per clone.

Male and female flowering, height, and D.B.H. of all ramets were measured at irregular intervals starting in 1969. Table 1-2 summarizes the measurements that were taken. Elevation above the stream was also estimated for all ramets.

The clonal composition varied greatly depending on the year of grafting. The total set of data was highly unbalanced, so each age group was analyzed separately. The data thus broken down by year were simplified into a group of nested designs:

<u>Source of variation</u>	<u>Expected mean squares</u>
Clone	$\sigma_w^2 + K\sigma_c^2$
Ramet/clone	σ_w^2

Table 1-1. Chemical analysis of soil samples taken from two portions of the Erambert orchard in 1972.

Constituent	Location	
	Lower elevation	Ridge
Organic matter (%) ¹	1.116	0.819
Total nitrogen (%) ²	0.0284	0.0185
pH ¹	5.3	5.5
Extractable phosphorous (ppm) (Bray II) ³	3.8	4.1
Exchangeable potassium (ppm) ¹	35	36

¹Jackson (1958)²Bradstreet (1965)³Bray and Kurtz (1945)

Table 1-2. Dates on which various traits were measured on all orchard ramets (indicated by "X").

Parameter	Year measured					
	1969	1970	1971	1972	1973	1976
Female strobili	X	X	X	X	X	X
Male strobili clusters		X	X	X	X	X
Cones	X	X	X	X	X	X
Stem height		X		X	X	X
Stem D.B.H.				X	X	X

"K" is the harmonic mean number of ramets in clones (Becker 1967). The genetic model is also very simple. The clonal component of variance, σ_c^2 , represents the genetic effect, and heritability is calculated:

$$h^2 = \frac{\sigma_c^2}{\sigma_c^2 + \sigma_w^2}$$

The model for computing genetic and environmental correlations between measured traits is similarly constructed. Since the ramets are vegetatively propagated, the clonal variance component contains all genetic variation, nonadditive as well as additive. The heritabilities derived are therefore broad-sense.

The number of ramets per clone in each age group varied widely, so 10 ramets grafted in 1966 were selected from each of 18 clones. The selected ramets were evenly spread over the orchard to represent the full range of site variation.

The sample ramets were distributed in the orchard as follows:

1. Lower elevation--three ramets from each clone located on the Iuka soils.
2. Middle elevation--four ramets from each clone on the Benndale soils.
3. Upper elevation--three ramets from each clone on the McLaurin soils.

In addition to the measurements indicated in Table 1-2, the following parameters were measured on the 180 sample ramets:

1. Total seed and sound seed (separated by ethanol flotation) from a five-cone sample taken in the fall of 1976, 1977, and 1978.

2. Weight per 100 seed in 1978.
3. Yearly diameter growth measured from an increment core (cores taken at 3 feet above ground) in fall 1976.
4. Counts of male strobili clusters and female strobili in 1977, 1978, and 1979.
5. Height and D.B.H. in 1977 and 1978.

In addition, depth of the A horizon was measured at three equally spaced points around each ramet, 5 feet from the trunk, with a soil auger. Soil samples from a depth of 10 centimeters (A₁ horizon) and 75 centimeters (B horizon) were bulked from the three locations, and sand, silt, and clay percentages were determined by the Bouyoucos hydrometer method for each depth.

A competition index (C.I.) was computed for each of the 180 sample ramets, based on spring, 1976, D.B.H., measurements of the study tree and the two trees 15 feet (4.6 m) in either direction in the row (between row spacing was 30 feet (9.1 m), and competition at that distance was considered negligible). The index was calculated as:

$$C.I. = \Sigma D.B.H.^2 \text{ (study tree).}$$

This is similar to an index that Daniels and Burkhardt (1975) found effective in describing competition effects on stand development in loblolly pines.

Environmental effects were analyzed in two ways: (1) by classifying the ramets by soil type (or elevational class) and analyzing flowering, height, and D.B.H.; and (2) by using regression and correlation to determine relationships of flowering and growth (as dependent variables) with soils, size of ramet, previous cone crop, etc. (as independent variables).

All count data were transformed to $\sqrt{\text{count} + 0.5}$. Tests of statistical significance were at the 0.05 level of probability.

Results and Discussion

Genetic Variation

Yields for all reproductive structures showed a large general increase with time, as would be expected in a young orchard (Fig. 1-1).

The 180 sample trees seemed to be fairly representative of orchard production, as they followed the production trend for the whole orchard. Large year-to-year variation aside from the general increase in production was evident, especially in female strobili numbers (Fig. 1-1a). There was an exceptionally good crop of female strobili in 1976, not only in this orchard but elsewhere in the area. Production the following year was lower than 1976, but it probably was near average.

Cone production (Fig. 1-1c) followed female flower production, though survival varied considerably, from 80% in 1970 and 1971 to 33% in 1973 and 1977. Male strobili production was very low during the early years, and then expanded tremendously after 1975 (Fig. 1-1b). It increased each year starting in 1976, but decreased in 1979. Female strobili, on the other hand, showed decreases in 1977 and 1978, and an increase in 1979. In comparing the yearly patterns of male and female flowering (Figs. 1-1a and 1-1b), it was evident that the two did not seem to be closely related; that is, the increase or decrease in female flowering did not correspond to an increase or decrease in male flowering.

Female flowering. Broad-sense heritabilities for female strobili production varied considerably from year-to-year (Table 1-3). Heritability seemed to increase sharply with age in the younger material,

Figure 1-1. Yearly variation in production of reproductive structures of loblolly pines at the Erambert Seed Orchard. A. Female. B. Male. C. Cones. Female strobili in 1975 were estimated from 1976 cone counts and 1976-1977 strobilus survival data. Grafts made in 1964 were included to amplify early flowering trends. The Y axis was square-root scale.

Line identities:

0	_____	0:	Entire orchard
S	_____	S:	180 sample ramets
4	_____	4:	1964 grafts

Table 1-3. Broad-sense heritabilities for female flowering by year for different aged grafts.

Year grafted	Clones	Ramets	-----Year examined-----						
			1969	1970	1971	1972	1973	1969-73 average ¹	1976
	No.	No.	-----h ² -----						
63	8	41	0.871	0.687	0.704	0.623	0.420	0.622	0.235
64	13	198	0.600	0.594	0.780	0.673	0.568	0.722	0.345
65	14	56	0.056	0.396	0.527	0.555	0.426	0.490	0.401
66	43	1106	0.326	0.584	0.486	0.595	0.481	0.606	0.441
66 ²	18	180	0.274	0.467	0.270	0.541	0.534	0.593	0.501
67	45	1351		0.268	0.298	0.475	0.370	0.439	0.558
68	34	388		0.477	0.430	0.577	0.304	0.423	0.565
69	34	206			0.204	0.422	0.276	0.356	0.391
70	47	186				0.431	0.299	0.395	0.617

¹This is the heritability of 1969-73 average flowering, not the average of the four heritabilities.

²Sample trees--180.

but then leveled off and perhaps even decreased with age. Curves were fitted to the change in variance with age and are shown in Figure 1-2. Variance and heritability were essentially zero before age 3, as only sporadic flowering occurred before that age. Genetic variance increased very rapidly from age 3 to age 5, and continued to increase but at a slower rate to age 13. Apparently the flowering trait was better expressed among larger trees. The environmental variance increased sharply at first, likely because of the large variation among ramets in graft union formation and in subsequent growth. It leveled off somewhat between ages 5 and 9 as more uniform growth occurred. After age 8 or 9, it increased sharply again, probably due to the large variation in competition among clones. At this age and spacing, 15 x 30 feet (4.6 m x 9.1 m), within-row competition was beginning to have an effect but was not uniform. Some of the ramets had essentially no competition because the ramets on either side were missing or were very small. Others had trees larger than themselves growing on either side. As a consequence, variance increased sharply as ramets were affected by competition in widely varying degrees.

Male flowering. Heritabilities for male strobilus production were lower than for female strobilus production, and more variable (Table 1-4). Significant heritable variation occurred only in the older material, probably due to the low frequency of male flowers before 1976 (Fig. 1-1b). It appeared, however, that eventually the heritability for male flowering would be nearly as high as that for female flowering in older material, probably above 0.4. The heritabilities for male flowering for grafts

Figure 1-2. Change in variance components of female flowering with age. The fitted regression equations for genetic variance ($\hat{\sigma}_g^2$) and environmental variance ($\hat{\sigma}_e^2$) curves and the respective coefficients of determination (r^2) were:

$$\hat{\sigma}_g^2 = 4.55 - 4.05a + 0.98a^2 - 0.07a^3 + .002a^4, \text{ where } a = \text{age in years}$$

$$r^2 = 0.791$$

$$\hat{\sigma}_e^2 = 6.24 - 7.48a + 2.59a^2 - 0.33a^3 + 0.01a^4$$

$$r^2 = 0.785$$

The curve for heritability was computed directly from estimated genotypic and environmental variances:

$$h^2 = \hat{\sigma}_g^2 / (\hat{\sigma}_g^2 + \hat{\sigma}_e^2)$$

The vertical axis is square-root scale.

Line identities:

+++++ : Genetic variance
 ----- : Environmental variance
 ***** : Heritability

Table 1-4. Broad-sense heritabilities for male flowering by year for different aged grafts.

Year grafted	Clones	Ramets	-----Year examined-----					
			1970	1971	1972	1973	1970-73 average ¹	1976
	No.	No.	-----h ² -----					
63	8	41	0.069	0.461	0.364	0.243	0.458	0.433
64	13	198	0.245	0.529	0.611	0.016	0.506	0.407
65	14	56	0 ³	0	0	0	0	0
66	43	1106	0.103	0.129	0.165	0.010	0.111	0.272
66 ²	18	180	0.002	0.102	0.168	0	0.055	0.208
67	45	1351	0.243	0.332	0.232	0.037	0.270	0.364
68	36	388		0	0.115	0.065	0.174	0.434

¹This is the heritability of 1969-73 average flowering, not the average of the four heritabilities.

²Sample trees--180.

³Negative heritabilities were assumed to be zero.

made in 1965 inexplicably were always slightly negative or zero (negative heritabilities were assumed to be zero). Heritabilities for female flowering for these same trees seemed reasonable (Table 1-3). And many, but not all, of the same clones were included in the 1964 grafts where heritability for 1970-1973 average male flowering was computed as 0.506. The range of clonal means for male flowering was much smaller in the 1965 grafts than in the 1964 grafts, however, and probably accounted for the low heritabilities. The 1970-1973 average clonal means for male flowering ranged from 0 to 140 clusters per ramet on the 1964 grafts. But male flowering ranged from 0 to only 20 clusters per ramet on the 1965 grafts. With respect to clonal variation, the 18 clones in the sample population seemed to be fairly representative of the 1966 grafts for both male and female flowering (Table 1-4).

Age and rootstock could bias clonal variation. The age of the ortet influenced growth (Franklin 1969) and flowering (Schmidtling and Griggs 1976) in slash pines. Ortets in this study did not vary greatly in age and were all reproductively mature, so age effects were probably minimal. Correlations based on the 1976 flower crop in the 1966 and 1967 grafts revealed no important age effect, as the correlation between ortet age and female flowering was $r = -0.053$, and between age and male flowering $r = -0.212$. Neither of these was significant at the 0.05 level. There was clearly no age bias in female flowering and very little, if any, in male flowering.

All ramets in this orchard were grafted on nursery-run seedling rootstocks, which surely affected variation in growth and flowering. Schmidtling (1978) found that rootstock variation significantly affected

flowering of loblolly pine grafts. This was true for different species of rootstock as well as different half-sib loblolly families used as rootstocks. Specific clonal reactions to grafting, such as incompatibility, could have increased clonal variation. But the rootstock variation undoubtedly contributed substantially to the within-clone (error or environmental variation), lowering heritabilities. Because of this, true broad-sense heritabilities were likely higher than those observed.

Cone and seed yields. Cone and seed production are even more important aspects of orchard performance than flowering because improved seed are the desired end product of any orchard. In addition to being affected by the same variables involved in production of the female strobili from which they are derived, cone and seed production are further affected by variations in conelet and seed survival. Much of this added variation is caused by insect predation, but other environmental and genetic factors may contribute to it (McLemore 1977).

Genetic variation in cone production was important, as heritabilities of cone counts were in the same range as heritabilities for female flowering. (Cone production figures for any given year should be compared to the previous year's flower production; e.g., the 1970 cone crop originated from the 1969 flower crop, etc.) The heritability estimates approached and sometimes exceeded 0.5 but they were highly variable (Table 1-5). Heritabilities for the 180 sample trees averaged slightly lower than the 1966 grafts as a whole. In addition to those listed in Table 1-5, the heritability estimate for cone production was 0.501 in 1977 and 0.648 in 1978 for the 180 sample trees. The genetic

Table 1-5. Broad-sense heritabilities of cone production, by year for different aged grafts.

Year grafted	Clones	Ramets	-----Year examined-----					
			1969	1970	1971	1972	1973	1976
	No.	No.	-----h ² -----					
63	8	41	0.593	0.808	0.647	0.375	0.154	0.714
64	13	198	0.550	0.523	0.565	0.763	0.244	0.649
65	14	56	0.571	0.396	0.368	0.329	0.154	0.679
66	43	1106	0.083	0.328	0.507	0.405	0.542	0.535
66 ¹	18	180	0.788	0.252	0.429	0.120	0.454	0.454
67	45	1351		0.030	0.238	0.102	0.424	0.534
68	36	388		0.264	0	0.518	0.518	0.300
69	34	206				0.342	0.367	0.368

¹Sample trees--180.

correlation between flowering and subsequent cone crops was high: $r = 0.905$ for 1976 female flowers with 1977 cones, and $r = 0.984$ for 1977 female flowers with 1978 cones. Those clones with the heaviest flower crops produced the most cones.

Conelet survival, i.e., the proportion of female flowers that produced cones, varied widely among clones, and averaged 32.7% for 1976-1977 and 63.8% for 1977-1978 (Tables 1-6 and 1-7). Conelet survival was moderately heritable: $h^2 = 0.356$ for the 1976-1977 crop and $h^2 = 0.453$ for the 1977-1978 crop.

Heavy-flowering clones had a slight tendency to produce a smaller proportion of surviving cones in the 1976-1977 crop, but not in the 1977-1978 crop. Genetic correlation for the 1976 female flower crop, with subsequent survival of that crop, was -0.121 . For the 1977-1978 crop, which was characterized by a smaller flower crop but much better survival, genetic correlation was 0.504 . Possibly the heavier drain on nutrients of the larger crops of developing cones adversely affected survival in a year where the overall crop was heavy. Insect predation could also have explained the difference. This factor was the major cause of conelet abortion in loblolly pine (McLemore 1977).

If insect control was poor in 1976-1977, the trees with larger flower crops could have presented a more favorable situation for insect population development. This would explain the trend for heavier flowering trees to have a smaller percentage of survivors. On the other hand, if insect control was better in 1977-1978, those populations could not have developed as fully in the heavier flowering trees. Consequently,

Table 1-6. Clonal means for flower, cone and seed yield for the 180 sample ramets in 1977.

Clone	1976 female flowers/ramet	Cones/ ramet	Conelet survival ¹	Sound seed/cone	Total seed/cone
	No.	No.	%	No.	No.
A	143.0	41.0	38.5	29.8	36.5
B	102.0	23.8	26.0	26.6	39.8
C	144.0	78.8	62.8	45.6	63.4
D	238.0	87.3	30.8	69.1	79.3
E	41.0	10.8	46.6	49.8	59.0
F	13.0	7.0	59.3	39.2	52.2
G	191.0	120.7	68.5	37.1	47.8
H	103.0	37.2	52.5	42.3	51.1
I	209.6	60.0	34.7	60.0	77.5
J	16.5	7.5	56.7	37.2	43.9
K	65.0	5.0	10.8	50.7	60.4
L	55.0	2.2	26.8	55.3	58.8
M	177.5	26.9	16.4	40.2	48.9
N	21.0	7.3	28.4	24.1	40.5
O	10.0	4.8	57.0	48.1	53.5
P	118.0	22.1	28.3	17.3	25.7
Q	97.0	9.0	14.2	25.6	30.6
R	239.5	97.0	45.9	56.4	81.1
Mean	110.2	36.0	32.7	41.9	52.8
Heritabili- ty	0.501	0.587	0.199	0.298	0.409

¹This column is based on individual tree data. Trees with no flowers were not included, so it is not the same as the percent that would be derived by dividing average 1978 cones per ramet by average 1976 flowers per ramet.

Table 1-7. Clonal means for flower, cone and seed yield for the 180 sample ramets in 1978.

Clone	1977 female flower/ramet	Cones/ ramet	Conelet survival ¹	Sound seed/cone	Total seed cone	Weight of 100 seed
	No.	No.	%	No.	No.	Grams
A	9.2	3.2	30.5	21.7	39.9	3.2
B	15.1	5.3	29.9	11.5	44.8	3.1
C	51.9	17.0	36.8	7.8	33.0	3.8
D	117.9	93.3	82.8	17.9	73.0	3.1
E	14.9	8.6	78.0	39.2	65.7	2.6
F	1.5	0.7	33.3	3.2	35.6	3.0
G	28.0	26.0	92.3	36.5	63.2	2.8
H	59.8	59.1	86.7	26.6	53.6	3.1
I	19.9	14.6	61.0	23.5	53.0	3.2
J	15.1	14.2	64.8	50.8	66.7	3.3
K	17.6	10.0	44.2	39.6	81.5	3.4
L	11.5	4.2	16.6	22.1	50.1	3.5
M	112.0	88.3	69.0	16.2	56.1	4.0
N	16.2	9.8	56.3	33.4	66.4	2.4
O	7.8	4.9	56.4	40.4	61.0	3.1
P	125.5	93.5	69.6	7.5	19.6	2.6
Q	82.1	49.2	52.3	10.8	40.5	3.5
R	275.1	202.9	80.6	11.6	41.0	4.4
Average	54.5	39.2	63.8	23.3	56.4	3.2
Heritabili- ty	0.629	0.618	0.274	0.307	0.268	0.366

there was a positive relationship between flowering and survival. Genetic correlation for conelet survival between the two crops was positive but weak ($r = 0.228$).

Average yields of total seed per cone varied from 42.3 in 1976 (Table 1-3) to 56.4 in 1978. The yield in 1977 (Table 1-6) was similar to that in 1978 (Table 1-7), 52.8 seed per cone. Clones varied widely in total seed per cone all 3 years (Tables 1-6, 1-7, and 1-8), with a three to fourfold difference between those having the largest and those having the smallest yields per cone. Heritabilities were moderately high for total seed per cone (0.241, 0.409, and 0.366 for 1976, 1977, and 1978, respectively).

Yearly averages of sound seed per cone varied much more than the total seed per cone. They ranged from 16 per cone in 1976 to nearly 42 per cone in 1977. Clonal averages of sound seed yields per cone also varied more widely than total seed, especially in 1976 and 1978. During those years there was a tenfold or elevenfold difference among clones. Proportion of total seed which were sound was about 38% in 1976 and 41% in 1978. In 1977, however, nearly 80% of the total seed was sound, and there was only a fourfold difference among clones.

The yearly differences in proportion of sound seed was probably due to variation in effectiveness of insect control. Apparently insect control was effective in 1977, but not so effective in 1976 and 1978. Losses to seed bugs (Leptoglossus corculus [Say]) occurred the year before cone harvest and were manifested as empty and aborted seed. Conelet/flower losses, on the other hand, occurred mainly in early spring

Table 1-5. Clonal means for cone and seed yields for the 180 sample ramets in 1976.

Clone	Cones per ramet	Sound seed per cone	Total seed per cone
	-----	No. -----	
A	7.6	9.5	30.8
B	2.4	18.1	51.9
C	22.1	24.1	61.1
D	16.5	12.9	40.4
E	1.0	15.9	33.1
F	0.1	7.0	25.0
G	18.5	35.4	56.9
H	8.5	18.5	45.3
I	26.1	9.9	46.1
J	0.3	53.5	75.5
K	0.0	-	-
L	0.8	5.7	57.7
M	9.0	13.0	53.3
N	2.7	4.4	18.6
O	0.9	4.0	17.5
P	50.8	7.2	23.2
Q	6.5	11.3	33.7
R	38.1	21.6	49.2
Mean	11.8	16.0	42.3
Heritability	0.45	0.25	0.24

during and shortly after flowering (McLemore 1977). The high survival rate of conelets for the 1977-1978 crop (71.8%), compared with the 1976-1977 crop (32.7%), also indicated better insect control. McLemore (1977) showed that most conelet losses in loblolly pines were caused by insects.

Data were not available to attest to the relative degree of insect losses for the years 1976 through 1978. Some survey data were available to provide an estimate of the overall seriousness of insect problems in this orchard. These data were collected in various years to assess the impact of insect loss and the effectiveness of various treatments.¹ In 1975, 85% of female strobili survived on trees sprayed periodically with the insecticide Guthion^R versus 64% on untreated checks. Cones from trees treated with the systemic insecticide Furadan^R averaged 47.6 sound seed per cone versus 14.3 sound seed per cone in untreated checks in 1976. For the 1977-1978 flower and cone crop, there was a 21.9% cone loss from trees treated with Furadan^R versus 39.6% from untreated checks. Cones, caged with a wire mesh to exclude insects, averaged 55 sound seed per cone in 1978. Uncaged checks averaged only 19 sound seed per cone. Apparently insects caused heavy losses of female strobili, cones, and seed in this orchard.

Clonal variation as well as yearly variation in conelet survival and seed yield could be related to variation in insect predation. Merkel et al. (1966) found evidence for inherent resistance to coneworm (Dioryctria amatella [Hulst.]) attacks in slash pine.

¹Data provided by Neil Overgaard, Entomologist, U.S.D.A., Forest Service, Pineville, Louisiana.

Year x clone interactions. In general, clonal variation in flowering followed the general yearly trend; i.e., all clones flowered well in good years such as 1975, and poorly in bad years such as 1977. The relative ranking of clones, however, changed considerably from year to year, as exemplified by 6 of the 18 sample clones shown in Figure 1-3. Those 6 clones were representative of the range of flowering performances of the 18 sample clones. The clones varied considerably in female flowering from year to year (Fig. 1-3a), and there seemed to be a long-term trend for some clones to move up or down in relative rank. Clone P was highly variable, and in the early years was the best flowering clone; but it has been surpassed by several other clones. Clone R, initially among the poorest, now has become the best.

Strong year x clone interactions were apparent in male flowering, also (Fig. 1-3b). For instance, Clone D was the best pollen producer during the first 3 years in which measurements were made, but it was average or only slightly above average the last 3 years. Clone R was at the bottom during the first 4 years and had no pollen, but it assumed the number one position the last 3 years. Clone P oscillated year to year from good to average. An important consequence of such year x clone interaction in pollen production is that the genetic makeup of the seed produced by the orchard will vary from year to year, even for seeds collected separately by female parent. The amount of selfing could also be expected to vary.

In an analysis of female and male flowering for the years 1976 through 1978, year x clone effects were significant and constituted an important part of the total variation for both male and female flowering (Table 1-9). But clonal effects were much greater, and heritabilities

Figure 1-3. Year-to-year clonal variation in male and female flowering of 6 representative clones from the 18 sample clones. Flowering of each clone is expressed as a percent above or below the mean for each year. A. Female flowering. B. Male flowering. Letters refer to clone designation.

Table 1-9. Analysis of variance and covariance of male and female flowering for 1976 through 1978 (year effect considered fixed, all others random).

Source of variation	Degrees of freedom	Expected Mean Squares
Clone (C)	17	$\sigma_e^2 + Y\sigma_R^2 + YR\sigma_c^2$
Ramet/Clone (R)	162	$\sigma_e^2 + Y\sigma_R^2$
Year (Y)	2	$\sigma_e^2 + R\sigma_{yc}^2 + CR\sigma_y^2$
Year x Clone	34	$\sigma_e^2 + R\sigma_{yc}^2$
Error	324	σ_e^2

Variance-Covariance Components				
	Variance Female	Covariance	Variance Male	Correlation Coefficient
Clone	10.88	10.95	17.02	0.805
Ramet	4.82	7.62	18.80	0.801
Year	4.17	-7.72	20.50	-0.835
Year x Clone	3.26	-0.69	3.22	-0.214
Error	5.55	1.45	12.70	0.173
Total	28.68		72.24	

for 1976-1978 average male and female flowering were 0.425 and 0.621, respectively. Although yearly variation and year x clone interactions were important, the average performance of a clone was highly heritable.

Correlation coefficients computed from the variance-covariance components showed that male and female flowering were well correlated by clone ($r = 0.805$) and by individual ramet ($r = 0.801$) over the 3 years (Table 1-9). The correlation coefficient for year ($r = -0.835$) was strongly negative, however. This indicates that yearly variation in female flowering has had an opposite basis than for male flowering, which was evident in comparing Figures 1-1a and 1-1b.

In spite of these interactions, female and male flowering for the whole orchard were correlated positively on a clonal basis, though the correlations were generally not as strong as in the sample trees. Those clones with the most female flowers generally were good pollen producers also. The genetic correlation between male and female flowering in 1976 was almost identical for the 1966 and 1967 grafts ($r = 0.589$ and $r = 0.582$, respectively). These were the most reliable figures, as grafts made in those 2 years had 39 and 45 clones represented, respectively. The 1976 flowering data for the 1966 grafts are shown in Figure 1-4.

One interesting aspect of Figure 1-4 was the number of clones in the upper left quadrant. These were below average for female strobili but above average for male strobili. If only female flower or cone production is used as a basis for preliminary rogueing of an orchard, some valuable pollen-producing clones might be eliminated. One clone

Figure 1-4. Scatter diagram of clonal means for female versus male flowering. Data were from 10-year-old grafts in 1976. Dotted lines indicate means for female flowering (vertical) and male flowering (horizontal). Both axes are square-root scale.

in particular averaged only 1.0 female strobili per ramet, but had over 50 male strobili clusters per ramet, which was more than twice the average (Fig. 1-4). It would be more logical to limit roguing to the clones in the lower left quadrant.

Contribution of each clone to the seed produced. Many tree improvement personnel are concerned that only a few of their clones produce the major part of their seed. One tree improvement cooperative estimates that 20% of the clones in their orchards produces 80% of the seed. This is the so-called "20/80 rule" (N.C. State University 1976). A strong clonal effect was evident in these data, although not as strong as "20/80."

In this study, sound seed per cone and total cone counts per ramet indicate that the top 4 of 18 clones (22%) produced 76%, 65%, and 62% of the total seed produced in 1976, 1977, and 1978, respectively. However, the top four clones were not the same each year. Figure 1-5 shows the strong year x clone interaction for seed produced for the top 7 of the 18 clones. Only one clone ("R" in Fig. 1-5) was included in the top four all 3 years. On the basis of total seed produced for all 3 years together, the top four clones produced 58.3% of the total seed.

The genetic correlations between number of female flowers and the number of sound seed produced from that particular flower crop were very high ($r = 0.857$ for the 1977 crop, and $r = 0.884$ for the 1978 crop). Clones which produced female flowers were the ones which produced the seeds, despite all the hazards which occurred between formation of the female strobilus and harvest of full seed.

Figure 1-5. Yearly seed production of the seven best seed producers of the 18 sample clones, expressed as a percent of the total production of all 18 clones each year.

The theoretical genetic contribution of each of the 18 clones was computed by using the proportion of sound seed and the proportion of pollen catkins contributed by each clone at time of pollination. This was done for the 1977 and 1978 seed crops (1975 pollen data were not available for the 1976 crop) and results are shown in Table 1-10. There was a distinct year x clone interaction, as there was with male and female flowering and seed produced. The top four clones contributed 49% of the genes for the 1977 and 1978 crops, respectively. These values are somewhat lower than those obtained from seed alone (65% and 62%, respectively). The present approach assumed that the male contribution of a given clone was proportional to the number of catkins it produced, which was surely not entirely true.

Clearly, the genetic quality of seed from an orchard can vary considerably from year to year. This will be true even if seed are collected from the same mother tree, since pollen composition will vary from year to year. This undoubtedly accounts for the seed crop year x genotype interaction observed by C. H. Lee (1978).

Environmental Variation

Soils. Although genetic variation accounted for a large proportion of the variation of many of the characters measured, environmental variation was also evident in this orchard. It was noted in 1969 that the trees in the lower elevations were growing better but flowering less abundantly than the trees located at higher elevations. Those differences seem to have held up over the years, especially for female flowering. This seemingly inverse relationship between growth and flowering suggested the present study.

Table 1-10. Theoretical genetic contribution of each of the 18 sample clones to the total output in 1977 and 1978. Based on sound seed and pollen produced in the year of pollination (selfs excluded). Ranked by 1977 proportion.

Clone	<u>Year</u>		Rank in 1978
	1977	1978	
	-----	% of total -----	No.
R	16.6	15.9	1
D	13.3	11.2	2
C	10.4	4.7	9
B	9.1	2.8	13
G	8.6	5.7	7
I	7.7	4.2	11
A	7.5	5.6	8
M	6.4	9.5	5
P	3.9	9.8	4
J	3.6	4.3	10
H	3.3	9.8	3
Q	2.9	6.4	6
L	1.7	2.0	15
E	1.5	2.4	14
K	1.1	3.1	12
F	1.0	0.0	18
N	0.9	1.6	16
O	0.5	1.0	17

According to a U.S. Forest Service soils survey, completed before the orchard was established, the orchard was planted on five soil series: Iuka, Benndale, McLaurin, Van Cluse, and Lucy loamy sands to sandy loams. The first three types predominated. Iuka soils are Entisols, and McLaurin and Benndale are Ultisols of similar taxonomy (Table 1-11). The soils did not vary greatly in their physical characteristics. Iuka, an alluvial soil located in the lower elevations near the stream, had the highest proportion of sand (85% and 90% at 10 cm and 75 cm depths, respectively) (Table 1-11). At the other extreme, McLaurin, which was located on the ridges, had the least sand at both depths (78% and 84% sand in the upper and lower samples, respectively). Benndale, which was intermediate in elevation, was intermediate in texture. Clay content of the surface horizons of these samples varied from 5% to 7%. Differences in textures were mainly a function of varying proportions of sand and silt.

The relationship of site variables, such as soil texture and elevation, to flowering were analyzed in two ways: (1) the soil series were used as a discrete classification variable; each sample tree was classified according to a soils map, and (2) regressions were used to relate soil and site variables to flowering, without regard to soil series.

The latter approach was probably the most valid, as soil variations were continuous and not discrete; and the soils around individual trees have been rather arbitrarily classified. However, the data can be presented in a much simpler way with the former approach, so both methods will be utilized.

Table 1-11. Description of the soils where the 130 sample trees were located.

Taxonomic description

Series	Family	Subgroup	Order
Iuka	Coarse-loamy, siliceous, thermic	Aquic Udifluvents	Entisols
Benndale	Coarse-loamy, siliceous, thermic	Typic Paleudults	Ultisols
McLaurin	Coarse-loamy, siliceous, thermic	Typic Paleudults	Ultisols

Measurements

Series	Elevation	Graph symbol	Depth A horiz.	Soil texture					
				10 cm depth			75 cm depth		
				sand	silt	clay	sand	silt	clay
			cm	-----%-----					
Iuka	Lower	1	31	85	10	5	90	5	5
Benndale	Middle	2	35	80	13	7	87	6	7
McLaurin	Upper	3	32	78	15	7	84	9	7

Female flowering. Measurements of flowering and growth generally confirmed earlier observations that flowering was best on soils where growth was poorest. In general, growth was best on the Iuka soils at lower elevations (Fig. 1-6). By fall of 1977 the sample ramets on Iuka soils averaged 11.1 m in height while those on Benndale and McLaurin soils averaged only about 10.3 m (Fig. 1-6a). Radial growth was clearly superior for ramets on the Iuka soil until 1973, when it was equaled or surpassed by those on the Benndale soil (Fig. 1-6b). As the sample trees grew larger, they seemed to be less influenced by soils.

By contrast, flowering was poorer on the soils on which growth was favored (Fig. 1-7). Flowering was always poorer on the Iuka soil for all years measured except the last, though the differences were statistically significant only in 1972 and 1973.

Although there were differences in flowering and growth of trees on the different soils, soil texture measurements were infrequently correlated with either flowering or growth. Female flowering was positively correlated with elevation in the early years. It was strongest in 1973 ($r = 0.296$) and weakest thereafter. This was opposite the early relationship between growth and elevation, but the trend toward decreasing the importance of elevation with time was similar.

The variable most strongly and consistently correlated with female flowering was D.B.H. Correlation increased with age; in 1973 the correlation between D.B.H. and female flowering was $r = 0.295$, and in 1976 it was $r = 0.524$. This seemed to contradict the negative relationship between growth and flowering by soil series. But the magnitude of these correlation coefficients allowed for considerable variation due to factors other than D.B.H. Correlations between D.B.H. and flowering were even

Figure 1-6. Growth of the 180 sample ramets by soil series.
A. Height. B. Radial growth, measured from
increment cores.

Line identities:

- 1 _____ 1: Iuka soils (lower elevation)
- 2 _____ 2: Benndale soils (middle elevation)
- 3 _____ 3: McLaurin soils (higher elevation)

A. HEIGHT

B. RADIAL GROWTH

Figure 1-7. Female flowering of the 180 sample ramets and the 1964 grafts by soil series. Vertical axis is square-root scale. Asterisk indicates differences were statistically significant.

Line identities:

- 1 — 1: Iuka soils (lower elevation)
- 2 — 2: Benndale soils (middle elevation)
- 3 — 3: McLaurin soils (higher elevation)
-: Fitted regression line for flowering/age

stronger when variation due to soil series was removed. This was done by computing correlation coefficients between D.B.H. and flowering separately within each of the three soil series, and then pooling the three values. In 1973, the within-soil correlation coefficient between D.B.H. and flowering was $r = 0.385$ compared to $r = 0.295$ overall; in 1976, the pooled correlation coefficient was $r = 0.553$ compared to $r = 0.524$ overall.

Flowering in a given year was always correlated positively with the size of the cone crop in the previous year. This was true even for the 1978 female crop, which was preceded by a cone crop varying from 0 to 390 cones per ramet. Correlations ranged from $r = 0.286$ for previous cone crop with female flowering in 1971 to $r = 0.644$ for previous cone crop with 1978 female flowering.

The positive correlation probably originated solely as a result of the positive correlation between successive flower crops, which was both genetic and environmental, and the close correlation between a flower crop and its subsequent cone crop. Positive correlation between cone crops and flowering in the subsequent year does not prove, by itself, that the drain on nutrients of developing cones would not affect flowering. But it suggests that the size of the cone crop, in an operational seed orchard, probably is not important in determining the next year's flower crop or inducing periodicity of cone crops.

Effects of competition on growth and female flowering were weak but significant. The correlation between competition index and 1976 female flowering was $r = -0.183$, and that between competition index and 1977 D.B.H. was $r = -0.255$.

In the stepwise multiple regressions, D.B.H., elevation, and height were significantly related to female flowering in 1973. Radial growth, summerwood percent, and percent sand in the A and B horizons were not significant. The equation

$$\sqrt{1973 \text{ female flowering} + 0.5} = 0.6 + 2.1 \text{ D.B.H.} + 0.05 \text{ elevation} - 0.28 \text{ height}$$

explained 29.2% of the variation in female flowering. The sign of the coefficient for height suggests that if D.B.H. and elevation are held constant, flowering was negatively related to height. The simple correlation coefficient between 1973 female flowering and height was positive but weak ($r = 0.151$).

Female flowering in 1977 was significantly related only to D.B.H., height, and competition index (Table 1-12). The equation

$$\sqrt{1977 \text{ female strobili} + 0.5} = 6.1 + 2.4 \text{ D.B.H.} - 0.5 \text{ height} - 2.4 \text{ CI}$$

explained 28% of the variation in female flowering. Elevation and soil texture did not enter into the equation, which agrees with the previous conclusions that the ramets seem to be more independent of site variation as they increase in size, but competition was important.

One important variable, moisture, was not measured in this experiment and could possibly account for some of the variation not explained in the multiple regressions. Drought, especially at critical times, can increase flowering in loblolly pines (Dewers and Moehring 1970, Gallegos 1978). Casual observations during soil sampling in mid-summer indicated that there was much less soil moisture at higher elevations in the McLaurin soils than at lower elevations in the Luka soils. This might have accounted for much of the difference in flowering performance, especially in the earlier years.

Table 1-12. Stepwise regression relating 1977 female flowering as a dependent variable with various independent variables.

Independent variables	Regression coefficient	Standard error	Partial F test
Intercept	6.06	2.80	4.68
1977 DBH	2.37	0.29	65.17
1977 height	-0.51	0.10	25.05
Competition index	-2.41	1.17	4.22

Independent variables not in the equation

Variable	Partial correlation	F to enter
Elevation	0.043	0.33
1976 DBH increment	-0.134	3.22
Sand % - A horizon	-0.049	0.43
Sand % - B horizon	-0.093	1.55

$$R^2 = 0.283$$

$$\text{Overall } F = 23.13$$

Male flowering. The pattern for male flowering was unlike that for female flowering (Fig. 1-8). For most years, male flowering was best on the Iuka soils, exactly opposite the pattern for female flowering. Differences in flowering by soil type were significant only in 1976 and 1977.

Size of the grafts might have been a more important factor in male flowering than in female flowering. Male strobilus production in Pinus is usually confined to vegetatively less vigorous branches in the lower part of the crown (Eggler 1961, Wareing 1957). It occurs on Southern pines mainly on branches in the lower crown that produce only one cycle of growth during the growing season (Eggler 1961, Greenwood 1979). Small trees, whether seed grown or grafted ramets, have a relatively small number of these less vigorous branches. Tree size would not be as important for female flowering, as female strobili are produced on more vigorous shoots, such as would occur over the entire crown of a smaller graft or in the upper crown of larger grafts. This might explain the lack of agreement between male and female flowering by soil type. The fact that almost no male flowering occurred in the sample trees before 1976 (Fig. 1-8) supported this hypothesis, because none of these trees would have had suppressed branches when young, regardless of soil type.

The only independent variables consistently correlated with male flowering were associated with current size. The coefficients ranged from $r = 0.156$ between 1973 male flowering and height to $r = 0.537$ between 1977 male flowering and D.B.H. In all years except 1976, site elevation was not related to male flowering. In 1976 the correlation was weakly negative ($r = -0.154$) which was opposite that for female flowering.

Figure 1-8. Male flowering of the 180 sample ramets and the 1964 grafts by soil series. Vertical axis is square-root scale. Asterisk indicates differences were statistically significant.

Line identities:

- 1—1: Iuka soils (lower elevation)
- 2—2: Benndale soils (middle elevation)
- 3—3: McLaurin soils (higher elevation)

In the stepwise regressions, only D.B.H. was correlated significantly with male flowering in 1973. The regression equation derived for 1977 male flowering was similar to that derived for 1977 female flowering, as the size variables were the first two entered into the equation. The equation

$$\sqrt{1977 \text{ male strobili clusters} + 0.5} = 1.7 + 4.0 \text{ D.B.H.} - 0.6 \text{ height} - 5.7 \text{ D.B.H. increment}$$

explained 37% of the variation in male flowering (Table 1-13). Competition index was just below the significance level required to enter the equation.

Cone and seed yields. It was anticipated that the drier soils might have a deleterious effect on conelet survival and seed yields (Gallegos 1978). However, that was not true. If any trend was apparent, it was opposite to that expected; i.e., yields tended to be poorer on the Iuka soils where growth was more favorable. Sound seed per cone, for instance, varied from 10.9 on the Iuka soils to 20.0 on the McLaurin soils in 1976.

Similar trends were noted for conelet survival. None of the statistical tests indicated significance, however, even though some of the means differed substantially. As mentioned previously, most of the variation in these traits was caused by variability in insect predation. Although there was fairly strong clonal variation in these traits (Tables 1-6, 1-7, and 1-8), the environmental variation seemed largely random, at least with respect to soil type.

Cone counts were included as an independent variable in all the analyses, with the expectation that large cone crops might have a deleterious effect on cone and seed yields. However, this was not true.

Table 1-13. Stepwise regression relating 1977 male flowering as a dependent variable with various independent variables.

Independent variables	Regression coefficient	Standard error	Partial F test
Intercept	1.69	3.978	0.18
1977 DBH	3.99	0.417	91.52
1977 height	-0.57	0.145	15.60
1976 DBH increment	-5.66	1.667	11.52

Independent variables not in the equation

Variable	Partial correlation	F to enter
Elevation	-0.092	1.51
Sand % - A horizon	-0.004	0.00
Sand % - B horizon	0.134	1.36
Competition index	0.134	3.20

$R^2 = 0.370$

Overall F = 34.4

The size of the cone crop was always uncorrelated or positively correlated to the cone and seed variables. The strongest example was the positive correlation between 1978 seed weight and 1978 cone crop. Variation in the 1978 cone crop was substantial, ranging from 0 to 425 cones per ramet. The overall correlation coefficient was $r = 0.424$. A large part of this was genetic ($r = 0.612$), indicating that those clones with large cone crops tended to have heavier seed.

Effects of rainfall. Summer rainfall varied considerably over the 10 years of the study (Fig. 1-9) and these variations might explain yearly variations in flowering. Promotive effects of drought during strobilus initiation were mentioned previously. Dewers and Moehring (1970) provide the best experimental evidence for the effects of moisture stress on reproduction. They subjected loblolly pines to four moisture regimes: (1) drought the entire growing season, (2) irrigated the entire growing season, (3) drought April through June, irrigated thereafter, and (4) irrigated April through June and drought thereafter. Treatments 1, 2, and 3 were approximately equivalent; trees under treatment 4 produced twice as many cones as the other treatments.

Figure 1-10 compares the timing of reproductive events in loblolly pines with a graphical representation of Dewers and Moehring's treatment 4. It was difficult to relate yearly increases in flowering to climatic variables since flowering was expected to increase each year, at least in the earlier years. However, some support for the hypothesis that a rainfall pattern approximating Dewers and Moehring's treatment 4 increased female flowering can be found by comparing Figure 1-9a with Figure 1-9c. Since the effects of moisture on female flowering have

Figure 1-9. Yearly variation in flowering compared to early spring and late growing season rainfall. A. Female Flowering. B. Male Flowering. C. Rainfall

Line identities:

- s—s: 180 sample ramets
- 4—4: 1964 grafts
- : Average early growing season (April, May, June) rainfall
- : Average late growing season (July, August, September) rainfall

been fairly well documented in the literature, it is more important to consider the effects of rainfall on male flowering, for which there is no literature.

Some workers (e.g., Giertych 1967) have claimed that treatments such as fertilization and hormonal applications might have opposite effects on male flowering from that on female flowering. However, since male and female strobili initiate and differentiate at different times, a treatment applied at one time might affect their development differently. Consequently, Greenwood and Schmidtling (1980) reported that such treatments as fertilization, subsoiling, or hormone application might promote both male and female flowering if the treatments are properly timed.

Considering the fact that male flower initiation occurs in early summer and female flower initiation occurs in late summer (Fig. 1-10), it is reasonable to assume that if drought could influence both male and female flowering, it should occur at different times. The opposite, or at least unrelated yearly variation in male flowering compared to female flowering, can be explained by differences in rainfall patterns. Rainfall in 1970 was characterized by low early summer rain and higher late summer rain (Fig. 1-10c). This was followed in 1971 by a good pollen crop (Fig. 1-10b, 1964 grafts) and a poor female flower crop (Fig. 1-10a). The rainfall pattern in 1972 was opposite that of 1970, with higher early summer rain and lower late summer rain. This pattern was followed by a poor pollen crop (Fig. 1-10b) and a good female flower crop (Fig. 1-10a), which was exactly opposite the 1971 pattern.

Figure 1-10. Approximate timing of reproductive events in loblolly pines (above) compared to Dewers and Moehring's (1970) best cone inducing treatment (below). Timing of reproductive events approximated from Greenwood (1979), Greenwood and Schmidtling (1980), Eggler (1961), Dorman and Barber (1956), and Sarvas (1962).

The greatest contrast, not only in rainfall pattern but also in male and female flowering, was between 1976 and 1978. There was a very large female flower crop and a poor pollen crop in 1976, whereas 1978 was characterized by a very good pollen crop and poor female flower crop (Figs. 1-10a and b). These two crops were preceded by rainfall patterns that were exactly opposite (Fig. 1-10c); i.e., higher early summer rain followed by lower late summer rain in 1975, and lower early summer rain followed by higher late summer rain in 1977.

Greenwood (1978) felt that the critical factor determining flowering was the existence of a quiescent bud for a sufficient length of time during the growing season to allow differentiation of primordia. Since male strobili are formed earlier than female, growth in male flowering buds would need to cease earlier than female flowering buds. This normally occurs, as male flowers are often found on branches that had only one cycle of growth the previous growing season (Eggler 1961, Greenwood 1979). An early growing season drought might discourage growth on buds normally expected to produce two or perhaps three cycles, allowing them to differentiate male strobili. This would not necessarily encourage female strobili if early drought is followed by abundant rain in late season, as this often causes renewed growth in buds located in the upper crown (Schmidtling and Scarbrough 1970) and suppresses female flowering due to late season bud growth. This could explain the opposite nature of the yearly variation in male flowering as compared with female flowering in this study.

A drought early in the growing season appears to favor male flowering, while a drought late in the growing season favors female flowering.

Moisture stress might exert its effect simply by limiting vegetative growth. Because of changes in rainfall patterns, this would cause not only yearly variation in flowering, but would also affect site variation caused by water availability.

Conclusions

Genetic Variation

Large genetic variation exists in fruitfulness in loblolly pines, with heritabilities ranging from 0.4 to 0.6, indicating that about half the observed variation is inherent. The biological significance of the substantial clonal variation is not clear. It seems to contradict the hypothesized advantage of sexual reproduction under natural forest conditions (i.e., high genetic variability through recombination), since only a few genotypes would produce a major portion of the reproduction.

Year x clone interactions in male and female flowering would return some of this variability to the system, because individual trees do not consistently produce a major part of the seed or pollen every year. The asynchrony in yearly variation between male and female flowering of clones provides further yearly variation. As a consequence, large genetic variation occurs among seed crops.

Evidence from Figure 1-2 shows that this large genetic variation might not be very important under natural forest conditions. Under increasing competition, environmental effects seem to increase. However, high genetic variation might be obtained under some natural conditions where competition is minimal, such as after a fire, storm, or insect epidemic where only a few trees are left standing.

Whether or not the high genetic variability is an artifact of orchard management, it is surely an important factor in tree improvement for two reasons. First, the number of clones included in many orchards might be much too small. In a 20-clone orchard, there is a good chance that only four or five of them make a significant contribution to orchard production. This provides a very narrow genetic base, and also increases the probability of inbreeding. Second, many clones never produce enough seed or pollen to justify the expense of maintaining them in an orchard. If pollen production is used as a criterion, the prospect for identifying the poorest clones at an early stage is not promising. Clones which are fruitful early continue to be fruitful. But some that show little reproductive activity in early years become fruitful later on. Strong year x clone interactions also make it imperative that fruitfulness be assessed over a period of several years. This information would normally be available for cones and seed, but not for pollen which is infrequently measured. If controlled pollinations for progeny tests are carried out in the orchard, these data could be easily obtained by assessing relative production when pollen is collected.

Another consequence of year x clone interactions is the unreliability of open-pollinated tests of orchard clones, if seeds from different crops are used in different tests. What might appear as family x site or family x planting year interactions could be partly due to pollen crop x year interactions, which cause large differences in male parentage from year to year. The same kind of variation could be expected in various kinds of "check" lots collected in different years.

Environmental Variation

The original observation that environmental conditions which favored growth did not necessarily favor flowering was reinforced upon examination of the data. Tree size and overall vigor were important in determining the size of the flower crop, but continuous growth in the year of initiation was unfavorable for large flower crops. Limited quantities of moisture, especially at critical times during the growing season, seemed important, and probably caused cessation of vegetative growth and allowed reproductive development.

There seemed to be more underlying similarities between male and female flowering than previously supposed. Genetic and environmental factors favoring female flowering appeared to influence male flowering as well. However, pollen production seems to be inadequate during early stages of an orchard.

The difference in the timing of initiation, however, might make it difficult to manage a seed orchard for optimum production of both male and female strobili. Continuous drought stress would affect the overall vigor of the tree and reduce flowering. May through June stress appeared to increase male flowering, while July through August stress increased female flowering. May through August stress might increase both but would be optimum for neither. If an orchard is to be managed (including irrigation) for both male and female flowering, it might be necessary to subdivide the orchard. The perimeter, or perhaps a portion windward to the prevailing winds at time of pollination, could be managed for pollen production and the rest for female flowering.

The results of this research indicate that the ideal orchard should be situated on a well-drained to droughty site, with an irrigation system. In the establishment phase and for 3 or 4 years thereafter, water, fertilizers, etc., should be provided to maximize growth to produce a tree large enough to provide good crops of female and male strobili. After the establishment phase, vigorous growth will no longer be necessary or desirable. In the long run, larger trees would make harvesting more difficult. In the short run, vigorous growth would take place at the expense of flowering.

When orchard ramets are 4 or 5 years old, irrigation should be provided as needed, except for July and August, in that portion to be managed for female flower production. After the orchard ramets are 6 to 7 years old, the part of the orchard managed for pollen production should be irrigated except during May and June. The additional period of optimum growth allows larger trees, which would be necessary for pollen production. Application of fertilizers should also be timed appropriately: June for the pollen production portion and August for the seed production portion. Other management practices such as mowing, subsoiling, and thinning may also be necessary, as will good insect control.

SECTION II
INHERITANCE OF PRECOCITY IN LOBLOLLY PINE
AND ITS RELATION TO GROWTH

Precocious flowering as well as abundant fruiting has obvious advantages in breeding programs and in the production of improved seed (Green and Porterfield 1962, Matthews 1963). It is possible the precocious flowering has already been selected for unintentionally, as tree breeders develop cultivated varieties from wild strains. Controlled mating and artificial regeneration may tend to multiply genes that favor seed production at an early age. This seems to have occurred in Scots pine, as the "Nye Branch" variety (Gerhold 1966) flowers precociously.

It is important to distinguish between fruitfulness and "ripeness to flower." Fruitfulness, which was treated at length in the first part of this dissertation, is a quantitative trait, as it consists of counts of reproductive structures. "Ripeness to flower," and precocity, the early expression of "ripeness to flower," are qualitative traits; i.e., either the tree has flowered or it has not. This concept also supposes that once flowering occurs, it is not reversible, even though flowering may not occur in subsequent years for various reasons.

Trees that direct a great deal of photosynthetic energy into reproductive development at an early age probably do so at the expense of growth (Romberger 1967). The study of the inheritance of fruitfulness and precocity is, therefore, important not only because of its obvious involvement with seed production and breeding strategy, but also because of its possible involvement with growth.

The present study was undertaken with two objectives in mind: (1) to determine the heritability of precocity and fruitfulness in loblolly pine seedlings, and (2) to explore the genetic relationship between fruitfulness, precocity, and growth.

Literature Review

Most woody plants are unable to flower until they attain a stage or condition known as "ripeness to flower" (Klebs 1918). Normally a mature tree is considered as having attained this stage and, in most cases, does not revert to the juvenile condition when propagated vegetatively (Schaffalitzky de Muckadell 1959). Vegetative propagation is the favored reproductive method for establishing seed orchards, because propagules from mature trees normally flower much sooner than seedlings of the same species (Barber and Dorman 1964).

All of the treatments and conditions which promote flowering in mature trees, such as fertilization, crown release, subsoiling, and drought stress, are effective in young trees as long as they have attained this "ripeness to flowering." However, these treatments do not seem to be effective prior to this stage of development (Robinson and Wareing 1969).

The stimulation of fruitfulness in woody plants therefore appears to be divided into two areas: increasing the number of flowers in mature trees, and shortening the juvenile phase to bring about "ripeness to flower." Precocity and fruitfulness may very well be related, though the former is a qualitative trait and the latter quantitative. No information seems to be available as to the relationship between these two traits in pines, but in pear and apple seedlings precocity and eventual productivity were unrelated (Visser et al. 1976).

Ability to shorten the juvenile phase could have great utility in tree breeding programs, since controlled crosses could be made early in the life cycle of a tree. This would allow a rapid turnover of generations and an increase in genetic gain. For instance, Greene (1969) reported potentially large volume gains by breeding precocious loblolly pines.

Processes governing the phase change from purely vegetative growth to reproductive growth have been the subject of a great deal of experimentation. Aside from being a feature of advancing age, phase change seems to be correlated with height in Virginia pines (Bramlett 1971) and loblolly pines (Schmidtling 1969). Robinson and Wareing (1969) concluded that the primary factor governing phase change was not dependent upon the plants passing through a certain number of growing seasons or attaining a certain size. They experimented with cuttings taken from Ribes nigrum L. seedlings of various ages, none of which had flowered. They found that the minimum size for flowering was less for cuttings from older seedlings than from younger seedlings. They then concluded that phase change occurred after the plant had passed through a certain minimum number of mitoses following embryo formation. This was correlated with, but not determined by, attaining a certain size.

Whether phase change is governed by age, size, or mitotic divisions, there does seem to be large genetic variation in this trait both between and within species. Mergen and Koerting (1957) found that flowering normally begins after about the 5th year in slash pine, but Smith and Konar (1969) found female strobili in cotyledon stage seedlings of that species.

There are several accounts of 1-year-old pine seedlings producing reproductive structures. Nursery-grown seedlings of P. tabulaeformis Carr. and P. mugo Turra produced male strobili at 1 year (Righter 1939, Mergen and Cutting 1957), and a P. rigida D. Don seedling of the same age produced female strobili (Namkoong 1960). Johnson and Critchfield (1978) found functional male and female strobili on P. contorta x banksiana hybrids at 1 year of age and presented evidence for the inheritance of precocity.

Precocious flowering was found to be inherited in Scots pine by Gerhold (1966) and in jack pine by Jeffers and Nienstaedt (1972), but they did not determine the mode of inheritance or its relationship to growth. Teich and Holst (1969) found that one form of precocity was related to a cone cluster trait, and that a simple dominant gene was involved in its inheritance, with a possible involvement of cytoplasmic inheritance. Wright et al. (1966) found substantial variation between provenances in precocity, but low family (within provenance) variation, and no relationship between precocity and growth.

In Virginia pine, which normally flowers at an early age, Bramlett (1971) found high narrow-sense heritability of fruitfulness in seedlings, and that flowering trees averaged taller than nonflowering trees. In another study, Bramlett and Belanger (1976) found that fruitfulness was highly heritable, but negatively correlated with height in parent-progeny correlations. In both cases, however, precocity was not measured directly. Flower counts in young seedlings, really more a measure of fruitfulness, were used.

In contrast to Bramlett's work, Varnell et al. (1967) found fruitfulness to have low narrow-sense heritability ($h^2 = 0.13$). Again their study measured fruitfulness and not precocity. Unfortunately, most of the authors of papers dealing with the heritability of fruitfulness (Bramlett 1971, Bramlett and Belanger 1976, Varnell et al. 1967) relied on counts of strobili which, even in young trees, would contain components of both ripeness (contrast between zero and one or more flowers) and fruitfulness (number of flowers in flowering trees). The two traits are obviously related, in the sense that one must occur before the other can be expressed. But they may be governed by separate genetic and environmental factors. At the other extreme, the two traits may be one and the same, the precocious trees being those with genomes for heavy fruitfulness.

Different answers to the question of how precocity is inherited may be obtained if counts of reproductive structures are used as opposed to proportion of trees flowering. In an analogous situation dealing with fusiform rust in loblolly pine, somewhat different results were obtained when proportion infected was used rather than number of galls (Blair 1970).

Visser et al. (1976) were able to deal with this problem by using age at first flowering as their precocity criterion. Their precocity trait was not related to the eventual fruitfulness of the seedlings, suggesting that genetic control was separate for the two traits. This kind of analysis is not possible in pines, or most other conifers, since flowering may never occur in many of the trees under plantation conditions in a relatively long (10 years) experiment.

This necessitated treating "ripeness to flower" as a threshold trait, and using measures of number of trees flowering rather than age at first flowering. Relationships among precocity, fruitfulness, and growth are important in tree breeding programs and have not been adequately determined.

Materials and Methods

Data from two experiments are included in this study, a 10-parent diallel and a half-sib progeny test.

Diallel. The 10 parents of the diallel were randomly selected loblolly pines located on the Harrison Experimental Forest in south Mississippi. These parent trees were crossed in all possible combinations, excluding selfs. The resulting seed were sown in the nursery in the spring of 1966, and the 1-year-old seedlings were bar-planted in January 1967 on the Harrison Experimental Forest. Spacing was triangular, with 9 feet (2.74 m) between rows and 10.39 feet (3.17 m) between trees in the rows. The experimental design was a randomized complete block of eight replications with eight trees per plot. Scions from the parent trees were grafted on potted seedling rootstocks in January of 1967, and the surviving grafts were included in the planting. The grafts did not grow as well as the seedlings initially, averaging only 1.9 meters tall at age 3 versus 2.2 meters for the seedlings. In the spring of the 2nd year, each graft was mulched with pine straw and fertilized with 7 pounds (3 kg) of 8-8-8 N-P₂O₅-K₂O fertilizer. As a result, the grafts averaged 5.5 meters tall at age 5 versus 3.8 meters for the seedlings. They were 11.3 meters tall at age 10 versus 10.6 meters for the seedlings.

Female flowers were counted on seedlings and grafts each spring from 1969 through 1975 (ages 2 through 8 years from planting) except 1973, when measurements on the grafts were not made. Heights were measured at ages 3, 5, and 10 years, diameters at 5 and 10 years, and crown width at age 5.

Flowering data were analyzed as binomial traits (zero or one, "ripeness to flower") where a tree was considered "ripe" if it had flowered in a given year or in any previous year. These traits were analyzed untransformed, both on an individual tree basis and on a plot mean basis. Analysis of a similar trait, fusiform rust, was carried out satisfactorily in this manner (Sohn 1977). Average number of flowers, square-root transformed, was also analyzed.

The flowering data from the grafts were used only for parent-progeny regressions. The data from the seedlings were analyzed by a general least squares analysis program for diallels, "DIALL" (Schaffer and Usanis 1969), on an individual tree basis and a plot mean basis.

The assumptions for the analysis of variance and the genetic variance expectations are the usual ones for nonrelated, random parents from a diploid population (Cockerham 1963). Effects accounted for with degrees of freedom (d.f.) adjusted for missing plots are shown in Table 2-1.

Negative components of variance were handled as recommended by Thompson and Moore (1963); i.e., a mean square smaller than a predecessor mean square, and whose component was included in it, was pooled with the predecessor and the result equated to both expectations.

Heritability (h^2) estimates were calculated by the formula:

$$h^2 = \frac{4 \sigma^2_{GCA}}{\text{Phenotypic variance}}, \text{ where the phenotypic variance} =$$

$$\sigma^2_{GCA} + \sigma^2_{SCA} + \sigma^2_{wp}.$$

When plot means were analyzed, heritability was computed as:

$$\frac{\sigma^2_{GCA}}{\text{Phenotypic variance}}, \text{ where phenotypic variance} = \sigma^2_{GCA} +$$

$$\sigma^2_{SCA} + \sigma^2_{p/8}.$$

Table 2-1. Form of analysis of variance and covariance for the diallel experiment.

Source	D.F.	Expected mean squares
Blocks	7	
General combining ability (GCA)	9	$\sigma^2_{wp} + C_2 \sigma^2_{SCA} + C_3 \sigma^2_{GCA}$
Specific combining ability (SCA)	35	$\sigma^2_{wp} + C_1 \sigma^2_{SCA}$
Error	1361 (276) ¹	σ^2_{wp} (σ^2_p)

¹Error degrees of freedom are adjusted for missing data.

σ^2_{wp} = Variance component due to error. DIALL computed this by subtraction, so it was a pooled error term containing both within- and among-plot variance.

σ^2_p = Variance component due to among-plot error in analyses based on plot means.

σ^2_{SCA} = Variance component due to specific combining ability.

σ^2_{GCA} = Variance component due to general combining ability.

The variance component coefficients C_1 , C_2 , C_3 , determined by DIALL, were $C_1 = 30.8$, $C_2 = 32.8$, $C_3 = 249.1$ for individual tree analysis, and $C_1 = 7.2$, $C_2 = 7.4$, $C_3 = 58.2$ for plot mean analysis.

The DIALL program computes the standard deviation of the variance components as

$$S.D. = \sqrt{\frac{\sum_i 2 a_i^2 (MS_i)^2}{DF_i + 2}}$$

where the a_i are the coefficients of the linear combination of the mean squares used to estimate the component (Anderson and Bancroft 1952).

Genetic correlations based on GCA components were calculated also.

Half-sib test. This experiment is of interest primarily because three of the families were selected for precocity. The test consisted of open-pollinated progeny of 24 trees, 21 of which were selected for the National Forest System's Southern Region Tree Improvement Program. Seed from the select trees were collected from the ortets, which were located in Mississippi, Alabama, Texas, North Carolina, and South Carolina.

The three trees selected for precocity were from a fertilizer study located on the Harrison Experimental Forest. Out of 4,000 loblolly pines in the study, 12 flowered 2 years after outplanting and 63 flowered after 3 years. All were on fertilized plots (Schmidtling 1971) and the enhanced flowering appeared to be related to attaining a certain height (Schmidtling 1969). The trees used in the present study were subjected to further selection, as only 3 of the total of 75 precocious trees produced enough seed in the 9th year to be included in this study. One of these (Pre-1) had flowered at age 2, the other two (Pre-2 and Pre-3) at age 3. All three precocious trees were larger than the plot means at 2 years of age as well as at 9 years of age when seed were collected (Table 2-2). The fact that they were taller than average at age 9 might have had an important role in determining their fruitfulness, as there was intense competition in the original stands at the 10 x 10 foot (3 x 3 m) spacing.

Table 2-2. Height and diameter of the three precocious parent trees used in the half-sib study compared to the means of the 100-tree plots where they were located.

Tree		Second year height	Ninth year height	Ninth year D.B.H.
		m	m	cm
Pre-1	Select tree	0.94	12.2	20.3
	Plot mean	0.77	11.7	16.7
Pre-2	Select tree	0.76	¹	19.1
	Plot mean	0.64	10.1	14.9
Pre-3	Select tree	0.73	11.7	15.5
	Plot mean	0.68	11.1	15.4

¹ Top broken

Seed collected from the 24 families were sown in the nursery in the spring of 1970, and the 1-year-old seedlings bar-planted in the winter of 1970-1971 at two locations on the Harrison Experimental Forest. Four replications of a randomized complete block were planted at each location, with four trees per plot and 10 x 10 foot (3 x 3 m) spacing. In spring of 1977, female flowers, conelets (1-year-old strobili), and cones were counted and height and D.B.H. were measured. At 4 and 5 years, fruitfulness was assessed by cone and conelet counts, respectively. This was conservative, because some trees without cones or conelets might have had flowers which aborted.

Mean number of trees flowering per plot was analyzed, and the analysis took the form:

Source of variation	D.F.
Location	1
Blocks in location	6
Families	23
Families x location	23
Error	138

The fixed model was assumed, and statistical significance was tested at the 0.05 level of probability.

Results and Discussion

Diallel. Approximately 5% of the seedlings flowered in 1969, or after 2 years in the field. Those are the ones that were considered precocious. Number flowering increased to over 30% in 1970, and 80% of the trees had shown some signs of reproduction (age 8) by 1975.

Seedlings actually started flowering before the grafts (Fig. 2-1), as there was almost no flowering among the grafts in 1969. Undoubtedly because of physiological maturity and special treatments the grafts received, they subsequently flowered better than the seedlings. They averaged over 10 female strobili each in 1974, whereas the seedlings averaged only about 2.0 each. Yearly variation in flowering of the seedlings was approximately parallel to that of the grafts.

Seedlings flowering in 1969 were taller than average at age 3 (Fig. 2-2a). The difference, although statistically significant, was very small (2.3 m versus 2.2 m for the overall average). Precocious individuals were still slightly taller than average at age 5, but by age 10 they were slightly shorter. Differences at ages 5 and 10 were not statistically significant. Precocious trees continued to flower better than the average (Fig. 2-2b). In 1973, the difference was largest, when the precocious trees averaged 12 flowers per tree and the others averaged only 6. Though the absolute difference varied widely, precocious trees had about twice as many flowers in all years measured. Possibly the precocious trees lost their initial height advantage because their energy was diverted into reproduction.

Figure 2-1. Flowering of the parent grafts and their seedling progeny in the diallel experiment. Vertical axis is square-root scale.

Line identities:

0 — 0: Grafts
 * — *: Seedlings

Figure 2-2. Growth and flowering of the precocious trees (flowering at age two) compared to the non-precocious trees in the diallel experiment. A. Height. B. Flowering. Vertical axis of B is square-root scale.

Line identities:

-----: Precocious
 —————: Non-precocious

The diallel analysis showed that all flowering characters exhibited some degree of heritability (Tables 2-3 and 2-4). These heritabilities are rather limited in application, and probably could not be used to accurately predict gain in many breeding situations. They were undoubtedly biased upwards because genotype x environment interaction was not estimated. Exact values are not important, but their relative magnitude is of interest.

General combining ability (GCA) values for flowering were all more than two standard deviations above zero, except for 8th-year ripeness on an individual tree basis (Tables 2-3 and 2-4). Specific combining ability (SCA) values for flowering traits were generally much smaller than GCA values. They differed from zero by two standard deviations only in three instances: 8th-year "ripeness," average number of flowers from individual tree data (Table 2-3), and average number of flowers from plot mean data (Table 2-4). Heritabilities ranged from 0.134 for 2nd-year "ripeness" to 0.609 for average number of flowers on individual tree data. Values for plot mean data were higher, ranging from 0.409 for 8th-year "ripeness" to 0.630 for average number of flowers. Thus, average number of flowers, a quantitative trait, was highly heritable both on an individual tree basis and on a family basis. This agrees with findings from the previous chapter. Precocity was much less heritable on an individual basis, but was moderately heritable on a family (plot mean) basis.

Table 2-3. Diallel statistics based on individual tree data for flowering and growth traits. Standard deviations are shown below general combining ability (GCA) and specific combining ability (SCA) statistics.

Trait	GCA	SCA	Error	h^2
Second-year "ripeness" ¹ (precocity)	0.00151 ±0.00072	0.00003 ±0.00034	0.0434	0.134
Third-year "ripeness" ¹	0.01270 ±0.00586	0.00185 ±0.00190	0.1929	0.238
Eighth-year "ripeness" ¹	0.55636 ±0.28038	0.44334 ±0.17952	10.0605	0.201
Average number of flowers ²	0.53342 ±0.23767	0.09305 ±0.04351	2.8761	0.609
Third-year height	0.04270 ±0.02400	0.02935 ±0.02442	2.3067	0.072
Fifth-year height	0.09017 ±0.05158	0.10353 ±0.05438	3.9821	0.096
Fifth-year D.B.H.	0.00778 ±0.00475	0.01602 ±0.00583	0.2768	0.104
Fifth-year crown width	0.16969 ±0.07854	0.05139 ±0.02625	1.8794	0.323
Tenth-year height	0.93879 ±0.47452	0.96583 ±0.30519	10.6353	0.299
Tenth-year D.B.H.	0.06061 ±0.03227	0.08875 ±0.02618	0.7316	0.275

¹ Having flowered by the year indicated
² Over the eight years measured

Table 2-4. Diallel statistics based on plot mean data for flowering and growth characters. Standard deviations are shown below General combining ability (GCA) and Specific combining ability (SCA) statistics.

Trait	GCA	SCA	Error	h^2
Second-year "ripeness" ¹ (precocity)	0.00229 ±0.00113	0.00020 ±0.00071	0.1947	0.465
Third-year "ripeness" ¹	0.01475 ±0.00675	0.00019 ±0.00213	0.6110	0.653
Eighth-year "ripeness" ¹	0.00701 ±0.00350	0.00448 ±0.00255	0.0453	0.409
Average number of flowers ²	0.58433 ±0.26870	0.17418 ±0.08518	1.3554	0.630
Third-year height	0.06173 ±0.03372	-0.00680 ±0.03366	1.0286	0.324
Fifth-year height	0.11456 ±0.06658	0.06539 ±0.07578	1.8476	0.279
Fifth-year D.B.H.	0.00783 ±0.00498	0.0140 ±0.00698	0.1299	0.221
Fifth-year crown width	0.15816 ±0.07381	-0.00639 ±0.02955	0.9058	0.583
Tenth-year height	0.83071 ±0.43881	0.83371 ±0.36203	5.0872	0.361
Tenth-year D.B.H.	0.05578 ±0.03164	0.09542 ±0.03308	0.3324	0.289

¹ Having flowered by the year indicated

² Over the eight years measured

Heritabilities of the growth variables were much lower than those for flowering (Tables 2-3 and 2-4). Only the GCA for crown width differed from zero by more than two standard deviations. Heritabilities for height seemed to increase with time, however. They reached 0.299 by the 10th year for individual tree height. In contrast to flowering, SCA values differed from zero by two standard deviations for several characters: 5th-year D.B.H., crown width, 10th-year height, and 10th-year D.B.H. on an individual basis, and for 10th-year height and 10th-year D.B.H. on a family basis. These results agree fairly well with those of Snyder and Namkoong (1978) in a longleaf pine diallel. Their heritabilities for growth traits were in the same range as those found here. They also noted significant SCA effects for many traits.

Genetic correlations among flowering traits were uniformly high and positive (Table 2-5), ranging from a low of 0.780 between average number of flowers and 2nd-year "ripeness" to a high of 1.0 between average number of flowers and 3th-year "ripeness." Individual tree and family correlations for each pair of traits were very close, as they should be.

Genetic correlations between all growth variables and flowering variables were negative except between 8th-year ripeness and 10th-year D.B.H., which was essentially zero on a family basis ($r = 0.065$). Correlations were generally not very strong. But uniformly negative signs indicate that selection based on fruitfulness or precocity alone would result in some loss in growth. The strongest genetic correlations were between 2nd-year "ripeness" (precocity) and various growth traits. They ranged from $r = -0.127$ between precocity and height at 3 years for individuals to $r = -0.654$ between precocity and crown width for plot means.

Table 2-5. Genetic (GCA) correlations among flowering variables and flowering and growth variables from the diallel analysis. Individual tree correlations are shown with correlations based on plot mean data below individual tree correlations in parenthesis.

	2nd year "ripeness" ¹	3rd year "ripeness"	8th year "ripeness"	Average number of flowers
Third-year "ripeness" ¹	0.936 ³ (0.931) ⁴	-	-	-
Eighth-year "ripeness" ¹	0.912 (0.780)	0.959 (0.898)	-	-
Average number of flowers ²	0.758 (0.826)	0.889 (0.870)	1.0 (1.0)	-
Third-year height	-0.127 (-0.292)	-0.116 (-0.167)	-0.440 (-0.401)	-0.419 (-0.526)
Fifth-year height	-0.364 (-0.467)	-0.350 (-0.366)	-0.532 (-0.367)	-0.460 (-0.537)
Fifth-year D.B.H.	-0.641 (-0.640)	-0.352 (-0.372)	-0.409 (-0.217)	-0.228 (-0.348)
Fifth-year crown width	-0.611 (-0.654)	-0.483 (-0.514)	-0.399 (-0.235)	-0.323 (-0.400)
Tenth-year height	-0.333 (-0.391)	-0.348 (-0.419)	-0.331 (-0.244)	-0.293 (-0.395)
Tenth-year D.B.H.	-0.536 (-0.544)	-0.370 (-0.354)	-0.241 (0.065)	-0.068 (-0.100)

¹ Having flowered by the year indicated

² Over the eight years measured

³ Correlation based on individual tree data

⁴ Correlation based on plot mean data

So even though precocious trees were significantly taller at age 3, this correlation was environmental since the genetic portion of the overall correlation was negative. Negative correlations between flowering traits and crown width were surprising, because it seems logical to assume that trees with larger crowns would have more cones. In this study, however, there was no genetic evidence for such an assumption.

Parent-progeny relations. Regression between mid-parent average flowering (average of the two parents for each cross) and progeny average flowering yielded a heritability of 0.518 (Fig. 2-3). This was slightly less than the heritability found in the diallel analysis, $h^2 = 0.609$ (Table 2-3). However, the most fruitful parents, in a quantitative sense, were not the ones which were producing the most precocious progeny. This was evident in Table 2-6. Parent one ranked fourth out of 10 for average flowering, but produced the most precocious progeny, 14.7%. The correlation between mid-parent average flowering of the grafts and precocity of the progeny was only $r = 0.355$. This increased sharply with subsequent measures of "ripeness" to a peak of $r = 0.680$ the 5th year (Fig. 2-4).

Correlations between mid-parent fruitfulness of the grafts and various growth measures of the progeny were all negative except for the correlation between 10th-year D.B.H. and parent fruitfulness ($r = 0.134$). Correlations between parent fruitfulness and 3rd-year height, 5th-year height, 5th-year diameter, and 10th-year height were all negative though weak, ranging from $r = -0.241$ for 3rd-year height to $r = -0.020$ for 5th-year diameter. Though probably not very important, correlations of that magnitude reinforce the findings of the diallel analysis in cautioning against selection for fruitfulness without considering other aspects.

Figure 2-3. Parent-progeny regression for average flowering for seven years in the diallel experiment. Both axes are square-root scale.

Table 2-6. Average flowering of the grafts compared to precocity and average flowering of the progeny in the Diallel planting.

Family	Parents (grafts) Average Flowering	Progeny ¹	
		Precocious ¹	Average Flowering
	No.	%	No.
7	14.62	12.7	2.54
9	12.04	3.2	2.05
4	4.09	5.2	1.5
1	3.52	14.7	2.35
8	3.40	6.1	1.77
6	1.93	4.4	.95
3	1.73	6.3	.91
5	1.22	1.4	.77
10	0.83	2.0	.80
2	0.65	2.9	.89

¹ Flowered at age two

Figure 2-4. Change in correlation with time between average fruitfulness of mid-parent and "ripeness to flower" of progeny. Last point marked "avg" is the correlation between mid-parent fruitfulness and progeny average fruitfulness.

Half-sib test. About 12.5% of the trees in the half-sib test flowered the 4th year (Table 2-7). Flowering increased to 15.6% the 5th year and to 26.3% the 6th year. Results of selection for precocity were evident. An average of 32.6% of individuals from the three precocious families flowered by 4 years compared with an average of 9.6% of the other families. Over 40% of Pre-1 (precocious family number one) progeny flowered by age 4. Only one family, Bud 12, equalled flowering of the poorest precocious family, Pre-3. Differences were statistically significant at all years and indicated that selection for precocity will result in early flowering progeny.

Growth of precocious selections was good, contrary to what one would expect from the negative correlations between flowering and growth in the diallel analysis. Precocious trees were all larger than average when selected, however (Table 2-2). Their progeny averaged 5.7 meters tall compared with 5.4 for the others, and 9.3 centimeters in diameter compared with 8.6 for the others. One precocious family, Pre-2, ranked first in diameter out of 24 families. This ranking was remarkable since the 21 nonprecocious families were intensively selected, and size was an important selection criterion. But geographic variation may be an important factor in this study, as 11 of the select trees were from areas of slower growing provenance; i.e., the Tal, Ban, Tex, and Sum sources from north and central Alabama, Texas, and South Carolina piedmont, respectively (Wells 1969, Wells personal communication). By excluding the latter, overall mean height of the remaining select trees was 5.88 meters and D.B.H. was 9.4 centimeters, slightly larger than precocious selections. But dropping these from the data does not change differences in flowering between precocious and select trees.

Table 2-7. Flowering and growth of the 24 families in the half-sib study.

Family	Tree Flowering By Age			Sixth Year Height	Sixth Year D.B.H.
	4 years	5 years	6 years		
	-----%-----			m	cm
Pre 1	40.6	50.0	62.5	5.21	8.7
Pre 2	30.2	44.8	64.6	6.22	10.7
Pre 3	27.1	33.3	54.2	5.66	8.5
Tal 115	21.9	21.9	33.3	4.57	6.9
Ban 57	15.6	18.8	41.7	4.42	7.4
Ban 71	12.5	12.5	21.9	5.17	8.3
Ban 34	7.3	7.3	17.7	4.84	7.5
Bud 12	27.1	33.3	40.6	5.69	9.6
Bud 20	12.5	12.5	25.0	5.21	9.3
Bud 1	3.1	3.1	13.5	5.93	8.8
Bud 11	0.0	0.0	0.0	5.73	9.2
Fra 39	15.6	21.9	30.2	6.40	10.4
Fra 165	3.1	10.4	10.4	5.66	8.6
Fra 211	13.5	13.5	32.3	6.63	10.3
Fra 119	6.3	9.4	15.6	5.52	8.4
Hom 10	9.4	12.5	16.7	5.86	9.4
Sum 35	12.5	12.5	31.3	4.72	8.0
Sum 160	9.4	16.7	32.3	5.14	8.2
Sum 145	6.3	6.3	34.4	4.73	7.8
Sum 73	6.3	6.3	13.5	5.06	8.1
Sum 41	0.0	0.0	12.5	5.49	8.6
Tex 204	7.3	7.3	7.3	4.78	7.7
Tex 18	6.3	13.5	13.5	5.67	8.9
Cro 2	6.3	6.3	6.3	6.14	10.0
Mean	12.5	15.6	26.3	5.44	8.7

Precocious trees performed better than expected, however, considering negative relationships that were found between growth and flowering in the diallel. As stated previously, the two-stage selection process probably favored fruitfulness as well as growth, since only dominant trees would be expected to flower under the very close crown competition in which they grew at age 9. In fact, the three precocious trees used were larger than their neighbors at age 9 (Table 2-2).

Conclusions

Precocious flowering appears to be moderately heritable, and selection for this trait can reduce the age of first flowering. Fruitfulness appears to be highly heritable, and the broad-sense heritability estimates of the previous chapter for fruitfulness appear to be on the low side. They probably are biased downward by rootstock effects. Estimates of broad-sense heritability include all genetic variation and should therefore be the upper limit for narrow-sense heritability. The narrow-sense heritability estimate of 0.609 from the diallel analysis for average flowering on an individual tree basis is higher than many of the estimates for broad-sense heritability from the previous chapter. A broad-sense estimate from Table 2-3 would be:

$$h^2 = 4(GCA + SCA)/\text{phenotypic variance} = 0.715$$

which is greater than any of the estimates from the clonal data.

The previous chapter concluded that size and overall vigor were positively related to flowering, but that prolonged vegetative growth discouraged reproductive development. Reproductive biologists tend to think in terms of "a transition" from vegetative growth to reproductive growth as part of an overall reproductive strategy (Cohen 1976). Obviously this does not happen in most forest trees, as growth and reproduction occur

within the same growing season. There is no complete transition from vegetative to reproductive growth as occurs in most herbaceous annuals.

Greenwood (1978) feels that the primary reason seedling pines do not flower is that they grow almost continuously during the growing season. He feels that a "quiescent" bud must be formed early in the season to allow strobilus initials to form.

Thus, whether one views the commencement of reproduction as a change-over from vegetative growth or as a process where a reduction in vegetative growth allows reproduction, a negative correlation between reproductive growth and vegetative growth should be expected. Although this study was limited by the fact that the conclusions are mainly based on an intensive analysis of only 10 parents, the expected negative relationship between growth and reproduction does seem to have a genetic basis in loblolly pines, which would seem to mitigate against selection based on flowering alone. The greater height of the precocious trees at age 3 was apparently an environmental relationship. The genetic correlations between precocity and all growth variables, including height at 3 years, though weak, were negative.

The fact that precocity and growth are only weakly correlated suggests that one could select for both of these traits simultaneously in a breeding program. The use of genetically induced precocity for obtaining large gains in growth by shortening generation time, however, hardly seems feasible.

SUMMARY AND CONCLUSIONS

Genetic Variability

Genetic variability in fruitfulness is certainly an important consideration in planning loblolly pine tree improvement programs. It is evident from this study that a relatively small proportion of orchard clones produce most of the progeny. Most of the genetic variation is additive, indicating that the use of seedling seed orchards would do little to solve the problem. In terms of genetic variability, the effective number of clones in a seed orchard may be less than half the actual number and could be further reduced by differences in reproductive phenology. In addition, the negative relationship between cone production in the parent trees and growth of the progeny indicates not only that few clones will be producing most of the seed, but that these are not the best clones with regard to progeny growth.

Under these conditions, early progeny testing assumes even more importance than previously. Including more selections in breeding programs also appear warranted. The ideal solution to the problem would be to find a way to increase flowering in the unfruitful clones. Unfortunately, the more fruitful clones are the ones which respond best to treatments such as fertilization. Beers' (1974) suggestion for fertilizing clones individually by "prescription" based on their previous response in seed production should, perhaps, be modified to include progeny test information in the form of an index similar to a selection index.

Relative response to fertilizers, in terms of increase in pounds of seed produced by each clone, would be included as well as relative growth of their progeny, to optimize economic gain.

Using precocious individuals to shorten generation time and increase genetic gain should be carried out with caution. In some breeding programs, selection as early as age 7 is being practiced. It would be tempting, but risky, to choose trees above average in growth from progeny tests primarily because they flower early. If precocious individuals are selected which are very much above average in growth, however, the risks are probably not great, since the heritability of precocity is only moderate to weak. Also, the genetic correlation with growth is not strong. Selection based on precocity alone seems to be clearly unwarranted.

Environmental Variability

There is ample evidence from previous studies showing that abundant production of seed reduces vegetative growth. The converse also appears to be true; i.e., reduced vegetative growth enhances the production of seed. The best conditions for vegetative growth appear to be less than optimum for reproductive growth. Some sites which have been carefully chosen for seed orchards may be too good. Previously, it was assumed that the best sites for vegetative growth would be the best for seed production, but it is apparent that conditions which favor cessation of growth early in the season are best for flowering.

Silvicultural treatments such as fertilization and irrigation need to be optimized to favor vegetative growth in the establishment phase, as size is very important in determining fruitfulness. After the orchard is in production, these silvicultural treatments need to be changed to optimize reproductive growth. This may require an adjustment in the attitude of seed orchard managers.

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Ronald Carl Schmidting was born November 21, 1937, in Detroit, Michigan. He attended and graduated from Monroe High School in Monroe, Michigan, in 1955. He attended the University of Michigan from 1955 to 1957. He returned to the University of Michigan in 1962 after serving in the U.S. Army, receiving a bachelor of science degree in 1964 and a master of science degree in botany in 1965. He was employed for 1 year as a biology instructor at Inter-American University in San Juan, Puerto Rico. He has been a Research Geneticist with the U.S. Forest Service in Gulfport, Mississippi, since 1967. From 1973 to present, doctoral work has been pursued at the University of Florida in forest genetics.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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