GENETIC VARIATION IN VIGOR IN A WHITE PINE INCOMPLETE DIALLEL CROSS EXPERIMENT AT AGE 6

H. B. Kriebel, J. H. Roberds, and R. V. Cox

Estimation of genetic parameters of a population by analysis of variance of F_1 progenies assumes the conditions defined by Eisenhart's "Model II". Random sampling of the population is required rather than selection of lines with particular characteristics of interest. The parameters to be estimated are the components of variance, rather than the means of the lines from which the progenies were derived (Eisenhart, 1947).

The use in forestry of the diallel cross for estimating genetic parameters of the population assumes (1) that the parent population is random-mating and in equilibrium, and (2) that the trees tested are a random sample of the population. A "modified diallel" crossing system must be used, in which families obtained by selfing are excluded from the analysis. The analysis may include or exclude reciprocals. General and specific combining ability components of variance provide estimates of additive and non-additive genotypic components of variance (Griffing, 1956).

The study reported herein is considered to be a reasonable approximation of these conditions. It was designed to estimate genetic and environmental components of variance in vigor in a small breeding population of native eastern white pine *(Pines strobus* L.) in central Ohio. Analyses of the experiment at ages 1, 2, and 3 were reported in an earlier paper, along with similar analyses of another diallel cross experiment and of open-pollinated progenies, all from the same breeding population (Kriebel, Namkoong, and Usanis, 1972).

Materials and Methods

The diallel crossing system included reciprocals for analysis of both the reciprocal component of variance and that attributable safely to maternal effects. Materials and methods used in crossing and in raising the seedlings prior to field planting were described in the earlier paper cited. In April, 1968, the potted trees were planted in the field in 4-tree plots replicated in 10 randomized blocks. Some of the 35 families were of necessity included in less than 10 replicates.

Measurements of total height were taken after 1 and 3 growing seasons in the field (i.e., at ages 4 and 6). We also measured 6th-year height increment, thinking that it might give a slightly more reliable assessment of the genotype at that age than total height, which is strongly influenced by transplanting and other early environmental effects.

We again used the general least squares analysis of Schaffer and Usanis (1969), but the procedure was modified to permit separation of the maternal and reciprocal components of variance. These had been combined in the nursery analyses. As before, our analyses assumed that the families tested were a random sample of all possible crosses in a diallel table and that epistatic components of variance were insignificantly small.

Heritability was estimated for (1) individual trees regardless of family, and (2) family means. The first heritability (h_1^2) is applicable to estimation of gain from mass selection among randomly placed individuals, whereas the second (h_2^2) is suitable for estimating gain in a progeny test of half-sib families with 4 trees per plot and 10 replications.

In the second case we assumed normal distribution of family means. We also assumed that environmental variation within full-sib plots is equal to environmental variation among individuals in half-sib plots. The formulas for estimating heritability and gain from mass selection are:

$$h_1^2 = \frac{4\sigma^2_{gca}}{2\sigma^2_{gca} + \sigma^2_{sca} + \sigma^2_{mat} + \sigma^2_{rec} + \sigma^2_{p} + \sigma^2_{w}}$$

and $\Delta G_1 = i_1 h_1^2$

and for half-sib family selection:

$$h_2^2 = \frac{\sigma^2_{gca}}{\frac{41\sigma^2_{gca}}{40} + \frac{\sigma^2_{sca}}{40} + \frac{41\sigma^2_{mat}}{40} + \frac{\sigma^2_{rec}}{40} + \frac{\sigma^2_{p}}{10} + \frac{\sigma^2_{w}}{40}}$$

and $\Delta G_2 = i_2 h_2^2$

where the components general combining ability, specific combining ability, maternal effect, reciprocal effect, plot variance, and with-plot variance are respectively symbolized by $\sigma^2_{gca}, \sigma^2_{sca}, \sigma^2_{mat}, \sigma^2_{rec}, \sigma^2_{p}$ and σ^2_{w} The plot error, σ^2_p, was derived from $\sigma^2_e = \frac{\sigma^2_w}{k} + \sigma^2_p$ by pooling the "among trees within plots' variances; k is the harmonic mean of the number of trees per plot, 3.8367 in 1968 and 3.7037 in 1970.

To estimate genetic gain from half-sib family selection in small test plantations of eastern white pine similar to the one studied, we used the mean and standard error of sixth-year height growth of the 29 full-sib families included in more than 3, and in most cases, 9 or 10 replications in the experiment. The statistic *s* was used as an estimate of σ, the population standard deviation, and various multiples of *s* were used as i_2 in the equation $\Delta G_2 = i_2 h_2^2$ Estimates of the gain from mating the parents of the best half-sib families were obtained by doubling i_2.

Estimated gain from mass selection in half-sib progeny tests was obtained by selecting at random 100 trees from the experiment. The mean sixth-year growth rate of the 100 trees and its standard deviation were computed. The latter was used as an estimate of σ, the standard deviation of individual trees in the plantation. Various multiples of s were used as i_1 in the equation $\Delta G_1 = i_1 h_1^2$.

Results

Variance component estimates, their standard errors, and heritabilities for the analyses at ages 4 and 6 are listed in Table 1. Estimates of genetic gain are shown in Table 2. The results showed that:

1. Environmental effects were somewhat larger than they were in the same progenies in the nursery. But they remained constant as a proportion of total variance during the first three years after plantation establishment. The ratio of all of the genetic components to the sum of components, i.e.,

$$\frac{\sigma^2_{gca} + \sigma^2_{sca} + \sigma^2_{mat} + \sigma^2_{rec}}{\sigma^2_{gca} + \sigma^2_{sca} + \sigma^2_{mat} + \sigma^2_{rec} + \sigma^2_{p} + \sigma^2_{w}}$$

   which had been 16 percent, 15 percent, and 10 percent successively during the first three years, was 8 percent at ages 4 and 6 and also in 6th-year height increment.
2. The dominance genetic variance was negative in all three estimates and at most represented a very minor part of the total genetic variance.
3. The maternal effect, which had increased greatly in the third year, increased still further during the first year in the plantation, as a percentage of total genetic variance. But thereafter it declined. Having been 23 percent, 25 percent and 63 percent of the genetic variance during the first 3 successive years, it increased to 78 percent at age 4, then declined to 52 percent at age 6, with a further drop to 42 percent of the genetic variance in 6th-year growth.
4. The reciprocal effect was moderately large at age 4, after one year in the field, but did not contribute to genetic variance in total height or height increment at age 6.
5. The estimates of heritability increased with age, reversing an earlier decline. Whereas heritability based on individual trees was .33, .28, and .19 at ages 1, 2, and 3, respectively, and dropped further to .11 at age 4, it was .28 at age 6 for total height and .32 for 6th-year height growth. On a plot mean bases, h^2 was .56, .54, .27, .23, .48 and .54 for the same successive measurements. Thus, for both individuals and family plots, h^2 was the same for 6th-year height growth as for total height at ages 1 and 2.
6. Though the error variance increased after field planting as compared with that in the nursery, samples consisting of 4-tree plots with 10 replicates were more efficient in reducing the error variance than the 10-tree plots with 4 replications used in nursery analysis. This increased efficiency just balanced the increase in environmental variance due to field planting, and the ratio of h^2 on a family-mean basis to that on an individual tree basis was about the same in the field as in the nursery.

Discussion

There was less of an increase in environmental variance after planting than was expected. In fact, the increase was twice as great after re-potting, the year prior to planting. A more efficient test design for the field than for the nursery (4-tree plots, 10 replications vs. large, variable-size plots and 4 replications) and careful planting techniques may be factors in the small increase.

The steady level of the environmental variance during the first 3 years in the field was one reason for the increasing heritability. Except for a moderate reciprocal component of variance during the first year in the field, the only important "genetic" components were the additive and maternal effects. During this period the maternal effect declined rapidly, by one third as measured by total height data and by nearly one half when its effect on 6th-year growth was compared with its effect on total height at age 4. Conversely, the additive effect, estimated by the *gca* component, increased 2 1/2 to 2 3/4 times depending on which measure of growth capacity was used at age 6.

Major changes in the components of variance from ages 1 to 6 and in other diallel material (Kriebel *et al.*, 1972) occurred the year after transplanting, due to re-potting, transfer from pots to nursery, or transfer from pots to the field. In each case an increase in environmental variation was accompanied by an increase in the maternal effect and a decrease in the additive effect.

The increase in maternal effect is difficult to understand. Possibly, conditions affecting trees growing in pots are more favorable to the phenotypic expression of the additive genetic component of growth, whereas a release of root confinement initially favors expression of the maternal effect. The biological basis of this is not clear; seed weight would not be expected to have a strong effect in the fourth year.

The results illustrate how changes in time as well as location can affect estimates of growth parameters and heritability. The major factor in the change with time appears to be transplanting shock.

The heritability estimates obtained from the data can be used to estimate genetic gain. Some estimates for different selection methods are shown in Table 2, based on the 6th-year height growth data. They are only approximations, because of the errors involved in the heritability estimates, but the selection differentials are probably based on reasonable estimates of population variability. If present trends continue, significant gains should be achieved from half-sib family selection in progeny tests similar to ours with moderate intensities of family selection (1.0 6 = 1 in 4 families, 1.5 6 = 1 in 13 families, 2.0 6 = 1 in 42 families). If the seed parents are crossed, gain can be doubled with the same selection differential. Large gains are also possible with individual tree selection.

Summary

Analysis was made of growth parameters in an incomplete diallel cross of eastern white pine with

reciprocals. The components estimated included general combining ability, specific combining ability, maternal effects, and reciprocal effects. The data were taken from an experimental plantation. Results were compared with those obtained from analyses at ages 1 to 3, prior to field planting.

Heritability increased between ages 4 and 6, reversing a decline among the potted trees in the lath house. Maternal effects were substantially larger than additive effects at age 4, but by age 6 the relationship was reversed. Neither dominance nor reciprocal effects were important factors.

The environmental component of variance increased only slightly after field planting, probably due to design efficiency and special planting techniques. Environmental variance was stable during the 3 years after planting.

The high variability of the material and comparatively high heritability estimates suggest that significant gain in vigor is possible in similar white pine plantations with both family and mass selection.

Table 1. Variance component estimates for the 1963 diallel cross at ages 4 and 6

Source	Variance component for Total Height at age 4	 Total Height at age 6	 Height Increment in the 6th year
Replication (Θ_b)	105.03	41.203	7.804
General Combining Ability (σ^2_{gca})	48.36	19.589	8.505
Specific Combining Ability (σ^2_{sca})	-61.89	-5.385	-1.971
Maternal effects (σ^2_{mat})	98.83	11.108	3.342
Reciprocal effects (σ^2_{rec})	40.76	-3.746	-1.937
Error (σ^2_e)	576.46	92.536	33.919
Plot error (σ^2_p)	231.49	43.717	15.480
Within-plot error (σ^2_w)	1323.55	195.275	73.756
Var (plot mean) $= \frac{41\sigma^2_{gca}}{40} + \frac{\sigma^2_{sca}}{40} + \frac{41\sigma^2_{mat}}{40} + \frac{\sigma^2_{rec}}{40} + \frac{\sigma^2_p}{10} + \frac{\sigma^2_w}{40}$	206.58	40.490	15.633
h^2 (plot) $= \sigma^2_{gca}$ /var (plot mean)	.23	.48	.54
Var (individual) $= 2\sigma^2_{gca} + \sigma^2_{sca} + \sigma^2_{mat} + \sigma^2_{rec} + \sigma^2_p + \sigma^2_w$	1729.45	276.241	104.204
h^2 (individual) $= 4\sigma^2_{gca}$ /var (individual)	.11	.28	.32

Table 2. Estimated genetic gain in *Pinus strobus* from different selection methods under test conditions

Selection Method	Selection differential *i*, in standard units (σ)	Genetic gain in 6th-year height growth cm.	 %
Family selection in test plantations (half-sib families)[1]	1.0	2.4	11
	1.5	3.7	16
	2.0	4.9	22
Parents of best half-sib families in test plantations intermated	1.0	4.9	22
	1.5	7.3	32
	2.0	9.8	43
Mass selection in test plantations[2]	2.0	7.1	27
	2.5	8.9	33
	3.0	10.7	40

[1] $\bar{x}$ = 22.6 ± 4.5 cm. for 6th-year height increment, n = 29 families

[2] $\bar{x}$ = 26.7 ± 11.1 cm. for 6th-year height increment, n = 100 randomly-selected trees

LITERATURE CITED

Eisenhart, C. 1947. The assumptions underlying the analysis of variance. Biometrics 3(1): 1-21.

Griffing, Bruce. 1956. A generalised treatment of the use of diallel crosses in quantitative inheritance. Heredity 10: 31-50.

Kriebel, H. B., G. Namkoong, and R. A. Usanis. 1972. Analysis of genetic variation in 1-, 2-, and 3-year old eastern white pine in incomplete diallel cross experiments. Silvae Genetica 21(1-2): 44-47.

Schaffer, H. E., and R. A. Usanis. 1969. General least squares analysis of diallel experiments. a computer program-DIALL. Genetics Department Research Report 1, North Carolina State University, 61 p.