P. strobus pollen grains in vitro. Dead pollen grains apparently produced some factor essential to germination of scattered grains, but they did not provide the stimulus to pollen tube growth given by live pollen. Pollen tubes were only two-thirds as long for viable grains in 10 percent dilutions as for those in undiluted viable pollen.

The species of pollen used as diluent at the 50 percent level may influence cone set. More cones were harvested when pollen of the seed parent species was used as diluent. The diluent species did not significantly influence total seeds per cone, proportion of seeds that were sound, or the germination in vitro of P. strobus pollen. The presence of dead pollen of a genetically incompatible species does not favor or disfavor hybrid seed production.

Additions of boric acid to dilutions containing 10 or 50 percent viable pollen did not have a significant effect on cone set or seed yield. The results of adding boric acid suggested that boron may increase both total number of seeds per cone and proportion of sound seeds. Further study is needed of the chemical form and concentration of boron in seed production.

Controlled intraspecific hybridizations produced more total seeds per cone, and controlled crosses produced twice as many sound seeds as were produced from open pollination by wind.

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Variation and Heritability of Fruitfulness in Slash Pine

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Introduction

Genetic studies of fruitfulness in Pinus are especially difficult because of the long generation time. Few species when grown from seed will flower before their fifth year. Even ramets from mature trees usually grow 2 to 3 years before flowering. After a tree begins to flower, production increases slowly and is erratic for another 2 to 5 years. Finally, if progeny are needed, a 20-month waiting period exists between pollination and seed fall.

The heritabilities we have obtained are incidental results of long-standing studies designed for other purposes. The limited data did not provide unequivocal estimates of heritability for either female flower (megasporangiate strobilus) production or cone yield, but the cumulative evidence from the flower and cone data provided a first-approximation of the genetic control of sexual reproduction in slash pine. For the sake of simplicity, the term "fruitfulness" is used here in the general sense of sexual reproduction or fecundity and refers to neither female flower production nor cone yield specifically.

Materials and Methods

Heritability of fruitfulness was studied in three plantations of slash pine (Pinus elliottii ENGELM. var. elliottii) located near Olustee in northeastern Florida, U. S. A. The first plantation, 0-132, was an informal arrangement of rooted cuttings from several trees originally chosen for their gum-yielding ability. Some clones had been distributed at random whereas others were In row plots. Seventeen clones, containing from 1 to 8 ramets and ranging in age from 14 to 17 years, were examined from the ground annually from 1961 through 1964 for cone yields. Although clonal differences were confounded to some extent with environmental differences, average annual cone production by ramet was analyzed as a completely random design and the resulting variance components were used in estimating broad-sense heritability.

The second plantation, 0-116, consisted of 6 control- and 8 wind-pollinated progenies of the selections in 0-132. The progenies were 16-years-old and were composed of from 1 to 7 individuals randomly located in each of 7 blocks. Cones were counted from the ground annually from 1961 through 1964. Average annual cone production per tree was subjected to the typical analysis of variance for randomized blocks. The within-plot mean square was determined by the method used by EHRENBERG (1963).

The third plantation, NS-112, contained 4- to 6-year-old air-layered propagules from each of 24 selected trees in 0-116. Every clone was represented in each of 8 treatments, and treatments were replicated twice. Since treatments were not the subject of this study,[2]) they were regarded as blocks. Treatment replications were regarded as subsamples. Female flowers, 1 to 2 months after pollination, were counted annually from 1962 through 1965 from a mobile platform about 11 feet high. Average annual flower production by ramet was analyzed as a randomized block design with an estimate of block-clone interaction. Variance

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[2]) Treatment effects are the subject of another report to be presented elsewhere (BENGTSON, G. W., in press).

components obtained from the analysis were used in estimating broad-sense heritability. The relationship between flower production by clones in NS-112 and cone production by their respective ortets in 0-116 was studied by regression and correlation analysis. Spacing in all plantations was 20 by 20 feet.

Results and Discussion

Variation. — The variation in cone and flower production was large *(Table 1)*. However, a considerable portion of this variation was associated with the history of the various plantations. For example, trees in 0-132 generally were more productive than trees in the other two plantations. Superiority of trees in 0-132 over those in NS-112 was expected. Trees in 0-132 were 14- to 17-years-old and had been flowering for several years. Trees in NS-112 were only 4- to 6-years-old and had just begun to bear flowers. Although 0-132 and 0-116 were about the same chronological age, the superior productivity of 0-132 over 0-116 is easily explained by the fact that 0-132 trees were established from rooted cuttings taken from sexually mature trees, whereas trees in 0-116 were grown from seed. Other dissimilarities between 0-132 and 0-116 which may contribute to the observed difference in cone yield were: (1) a larger proportion of the trees in 0-132 were on the edge of the plantation where conditions for flowering were more favorable, and (2) a variation in site quality between the two plantations.

The data *(Table 1)* also gave an idea of the magnitude of variation among and within both clones and families. Although within-clone differences were often large, some clones in 0-132, such as G-12, G-35, and G-37, were heavy cone producers; others, such as G-28, G-29, G-31, and G-36, were poor cone producers. Similar clonal differences were apparent in the NS-112 data. Family differences, on the other hand, were relatively small compared to clonal differences (in *Table 1*, compare 0-116 and 0-132).

Variation within families *(Table 1*, 0-116 data), which should not exceed the variation among families, seemed quite large. Similarly, in NS-112, considerable variation usually occurred among clones having one or more parents in common. Clones having G-3 as a parent were an exception — all four such clones were poor flower producers.

Another important aspect of variation, which is not shown in *Table 1*, concerns the difference in the time at which young trees reach the flowering stage. Certain clones in NS-112 began flowering earlier than others, but some of the late starters showed signs of greater ultimate productivity.

Broad-sense heritabilities. — Broad-sense heritabilities for cone yields on 14- to 17-year-old rooted cuttings in 0-132 and for flower production on 4- to 6-years-old airlayered propagules in NS-112 were 0.50 and 0.49, respectively *(Tables 2 and 3)*. Although these estimates are based on reasonably large samples of 16 clones in 0-132 and 24 clones in NS-112, they are subject to certain restrictions. For instance, in 0-132 the age differential within the plantation and nonrandomized arrangement of some clones probably caused an upward bias in the heritability for cone yields. The heritability for flower production may be affected similarly in NS-112 where the trees have been flowering erratically, possibly because of their youthfulness.

Correlation analysis of flower production of NS-112 clones and cone production of their respective ortets in 0-116 *(Table 4)* yielded a coefficient of 0.51 ($p < 0.01$). This suggests a trend toward moderately strong genetic control of fruitfulness. However, the correlation is due largely to the values for a single clone (G-1 × G-2, 4-2-7) and its ortet and is of doubtful value.

The broad-sense heritabilities, as well as the ramet-ortet correlation coefficient, may be biased upwards by variation associated with cloning ("c" effects variation) which results from nongenetic differences among ortets (LIBBY and JUND, 1962). The 0-132 clones may contain large amounts of "c" effects variation because their ortets were quite heterogenous with respect to age, size, location, and density of

Table 1. — Averages and ranges of annual flower or cone production for clones and progenies.

0-132[1]				0-116[1]				NS-112[2]				
Clone	Ramets	Cones per tree		Progeny	Trees	Cones per tree		Clone		Ramets	Flowers per tree	
		Mean	Range			Mean	Range				Mean	Range
G—1	6	78	50—105	G—1 × G—2	28	14	0—79	G—1 × G—2	2—5—6	16	1	0—12
G—2	8	42	17— 61	G—1 × G—7	26	14	0—34		4—2—7	16	27	0—86
G—3	2	30	24— 37	G—3 × G—2	26	9	0—38		6—9—6	16	19	1—64
G—4	6	45	25— 74	G—3 × G—6	12	10	0—51	G—1 × G—7	2—1—4	16	3	0—11
G—5	3	72	53—103	G—6 × G—3	13	8	0—20		3—3—5	16	11	0—50
G—7	1	22	—	G—6 × G—8	27	8	0—47	G—1 × W	1—3—7	16	10	0—29
G—10	2	30	6— 53	G—1 × W	38	8	0—29	G—2 × W	1—6—4	16	2	0— 8
G—11	4	83	54—111	G—2 × W	38	7	0—25		3—8—3	16	0[3]	—
G—12	2	107	66—147	G—3 × W	37	14	0—36		4—7—5	16	1	0— 3
G—28	3	16	0— 36	G—4 × W	18	15	0—77		7—5—4	16	5	0—20
G—29	1	14	—	G—6 × W	36	6	0—31	G—3 × G—2	1—1—4	16	0[3]	—
G—31	1	9	—	G—8 × W	17	5	0—15	G—3 × G—6	7—7—1	16	0[3]	—
G—34	1	33	—	G—23 × W	33	10	0—47	G—3 × W	7—4—3	16	3	0—10
G—35	3	132	81—204	G—25 × W	39	4	0—30	G—4 × G—1	2—3—4	16	10	0—45
G—36	2	16	9— 12						6—4—7	16	22	2—59
G—37	3	100	60—141						6—9—7	16	45	3—90
G—38	1	68	—					G—4 × W	4—3—2	16	10	0—24
									6—2—3	16	0[3]	—
								G—6 × G—3	2—9—1	16	2	0—22
								G—8 × W	7—9—5	16	3	0— 9
								G—10 × G—7	2—7—3	16	16	0—37
									3—9—6	16	2	0— 8
									4—7—3	16	3	0—10
								G—25 × W	4—10—5	16	1	0— 2

[1] Data obtained annually from 1961 through 1964.

[2] Data obtained annually from 1962 through 1965.

[3] Flowers were produced on some ramets, but the average was less than 0.5.

Table 2. — Analysis of variance of average annual cone production in clonal plantation 0—132, 1961—64.

Source	Degrees of freedom	Mean squares	F	Variance component estimates
Between clones	16	3336	3.79***	$\sigma_c^2 = 880$
Within clones	32	880		$\sigma_e^2 = 880$

*** Significant at the 0.5 percent level of confidence.

$$h^2 = \frac{\sigma_c^2}{\sigma_c^2 + \sigma_e^2} = 0.50$$

Table 3. — Analysis of variance of average annual female flower production in clonal plantation NS-112, 1962—1965.

Source	Degrees of freedom	Mean squares	F	Variance component estimates
Blocks	7	434		
Clones	23	1918	14.86**	$\sigma_c^2 = 112$
Interaction	161	129	1.24 N.S.	$\sigma_{cb}^2 = 13$
Error	192	104		$\sigma_e^2 = 104$

** Significant at the 1.0 percent level of confidence.

$$h^2 = \frac{\sigma_c^2}{\sigma_c^2 + \sigma_{cb}^2 + \sigma_e^2} = 0.49$$

Table 4. — Female flower production of NS-112 clones and cone production of their respective ortets in 0—116.

Clone and ortet designation	Mean annual flower production[1] of clones	Mean annual cone production[2] of ortets
G—1 × G—2, 2—5—6	1	4
4—2—7	27	79
6—9—6	19	5
G—1 × G—7, 2—1—4	3	19
3—3—5	11	7
G—1 × W, 1—3—7	10	0
G—2 × W, 1—6—4	2	15
3—8—3	0	0
4—7—5	1	5
7—5—4	5	3
G—3 × G—2, 1—1—4	0	0
G—3 × G—6, 7—7—1	0	2
G—3 × W, 7—4—3	3	0
G—4 × G—1, 2—3—4	10	1
6—4—7	22	11
6—9—7	45	23
G—4 × W, 4—3—2	10	5
6—2—3	0	3
G—6 × G—3, 2—9—1	2	12
G—8 × W, 7—9—5	3	11
G—10 × G—7, 2—7—3	16	3
3—9—6	2	0
4—7—3	3	10
G—25 × W, 4—10—5	1	0

[1] Based on observations of 16 ramets in every clone in each of 4 consecutive years.

[2] Based on observations in each of 4 consecutive years.

surrounding stand. The ortets of the NS-112 clones, on the other hand, were relatively uniform in respect to these factors. Unfortunately, the amount of bias due to "c" effects variation cannot be determined from this study.

The broad-sense heritabilities and the ramet-ortet correlation coefficient, taken together and allowing for possible bias, indicated moderate genetic control of fruitfulness in slash pine. This conclusion is supported by two repeatability measurements from widely different sources. First, the repeatability of first-year conelet production, as determined from 4 annual counts of conelets 2 to 3 months after pollination on 19 individual slash pine trees near Olustee, Florida, U. S. A., was 0.60.[3] Second, a repeatability of 0.38 was determined by Campbell (1964) from data published by Arnborg and Hadders (1957) on female flower production in clones of Scotch pine at Nedansjö, Sweden. Further corroboration of this conclusion comes from Goddard's (1964) correlation coefficient of 0.281 for 1964 flower production between 2 ramets for each of 232 slash pine clones near Gainesville, Florida, U. S. A.

Narrow-sense heritability. — A narrow-sense heritability estimate of 0.13 was obtained for cone yield in 16-year-old control- and wind-pollinated progeny in 0-116 *(Table 5).* This heritability showed that additive genetic variance was low.

The large difference between the one narrow-sense heritability and the two broad-sense heritabilities suggests that additive genetic variance accounts for a relatively small amount of the genetic control of fruitfulness. This means that genetic gains in seed production would be relatively small in selective breeding programs that require high additive genetic variance.

However, fruitfulness is a peculiar trait in comparison with other traits (i. e., gum yield, growth rate) that are usually included in a breeding program. Seedlings with high seed-production potential are not especially needed for commercial forest planting because the vast majority of stands are being, and will continue to be, replanted artificially.

Yet, desirable seed orchard trees should be heavy seed producers. In clonal orchards, the relative amount of additive vs. nonadditive genetic variance is not important. High total genetic variance will assure that if selections are fruitful the vegetative propagules will also be fruitful. In contrast, appreciable additive genetic variance is needed to assure high seed production in the first-generation progenies planted in seedling seed orchards.

Since moderately high total genetic variance for fruitfulness was found in this study, use of this trait as a criterion in selection would likely be successful in clonal orchards. In seedling seed orchards special techniques will probably be necessary to attain appreciable gains in seed production. More study is needed, however, on the nature of the inheritance of fruitfulness in slash pine.

Summary

Heritability of fruitfulness was estimated by studying female flower and cone production in three slash pine plantations in northeastern Florida, U. S. A. Broad-sense heritabilities of 0.50 and 0.49 were determined from cone yields in 14- to 17-year-old rooted cuttings and from flower production in 4- to 6-year-old air-layered propagules, re-

Table 5. — Analysis of variance[1] of average annual cone production in progeny plantation 0—116, 1961—1964.

Source	Degrees of freedom	Mean squares	F	Variance component estimates
Block	6	45		$\sigma_t^2 = 5$
Progenies	13	69	1.86*	$\sigma_{pa}^2 = 9$
Plots within blocks	78	37	1.0 N.S.	$\sigma_{pl}^2 = 110$
Within plots	291	110		

* Significant at the 5 percent level of confidence.

[1] Computational procedure may be found in Eklundh Ehrenberg (1963).

Genetic variance = $\sigma_g^2 = 16$

Environmental variance = $\sigma_e^2 = 100$

$$h^2 = \frac{\sigma_g^2}{\sigma_g^2 + \sigma_e^2 + \sigma_{pa}^2} = 0.13$$

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[3] From data soon to be published.

spectively. A narrow-sense heritability of 0.13 was determined from cone yields in 16-year-old progeny.

The broad-sense heritabilities indicated moderate genetic control of fruitfulness. The narrow-sense heritability indicated a low additive genetic component. An appreciable amount of nonadditive genetic variance was suggested by the large difference between the narrow-sense heritability and the broad-sense heritabilities and by the variation in flower and cone production.

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Effects of Clone and Light Intensity on Photosynthesis, Respiration and Growth of Aspen-Poplar Hybrids[1]

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Introduction

A naturally-occurring aspen-poplar hybrid (*Populus grandidentata* × *P. alba*) shows promise as a timber tree in southeastern Iowa. It has the superior form and growth habit of bigtooth aspen and the rapid growth rate of white poplar. Mean annual growth rate of the hybrid is 3½ times greater than the growth rate of native oaks on the same site at age 24 (McComb and Hansen 1954). To date, four clones have been identified, the Shimek and Sherrill in Van Buren County, and the Crandon and Hansen in Lee County. The Shimek and Sherrill clones have been described in detail by Little *et al.* (1957). To maintain the existing but unknown superior genotype, stem cuttings have been used exclusively for planting material. However, survival and growth of outplanted cuttings of the Shimek and Sherrill clones have been low. Little information is available concerning survival and growth of the Crandon and Hansen clones. Therefore, fundamental investigations of physiological variation among the four clones have been initiated to determine the causes of poor survival and growth and to determine variation in gene-controlled production.

To determine physiological variation among the four clones, rates of physiological processes were measured under controlled environmental conditions. Because of their importance as yield determining processes, photosynthesis and respiration were chosen as dependent variables for the initial investigation of among-clone physiological variation. Because light intensity strongly affects rates of photosynthesis, and thus may affect survival and growth, rates of photosynthesis and respiration were determined at several light intensities. To test the feasibility of using such physiological data in the development of rapid selection methods, the relationship must be known between rates of physiological processes and growth and distribution of assimilate. Therefore, growth and distribution of assimilate also were determined for the four clones.

Thus, the dependent variables included in this study were (1) rates of photosynthesis (2) rates of respiration (3) growth and (4) distribution of assimilate. The independent variables were (1) clone and (2) light intensity. The hypotheses tested were:

1. Differences in photosynthesis and respiration of aspen-poplar hybrids exist among clones and light intensities.
2. Differences in growth and distribution of assimilate of aspen-poplar hybrids exist among clones.

An excellent summary of the research on the effect of environmental factors on tree photosynthesis and respiration was written by Kramer (1957). Studies showing differences in photosynthesis, respiration and/or growth among seed sources or clones of trees include investigations by Huber and Polster (1955), Rüsch (1959), Huber and Rüsch (1961), McGregor *et al.* (1961), Krueger and Ferrell (1962), Polster and Weisse (1962), Bourdeau (1963), Gatherum (1965), and others.

Materials and Methods

Photosynthesis and respiration of aspen-poplar hybrids were determined (1) at light intensities of 560, 1,300, 2,000, 3,300 and 6,000 foot-candles and (2) for four clones, Hansen, Sherrill, Crandon and Shimek, obtained originally from naturally-occurring stands in southeast Iowa. The study was established as a simple split-plot experiment with four replicates of five light intensity plots, each divided into four clone sub-plots. Photosynthesis and respiration of intact potted plants were measured in a gas-tight, refrigerated, controlled-environment chamber described by Broerman *et al.* (1966). A Beckman L/B infra-red analyzer, model 15 A, was used to measure the uptake and evolution of CO_2 within the chamber. In addition, growth and distribution of assimilate of aspen-poplar hybrids were determined for each of the four clones. This study was established as a randomized complete block design with 20 replicates of four-clone plots.

Stem cuttings of the four clones were obtained from a clonal orchard in December, 1963. The cuttings were (1) graded by diameter, .60 of an inch, and length, 9 inches, to minimize variation related to cutting size, (2) placed in polyethylene bags and treated with a fungicide and (3) stored in a refrigerated seed house at 38° F until May 8, 1964. At this time, the cuttings were butt-end treated with 100 ppm-concentration of indole-butyric acid for 24 hours and potted in 1-gallon pots in a soil mixture of one-third sand, one-third peat and one-third Clarion loam. The potted plants were grown in the State Forest Nursery at Ames

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