The Inheritance of Precocity and its Relationship with Growth in Loblolly Pines1)

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Abstract

Genetic variation in precocity and fruitfulness was examined in open-pollinated families and diallel crosses of loblolly pines *(Pinus taeda* L.). Genetic variation in average amount of flowering was very strong among families in a diallel and most of the genetic variation was additive. Diallel analyses and parent-progeny regressions yielded narrow-sense heritability estimates of 0.61 and 0.52, respectively. The inheritance of 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. Although results of a half-sib progeny test suggest that simultaneous selection for precocity and growth could be successful, it would not be advisable in loblolly improvement programs.

Key words: Diallel, flowering, heritability, genetic correlation, general combining ability, ripeness to flower.

Zusammenfassung

Bei frei abgeblühten Familien und Kreuzungsdiallelen von *Pinus taeda* L. wurde die genetische Variation in Frühreife und Fruchtbarkeit untersucht. Die genetische Variation in der durchschnittlichen Blühbereitschaft war zwischen Familien sehr groß und der größte Teil der genetischen Variation war additiv. Diallel-Analysen und Eltern-Nachkommenschafts-Regressionen erbrachten Heritabilitätsschätzwerte im engeren Sinne von 0,61 bzw. 0,52. Die Erblichkeit der Frühreife war nicht so hoch wie die der durchschnittlichen Blühbereitschaft, da sie auf Einzelbaumbasis nur 0,13 und auf Familienbasis nur 0,47 betrug. Blühmerkmale waren mit Wachstumsmerkmalen negativ korreliert, was anzeigt, daß eine Selektion auf die durchschnittliche Blühbereitschaft oder Frühreife allein zu einem Verlust an Höhenwachstum führt. Obwohl die Ergebnisse einer Halbgeschwister-Nachkommenschaftsprüfung anzeigen, daß eine gleichzeitige Selektion auf Frühreife und Wachstum erfolgreich sein kann, wäre dies in *Pinus taeda*-Züchtungsprogrammen nicht ratsam.

Introduction

Most woody plants are unable to flower until they pass through a juvenile period and attain a stage or condition known as "ripeness to flower." In many tree species, the extended length of the juvenile period is a serious obstacle to advanced generation breeding.

Genetic variation in the length of the juvenile period in pines has been documented (Gerhold 1966, Jeffers and Nienstaedt 1972, Teich and Holst 1969, and Schröck 1957). Greene and Porterfield (1962) have suggested utilizing this variation in tree improvement programs to shorten generation intervals by selecting for precocious flowering. But little information is available on the genetic relationship between precocity or fruitfulness and growth.

Greenwood (1978) suggests that seedling pines do not flower because they grow almost continuously during the the growing season, and that a quiescent bud must be formed early in the season to allow strobili initials to form. Whether or not growth cessation is necessary to allow reproduction, it seems likely that reproduction will lead to slower growth. Trees that direct photosynthetic energy to reproductive development at an early age probably do so at the expense of growth (Romberger 1967).

Fielding (1960) has estimated that 16 percent of the mean annual increment of a pine plantation was diverted to reproductive structures. Thus, a negative correlation between reproductive growth and vegetative growth might then be anticipated.

Wright *et al.* (1966) found substantial variation between provenances for precocious flowering in Scots pine, but low family (within provenance) variation and no relationship between precocity and growth. In Virginia pine *(P. virginiana* Mill.), which normally flowers at an early age, Bramlett (1971) found high narrow-sense heritability of fruitfulness in seedlings ($h^2 = 0.59$ and 0.65), and that flowering trees on the average ware taller than nonflowering, or precocity, as also a qualitative trait, and is defined Belanger (1976) found that fruitfulness was heritable but negatively correlated with height in parent-progeny correlations.

Although the terms "early fruitfulness," "precocious flowering," and "ripeness to flower" are often used interchangeably, they have slightly different meanings. Ripeness to flower is a qualitative trait, either the tree has flowered or it has not. The ripeness to flower concept assumes that once flowering occurs, it is not reversible, even though flowering may not occur in subsequent years. In this study, a tree is considered to have attained ripeness at any given age if it had flowered previously. Precocious flowering, or precocity, as also a qualitative trait, and is defined as the early manifestation of ripeness to flower. Fruitfulness or early fruitfulness, on the other hand, is considered a quantitative trait and consists of counts of reproductive structures. In most previous work on flowering in pines, fruitfulness was measured.

Since a tree must attain ripeness to flower before it can be fruitful, the two traits are obviously related, but not necessarily the same.

In an analogous situation dealing with fusiform rust in loblolly pine *(P. taeda* L.), somewhat different results were obtained when proportion infected was used rather than number of galls (Blair 1970). Visser *et al.* (1976) used age at first flowering, a trait similar to ripeness, which was not related to the eventual fruitfulness of the seedlings, suggesting that genetic control is separate for the two traits.

In this study, ripeness to flower and precocity were treated as threshold traits by measuring proportion of trees flowering at given ages. The objective was to determine

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the heritability of precocity and fruitfulness in loblolly pine seedlings and to explore the genetic relationship among fruitfulness, precocity, and growth.

Materials and Methods

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

Diallel. Ten randomly selected mature loblolly pine trees, located on the Harrison Experimental Forest in south Mississippi, were crossed in all possible combination, excluding selfs, to give 90 seed lots. The seed was 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 2.74 m between rows and 3.17 m between trees in the rows. The experimental design was a randomized-complete block of 8 replications with 8-tree row plots and 45 plots per block (reciprocal crosses were combined). Scions from the parent trees were grafted on potted seedling rootstocks in January 1967 and included in the planting.

Female flowers were counted on seedlings and grafts each spring at ages 2 through 8 years except at age 6 when measurements on the grafts were not made. Trees flowering at age 2 were considered precocious. 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), where a tree was given the value one if it had flowered in a given year or in any previous year. This procedure not only allows estimation of both individual and family heritabilities from qualitative data, but also provides better estimates of predicted gain than using transformed plot means (Sohn and Goddard 1979). 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), assuming nonrelated, random parents from a diploid population (Cockerham 1963) *(Table 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 for individual trees were calculated by the formula:

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

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

When plot means were analyzed, family heritability was computed as:

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

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

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

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

where the a_i are the coefficients of the linear combination of the mean squares used to estimate the components (Anderson and Bancroft 1952). GCA and SCA values differing from zero by more than two standard deviations were considered significant. Genetic correlations based on GCA components were calculated also.

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

[1] Error degrees of freedom are adjusted for missing data. Out of a total of 360 plots in the study, 39 were missing.

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.

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

Half-sib test. Open-pollinated progenies of 24 loblolly pine trees were included in the half-sib test. Three of the trees were selected for precocity and 21 were selected from the National Forest System's tree improvement program in Mississippi, Alabama, Texas, North Carolina, and South Carolina. The 3 trees selected for precocity were from an experimental planting of 3,451 loblolly pines in which 12 trees flowered 2 years after outplanting and 62 flowered after 3 years. The 3 trees were subjected to further selection for flowering as they were the only ones in the total of 75 precocious trees which produced enough seed in the 9th year to be included. One of these (Pre-1) had originally flowered at age 2, and the other two (Pre-2 and Pre-3) at age 3. All three precocious trees were also taller than the plot means at 2 years of age as well as at 9 years of age when seed were collected. The fact that they were taller than average at age 9 probably had an important role in determining their fruitfulness. There was intense competition in the original stands at the 3 × 3 m spacing, and only dominant trees would be expected to flower (Fowells and Schubert 1956).

Seed from the 24 families were sown in a nursery. The 1-year-old seedlings were bar-planted at two locations in south Mississippi. Four replications of a randomized complete block were planted at each location, with four trees per plot and 3 × 3 m spacing. At age 6, female flowers, conelets (1-year-old strobili), and cones were counted, and height and d.b.h. were measured. Fruitfulness at ages 4 and 5 was assessed by cone and conelet counts at age 6. Mean number of trees flowering per plot was analyzed. The fixed model assumed for the analysis of variance. Statistical significance was tested at the 0.05 level of probability.

Results and Discussion

Diallel. Approximately 5 percent of the diallel progeny had female flowers after 2 years in the field. The number with female flowers increased to over 30 percent by age 3, and to 80 percent by age 8. Although the seedlings flowered better than the grafts at age 2, the grafts subsequently flowered much better than the seedlings *(Fig. 1).* This was undoubtedly due to physiological maturity of the grafts. The grafts averaged 10 female strobili each at age 7, whereas the seedlings averaged only 2 each. Yearly variation in flowering of the seedlings was approximately parallel to that of the grafts.

At age 3, the precocious seedlings were taller than nonprecocious (*Fig. 2*). Although statistically significant in a t-test, the difference was small (2.3 m versus 2.2 m for the nonflowering seedlings). By ages 5 and 10, there were no differences in height. Precocious trees continued to flower better than the nonprecocious trees. At age 6, the difference in flowering was largest, when the precocious trees averaged 12 flowers per tree and the nonprecocious averaged only 6. Though the absolute difference varied widely, precocious trees had about twice as many flowers each year that they were measured.

The diallel analysis showed that precocity and fruitfulness were heritable. General combining ability (GCA) values for flowering were all significant. Specific combining ability (SCA) values for flowering traits were generally much smaller than GCA values and were significant only for average number of flowers (*Table 2*). Heritabilities ranged from 0.13 for 2nd-year ripeness to 0.61 for average number of flowers on individual trees. Values using family means were higher, ranging from 0.47 for 2nd-year ripeness to 0.65 for 3rd-year ripeness. Average number of flowers, a quantitative trait, was highly heritable both on an individual tree basis and on a family basis (0.61 and 0.63, respectively). This agrees with findings from previous work (Schmidtling 1980). Precocity was much less heritable on an individual basis ($h^2 = 0.13$), but was moderately heritable on a family (plot mean) basis ($h^2 = 0.47$).

Heritabilities of the growth variables were lower than those for flowering (*Table 2*). Only the GCA for crown width was significant. Heritabilities for height seemed to increase with time, however, reaching 0.30 by the 10th year for individual tree height. In contrast to flowering, SCA values were significant for several characteristics: 5th-year d.b.h., 10th-year height, and 10th-year d.b.h. on an individual basis, and 10th-year height and 10th-year d.b.h. on a family mean basis. Genetic variation in this

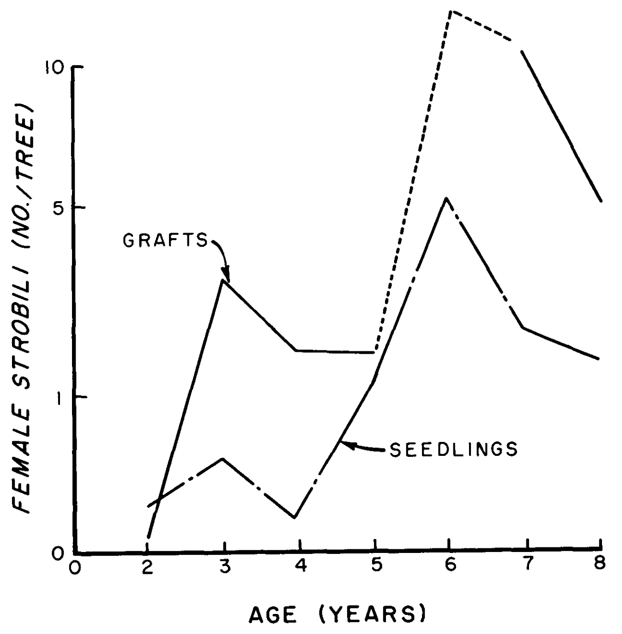

Figure 1. — Flowering of the parent grafts and their seedling progeny in the diallel experiment. Vertical axis is square-root scale. Data for the grafts at age 6 were missing, and this point is estimated using flowering data from a near-by clone bank of grafted loblolly.

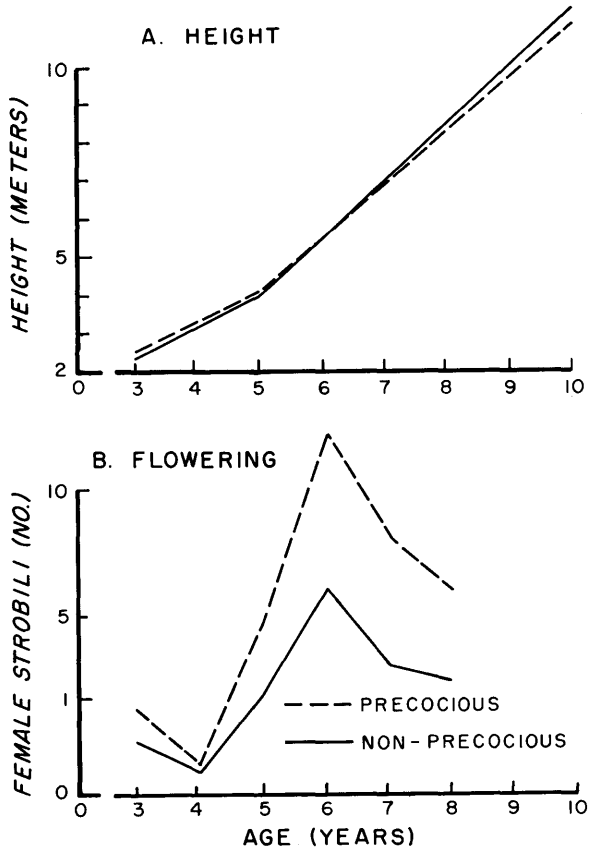

Figure 2. — Growth and flowering of the precocious trees (flowering at age two) compared to the non-precocious trees in the diallel experiment. A. Height. B. Flowering. Vertical axis of B is square-root scale.

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

[1] Having flowered by the year indicated.

[2] Over the eight years measured.

[3] Since heritabilities are based on one location they may be biased upwards, since there is no estimate of genotype × environment interactions.

	Individual tree basis			Family (Plot mean) basis		
Trait	GCA	SCA	h^2 [3]	GCA	SCA	h^2 [3]
Second-year "ripeness"[1] (precocity)	0.0015 ±0.0007	0.0000 ±0.0003	0.13	0.0023 ±0.0011	0.0002 ±0.0007	0.47
Third-year "ripeness"[1]	0.0127 ±0.0059	0.0019 ±0.0019	0.24	0.0148 ±0.0068	0.0002 ±0.0021	0.65
Average number of flowers[2]	0.5334 ±0.2377	0.0937 ±0.0435	0.61	0.5843 ±0.2687	0.1742 ±0.0852	0.63
Third-year height	0.0427 ±0.0240	0.0294 ±0.0244	0.07	0.0617 ±0.0337	-0.0068 ±0.0337	0.32
Fifth-year height	0.0902 ±0.0516	0.1035 ±0.0544	0.10	0.1146 ±0.0666	0.0654 ±0.0758	0.28
Fifth-year D.B.H.	0.0078 ±0.0048	0.0160 ±0.0058	0.10	0.0078 ±0.0050	0.0140 ±0.0070	0.22
Fifth-year crown width	0.1697 ±0.0785	0.0514 ±0.0263	0.32	0.1582 ±0.0738	-0.0064 ±0.0296	0.58
Tenth-year height	0.9388 ±0.4745	0.9658 ±0.3052	0.30	0.8307 ±0.4388	0.8377 ±0.3620	0.36
Tenth-year D.B.H.	0.0606 ±0.0323	0.0888 ±0.0262	0.28	0.0558 ±0.0316	0.0954 ±0.0331	0.29

Table 3. — Genetic (GCA) correlation among flowering and growth variables from the diallel analysis (based on plot means).

[1] Having flowered by the year indicated.

[2] Over the eight years measured.

[3] All correlation coefficients differed by more than two standard deviations from zero.

	2nd year "ripeness"[1]	3rd year "ripeness"	Average number of flowers
Third-year "ripeness"[1]	0.93 [3]	-	-
Average number of flowers[2]	0.83	0.87	-
Third-year height	-0.29	-0.17	-0.53
Fifth-year height	-0.47	-0.37	-0.54
Fifth-year D.B.H.	-0.64	-0.37	-0.35
Fifth-year crown width	-0.65	-0.51	-0.40
Tenth-year height	-0.39	-0.42	-0.39
Tenth-year D.B.H.	-0.54	-0.35	-0.10

diallel is similar to that found by Snyder and Namkoong (1978) in a longleaf pine diallel. Heritabilities in their study for growth traits were in the same range as those found here. They also noted significant SCA effects for many traits.

Genetic (GCA) correlations based on family mean data agreed very closely with those based on individual trees. Genetic correlations among flowering traits were uniformly high and positive *(Table 3)*, ranging from 0.83 between average number of flowers and 2nd-year ripeness to 0.93 between 2nd-year ripeness and 3rd-year ripeness.

Genetic correlations between all growth variables and flowering variables were negative. The 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, ranging from $r = -0.29$ between precocity and height at 3 years for individuals, to $r = -0.65$ between precocity and crown width for plot means.

So, even though precocious trees were significantly taller than nonprecocious trees at age 3, the height difference was environmental since the genetic portion of the overall correlation between height and precocity 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.

Table 4. — Average flowering of the grafts compared to precocity and average flowering of the progeny in the diallel planting.

Family	Parents (grafts)	Progeny	
	Average number of flowers [1]	Percent individuals flowering at age 2	Average number of flowers [1]
7	14.6	12.7	2.5
9	12.0	3.2	2.1
4	4.1	5.2	1.5
1	3.5	14.7	2.3
8	3.4	6.1	1.8
6	1.9	4.4	.9
3	1.7	6.3	.9
5	1.2	1.4	.8
10	0.8	2.0	.8
2	0.6	2.9	.9

[1] Over the 8 years measured.

Parent-progeny relations. Regression between mid-parent average (average of the two parents for each cross) and progeny average for number of flowers yielded a heritability of 0.52. This was slightly less than the heritability found in the diallel analysis, $h^2 = 0.61$ *(Table 2)*. However, the most fruitful parents, in a quantitative sense, were not necessarily the parents which produced the most precocious progeny *(Table 4)*. Parent 1 ranked 4th out of 10 for average flowering, but produced the most precicious progeny, 14.7 percent. The correlation between mid-parent average flowering of the grafts and precocity of the progeny, although positive and significant, was only $r = 0.36$.

Correlations between mid-parent fruitfulness and various growth measures of the progeny were all negative except for the correlation between 10th-year d.b.h. and parent fruitfulness ($r = 0.13$). 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 $r = -0.24$ for 3rd-year height to $r = -0.02$ for 5th-year diameter. Though correlations of this magnitude probably are not very important, they reinforce the findings of the diallel analysis in cautioning against selection or roguing for fruitfulness without considering other aspects, since there may be a tendency for the most fruitful parents to produce slower growing progeny.

Half-sib test. About 12 percent of the trees in the half-sib test flowered the 4th year. Flowering increased to 16 percent the 5th year and to 26 percent the 6th year. Family and location effects were statistically significant, but the family × location interaction was not.

Results of selection for precocity were evident. An average of 33 percent of individuals from the three precocious families flowered by age 4 compared with an average of 10 percent of the other families. Over 40 percent of Pre-1 progeny flowered by age 4. Only one nonprecocious family equalled flowering of the poorest precocious family, Pre-3, with 27 percent flowering by the 4th year. The realized gain of 23 percent in frequency of trees with flowers at age 4 is slightly higher than one would expect from the diallel experiment. The selection differential for the precocious parents was about 0.022 (75 trees flowering at ages 2 or 3 out of a total of 3451 trees). According to Falconer (1960) heritability is expressed as:

$$h^2 = (\text{realized gain X2})/\text{selection differential} =$$
$$= (0.23\text{X}2)/0.022 = 0.21$$

This is higher than the 0.13 heritability in the diallel but is probably biased upwards because of the further selection for fruitfulness at age 9, since only 3 of the original 75 selections had enough cones at that time to be included.

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 progeny were significantly larger than the nonprecocious progeny-averaging 5.7 m tall versus 5.4 m for height and 9.3 cm versus 8,6 cm for diameter. Caution in interpretation is needed here, since geographic variation has likely biased these results. Eleven of the 21 National

Forest selections were from areas of slower growing provenance; i.e., from north and central Alabama, Texas, and South Carolina Piedmont (Wells 1969, Wells personal communication). By excluding the slow growing provenances, mean height and diameter of the remaining trees were not significantly different from the precocious selections. After dropping these slower growing provenances from the analysis, flowering differences between precocious and select trees still remain significant.

Theoretically, one could increase genetic gain in breeding programs by utilizing precocious flowering for a more rapid turnover of generations. In order to be practical, breeding such precocious trees would need to be combined with rogueing based on later evaluation of the select trees, since growth evaluation at age 2 would be very uncertain. This is approximately what occurred in the half-sib study. The precocious trees were selected at ages 2 and 3 for flowering; they were then indirectly selected for growth at age 9, since the close competition prevented all but strongly dominant trees from having cones. It is possible that in a two-stage selection process, as in this half-sib study, both of these traits could be improved simultaneously. In this study, the precocious selections flowered earlier and grew as well as the National Forest selections, which were selected for growth.

Conclusions

Precocious flowering in loblolly pine appears to be heritable, and selection for this trait can be effective. Fruitfulness is highly heritable, and the broad-sense heritability estimates determined from clonal studies (around 0.5) appear to be low (Schmidtling 1980). In the present study (of 10 parents only), a negative relationship between growth and flowering had a genetic basis.

Although the results of the half-sib study suggest that it is possible to breed for both traits simultaneously, in practical programs this would not be advisable. To use precocity to produce long-term gains in growth would require that the heritability of precocity be high, the correlation between precocity and growth be near-zero or positive, and costs of testing be reasonable. On the basis of the diallel and the half-sib test, I conclude that using precocity for turning over generations for selection for growth would not be advisable for improvement in loblolly pine. Physiologically inducing precocity would seem to be a more reasonable approach to shortening generation time.

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Literature Cited

Anderson, R. L., and Bancroft, T. A.: Statistical theory in research. McGraw-Hill, New York. 399 p. (1952). — Blair, R. L.: Quantitative inheritance of resistance to fusiform rust in loblolly pine. Ph. D. Thesis, N. C. State Univ., Raleigh, 87 p. (1970). — Bramlett, D. L.: Correlations between reproductive and vegetative growth in a 6-year-old Virginia pine plantation. U.S.D.A. For. Serv., Southeast. For. Exp. Stn. Res. Pap. SE-88, 6 p. (1971). Bramlett, D. L., and Belanger, R. P.: Fertilizer and phenotypic selection increase growth and flowering in young Virginia pine. For. Sci. 22: 461—467 (1976). — Cockerham, C. C.: Estimation of genetic variances. *In* Stat. Genet. and Plant Breed. Symp. W. D. Hanson and H. F. Robinson, eds. Natl. Acad. Sci. Nat. Res. Counc. Publ. 982, p. 53—94. Wash., D. C. (1963). — Falconer, D. S.: Introduction to quantitative genetics. Ronald Press, New York. 365 p. (1960). — Fielding, J. M.: Branching and flowering characteristics of Monterey pine. Forestry and Timber Bureau (Canberra), Bull. 37, 59 p. (1960). — Fowells, H. A., and Schubert, G. H.: Seed crops of forest trees in the pine region of California. U.S.D.A. Tech. Bull No. 1150, 48 p. (1956). — Gerhold, H. D.: Selection for precocious flowering in *Pinus sylvestris*. *In* Joint Proc. Second Genet. Workshop, Soc. Am. For. and Seventh Lake States For. Tree Improv. Conf. U.S.D.A. For. Serv., North Cent. For. Exp. Stn. Res. Pap. NC-6, p. 4—7 (1966). — Greene, J. T., and Porterfield, H. D.: Early cone production in loblolly pine through selection and control pollination. Ga. Acad. Sci. Bull. 20, 6 p. (1962). — Greenwood, M. S.: Flowering induced on young loblolly pine by out-of-phase dormancy. Science 201: 443—444 (1978). — Jeffers, R. M., and Nienstaedt, H.: Precocious flowering and height growth of jack pine full-sib families. *In Proc.* Work. Party on Progeny Test., Ga. For. Res. Counc. Publ., p. 19—23 (1972). — Romberger, J. A.: Flowering as a problem in developmental physiology. *In* 14th Int. Union For. Res. Organ. Congr., Sec. 22, 14 p. (1967). — Schaffer, H. B., and Usanis, R. A.: General least squares analysis of diallel experiments--a computer program--DIALL. Genet. Dept. Res. Rep. 1, 61 p. N.C. State Univ., Raleigh (1969). — Schröck, O.: Beobachtungen an der Nachkommenschaft einer Zapfensuchtkiefer. Silvae Genetica 6: 169—178 (1957). — Schmidtling, R. C.: The genetic and environmental basis of fruitfulness and growth in loblolly pines. Ph. D. diss. Univ. Fla., Gainesville. 104 p. (1980). — Snyder, E. B., and Namkoong, G.: Inheritance in longleaf pine: A diallel crossing experiment. U.S.D.A. For. Serv., South. For. Exp. Stn. Res. Pap. SO-140, 31 p. (1978). — Sohn, S. I. and Goddard, R. E.: Influence of infection percent on improvement of fusiform rust resistance in slash pine. Silvae Genetica 28: 173—180 (1979). — Teich, A. H., and Holst, M. J.: Genetic control of cone clusters and precocious flowering in *Pinus sylvestris*. Can. J, Bot. 47: 1081—1084 (1969). — Thompson, W. A., Jr., and Moore, J. R.: Non-negative estimates of variance components. Technometrics 8: 441—449 (1963). — Visser, T., Verbaech, J. J., and Devries, D. P.: A comparison of apple and pear seedlings with reference to the juvenile period. I. Seedling growth and yield. Euphytica 25: 343—351 (1976). — Wells, O. O.: Results of the southwide pine seed source study through 1968—69. *In* Proc. 10th South. For. Tree Improv. Conf., p. 117—129 (1969). — Wright, J. W., Lemmien, W. A., and Bright, J.: Early flowering patterns in Scotch pine. Mich. Agric. Exp. Stn. Q. Bull. 49, p. 189—199 (1966).