Genotype x Environment Interaction and Genotypic Stability in Loblolly pine *)

V. Effects of genotype × environment interaction on genetic variance component estimates and gain predictions

By F. OWINO1), R. C. KELLISON2) and B. J. ZOBEL3)

(Received Juli / September 1976)

Introduction

It is important to accurately estimate the magnitude and relative proportion of the various components of genetic variance in order to understand the underlying type of gene action that controls the trait of interest. For example, general combining ability variance is a measure of additive effects of genes and of additive X additive epistatic interactions while specific combining ability variance is a measure of dominance and epistatic types of gene action. Genotype X environment interaction can cause upward biases an these estimates (COMSTOCK and MOLL 1963) and, therefore, can lead to erroneous choices of breeding methods. Recent investigations by BARKER (1973) based on a large loblolly pine heritability study planted at two locations suggest that there could be substantial biases in genetic gain predictions due to genotype X location interactions for some traits like tracheid length, diameter, volume and dry weight.

The specific objectives ob the present investigation were as follows:

1. To estimate the magnitudes of additive and dominance genetic variances and additive genetic × environment interaction variance for height growth in loblolly pine.
2. To determine the effects of the estimated additive genetic X environment interaction variance on genetic gain prediction.
3. To compare local, intermediate and wide crosses with respect to their genetic gain stability as measured by the ratio additive genetic X environment interaction variance to additive genetic variance.
4. To study the relative importance of the estimated genotype X environment interaction variance on different schemes of selection currently used in tree breeding.

The fundamental concept involved in this study is that, when genotype X environment interactions are prasent, and the estimates from a single location test are used for a general genetic gain prediction, the heritability estimate is inflated as follows:

$$h^2 = \frac{\sigma^2_A + \sigma^2_{AE}}{\sigma^2_A + \sigma^2_D + \sigma^2_{AE} + \sigma^2_{DE} + \sigma^2_E}$$

whereas it should be

$$h^2 = \frac{\sigma^2_A}{\sigma^2_A + \sigma^2_D + \sigma^2_{AE} + \sigma^2_{DE} + \sigma^2_E}$$

Materials and Methods

Sets of intra- and inter-population crosses were tested over several locations. The half-diallel mating design was used for the intra-population (within orchard) crosses while N.C. design II (COMSTOCK and ROBINSON, 1948) was used for inter-population crosses. The mating matrix was of small dimension for both designs being 4 × 4 for the half-diallel and 4 X 14 or 4 X 15 for the N.C. design II experiments.

Because of seed shortage, not all the sets of crosses were represented in all the test locations and this resulted in great imbalance in the data.

Table 1. — Form of analysis of variance for estimating variance components for the N.C. design II and partial diallel experiments, based on plot mean values.

Source of variation1)	DF	Expected mean squaree)
Location	1 — 1	
GCA	p — 1	$(\sigma^2_{w/k} + \sigma^2_p) + c_1\sigma^2_{gca.l} + c_2\sigma^2_{sca} + c_3\sigma^2_{gca}$
SCA	p(p — 3)/2	$(\sigma^2_{w/k} + \sigma^2_p) + c_4\sigma^2_{gca.l} + c_5\sigma^2_{sca}$
GCA × location	(1 — 1) (p — 1)	$(\sigma^2_{w/k} + \sigma^2_p) + c_6\sigma^2_{gca.l}$
Pooled error		$(\sigma^2_{w/k} + \sigma^2_p)$

1) GCA = general combining ability.
SCA = specific combining ability.
Pooled error includes all possible interactions with replications.

2) σ^2_{gca} = variance due to general combining ability.
σ^2_{sca} = variance due to specific combining ability.
= plot to plot variance.
σ^2_w = within plot variance.
$\sigma_{gca.l}$ = variance due to general combining ability x location interaction.
k = harmonic mean of the number of trees per plot.
c. = coefficients determined by least squares method.

Statistical Models and Data Analysis

For variance component estimation the least squares method (cf SCHAFFER and USANIS 1969) was used. Such analyses are based on the following statistical model

---

* This study was carried out in partial fulfilment of the requirements for the Ph. D. degree, North Carolina State University, 1975. Unfortunately part IV of this paper can only be published in one of the next issues of Silvae Genetica.

1) Lecturer, Botany Department, University of Nairobi, Kenya.

2) Associate Professor, Forest Genetics, North Carolina State University, Raleigh.

3) Professor of Forest Genetics, North Carolina State University, Raleigh.

where

$$Y_{klji} = mu + e_k + r_{l(k)} + g_j + g_l + s_{lj} + (eg)_{kj} + (eg)_{kl} + e_{klji}$$

where

Y_{klji} = family mean in the l^{th} replication at the k^{th} environment involving a cross between the i^{th} and the j^{th} genotypes.
mu = population mean.
e_k = effect of the k^{th} environment
$r_{l(k)}$ = added effect of the l^{th} replication in the k^{th} environment.
g_j = general combining ability effect for the j^{th} female.
g_i = general combining ability effect of the i^{th} male.
s_{ij} = specific combining ability effect for the cross between i^{th} male and j^{th} female.
$(eg)_{kj}$ = location by general combining ability interaction involving k^{th} location and j^{th} female.
e_{klji} = residual.

The expectation mean squares for the corresponding analysis of variance is shown in *Table 1*.

For genetic interpretation of these components, the routine procedure is to equate them to covariances of certain relatives and then interpret these covariances in terms of the appropriate genetic components of variation. The procedure and associated assumptions have been detailed by Dudley and Moll (1969).

Thus,

$$\text{Cov (Half sibs)} = \left(\frac{1+F}{4}\right)\sigma^2_A + \left(\frac{1+F}{4}\right)^2\sigma^2_{AA} + \left(\frac{1+F}{4}\right)^3\sigma^2_{AAA} + \ldots$$

and

$$\text{Cov (Full sibs)} = \left(\frac{1+F}{4}\right)^3\sigma^2_{AD} + \left(\frac{1+F}{2}\right)^4\sigma^2_{DD} + \ldots$$

Where all the parents have the same inbreeding coefficient. With the added assumption of F = 0.

$$\sigma^2_{gca} = \text{Cov (Half sibs)} = 1/4\,\sigma^2_A + 1/16\,\sigma^2_{AA} + 1/64\,\sigma^2_{AAA} + \ldots$$

$$\sigma^2_{sca} = \text{Cov (Full sibs)} - 2\,\text{Cov (Half sibs)} = 1/4\,\sigma^2_D + 1/8\,\sigma^2_{AA} + 1/8\,\sigma^2_{AD} + \ldots$$

On further assumption of no epistasis;

$$\sigma^2_{gca} = 1/4\,\sigma^2_A \text{ and } \sigma^2_{sca} = 1/4\,\sigma^2_D$$

Similary, $\sigma^2_{gca \times l} = 1/4\,\sigma^2_{AE}$

Equations for genetic gain predictions are similar to those of Namkoong *et al.* (1966), Shelbourne (1969) and Namkoong (1974). The selection intensities assumed in the calculations are given in *Appendix 1*. The formulae for genetic gain predictions are shown in *Appendix 2*.

Results and Discussion

The estimates of variance components are shown in *Table 2* for ten sets of crosses. Four of these crosses have been

Appendix 1. Selection intensities assumed in the calculations of genetic gains.

Selection intensity	Value	Description
i_1	3.37	For selection in the wild or base plantation, i, e., 1 plus tree per 1000 searched. Applicable to all schemes
i_2	1.27	Selection of 1 out of 4 among first stage selections based on half-sib family assessment. Applicable to schemes 2 and 3
i_3	1.40	For selection of best individual in the half-sib family. Applicable to scheme 2 only.
i_4	1.27	For selection of the best full-sib families. Applicable to scheme 4 only.
i_5	1.40	For selection of the best individual within a full-sib family. Applicable to scheme 4 only.

Appendix 2. — Formulae used in genetic gain prediction for four different selection schemes[1]).

Scheme 1	$G_1 = \dfrac{i_1\,\sigma^2_A}{\sqrt{\sigma^2_{w/k} + \sigma^2_p + \sigma^2_A + \sigma^2_{AE} + \sigma^2_D}}$
Scheme 2	$G_2 = \dfrac{i_1 \cdot 1/2\,\sigma^2_A}{\sqrt{\sigma^2_{w/k} + \sigma^2_p + \sigma^2_A + \sigma^2_{AE} + \sigma^2_D}} + \dfrac{i_2 \cdot 1/4\,\sigma^2_A}{\sqrt{\dfrac{(\sigma^2_{w/k} + \sigma^2_p)}{knl} + \dfrac{2\sigma^2_{AE}}{l} + 1/4\,\sigma^2_A}} + \dfrac{i_3 \cdot 3/4\,\sigma^2_A}{\sqrt{\sigma^2_{w/k} + \sigma^2_p + \dfrac{2\sigma^2_{AE}}{l} + 3/4\,\sigma^2_A + \sigma^2_D}}$
Scheme 3	$G_3 = \dfrac{i_1 \cdot 1/2\,\sigma^2_A}{\sqrt{\sigma^2_{w/k} + \sigma^2_p + \sigma^2_A + \sigma^2_{AE} + \sigma^2_D}} + \dfrac{i_2 \cdot 1/2\,\sigma^2_A}{\sqrt{\dfrac{(\sigma^2_{w/k} + \sigma^2_p)}{knl} + \dfrac{2\sigma^2_{AE}}{l} + \dfrac{\sigma^2_D}{f} + \dfrac{\sigma^2_A}{4}}}$
Scheme 4	$G_4 = \dfrac{i \cdot 1/2\,\sigma^2_A}{\sqrt{\sigma^2_{w/k} + \sigma^2_p + \sigma^2_A + \sigma^2_{AE} + \sigma^2_D}} + \dfrac{i_4 \cdot 1/2\,\sigma^2_A}{\sqrt{\dfrac{\sigma^2_{w/k} + \sigma^2_p}{knl} + \dfrac{2\sigma^2_{AE}}{l} + \dfrac{\sigma^2_D}{4} + \dfrac{\sigma^2_A}{2}}} + \dfrac{i_5 \cdot 1/4\,\sigma^2_D}{\sqrt{\sigma^2_{w/k} + \sigma^2_p + \dfrac{2\sigma^2_{AE}}{l} + 3/4\,\sigma^2_A + \sigma^2_D}}$

---

[1]) See legend to *table 4*.

Table 2. — Variance components estimates from sets of N.C. design II and partial diallel experiments.

Mating designation	Cross type[1]	Variance components for: Location	Replication	GCA	SCA	GCA × l	Residual
Weyerhaeuser ×	L	7.6905	.4117	—.1196	.3313	—.0521	3.9245
Weyerhaeuser		±6.3334	±.3049	±.6169	±.9110	±.0511	± .5045
Hoerner-Waldorf ×	L	8.5266	.2524	.0700	—.1412	—.0284	2.6310
Weyerhaeuser		±7.0088	±.1763	±.0732	±.0543	±.0739	± .3133
Hoerner-Waldorf ×	L	2.6714	.8658	.0868	.1358	—.1372	3.7284
Albemarle		±2.3297	±.4835	±.1423	±.2088	±.-559	± .4875
Hoerner-Waldorf ×	L	3.6000	.5818	0.354	—.0360	.0090	3.0400
Westvaco		±2.3574	±.2317	±.0411	±.0514	±.0574	± .2574
Hoerner-Waldorf ×	I	5.2130	.5885	.1034	.0661	—.1039	2.7673
Continental Can		±4.3030	±.3571	±.0739	±.0899	±.0550	± .4220
Hoerner-Waldorf ×	I	5.5392	.6623	.0589	.0126	.0734	3.1815
Continental Can		±4.0675	±.3248	±.1112	±.1331	±.1338	± .3614
Weyerhaeuser ×	I	5.7727	.5711	—.0246	.0447	.0904	2.2282
Kimberly-Clark		±4.2904	±.2719	±.0867	±.0783	±.1154	± .1682
Weyerhaeuser ×	W	3.6993	.1992	.1114	—.0532	.1052	3.2147
Texas		±3.1014	±.1388	±.1119	±.067	±.1004	± .2959
Hoerner-Waldorf ×	W	1.8234	.4853	.1752	.2178	.0154	4.5710
Texas		±1.6331	±.4959	±.2219	±.6411	±.2301	±1.3529
Hoerner-Waldorf ×	W	7.0253	.3089	—.0305	—.0908	.1142	3.7302
Louisiana		±5.8511	±.2116	±0.941	±.0962	±.1496	± .3976
Average[2]		5.5027	.4771	.0713	.1223	.0461	3.2637

[1] L = local crosses.
I = intermediate between local and wide crosses.
W = Wide crosses.

[2] Negative estimates equated to zero before calculating the average.

Table 3. — Average variance components for three levels of genetic diversity.

Variance Component	Type of cross: local	Intermediate	Wide
Location	6.2915	5.5083	4.1827
Replication	.4865	.5242	.3311
GCA	.0481	.0411	.0371
SCA	0.0352	0.0411	0.0726
GCA × location	.0023	.0546	.0783
Residual	3.2417	2.7252	3.8386
$\frac{\text{GCA} \times \text{LOC}}{\text{GCA}}$	.0478	1,3284	2.4018
$\frac{\text{SCA}}{\text{GCA}}$	.7318	1.0042	1.9569

Table 4. — Predicted genetic gains (percent of the overall mean height of 10.45 ft.) for four selection schemes.

Selection scheme[1]	Test A[2]	Test B[3]
Scheme 1	4.47	7.37
Scheme 2	10	24
Scheme 3	11	26
Scheme 4	12	25

[1] Scheme 1 = simple recurrent selection
Scheme 2 = mass selection plus seedling seed orchard breeding strategy where controlled pollination is carried out with the first stage selections.
Scheme 3 = mass selection plus half-sib family selection.
Scheme 4 = mass selection plus full-sib family selection.

[2] Test A = genetic gain prediction taking account of the estimated magnitude σ^2_{AE}.

[3] Test B = genetic gain prediction based on the assumption that $\sigma^2_{AE} = 0$

designated local, 3 have been designated intermediate and 3 have been designated wide based on the distance between the populations of origin. Generally, the component of specific combining ability was found to be larger than that for general combining ability.

The averages over all sets of the crosses *(Table 2)* have been used for genetic interpretations are outlined above and the derived components have been used in genetic gain equations, as shown *in Appendix 2*. By comparing test A and test B it can be seen that the assumption of $\sigma^2_{AE} = 0$ in gain predictions in loblolly pine breeding can result in great upward biases.

The most important finding in this study is that bias caused by additive genetic × location interaction is almost the same relative magnitude for the four selection schemes considered here. This bias can result in additive genetic variance estimates twice as much as the actual value and this in turn can result in about twice as much predicted genetic gains as should be the case *(Table 4)*.

Summary

The observed magnitude of additive genetic × environment interaction variance was large enough to cause upward biases on heritability estimates and genetic gain predictions of up to 60% for mass selection and upto 100% for mass selection plus half sib family selection, mass selection plus full sib family selection, and mass selection followed by a seedling seed orchard breeding strategies.

Key words: Pinus taeda, genotype × environment interaction, wide crosses, genetic gain predictions, diallel analysis.

Zusammenfassung

Zweck der Studie ist es, den Einfluß von Genotyp — Umwelt Interaktionen auf den geschätzten genetischen Gewinn für rekurrente Selektion und verschieden kombinierte Selektions-Schemata für den Höhenwuchs bei *Pinus taeda* zu untersuchen. Auf mehreren Standorten wurden Nachkommenschaften aus kontrollierten Kreuzungen geprüft und Varianzkomponenten u. a. für GCA, SCA und GCA × Orte berechnet. Es wird gezeigt, daß bei Nichtberücksichtigung der Interaktionskomponente GCA × Orte eine Überschätzung des erwarteten genetischen Gewinnns eintritt, der von +2% für einfache recurrente Selektion bis zu 136% je nach Selektionsmethode reicht.

Literature Cited

Barker, J. A.: Location effects on heritability estimates and gain predictions for ten-year-old loblolly pine. Unpublished Ph. D. dessertation, Department of Forestry, North Carolina State University at Raleigh (1973). — Comstock, R. E. and Moll, R. H.: Genotype-environment interactions. pp. 164—196. In Hanson, W. D. and Robinson, H. F. (ed.) Statistical Genetics and Plant Breeding. NAS — NRC Publ. 982 (1963). — Comstock, R. E. and Robinson, H. F.: The components of genetic variance in populations. Biometrics 4: 254—266 (1948). — Dudley, W. J. and Moll, R. H.: Interpretation and use of estimates of heritability and genetic variances in plant breeding. Crop Sci. 9: 257—261 (1969). — Nomkoong, G.: Forest Genetics: Quantitative theory and application. U.S. Dep. Agr., For. Serv., Agr. Handb. (in press) (1974). — Namkoong, G., Snyder, E. B. and Stonecypher, R. W.: Heritability and gain concepts for evaluating breeding systems such as seedling orchards. Silvae Genet. 15: 76—84 (1966). — Schaffer, H. E. and Usanis, R. A.: General least squares analysis of diallel experiments, a computer program DIAL. Department of Genetics Research Report No. 1, North Carolina State University at Raleigh (1969). — Shelbourne, C. J. A.: Tree Breeding methods. Forest Res. Inst., New Zealand Forest Service, Tech. Paper No. 55 (1969).

Clone Influences Maturation of Unpollinated Strobili in Southern Pines

By B. F. McLemore

Southern Forest Experiment Station
Forest Service, U. S. Department of Agriculture
Pineville, Louisiana 71360

(Received February 1977)

Introduction

The abortion of female strobili in conifers is a well-known phenomenon, variously attributed to insects, climatic conditions, insufficient nutrients, and lack of pollination. Sarvas (1962) stated in the genus *Pinus* female strobili will dry and drop to the ground if all the ovules are unpollinated. Allen (1941), however, reported that abortion of Douglas-fir *(Pseudotsuga menziesii* (Mirb.) Franco) conelets was not associated with lack of pollen since unpollinated cones showed fewer abortions than pollinated cones on test trees. A preliminary study at Pineville, Louisiana, showed that unpollinated strobili on three loblolly *(Pinus taeda* L.) clones developed into mature cones, whereas all unpollinated strobili on a fourth clone aborted. The present study was installed to determine if the retention of unpollinated conelets is a clonal characteristic.

Methods

Sample trees were 7- to 10-year-old grafted southern pines located in the Kisatchie National Forest's Stuart Seed Orchard near Pollock, Louisiana. The trees had been producing female strobili for 2 or 3 years and were 20 to 30 feet tall when the study was installed.

The two treatments consisted of unpollinated, bagged strobili and wind-pollinated, unbagged strobili (control). Both treatments were applied to 18 loblolly, 7 shortleaf (*P. echinata* Mill.), 5 slash (*P. elliottii* Engelm.), and 5 longleaf (*P. palustris* Mill.) clones. On two ramets of each clone, 10 female strobili were bagged and 10 were tagged for observation as wind-pollinated controls. Bags were removed after 4 to 6 weeks, when strobili were no longer receptive. Conelet mortalities were determined every 2 to 4 weeks during spring and summer of the first year and twice during the second year. The arcsin $\sqrt{\text{proportion}}$ transformation was used for analyzing the percentage of losses at the 0.05 level of significance.

Results

Twelve of the 18 loblolly clones, 3 of the 5 slash clones, 1 of the 7 shortleaf clones, and 1 of the 5 longleaf clones developed mature cones from unpollinated strobili. Some of these same clones were observed for an additional year, and results were consistent. The four loblolly clones from the preliminary test responded the same way in this study: three produced mature cones from unpollinated strobili, and one aborted all such cones. Of the two slash clones observed for 2 years, one consistently produced fully developed cones, and one consistently aborted all unpollinated strobili. On the one shortleaf clone that produced unpollinated cones, cones were observed to mature during the first growing season for 2 consecutive years (Mc Lemore 1975).

Unpollinated cones were smaller than pollinated cones

Table 1. — Proportion of conelet losses in four southern pines

	Loblolly	Slash	Shortleaf	Longleaf
Clones observed, no.	18	5	7	5
Clones producing cones from unpollinated strobili, no.	12	3	1	1
Losses from all clones, percent				
Pollinated	42	51	70	55
Unpollinated	81	67	92	96
Losses from all clones, percent those aborting all unpollinated strobili, percent				
Pollinated	49	40	80	35
Unpollinated	68	44	45	80