Patterns of Genetic and Environmental Variance in a Short-term Progeny Test of Loblolly Pine

by E. C. Franklin

Abstract.--Thirty-five loblolly pine families from eastern North Carolina, South Carolina and Georgia orchards of 4 companies were grown for 5 years in a short-term progeny test in Charleston, SC. The four spacings were 33, 50, 67, and 100 cm square. Each spacing consisted of 4 randomized complete blocks of sixteen-tree square plots. The objectives were (1) to determine if young trees grown at close spacing would mimic the genetic and environmental variance patterns of stands at conventional spacings at much older ages, and (2) to compare families on the basis of their competitive performance with varying numbers of sibling versus nonsibling competitors. Patterns of additive genetic variance which evolved in the closely spaced tests followed very closely those patterns found in older tests grown at conventional spacing. No differences were found in height, diameter and volume growth between groups of 8 trees containing 3, 5 or 8 sibling competitors.

Additional keywords: Short-term progeny testing, selection, heritability, Pinus taeda L., tree improvement, competition.

Director, Small Woodlot Forestry Research and Development Program, School Forest Resources, N.C. State University, Raleigh, NC.

Acknowledgements. This paper is a preliminary review of a large study which is continuing through the concerted efforts of many people. I thankfully recognize the contributions and continuing cooperation of the staff of the USDA Forest Service Research Laboratory at Charleston, SC for their diligent efforts in acquiring the data; the N.C. State Tree Improvement Cooperative for use of progeny test data; Continental Forest Industries, Savannah, GA, Union Camp Corporation, Savannah, GA, Westvaco Corporation, Summerville, SC, and Weyerhaeuser Company, New Bern, NC for supplying the seed. I recognize the large individual contributions of the two supervisory technicians who have in turn shepparded this project from its inception: William S. Dvorak and Edgar L. Davenport both formally based at Charleston, SC with the Southeastern Forest Experiment Station. Lastly, thanks to my staff for the extra effort they continue to devote to this project.

INTRODUCTION

Rate of genetic improvement of any long-lived organism can be increased by early testing and selection if certain genetic relationships exist between juvenile and mature growth phases. Most research on maturation in woody perennials concerns fruit and seed production because of "the economic importance of these traits to crop yields. With commercial forest species, products are more varied and problems are compounded by less environmental control, and by the size, complexity and longevity of individual trees and stands.

Strategies for dealing with juvenile-mature phase change vary according to genetic and environmental characteristics of the traits involved. For many traits such as wood density and fiber length, careful sampling has shown that single samples at almost any age will yield good estimates of relative whole-tree values for individuals and families, because variation patterns with age are systematic and very regular. In contrast, parameters measuring growth rate are influenced by age and environment to a much greater extent. Recent research has pointed to a need for much better understanding of the effects of age and associated stand environment on juvenile-mature relationships.

Analyses of long-term progeny tests of four North American conifers led to the development of a hypothetical model to describe genetic phase changes in the growth of stands (Franklin, 1979). The model divides stand development into three genetic phases based on the behavior of the additive genetic variance and the heritability of the trait (Fig. 1). The juvenile genotypic phase is characterized by extremely low levels of additive genetic variance with a peak in heritability (juvenile genetic culmination) in the early to middle part of the phase. The mature genotypic phase is characterized by rapidly increasing additive genetic variance and heritability with a peak in heritability (mature genetic culmination) occuring early in the phase . The codominance-suppression phase is characterized by a rapid decline in additive genetic variance and an especially rapid decline in heritability *as* mortality removes suppressed trees and the stand approaches uniformity in stocking, and heights of dominants and codominants.

Recent results show that levels of additive genetic variances for height, diameter and volume growth vary widely but systematically in the course of stand development (Namkoong et al. 1972, Namkoong and Conkle 1976, Franklin 1979). The implication of-these results for selecting in natural stands and plantations *at* conventional spacing is that selection should be done around half-rotation age. In the hypothetical model, this is called the mature genotypic phase (Franklin 1979). A much greater rate of genetic gain per unit time could be obtained if selections could be done at younger ages. Because trees are so plastic in their growth response to environmental influences, particularly spacial relationships, I developed the hypothesis that stands of trees growing close together might simulate stand development at very young ages typical of more widely spaced stands at much older ages. From a practical point of view, once a poorly competing family falls behind, it never catches up. So why wait ten to twenty years at conventional spacing to develop enough competition to make that happen?

METHODS

The experimental design consisted of four separate trials grown at 33, 50, 67, and 100 cm square spacings in a small agricultural field at the USDA Forest Service Laboratory in Charleston, SC. Each trial contained 4 replications of 35 16-tree square family plots. The families were orchard open-pollinated from four companies in North Carolina, South Carolina and Georgia (Table 1). Clones were chosen on the basis of having been crossed with large numbers of other clones and of having 12- to 16-year measurements in progeny tests at conventional spacings.

Table 1.--Companies which made seed available from selected clones in their commercial production orchards

Company	No. Families	Provenance
Continental Forest Industries	8	GA Piedmont
Union Camp Corporation	8	GA/SC Coastal Plain
Weyerhaeuser Company	14	NC Coastal Plain
Westvaco Corporation	5	SC Coastal Plain
	35	

Families totaling about 12,000 trees were grown as container stock in a greenhouse and outplanted in early June, 1978 at 12 weeks of age. The site was prepared by raking and disking; only grasses remained on the site. Survival was generally good but some replacement planting was done during the first 6 months of the study. Competition from grasses was controlled until crown closure by mowing in the 100-cm spacing and with herbicides in the closer spacings. Soil tests indicated no fertilization was needed. Infestations of spider mites and tipmoths were controlled with periodic spraying of insecticides.

Measurements of total height were made during the second through the ninth growing months over a five-year period. December, January and February were classified as non-growing months and excluded from the measurement schedule. Measurements in the 10th through the 19th growing months included height and diameter. Diameters were measured first at one inch above the ground (10th month) then at mid-height (15th through 23rd growing months) and from then on at 4 1/2 feet above ground. Heights and diameters were measured in alternate growing months in the 21st through the 37th growing months. An index of volume equal to diameter squared times height was used.

Cumulative mortality, total phenotypic variance, additive genetic variance, environmental variance, and heritability were estimated for each measurement. Variances were interpreted based on the simpliest additive model:

$$P = A + E, \quad \text{and} \quad h^2 = \frac{A}{P},$$

where:

P is phenotypic variance,

A is additive genetic variance,

E is environmental variance, and

h^2 is individual tree, narrow-sense heritability.

RESULT

Mortality

Cumulative mortality did not begin to reflect large differences in growing space until the fourth and fifth years of the study. In 1981, the amount of mortality sharply increased in the 33-cm spacing, and in 1982 in the 50-cm spacing (Table 2).

Genetic Variances

The rapid increase in additive genetic variance, marking the juvenile/mature phase change (as interpreted based on Fig. 1), occurred in the 9th growing month for height and the 21st growing month for diameter and volume in all spacings (Table 3). Similarly, highest heritability in the mature genotypic phase (mature genetic culmination) occurred at 15 months for height and 23 months for diameter and volume in all spacings except 21

Table 2.--Culmulative mortality percentages by spacing and growing season

YEAR	SPACING (CM) 33	50	67	100
	--Percent--			
78	2	2	1	2
79	4	3	2	5
80	9	4	2	6
81	43	8	4	6
82	67	22	12	10

Table 3.--Number of growing months to reach the juvenile/mature phase change as interpreted based on the model by Franklin (1979)

TRAIT	SPACING (CM) 33	50	67	100
	--Months--			
Height	9	9	9	9
Diameter	21	21	21	21
Volume[a]	21	21	21	21

[a] Volume index based on diameter squared times height.

months for volume at 33—cm spacing (Table 4). The mature genetic culmination heritability was highest for height, with the two intermediate spacings yielding the highest values. Heritabilities for diameter and volume were lowest at the 33—cm spacing and trended higher at the wider spacings (Table 5). All heritabilities steadily decreased after reaching the mature onetic culmination, except heritability for height at the 100—cm

Table 4.--Number of growing months to reach mature genotypic (maximum heritability) as interpreted based on the model by Franklin (1979)

	SPACING (CM)			
TRAIT	33	50	67	100
	Months			
Height	15	15	15	30[a]
Diameter	23	23	23	23
Volume[b]	21	23	23	23

[a] In the 100-cm spacing, a sharp, distinct peak occurred at 15 months, but a rounded, less distinct peak which was .05 units higher, ocurred at 30 months.

[b] Volume index based on diameter squared times height.

Table 5.--Heritability at mature genotypic culmination as interpreted based on the model by Franklin (1979)

	SPACING			
TRAIT	33	50	67	100
	Heritability			
Height	.73	.87	.90	.70
Diameter	.37	.45	.64	.60
Volume[a]	.36	.50	.60	.63

[a] Volume index based on diameter squared times height.

spacing.[2] For height this was a period of 22 growing months over 3 seasons, and for diameter and volume, a period of 14 growing months over 2 seasons (Figs. 2, 3, 4).

The 16-tree square plots provided a test for trends in competitive influence of sibling versus nonsibling neighbors.

---

[2] In the 100-cm spacing, a sharp, distinct peak occurred at 15 months, but a rounded, less distinct peak which was .05 units higher, occurred at 30 months.

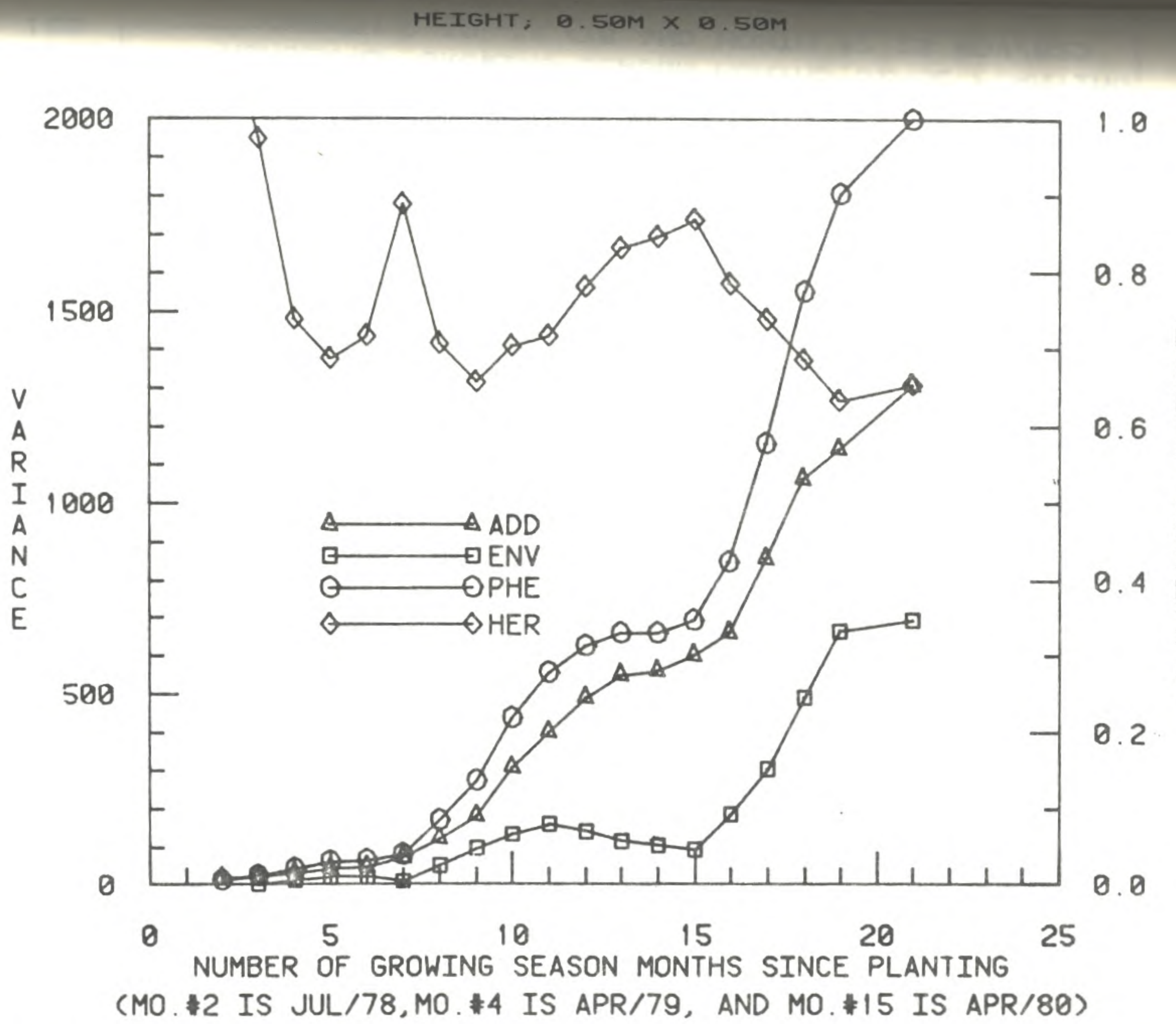
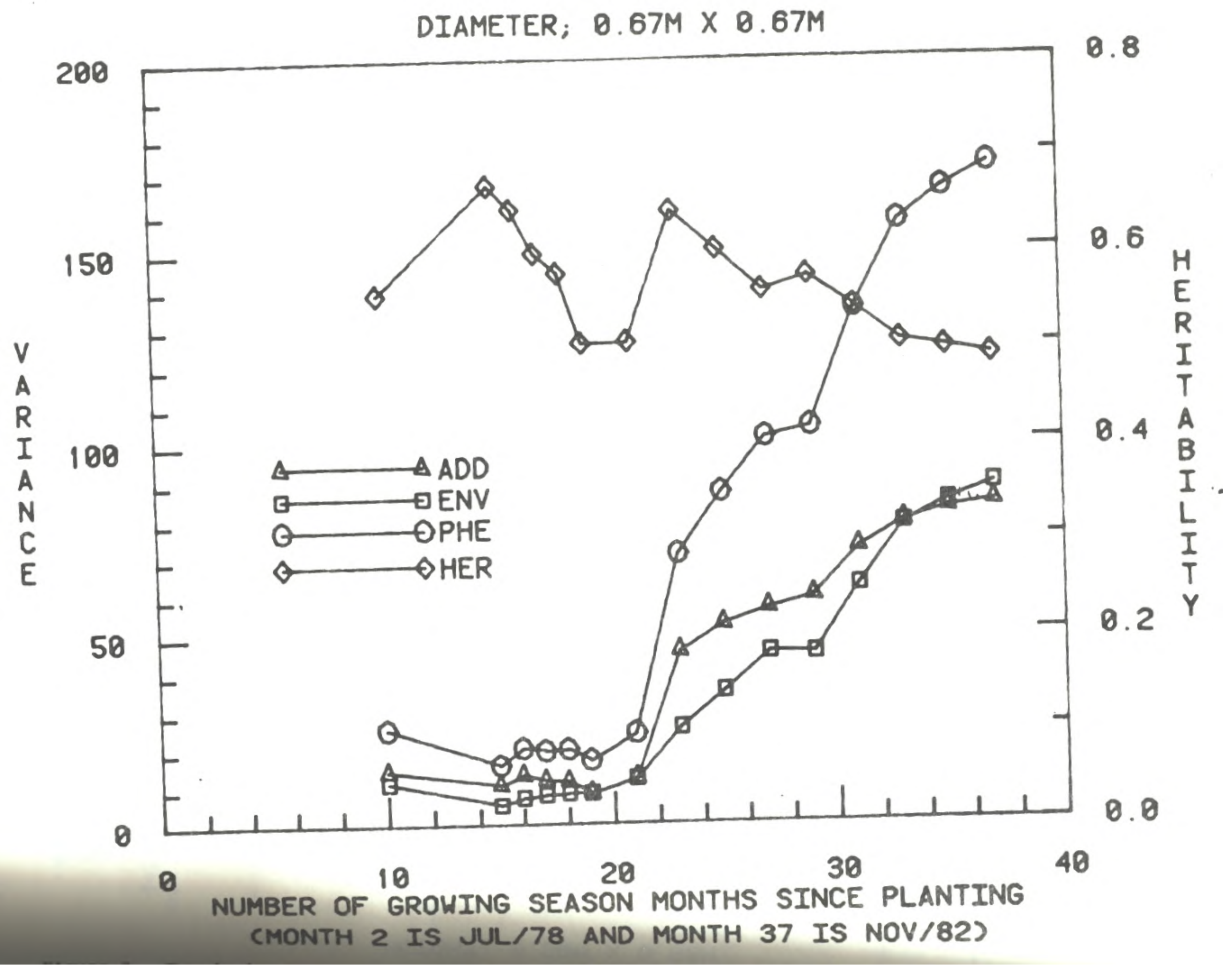


Figure 2.--Trends in the additive (ADD), environmental (ENV), and phenotypic (PHE) variances, and in the heritability ratio (HER = ADD/PHE) of height of 35 loblolly pine families growing at a 1/2-meter square spacing through 37 growing months.


DIAMETER; 0.67M X 0.67M
VARIANCE
0
50
100
150
200
HERITABILITY
0.0
0.2
0.4
0.6
0.8
ADD
ENV
PHE
HER
0
10
20
30
40
NUMBER OF GROWING SEASON MONTHS SINCE PLANTING
(MONTH 2 IS JUL/78 AND MONTH 37 IS NOV/82)

(MONTH 2 IS JUL/78 AND MONTH 37 IS NOV/82)

Figure 3.--Trends in the additive (ADD), environmental (ENV), and phenotypic (PHE) variances, and in the heritability ratio (HER = ADD/PHE) of diameter of 35 loblolly pine families growing at a

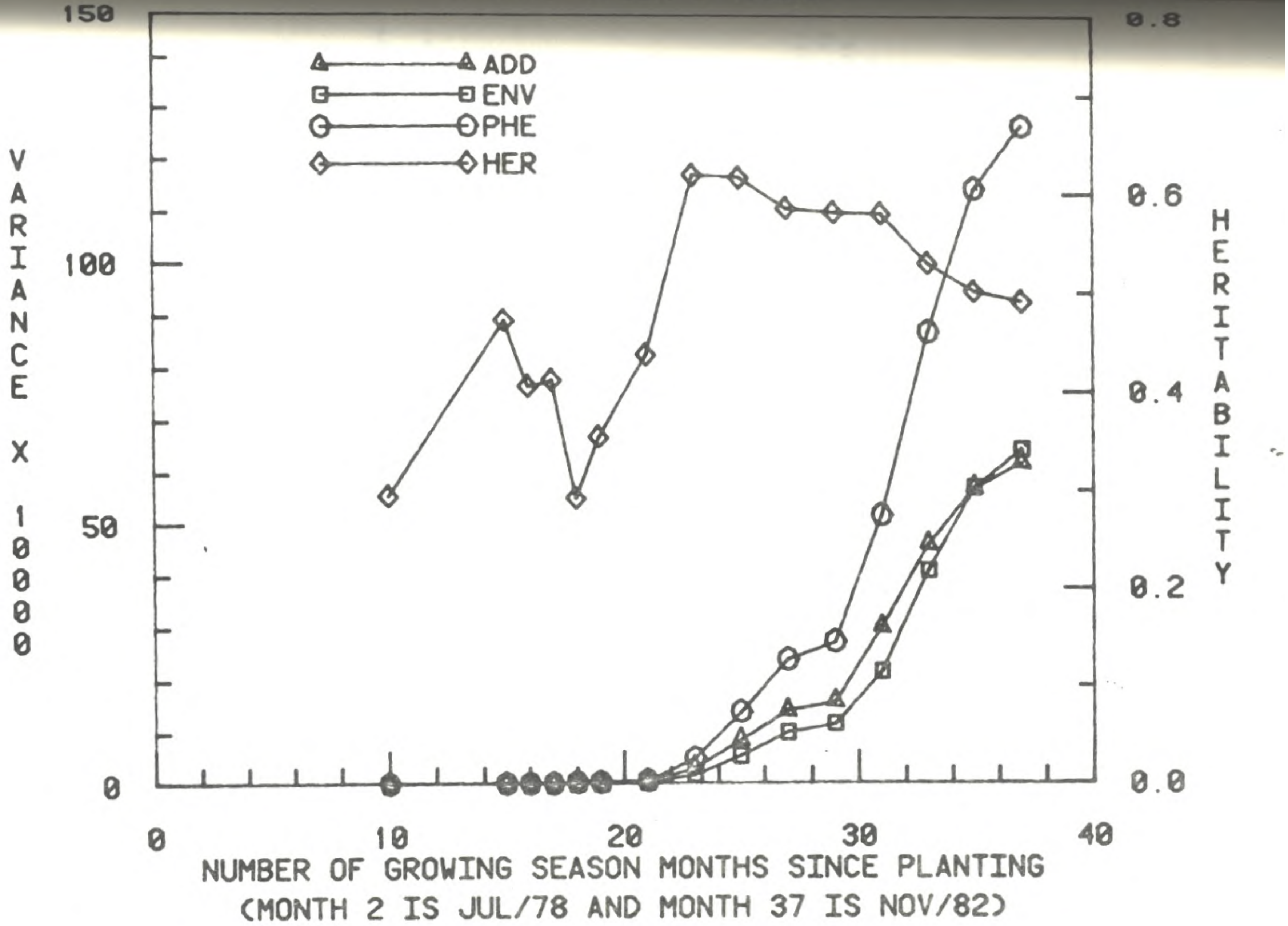


Figure 4.--Trends in the additive (ADD), environmental (ENV), and phenotypic (PHE) variances, and in the heritability ratio (HER = ADD/PHE) of volume of 35 loblolly pine families growing at a 1-meter square spacing through 37 growing months.

The 4 corner trees had 3 sibling and 5 nonsibling competitors. The 8 internal trees on the outside rows had 5 sibling and 3 nonsibling competitors. The 4 internal trees had all sibling competitors (Fig. 5). Analyses of variance were run for all traits and spacings at 37 months and repeated for the 33 cm spacing at 25 months. Results showed no differences between sibling competitor groups. Regression of growth parameters on increasing numbers of sibling competitors per group failed to demonstrate any trends.

DISCUSSION

The hypothesis under test was that for purposes of genetic interpretaion and testing, families of trees grown at very close spacings in a short period of time would mimic the development of stands of those same families grown at conventional spacing, over a much longer period of time.

Under this hypothesis based on the model (Fig. 1), the following would be expected if the hypothesis was acceptable:

1. A distinct phase change from the juvenile genotypic to mature genotypic phase marked by a rapid increase in additive genetic variance from a level hardly varying from nil.

2. A relatively high but decreasing heritability in the juvenile genotypic phase.

3. A very rapid rise in heritability to a distinct peak early in the mature genotypic phase, then a gradual decline toward the codominance-suppression phase change.

4. A sharp decline in additive genetic variance marking the boundary of the codominance-suppression phase accompanied by a plummeting heritability.

With only one minor exception (footnote 2), trends for each trait at each spacing fit perfectly through item 3. Thus, the results obtained so far are consistent with the hypothesis, but are inconclusive, because results have not reached the boundary of the codominance-suppression phase.

Comparing the behavior of the variances for the short-term tests with those of the longer-term tests, the scale indicates that development in the short-term test is well into the mature genotypic phase. Indeed, the rapid decline of the additive genetic variance is expected to occur soon. The closer the spacing the sooner the decline is expected. At the 33-cm spacing, 15% of the families have 10 or fewer trees remaining out of the original 64. When whole families start dropping out, the

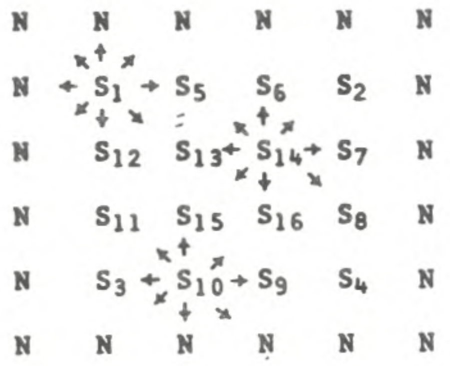


Figure 5.--Competitive spacial relationships between sibling and nonsibling trees with a 16-tree square plot: $S_{1,2,3,4}$ have 3 sibling 5 nonsibling competitors; $S_{5,6,7,8,9,10,11,12}$ have 5 sibling, 3 nonsibling competitors, $S_{13,14,15,16}$ have 8 sibling competitors.

additive genetic variance is expected to plummet. This trend is expected in each spacing as mortality increases (Table 2).

These results are interesting but what is the practical significance of short-term testing? Can these tests be used to pick families which are genetically superior under conventional silvicultural regimes? This topic will be developed in a subsequent paper. Preliminary results indicate that short-term tests will be useful but that the choice of parameters to express superiority will be critical. More emphasis must be placed on yield per unit area rather than individual tree superiority or the superiority of families based on the average tree. For example, a family which combines fast growth and good survival against competition is expected to produce somewhat smaller but more uniform trees and higher yields per unit area than a family with poor or erratic survival leading to production of a few large trees. If silvicultural techniques such as planting at wide spacing are to be used, where competition is not an important environmental parameter, short-term tests at close spacing may not be appropriate in the development of genetic strains for that use.

Sibling Versus Non-sibling Competitive Ability

The apparent lack of differences between groups of trees with varying numbers of sibling versus nonsibling competitors is not unexpected with the relatively low level of genetic control obtained with orchard open-pollinated families. With full-sib families real effects may be found, and with certain clonal combinations real effects will almost certainly be found. Whether those effects will be large enough to be important remains to be demonstrated.

LITERATURE CITED

Franklin, E. C. 1979. Model relating levels of genetic variance to stand development of four North American conifers. Sil. Genet. 5-6: 207-212.

Namkoong, G. and Conkle, M. T. 1976. Time trends in genetic control of height growth in ponderosa pine. For. Sci. 22:2-12.

Namkoong, G., R. A. Usanis, R. R. Silen. 1972. Age-related variation in genetic control of height growth in Douglas-fir. Theor. and Appl. Genet. 42:151-159.