THEORETICAL AND APPLIED ASPECTS OF SHORT-TERM PROGENY TESTING IN LOBLOLLY PINE

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Abstract.--Patterns of stand development based on trends in genetic and environmental variances were similar to those previously found for several North American conifers grown at conventional spacing. Trials at 33, 50, 67 and 100 cm square spacings all showed similar patterns of change in genetic and environmental variances over time. For practical as well as theoretical reasons, the widest spacings, 67 and 100 cm offered the most promise for applied short-term testing. Sibling correlations for volume index generally peaked and leveled off at 2 to 3 years of age in all spacings with maximum correlations reaching 0.47 in the 100 cm spacing. In practical terms, 8 of 9 top-ranking families in the 100 cm spacing, were from the top 50% of parents ranked on the basis of long-term tests. Volume per tree and volume per unit area had consistently higher sibling correlations than height. In the 100 cm spacing, sibling correlations for height continued to increase through age 10 years while those for volume remained steady. At the 33 cm spacing, sibling correlations dropped sharply as mortality exceeded 75%. Results indicated that at 3 years from planting, short-term, closely spaced tests can provide a very efficient means of culling large base populations for volume growth. This could substantially reduce the cost of testing for other more complex traits such as structural quality and chemical composition of wood.

Keywords: Pinus taeda L., short-term progeny testing, close spacing, genetic variance, heritability.

INTRODUCTION

The concept of interpreting phases of stand development in terms of progressively changing environments for tree growth, and the resulting changes in expression of genetic and environmental variances was generalized by Ford (1975, 1976). Specific examples in western conifers were reported by Namkoong et al. (1972) and by Namkoong and Conkle (1976). These concepts were integrated into a genetic model of stand development by Franklin (1979) for Douglas-fir (Pseudotsuga menziesii [Mirb] Franco) and ponderosa pine (Pinus ponderosa Dougl. ex Laws), and two eastern conifers: loblolly (Pinus taeda L.) and slash pines (Pinus elliotti Engelm.). Short-term progeny testing has been successfully applied for at least 25 years in southern pines (Squillace and Gansel 1968, Franklin and Squillace 1973) and in eucalypts (Franklin 1986). There is no question that when properly applied, it works well. We need to understand more about why it works and thereby make it work better.

In 1978, a study was begun at the USDA Forest Service's Forestry Sciences Laboratory in Charleston, SC to test two hypotheses:

1. That young stands grown at close spacings would display the same patterns of change in genetic and environmental variances as older stands at conventional spacings.

2. That accelerated stand development could be used to increase the precision of short-term progeny testing by carefully monitoring genetic phases of stand development and the corresponding changes in levels of genetic and environmental variances.

METHODS

The experimental design consisted of four adjoining trials grown at 33, 50, 67, and 100 cm square spacings in a small agricultural field near the laboratory. Each trial was a randomized complete block of 4 replications of 35 families, in 16-tree square plots (Table 1).

Table 1. Companies which made seed available from selected clones in their commercial production orchards (after Franklin, 1983)

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	5	SC Coastal Plain

Measurements of total height were made each growing month over a five-year period. December, January and February were classified as non-growing months and excluded from the measurement schedule. Measurements in the 11th, 17th and all growing months thereafter included total height and diameter. Diameters were measured first at one inch above the ground (11th month) then at mid-height (17th through 23rd growing months) and at 4 1/2 feet above ground thereafter. Heights and diameters were measured in alternate growing months in the 21st through the 33rd growing months, the 36th through the 42nd growing months, and individually in the 51st, 69th and 88th growing months.

Two indices of volume were used. Volume per tree was indexed as diameter squared times total height, and that quantity was divided by original growing space to index yield per unit area. For the yield index, zero yield was recorded for dead trees so mortality did not reduce the number of trees in the model, but did reduce the average yield.

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

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

where:

P is phenotypic variance,
A is additive genetic variance,
E is environmental variance, and
h^2 is individual narrow-sense heritability (Franklin 1983).

Height and volume family performance levels for conventional progeny trials were supplied by the NC State University-Industry Tree Improvement Cooperative. These arrays were compared to the corresponding family means for height, volume and yield indices from the short-term tests using product-moment correlations.

RESULTS

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 other spacings (Franklin 1983). Rate of mortality through time was inversely proportional to original area per tree, but by the 88th growing month (10th year) the three closest spacings had achieved about the same average space per tree, while the 100 cm spacing had more growing space but was still showing a high rate of mortality (Table 2).

Table 2. Trends in mortality and subsequent average spacing after 69 and 88 growing months from planting

Original square spacing cm	Original area per tree m^2	Mortality at 69 months %	Mortality at 88 months %	Area per tree at 69 months m2	Area per tree at 88 months m2
33	.111	91	95	1.25	2.09
50	.250	76	86	1.05	1.79
67	.458	63	78	1.20	2.01
100	1.000	44	63	1.80	2.70

Patterns of Genetic Variance and Heritability

In terms of the model proposed by Franklin (1979), the juvenile and mature genotypic phases were readily observable (Table 3). The transition into the codominance-suppression phase was apparent for height in the three wider spacings (Figure 1), but was not observed at the 33 cm spacing. Neithervolume nor yield indices had reached the codominance-suppression phase through 88 growing months (Figure 2).

Additive genetic variances for height showed a generally rising trend through the 69th growing month at the 50, 67 and 100 cm spacings. At the 88th growing month, additive genetic variance had decreased at the three wider spacings. This accelerated the already decreasing trend in heritability, which had been decreasing steadily since the mature genetic culmination (MGC). In the 33 cm spacing, additive genetic variance for height and volume

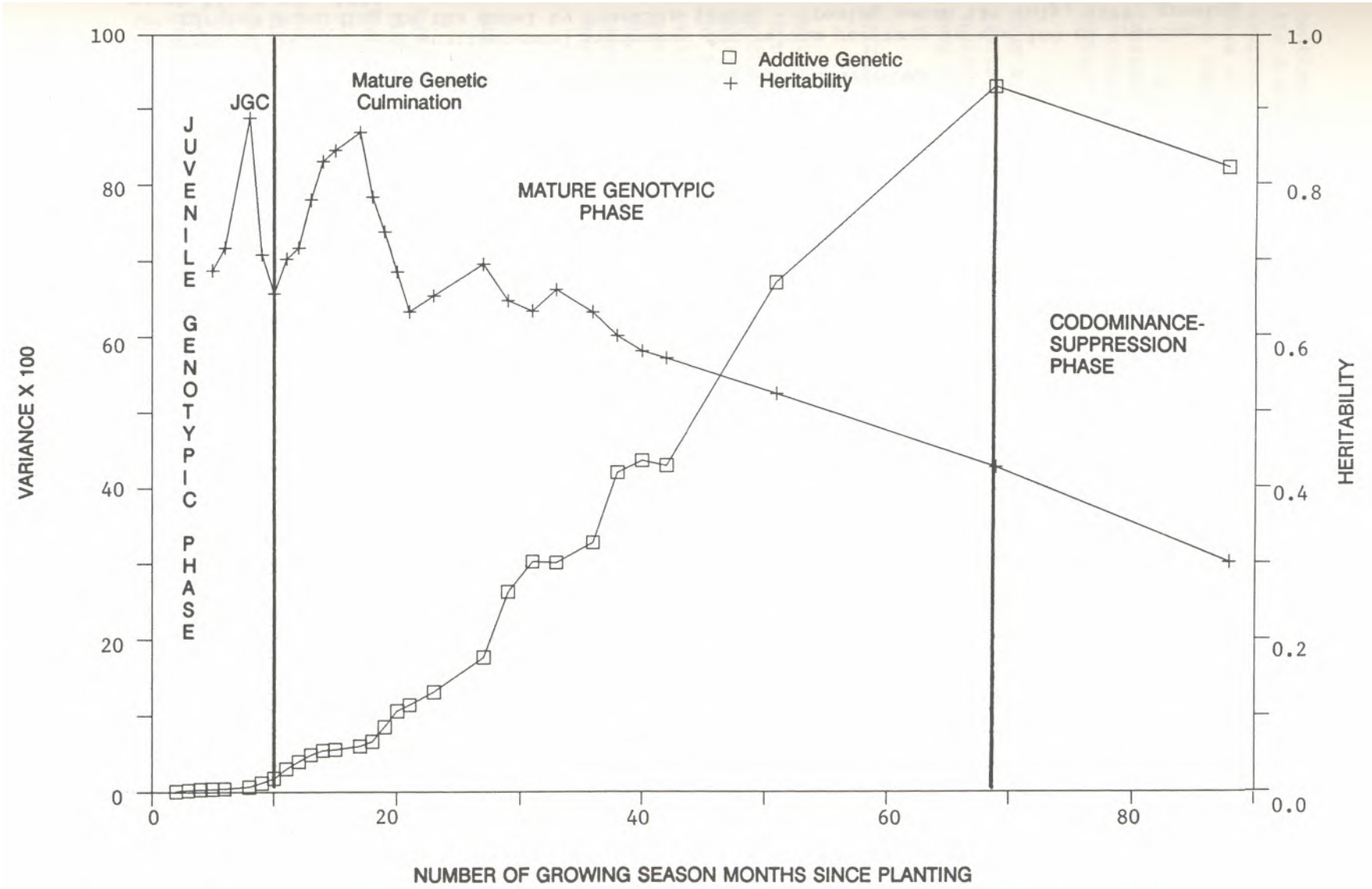

Figure 1. Patterns of genetic and environmental variances for height in the 50 cm spacing, interpreted according to the model by Franklin (1979). Growing month 2: July, 1978; growing month 88: March, 1988.

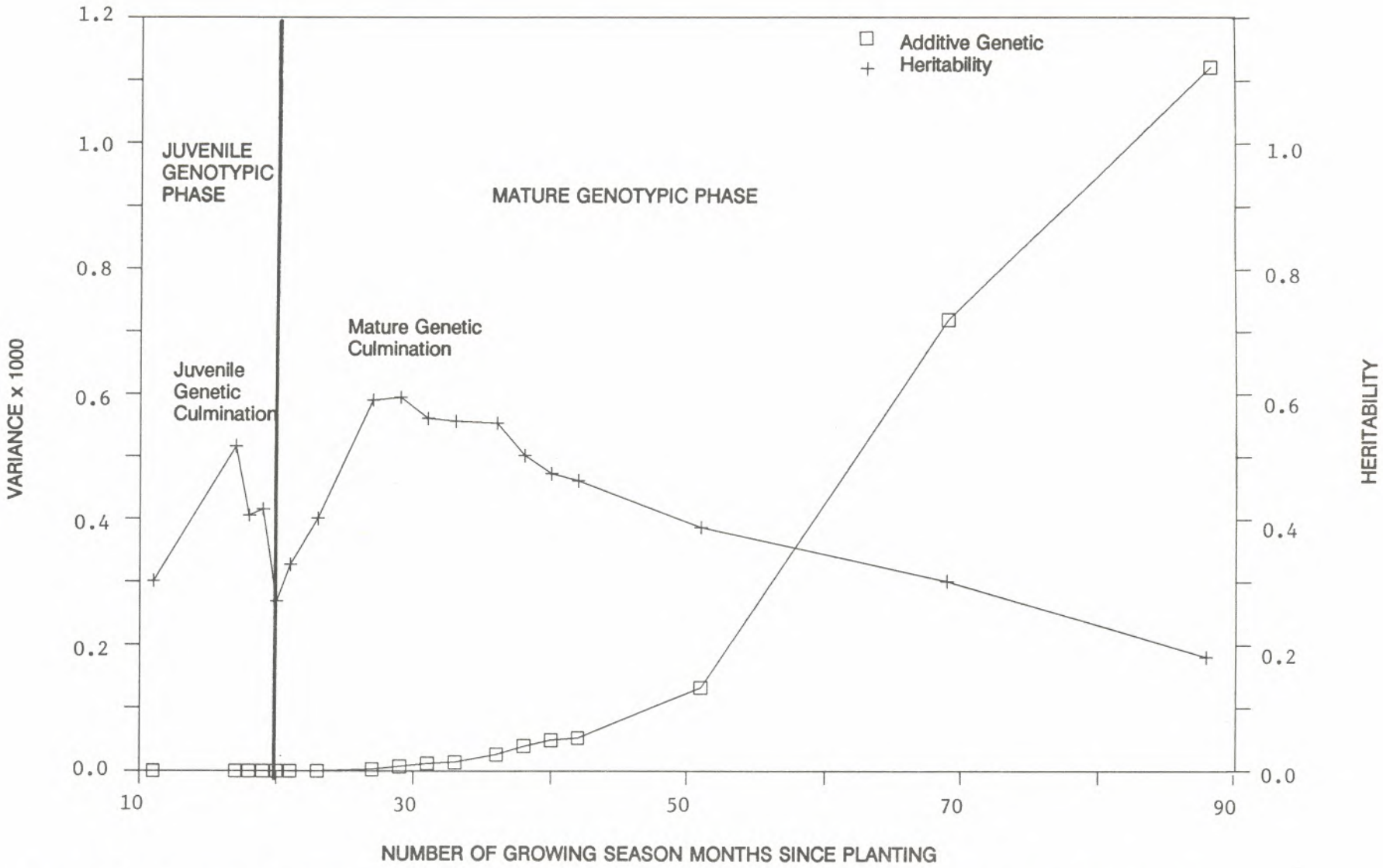

Figure 2. Patterns of genetic and environmental variances for volume per tree in the 100 cm spacing, interpreted according to the model by Franklin (1979). Growing month 11: July, 1979; growing month 88: March, 1988.

continued to increase, and at the 69th growing month, heritability reversed its downward trend and started to increase. These results are probably spurious since by the 69th month only about 200 (9%) of the original trees were alive. This reversal in trend of heritability in the 33 cm spacing did not occur with the yield index, which was analyzed with the full model.

Additive genetic variances for volume and yield indices generally increased throughout the course of the study in all four spacing trials. In contrast, heritabilities decreased at relatively steady rates from the MGC through the 88th growing month.

Heritabilities for height at the MGC ranged from 0.62 to 0.89 over the four spacings, with the intermediate spacings having the higher values. Heritabilities for volume index ranged from 0.36 to 0.63 with the 33 cm spacing having by far the lowest value. Heritabilities for yield index ranged from 0.29 to 0.59 with the 33 cm spacing again having the lowest value (Table 3)

Correlations with Conventional Tests

For height, sibling correlations with performance levels in conventional tests were near zero during the first few months, then gradually increased through about 40 months. Correlations then decreased markedly through 88 months at the three closer spacings. In the 100 cm spacing, correlations continued to increase through 88 months. Patterns of change in correlations for both volume and yield indices were similar. Correlations increased rapidly from 11 to 18 growing months, then leveled off in the 50 and 100 cm spacings, gradually decreased in the 33 cm spacing, and gradually increased in the 67 cm spacing. Yield index tended to decrease less rapidly than volume index. In almost all cases, the MGC was a stage where correlations were at or near their highest levels for volume and yield indices (Table 3).

DISCUSSION

The Model

Patterns of genetic and environmental variances and heritability for height, volume and yield through 88 growing months (10 years) were very similar to those previously reported for loblolly pine through 25 years and Douglas-fir through 53 years. The similarities between the four spacing trials in this study, and between this study and previous studies suggests that a relatively consistent pattern of changes in genetic and environmental variances does occur, and that planting at closer spacings can shorten the time required to see this pattern develop. However, the range of spacings used in this study did not result in any appreciable differences in patterns of development except in rate of mortality. Most mortality, even at the closest spacing (33 cm), occurred well after the MGC for volume and yield indices (27-29 months).

Table 3. Number of growing months to reach successive stages in a stand development model (Franklin 1979), and corresponding heritabilities and correlations with results of older trials

Trait	Spacing	Juvenile genetic culmination (mo)	Juvenile mature phase change (mo)	Mature genetic culmination (mo)	Codominance-suppression phase change (mo)	Individual Narrow-Sense Heritability at the MGC1 h2	Correlation at MGC1 for volume r	Highest correlation at any age r
Height	33	8	13	17	NO2	.72	.32	.37
	50	8	10	17	69	.87	.32	.39
	67	8	10	17	69	.89	.19	.27
	100	8	12	17/363	69	.62	.25	.38
Volume per Tree								
	33	18	21	23	NO	.36	.38	.42
	50	18	20	27	NO	.50	.32	.32
	67	17	23	27	NO	.60	.26	.36
	100	17	20	29	NO	.63	.47	.48
Yield (Volume per Unit Area)								
	33	18	21	27	NO	.29	.42	.42
	50	18	20	27	NO	.49	.32	.32
	67	17	23	27	NO	.59	.36	.36
	100	17	20	27	NO	.48	.44	.47

Mature genetic culmination.

[2]Not observed through 88 growing months.

[3]In the 100-cm spacing, a sharp, distinct peak occurred at 17 months, but a rounded less distinct peak which was 0.05 units higher occurred at 36 months.

This study has shown that accelerated stand development can be obtained by planting loblolly pine at square spacings of from 33 to 100 cm. It has failed to show any shortening of the cycle of development due to reduction of spacing within the range tested.

Operational Testing

With regard to operational use of short-term progeny testing, results of this study indicated that over the range of spacings tested, the same results will be obtained in rate of change in genetic structure. Other criteria of importance might include statistical stability, size of heritability at the MGC, strength of correlations with conventional tests, efficient use of space and ease of measurement (Table 3). The 33 cm spacing proved to be the poorest with regard to these criteria. It was difficult to measure, yielded low heritabilities, especially for volume, and by the end of 10 years most (95%) of its trees were dead. This precludes the use of the study for other traits such as wood quality. The 50 cm spacing was marginally to substantially better but still not as good as the 67 and 100 cm trials.

The best trait to use as indicated from these results is either volume per tree or yield (volume per unit area). If mortality is a factor to be considered, volume per unit area is the preferred trait. In this study, mortality was very light at the MCC, so both traits behaved similarly. Volume per tree had slightly higher heritabilities than yield at MCC, and equally high correlations with long term tests.

There were two criteria examined in this study to determine the optimum time to measure a short-term test: the highest heritability (MCC) during the mature genotypic phase, and the time when the correlation with long-term conventional tests were highest. Results of the study indicated 27 to 29 growing months or about 3 years from planting as the optimum age at which to measure. This was the point of maximum heritability (MGC) and also a time when correlations with long-term tests were at or near their highest values for volume and yield indices. In practical terms, a correlation of 0.47 for volume per tree in the 100 cm spacing meant that of 9 families in the top 25% in the short-term test, 8 were in the top 50% of the long-term test. Thus, the correlations are high enough to prove the value of short-term tests, however we would like to see even higher correlations in future tests. Higher correlations might have been obtained if only local families had been used. Families from Westvaco's orchard consistently had extremely high correlations (0.90+) with older tests for height, volume and yield indices. Families from a piedmont source showed much lower correlations. Use of control-rather than orchard open-pollinated material would be expected to strengthen correlations because each orchard has a unique pollen background. Use of genetically proven check families would also be expected to improve precision in short-term tests (Franklin and Squillace 1973).

CONCLUSIONS

Short-term progeny tests in this study reduced the optimum time of measurement for height in loblolly pine from 10 years to 2 years and for volume from 20 years to 3 years based on results by Franklin (1979). Patterns

of genetic and environmental variances and heritability through time in the short-term tests were similar to those previously found in long-term tests, but in a much compressed time-frame. A ten-fold difference in growing space per tree did not affect the optimum time for measurement in this study. Other considerations indicated that the 67 and 100 cm spacings were preferable over closer spacings. Correlations of short-term and long-term test results were high enough to be useful, but could probably be improved by use of local seed sources, control-crossed material, and genetically proven checks.

LITERATURE CITED

Ford, E. D. 1975. Competition and stand structure in some even-aged plant monocultures. J. Ecol. 63:311-333.

Ford, E. D. 1976. Competition, genetic systems and improvement of forest yield. In: Cannell, M. G. R. and Last, F. T. (eds) Tree Physiology and Yield Improvement. Academic Press, NY. pp. 464-472.

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

Franklin, E. C. 1983. Patterns of genetic and environmental variance in a short-term progeny test of loblolly pine. Proc. 17th Sou. For. Tree Improv. Conf., Athens, GA: pp. 332-343.

Franklin, E. C. 1986. Estimation of genetic parameters through four generations of selection in Eucalyptus grandis. Proc. IUFRO Conf.; Breeding Theory, Progeny Testing and Seed Orchards. Williamsburg, VA: pp. 12-17.

Franklin, E. C. and A. E. Squillace. 1973. Short-term progeny tests and second generation breeding in slash pine. Can. J. For. Res. 3(3):165-169.

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

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

Squillace, A. E. and C. R. Gansel. 1968. Assessing the potential oleoresin yields of slash pine progenies at juvenile ages. USDA SEFES Res. Note SE-95.

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