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Genetic Variation in Fruitfulness in a Loblolly Pine (*Pinus taeda* L.) Seed Orchard¹⁾

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Abstract

In a loblolly pine seed orchard in South Mississippi, more than 50 percent of the variation in female flowering, cone production, and seed production, and about 40 percent of the variation in male flowering was attributable to genetic effects.

Although the more fruitful clones tended to produce an abundance of strobili every year, there were year × clone interactions for male and female flowering. This indicates that the genetic makeup of seeds collected from year to year may vary considerably, even if collected separately by clone.

Key words: Heritability, pollen, seed, *Pinus taeda* L., genotype × environment interactions.

Zusammenfassung

In einer *Pinus taeda* L. Samenplantage in Süd-Mississippi ließen sich bei der Variation im weiblichen Blühverhalten, der Zapfen- und Samenproduktion mehr als 50% und bei der Variation im männlichen Blühverhalten ca 40% auf genetische Effekte zurückführen. Obwohl die fruchtbaren Klone in jedem Jahr zu einer starken Blütenproduktion neigten, gab es bei den männlichen und den weiblichen Blüten eine Interaktion zwischen Jahr und Klon. Dies zeigt, daß die genetische Zusammensetzung gesammelter Samen trotz klonweise getrennter Ernte von Jahr zu Jahr beträchtlich variiert.

Introduction

Large differences often exist in fruitfulness between southern pine clones. This could be a serious problem in seed production if only a few clones in a orchard produce most of the seed. BERGMAN (1968) estimated that 2 of 15 clones produced over half of the seed in a loblolly pine (*Pinus taeda* L.) orchard. Others estimate that 20 percent of the clones produced 80 percent of the seed (North Caro-

lina State University 1976). A less pessimistic estimate was provided by BEERS (1974) who found that the top 20 percent of clones in seed production produced 56 percent of the seed in a slash pine (*P. elliotii* ENGLM.) orchard. DANBURY (1971) estimated that seed production could be increased by 50 percent and that seed cost could be 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 correlated genetically. Inherent fruitfulness can be especially important, since as a general rule trees which are inherently unfruitful do not respond well to flower inducing treatments (BERGMAN 1968).

The inherent ability of the individual tree to flower is the most important factor influencing fruitfulness in southern pines (SCHMIDTLING 1974, SHOULDERS 1967). It is important to consider this variation in the experimental design of seed orchard studies. In several fertilizer experiments, from 33 percent (SCHMIDTLING 1974) to 56 percent (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 0.40 to 0.70 for loblolly (SCHMIDTLING 1974) corroborate this observation.

Inherent variation in male flowering is also large, but the effects are seldom quantified. Male strobilus production is more difficult to assess than female strobilus production because catkins are numerous and do not persist after pollen is shed. BARNES and BENGSTON (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 are not closely correlated. STERN and GREGORIUS (1972) found that the correlation between male and female flowering in Scots pine (*P. sylvestris* L.) is weak. SCHULTZ (1971) found a negative genetic correlation between male and female flowering in slash pine. This relationship between

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male and female flowering could be an important consideration in seed orchard management. If DANBURY'S (1971) suggestion is followed and 50 percent of the clones are rogued on the basis of seed production, some of the best pollen producers in the orchard may be eliminated. This in turn would narrow the genetic base and perhaps eliminate some of the better genotypes.

Flowering and seed yield data collected from a loblolly pine seed orchard over a period of several years were examined in this report. The objectives of the study were 1) to determine the extent of genetic control of male and female flowering and their intercorrelations and 2) to study flowering patterns over time.

Materials and Methods

The study was conducted in a U. S. Forest Service seed orchard, located in South Mississippi 25 miles (40 km) southeast of Hattiesburg. The orchard was composed of ramets from 50 superior loblolly pine selections located in the National Forests of South Mississippi. There were about 4,000 ramets of these clones planted at 4.6×9.1 m spacing.

The ortets ranged from 31 to 67 years and more than half were between 43 and 54 years of age. All were reproductively mature, as some evidence of cone production was required when selected or after release and fertilization.

The orchard was established from 1963 to 1972 with 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 of all ramets were measured each year from 1969 through 1973, and in 1976.

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

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

"K" is the harmonic mean number of ramets in clones (BECKER 1967). The clonal component of variance, σ_c^2 , re-

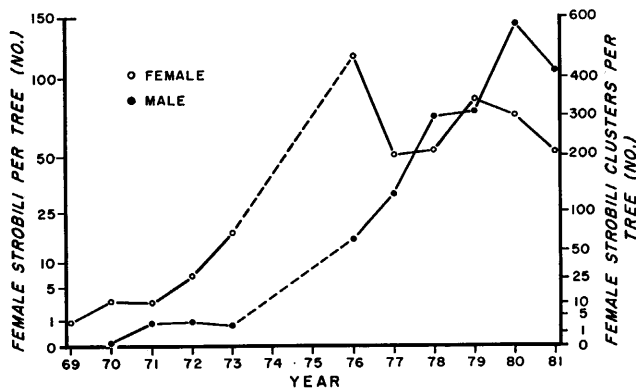


Figure 1. — Yearly variation in male and female strobili in a loblolly pine seed orchard in South Mississippi. Vertical axes are square-root scale. * Attention: Female on the right side of the figure should read male.

Table 1. — Clonal means for flower, cone and seed yield for the 180 sample ramets.

Clone	Cones per ramet	Female flowers/ramet		Conelet survival		Sound seed per cone		
		1976 No.	1977 No.	1976-77 Percent	1977-78 Percent	1976 No.	1977 No.	1978 No.
A	7.6	143	9	38	30	9	29	21
B	2.4	102	15	26	29	18	26	11
C	22.1	144	51	62	36	24	45	7
D	16.5	238	117	30	82	12	69	17
E	1.0	41	14	46	78	15	49	39
F	0.1	13	1	59	33	7	39	3
G	18.5	191	28	68	92	35	37	36
H	8.5	103	59	52	86	18	42	26
I	26.1	209	19	34	61	9	60	23
J	0.3	16	15	56	64	53	37	50
K	0.0	65	17	10	44	--	50	39
L	0.8	55	11	26	16	5	55	22
M	9.0	177	112	16	69	13	40	16
N	2.7	21	16	28	56	4	24	33
O	0.9	10	7	57	56	4	48	40
P	50.8	118	125	28	69	7	17	7
Q	6.5	97	82	14	52	11	25	10
R	38.1	239	275	45	80	21	56	11
Mean	11.8	110	54	39	57	16	41	23
h ²	0.45	0.50	0.63	0.20	0.27	0.25	0.30	0.31

presents the genetic effect, and broad-sense heritability is calculated:

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

The number of ramets per clone in each age group varied widely, so 10 ramets grafted in 1966 were randomly selected from each of 18 clones. In addition to the observations of strobilus production made on all ramets from 1969 through 1976, the following traits were measured on the 180 sample ramets:

1. Total seed and sound seed (separated by ethanol flotation) from a five-cone sample taken from each ramet in the fall of 1976, 1977, and 1978.
2. Seed weight in 1978.
3. Counts of male strobili clusters, female strobili and cones each year from 1977 through 1981.

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

Results and Discussion

The number of female flowers generally increased with time as expected in a young orchard (Fig. 1). The 180 sample trees followed the production trend of the whole orchard.

In addition to the general yearly increase in female strobili production, there was considerable year-to-year variation (Fig. 1). An exceptionally good crop of female strobili in 1976 was followed with a nearly average crop in 1977.

Male strobili production increased with age, similar to the female strobili production trend (Fig. 1). In addition to the general yearly increase in male flowering, there was also year-to-year variation as in female flowering. The yearly patterns of male and female flowering did not



Figure 2. — 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.

seem to be related; that is, the increase or decrease in female flowering did not correspond to an increase or decrease in male flowering.

Inherent variation. Clonal variation in male and female flowering was high. Broad-sense heritabilities for female strobilus production averaged around 0.50 but varied by year and age of ramets. Using the sample ramets as an example, average female flower counts per ramet ranged from 10 to 239 in 1976 and from 1 to 275 in 1977 (Table 1). The average number of female flowers was 110 in 1976 and 54 in 1977, with corresponding heritabilities of 0.50 and 0.63, respectively.

Heritabilities for male strobilus production were more variable than for female strobilus production, ranging from near 0 to 0.6 and averaging 0.4. Due to the low frequency of male flowers before 1976 (Fig. 1), early heritabilities for male flowering were generally very low. As male flowering increased with age, so did heritability.

The broad-sense heritabilities estimated in this experiment are lower than those estimated from diallel crosses in loblolly (SCHMIDTLING 1981). Rootstocks cause substantial variation in flowering (SCHMIDTLING 1978). Since the orchard ramets were grafted on nursery-run seedlings, the within-clone variance would include rootstock effects which would lower heritability. If rootstock variation were controlled through the use of clonal rootstocks or rooted cuttings, clonal variation would likely be higher.

Female and male flowering for the whole orchard were positively correlated on a clonal basis. The genetic correlation between male and female flowering in 1976 was 0.59 for 10 year old grafts (39 clones) and 0.58 for 9 year old grafts (45 clones). Generally, clones with the most female flowers were good pollen producers, but some clones that were below average for female strobili were well above average for male strobili (Fig. 2). If only female strobilus or cone production is used as a basis for roguing an orchard, some valuable pollen-producing clones might be eliminated. One clone in particular averaged only 1 female strobilus per ramet, but had over 50 male strobili clusters per ramet, which was more than twice the average (Fig. 2). It would be more logical to limit roguing to the clones in the lower left quadrant of Fig. 2.

The average heritability estimate for cone production over all ages and years was 0.51, about the same as for female flowering. Conelet survival in the sample ramets

averaged 39 percent for 1976—1977 and 57 percent for 1977—1978 (Table 1). The heritability of conelet survival was 0.20 for the 1976—1977 crop and 0.27 for the 1977—1978 crop.

Average yields of total seed per cone for the sample ramets were 42.3 in 1976, 56.4 in 1978, and 52.8 in 1977. Clones varied widely in total seed per cone all 3 years, with a three to fourfold difference between those having the largest and those having the smallest yields per cone. Heritabilities for total seed per cone were 0.24, 0.41, and 0.37 for 1976, 1977, and 1978, respectively.

Variation in clone and seed production is a function of female strobili production and variations in conelet and seed survival. Although much of this added variation might be caused by insect predation (McLEMORE 1977). Other environmental and genetic factors may contribute to it also, such as inadequate pollen, lack of reproductive synchrony, or physiological stress.

Yearly averages of sound seed per cone varied much more than the total seed per cone (Table 1). There were averages of 16, 41 and 23 seed per cone in 1976, 1977 and 1978 respectively. 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 more than a tenfold difference among clones. About 38 percent of the total seed were sound in 1976 and 41 percent in 1978. In 1977, 79 percent of the total seed were sound, with only a fourfold difference among clones.

The yearly differences in proportion of sound seed was probably due to variation in insect predation. Losses to seed bugs (*Leptoglossus corculus* [SAY]) occur the year of cone harvest and are manifested as empty and aborted seed. Insects are also the primary cause of conelet/flower losses, which occur mainly in early spring during and shortly after flowering (McLEMORE 1977). The decrease in

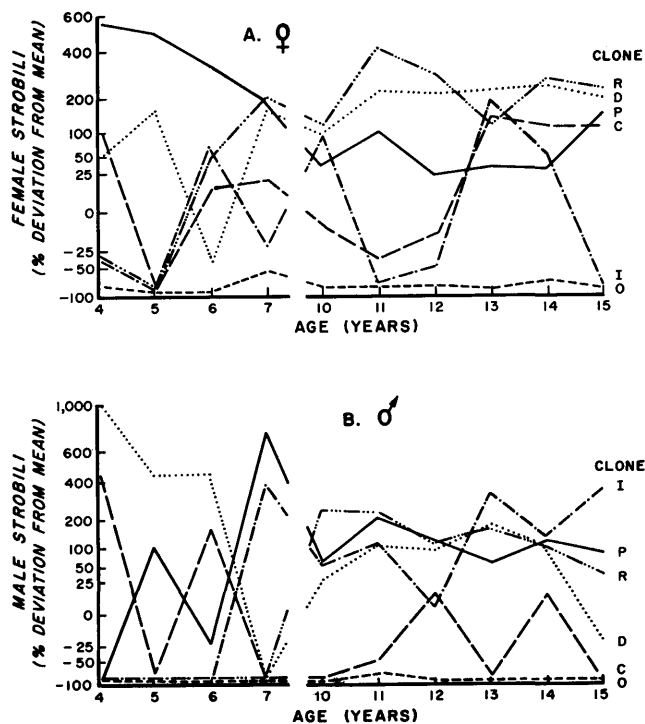


Figure 3. — Year-to-year clonal variation in male and female flowering of 6 representative clones from the 18 sample clones. Flowering of each clone is expressed as a percent above or below the mean for each year. Vertical axes are square-root scale.

sound seed per cone from 1977 to 1978 probably is a result of an increase in seed bug population associated with the large cone crop in 1977.

Year × clone interactions. In general, clonal variation in flowering followed the general yearly trend; i.e., all clones flowered well in good years such as 1976, and poorly in bad years such as 1977. The relative ranking of clones changed from year to year, however. This is exemplified in Fig. 3 by 6 clones that represent the range of flowering performances of the 18 sample clones. The clones varied considerably in female flowering from year to year (Fig. 3a), and there seemed to be a long-term trend for some clones to move up or down in relative rank. Clone P was the best flowering clone in the early years; but it has been surpassed by several other clones. Clone R, initially among the poorest, now has become one of the best. Clone I varied widely from year to year.

Strong year × clone interactions were also apparent in male flowering (Fig. 3b). For instance, Clone D was the best pollen producer during the first 3 years in which measurements were made, but it was only average for the last 3 years. Clone I was at the bottom during the first 3 years and had no pollen, but it assumed the number one position the last 3 years. Clone C oscillated (from) year to year from poor to above average. An important consequence of such year × clone interaction in pollen production is that the genetic composition of the seed produced by the orchard may vary from year to year, even for seeds collected separately by female parent.

In an analysis of female and male flowering for the years 1976 through 1978, clonal effects were very large but year × clone effects were significant and constituted an important part of the total variation for both male and female flowering (Table 2). The correlation coefficients show that male and female flowering were well correlated by clone ($r = 0.81$) and by individual ramet ($r = 0.80$) over the 3 years. The negative correlation coefficients between male and female flowering across years ($r = -0.84$) and for a given clone across years (year × clone $r = -0.21$) quantify the interactions for male and female flowering evident in Figs. 1 and 3, respectively. Large yearly increases in male flowering were associated with decreases or only slight increases in female flowering for 1976 through 1978 (Fig. 1).

At the clonal level, yearly fluctuations in male flowering (Fig. 3b) did not correspond to changes in female flowering (Fig. 3a).

Under natural conditions, consecutively good cone crops would not be selectively advantageous, since predator populations would increase to consume a large proportion of the output. Yearly variation, therefore, functions to keep predator populations low (FORCELLA 1980). Year × genotype interactions may serve a similar function by shifting reproduction to different trees each year.

The lack of correlation in yearly variation between male and female flowering may also have adaptive significance. It would seem logical to assume that male and female flowering should be highly correlated from year to year to realize the maximum in reproductive potential. The fact that they are not correlated is undoubtedly a consequence of different times of primordia initiation (GREENWOOD and SCHMIDLING 1981) but could also serve to disrupt the life cycle of insects which feed on both pollen and cones. *Dioryctria disclusa* has one life cycle per year which begins with larvae feeding on maturing pollen catkins in loblolly pines. The larvae moves to feed on deve-

Table 2. — 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	Male/Female Covariance	Variance Male	Male/Female 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	11.61	72.24	0.366

loping cones on the same tree after pollen shed (DEBARR, pers. comm.). Thus, yearly fluctuation in pollen production relative to cone production would serve to interrupt the life cycle of this insect.

Clonal contribution to seed production: Many tree improvement workers are concerned that only a few of their clones produce the major part of their seed. One tree improvement cooperative estimates that 20 percent of the clones in their orchards produce 80 percent of the seed. This is the so-called "20/80" rule" (North Carolina State University 1976). A strong clonal effect was evident in these data, although not as strong as "20/80."

In this study, the top 4 of 18 clones (22 percent) produced 76 percent, 65 percent, and 62 percent of the total sound seed produced in 1976, 1977, and 1978, respectively. However, the top 4 clones were not the same clones each year. Fig. 4 shows the strong year × clone interaction for seed produced for the top 7 of the 18 clones. Only Clone R was included in the top 4 all 3 years. If a 3-year average is used, the top 4 clones produced 58 percent of the total sound seed. The yearly fluctuation in pollen production (Fig. 3b) would cause even greater genetic variation in the

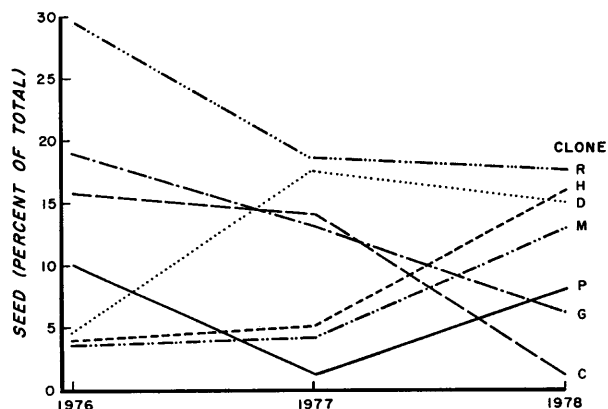


Figure 4. — Yearly seed production of the 7 best seed producers of the 18 sample clones, expressed as a percent of the total production of all 18 clones each year.

seed produced, and the contribution of the top clones to the overall genetic makeup of the seed produced would be less than 58 percent.

The genetic correlations between number of female flowers and the number of sound seed per ramet produced from that particular flower crop were 0.86 for 1977 and 0.88 for 1978. 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.

There was a very low correlation among years for each clone for either sound seed yields or conelet survival. Although the correlation coefficient between years for female flowering was high ($r = 0.63$) the correlations between years for conelet survival and between years for sound seed were low.

Conclusions

The number of clones which should be included in a seed orchard is a matter of controversy. This paper does not attempt an answer, but points out the importance of considering complex interactions as well as clonal variation.

The large clonal component of variation is an important factor because many clones never produce enough seed or pollen to justify the cost of their maintenance in an orchard. The "genetic base" of the average orchard, however, may not be as narrow as this clonal variation seems to indicate. If variation in pollen production as well as variation in seed production over a period of several years is considered, the genetic base includes a large proportion of the orchard.

The prospect for identifying the poorest clones at an early stage is not promising. Although clones which are fruitful early tend to continue to be fruitful, some that show little reproductive activity in early years become fruitful later on. Strong year \times clone interactions also make it imperative that fruitfulness, including pollen production, be assessed over a period of several years.

As a consequence of year \times clone interactions in pollen production, open-pollinated seed of orchard clones could vary genetically from year to year. What might appear as family \times site or family \times planting year interactions could be partly due to pollen crop \times year interactions, which cause large differences in male parentage from year to year. This undoubtedly accounts for the seed crop year \times genotype interaction observed by C. H. LEE (1978). The same kind of variation could be expected in various kinds of "check" lots collected in different years. A more realistic evaluation of gain could be obtained by mixing seed from several years production.

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Isoenzyme Variation within and among Populations of European Black Pine (*Pinus nigra* Arnold)

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Summary

Genetic variation in 28 natural populations of European black pine (*Pinus nigra* ARNOLD) is studied at the enzyme level. Using techniques of gel electrophoresis, we have characterized the isoenzyme patterns of esterase (Est), acid phosphatase (Acph) and leucine aminopeptidase (Lap) in dormant seeds. The samples examined are from 19 loca-