Theor Appl Genet (1987) 73:371–378

Testcross selection theory*

N.M. Cowen**

Department of Agronomy, University of Missouri, Columbia, MO, USA

Received June 20, 1986; Accepted September 15, 1986
Communicated by A.R. Hallauer

Summary. The purpose of this paper is to extend the theoretical basis for testcross selection theory from models assuming two alleles per locus to a model which is general for number and frequency of alleles. The expectations of genetic variances expressed among and within testcross families is presented for both inbred and population testers. Predicted change due to selection in testcross, non-inbred and selfed population performance with testcross selection are derived. Expected changes in testcross heterosis and inbreeding depression in the population are also derived. Approximate confidence intervals for predicted selection response are developed and appropriate sets of progeny to evaluate in order to estimate parameters of interest are identified.

Key words: Heterosis – Inbreeding – Prediction – Genetic variance – Genetic theory

Introduction

Testcross progeny of individuals or lines from breeding populations are commonly used to identify lines with superior hybrid performance in combination with the tester or combining ability (Hallauer and Miranda 1981).

Recurrent selection of a population using a tester is a common procedure for improving the combining ability of the population (Hallauer and Miranda 1981; Horner et al. 1973; Russell et al. 1973; Horner et al. 1976). Currently, the theoretical basis for the expected genetic variances among and within testcrosses, and predicted response to selection requires the assumption of two alleles per locus (Hallauer and Miranda 1981; Rawlings and Thompson 1962). This assumption is overly restrictive, and application of current theoretical models to populations with multiple alleles may yield inaccurate results.

The purpose of this paper is to extend the theoretical model for testcross selection from two alleles per locus to a model which is general for number and frequency of alleles.

The population

The population that is considered is assumed to be in linkage equilibrium, with no linkage of genes affecting the trait, and no epistasis. Thus, all variances and quadratic components defined for the population will be the sum of the values for the individual loci, and consideration can be given to a single locus. The structure of the noninbred population at a single locus is

$$\sum_i \sum_j p_i p_j A_i A_j,$$

and the structure at a level of inbreeding where the inbreeding coefficient = F is

$$F \sum_i p_i A_i A_i + (1 - F) \sum_i \sum_j p_i p_j A_i A_j,$$

where p_i is the frequency of allele A_i in the population. The structure of the fully inbred (F = 1) population is $\sum p_i A_i A_i$. Assuming a model which allows dominance, but no epistasis, the genotypic value for $A_i A_j$ is

$$G_{ij}^* = \mu + \alpha_i + \alpha_j + \delta_{ij},$$

where μ is the population mean genotypic value, α_i and α_j are the additive effects of alleles A_i and A_j fit by

* Contribution from the Missouri Agricultural Experiment Station. Journal Series No. 10063

** Current address: United Agriseeds, P.O. Box 4011, Champaign, IL 61820, USA

least squares, and δ_{ij} is the dominance deviation. By definition

$$\sum_i p_i \alpha_i = \sum_j p_j \alpha_j = 0 .$$

All genotypic values in the remaining discussion will be coded by substracting μ: $G_{ij} = G^*_{ij} - \mu$.

Genetic variances among and within progenies

Consider an inbred tester with genotype $A_k A_k$. The additive effect of allele A_k is defined as the deviation of the mean of all testcrosses from the mean of the population:

$$\alpha_K = \sum_i p_i G_{ik} .$$

Any dominance deviation is defined as the difference between the genotypic value and the predicted value based on the additive effects of the alleles.

The gametic output of an individual $A_i A_j$ is

$$\tfrac{1}{2}(A_i + A_j) .$$

The genetic structure of the testcross of this individuals is

$$\tfrac{1}{2}(A_i A_k + A_j A_k) .$$

The coded genotypic value of the testcross is thus

$$\tfrac{1}{2}[(\alpha_i + \alpha_k + \delta_{ik}) + (\alpha_j + \alpha_k + \delta_{jk})] .$$

The variance expressed among and within testcrosses are linear functions of the additive genetic variance in the population

$$\sigma^2_A = 2 \sum_i p_i \alpha_i^2 ;$$

the covariance of additive and testcross dominance deviations

$$\mathrm{Cov}(AD_T) = \sum_i p_i \alpha_i \delta_{ik} ;$$

and the variance of the testcross dominance deviations

$$V(D_T) = \sum_i p_i \delta^2_{ik} .$$

The total variance expressed among testcross individuals is constant with inbreeding in the population because the gametic output of the population does not change. The genetic structure of population testcross is

$$\sum_i p_i A_i A_k .$$

The variance expressed among individuals is obtained as the mean of the squared genotypic values minus the squared mean genotypic value; i.e.,

$$\begin{aligned}
&\sum_i p_i (\alpha_i + \alpha_k + \delta_{ik})^2 - \alpha_k^2 \\
&= \sum_i p_i \alpha_i^2 + 2 \sum_i p_i \alpha_i \alpha_k + 2 \sum_i p_i \alpha_i \delta_{ik} + \alpha_k^2 \\
&\quad + 2 \sum_i p_i \alpha_k \delta_{ik} + \sum_i p_i \delta^2_{ik} - \alpha_k^2 \\
&= \sum_i p_i \alpha_i^2 + 2 \sum_i p_i \alpha_i \delta_{ik} + \sum_i p_i \delta^2_{ik} \\
&= \tfrac{1}{2} \sigma^2_A + 2\,\mathrm{Cov}(AD_T) + V(D_T) .
\end{aligned}$$

If we consider testcrosses of individuals from a generation with inbreeding level F, the total variability may be subdivided into portions expressed among and within testcross families. The variance among testcross families may be obtained as the mean of the squared, coded, family genotypic means minus the squared mean genotypic value, i.e.

$$\begin{aligned}
&F \sum_i p_i (\alpha_i + \alpha_k + \delta_{ik})^2 \\
&\quad + (1 - F) \sum_i \sum_j p_i p_j [\tfrac{1}{2}(2\alpha_k + \alpha_i + \alpha_j + \delta_{ik} + \delta_{jk})]^2 - \alpha_k^2 \\
&= F \sum_i p_i \alpha_i^2 + 2F \sum_i p_i \alpha_i \delta_{ik} + F \sum_i p_i \delta^2_{ik} - (1 - F)\alpha_k^2 \\
&\quad + (1 - F)\alpha_k^2 + \tfrac{1}{2}(1 - F) \sum_i p_i \alpha_i^2 + (1 - F) \sum_i p_i \alpha_i \delta_{ik} \\
&\quad + \tfrac{1}{2}(1 - F) \sum_i p_i \delta^2_{ik} \\
&= \tfrac{1}{4}(1 + F)\sigma^2_A + (1 + F)\,\mathrm{Cov}(AD_T) + \tfrac{1}{2}(1 + F)\,V(D_T) .
\end{aligned}$$

The variance expressed within testcrosses is the difference between the total variance and the variance expressed among testcross families. The coefficients of these three variances or quadratic components expressed among and within testcross families for several levels of inbreeding are given in Table 1. The coefficient of the three components among families are all linear functions of $1 + F$, while the coefficients for within families are all linear function of $1 - F$.

Now consider a population rather than an inbred line as a tester. The tester may not be in equilibrium, but I will assume that the gametic output of the tester is identical to the gametic output of the tester population at equilibrium. The gametic output of the tester population is assumed to be

$$\sum_k p_k A_k ,$$

where p_k is the frequency of allele A_k in the tester. Given an individual $A_i A_j$, the genetic structure of its testcross is

$$\tfrac{1}{2}\left[\sum_k p_k (A_i A_k + A_j A_k)\right] .$$

The coded genotypic value of an individual $A_i A_k$ is

$$G_{ik} = \alpha_i + \alpha_k + \delta_{ik}$$

Table 1. Variances among and within testcross families using an inbred tester

Generation of testcross		Among			Within		
Individual	Line	σ_A^2	$\mathrm{Cov}(AD_T)$	$V(D_T)$	σ_A^2	$\mathrm{Cov}(AD_T)$	$V(D_T)$
S_0	S_1	0.25	1	0.5	0.25	1	0.5
S_1	S_2	0.375	1.5	0.75	0.125	0.5	0.25
S_2	S_3	0.438	1.75	0.875	0.063	0.25	0.125
S_3	S_4	0.469	1.875	0.938	0.031	0.125	0.063
S_4	S_5	0.484	1.938	0.969	0.016	0.063	0.031
S_5	S_6	0.492	1.969	0.984	0.008	0.031	0.016
S_n	S_{n+1}	$\frac{1}{4}(1+F_n)$	$(1+F_n)$	$\frac{1}{2}(1+F_n)$	$\frac{1}{4}(1-F_n)$	$(1-F_n)$	$\frac{1}{2}(1-F_n)$
S_∞	S_∞	$\frac{1}{2}$	2	1	0	0	0

where

$$\alpha_k = \sum_i p_i G_{ik}$$

and δ_{ik} is a testcross dominance deviation. The mean additive effect of alleles in the tester are defined as:

$$\bar{\alpha}_. = \sum_k p_k \alpha_k;$$

the mean testcross dominance deviation of allele A_i as:

$$\bar{\delta}_{i.} = \sum_k p_k \delta_{ik};$$

and the mean testcross dominance deviation of allele A_k as:

$$\bar{\delta}_{.k} = \sum_i p_i \delta_{ik}.$$

It can be shown that

$$\sum_i \sum_k p_i p_k \delta_{ik} = \sum_i p_i \bar{\delta}_{i.} = 0.$$

The variances expressed among and within testcross families are linear functions of six populations variances or quadratic components. The components are: the population additive genetic variance

$$\sigma_A^2 = 2 \sum_i p_i \alpha_i^2;$$

the covariance of population additive effects and mean testcross dominance deviations

$$\mathrm{Cov}(A\,\bar{\delta}) = \sum_i p_i \alpha_i \bar{\delta}_{i.};$$

the variance of the mean testcross dominance deviations

$$V(\bar{\delta}) = \sum_i p_i \bar{\delta}_{i.}^2;$$

the additive genetic variance within the tester

$$\sigma_{ATC}^2 = 2 \sum_k p_k \alpha_k^2;$$

the covariance of tester additive effects and mean testcross dominance deviations

$$\mathrm{Cov}(A\,\bar{\delta})_{TC} = \sum_k p_k \alpha_k \bar{\delta}_{.k};$$

and the variance of the testcross dominance deviations

$$V(\delta) = \sum_i \sum_k p_i p_k \delta_{ik}^2.$$

The genetic structure of the population testcross is

$$\sum_i \sum_k p_i p_k A_i A_k;$$

with coded, mean genotypic value of

$$\sum_i \sum_k p_i p_k (\alpha_i + \alpha_k + \delta_{ik}) = \sum_i p_i (\alpha_i + \bar{\alpha}_. + \bar{\delta}_{i.}) = \bar{\alpha}_..$$

The total variance expressed among individuals in the population testcross is

$$\begin{aligned}
&\sum_i \sum_k p_i p_k (\alpha_i + \alpha_k + \delta_{ik})^2 - \bar{\alpha}_.^2 \\
&= \sum_i p_i \alpha_i^2 + \sum_k p_k \alpha_k^2 + 2 \sum_i p_i \alpha_i \bar{\delta}_{i.} + 2 \sum_k p_k \alpha_k \bar{\delta}_{.k} \\
&\quad + \sum_i \sum_k p_i p_k \delta_{ik}^2 - \bar{\alpha}_.^2 \\
&= \tfrac{1}{2}\sigma_A^2 + \tfrac{1}{2}\sigma_{ATC}^2 + 2\,\mathrm{Cov}(A\,\bar{\delta}) + 2\,\mathrm{Cov}(A\,\bar{\delta})_{TC} + V(\delta) - \bar{\alpha}_.^2
\end{aligned}$$

Using arguments similar to those presented for an inbred tester, the variance expressed among testcross families of individuals with inbreeding coefficient F is

$$\tfrac{1}{4}(1+F)\,\sigma_A^2 + (1+F)\,\mathrm{Cov}(A\,\bar{\delta}) + \tfrac{1}{2}(1+F)\,V(\bar{\delta}).$$

It is obvious, since the variance within families is the difference between total variance and the among families variance, that the variance within testcross families is a linear function of all six variances or quadratic components, and is equal to

$$\begin{aligned}
&\tfrac{1}{4}(1-F)\,\sigma_A^2 + \tfrac{1}{2}\sigma_{ATC}^2 + (1-F)\,\mathrm{Cov}(A\,\bar{\delta}) \\
&\quad + 2\,\mathrm{Cov}(A\,\bar{\delta})_{TC} + V(\delta) - \tfrac{1}{2}(1+F)\,V(\bar{\delta}) - \bar{\alpha}_.^2.
\end{aligned}$$

The only real simplification in these linear functions results when the tester population is identical to the population that is being improved. Under these conditions;

$$\sigma_{ATC}^2 = \sigma_A^2; \quad \mathrm{Cov}(A\,\bar{\delta}) = \mathrm{Cov}(A\,\bar{\delta})_{TC} = 0;$$

$$V(\bar{\delta}) = 0; \quad \bar{\alpha}_. = 0;$$

and $V(\delta) = \sigma^2_D$ for the population. The variance expressed among testcross families reduces to $\frac{1}{4}(1+F)\,\sigma^2_A$, and the variance expressed within families reduces to $[1-\frac{1}{4}(1+F)]\,\sigma^2_A + \sigma^2_D$. These are the expectations of the variance expressed among and within half sib families (Hallauer and Miranda 1981). The coefficients for σ^2_A, $\mathrm{Cov}(A\,\bar{\delta})$ and $V(\bar{\delta})$ expressed among testcross families when the tester is a population are identical to those for σ^2_A, $\mathrm{Cov}(ADT)$ and $V(D_T)$, respectively, shown in Table 1.

The additive genetic variance used here is that of the equilibrium population. The proportion of σ^2_A expressed among testcrosses depends on the inbreeding level of the progeny testcrossed, and is the same for both inbred and noninbred testers. Both $\mathrm{Cov}(AD_T)$ and $\mathrm{Cov}(A\,\bar{\delta})$ can, by definition, be negative. Hence, the total variability expressed among testcross families may not increase with inbreeding in the population. The variability among testcross families may be zero in two instances. First the trivial case when all components are zero; and second when $\mathrm{Cov}(AD_T) = -\frac{1}{4}\sigma^2_A - \frac{1}{2}V(D_T)$ or $\mathrm{Cov}(A\,\bar{\delta}) = -\frac{1}{4}\sigma^2_A - \frac{1}{2}V(\bar{\delta})$. These are the lower limits for these two covariances. Combinations of population and tester where this situation occurs will not be used for selection because there will be no genetic variability among testcrosses at any inbreeding level of the population.

Predicted selection response

Predicted selection response can be obtained as the products of the selection differential and the regression of progeny testcross mean performance in cycle t + 1 on parental testcross mean performance in cycle t (Hallauer and Miranda 1981). The individuals or lines that are testcrossed are related through an S_0 individual.

The regression function involved is the ratio of the covariance of testcross family means to the variance of testcross means in cycle t. If intermating takes place exclusively among selfed progeny of selected individuals then the regression of testcross progeny means is on mid parent value. The denominator of the regression equation is thus the variance of mid-parent values or $\frac{1}{2}$the variance of a testcross mean in cycle t.

Assuming no environmental covariance between relatives, then the covariance of testcross family means is obtained in two parts. First, consider an S_n individual whose genotype is $A_i A_i$; the gametic output of this individual is A_i. With the inbred tester described above the testcross of this individual is genetically:

$A_i A_k$;

with genotypic value:

$\alpha_i + \alpha_k + \delta_{ik}$.

The gametic output of the population is:

$\sum_l p_l A_l$.

The genetic structure of the S_0 progeny of this S_n individual when recombined with the population is:

$\sum_l p_l A_i A_l$.

If these S_0 progeny are self-pollinated to the S_n their genetic structure is:

$$\frac{F_n}{2}(A_i A_i + \sum p_l A_l A_l) + \frac{(1-F_n)}{2}\sum_l p_l A_i A_l .$$

The genetic structure of the testcross progeny of these S_n individuals is:

$$\frac{F_n}{2} A_i A_k + \frac{F_n}{2}\sum_l p_l A_l A_k$$

$$+\left(\frac{1-F_n}{2}\right)\left(A_i A_k + \sum_l p_l A_l A_k\right) = \frac{1}{2}\left(A_i A_k + \sum_l p_l A_l A_k\right);$$

with genotypic value:

$$\frac{1}{2}\left(\alpha_i + \sum_l p_l \alpha_l + 2\,\alpha_k + \delta_{ik} + \sum_l p_l \delta_{lk}\right).$$

The product of the genotypic value of the testcross family means of the S_n individual and its S_n progeny following intermating is:

$$(\alpha_i + \alpha_k + \delta_{ik})\left(\frac{1}{2}\alpha_i + \frac{1}{2}\sum_l p_l \alpha_l + \alpha_k + \frac{1}{2}\delta_{ik} + \frac{1}{2}\sum_l p_l \delta_{lk}\right).$$

Second, consider an S_n individual which is genetically $A_i A_j$; the gametic output of this individual is

$\frac{1}{2}(A_i + A_j)$.

The genetic structure of the testcross progeny of this individual with the inbred tester is:

$\frac{1}{2}(A_i A_k + A_j A_k)$;

with genotypic value:

$\frac{1}{2}(\alpha_i + \alpha_j + 2\,\alpha_k + \delta_{ik} + \delta_{jk})$.

The S_0 progeny from the cross of this individual with the population has genetic structure:

$\frac{1}{2}\sum_l p_l (A_i A_l + A_j A_l)$;

resulting in an S_n progeny which has genetic structure:

$$\frac{1}{2}\left[\frac{F_n}{2}\left(A_i A_i + A_j A_j + 2\sum_l p_l A_l A_l\right)\right.$$

$$\left. + \frac{(1-F_n)}{2}\sum_l p_l (A_i A_l + A_j A_l)\right].$$

The genetic structure of the testcross of this S_n progeny is:

$$\frac{1}{2}\left[\frac{F_n}{2}\left(A_i A_k + A_j A_k + 2\sum_l p_l A_l A_k\right) + (1-F_n)\left(\tfrac{1}{2} A_i A_k + \tfrac{1}{2} A_j A_k + \sum_l p_l A_l A_k\right)\right];$$

with genotypic value:

$$\tfrac{1}{4}\left(\alpha_i + \alpha_j + 4\alpha_k + \delta_{ik} + \delta_{jk} + 2\sum_l p_l \alpha_l + 2\sum_l p_l \delta_{lk}\right).$$

The product of the genotypic values of the testcrosses of this S_n individual and its S_n progeny following intermating is:

$$1/8\,(\alpha_i + \alpha_j + 2\alpha_k + \delta_{ik} + \delta_{jk}) \cdot \left(\alpha_i + \alpha_j + 4\alpha_k + \delta_{ik} + \delta_{jk} + 2\sum_l p_l \alpha_l + 2\sum_l p_l \delta_{lk}\right).$$

The covariance of S_n testcross family means with the testcross family means of their S_n progeny is thus:

$$\begin{aligned}
&F_n \sum_i p_i \left[(\alpha_i + \alpha_k + \delta_{ik}) \cdot \left(\tfrac{1}{2}\alpha_i + \tfrac{1}{2}\sum_l p_l \alpha_l + \alpha_k + \tfrac{1}{2}\delta_{ik} + \tfrac{1}{2}\sum_l p_l \delta_{lk}\right)\right] \\
&+ (1-F_n) \sum_i \sum_j p_i p_j\, 1/8 \left[(\alpha_i + \alpha_j + 2\alpha_k + \delta_{ik} + \delta_{jk}) \cdot \left(\alpha_i + \alpha_j + 4\alpha_k + \delta_{ik} + \delta_{jk} + 2\sum_l p_l \delta_{lk}\right)\right] - \alpha_k^2 \\
&= \frac{F_n}{2}\sum_i p_i \alpha_i^2 + F_n \sum_i p_i \alpha_i \delta_{ik} + F_n \alpha_k^2 + \frac{F_n}{2}\sum_i p_i \delta_{ik}^2 \\
&+ \left(\frac{1-F_n}{4}\right)\sum_i p_i \alpha_i^2 + \left(\frac{1-F_n}{2}\right)\sum_i p_i \alpha_i \delta_{ik} \\
&+ (1-F_n)\alpha_k^2 + \left(\frac{1-F_n}{4}\right)\sum_i p_i \delta_{ik}^2 - \alpha_k^2 \\
&= \frac{1+F_n}{8}\sigma_A^2 + \frac{1+F_n}{2}\mathrm{Cov}(AD_T) + \frac{1+F_n}{4}V(D_T).
\end{aligned}$$

The covariance of testcross family means with a population as a tester is:

$$\frac{1+F_n}{8}\sigma_A^2 + \frac{1+F_n}{2}\mathrm{Cov}(A\,\bar{\delta}) + \frac{1+F_n}{4}V(\bar{\delta}).$$

The form of the selection response equation with an inbred tester for testcrosses of S_n individuals is:

$$(\bar{X}_{STC} - \bar{X})\left\{\frac{\frac{1}{2}\left[\frac{1+F_n}{4}\sigma_A^2 + (1+F_n)\mathrm{Cov}(AD_T) + \left(\frac{1+F_n}{2}\right)V(D_T)\right]}{\frac{1}{2}\mathrm{Var}(\bar{X}_{TC})_{S_n}}\right\}$$

where $\bar{X}_{STC}$ and $\bar{X}$ are the mean of the selected testcross families and the grand mean, respectively, $\mathrm{Var}(\bar{X}_{TC})$ is the phenotypic variance of a testcross family mean and all other terms are defined above. The term $\mathrm{Var}(\bar{X}_{TC})_{S_n}$ is equal to:

$$\frac{\sigma_E^2}{RL} + \frac{\sigma_{GE}^2}{L} + \sigma_G^2;$$

where σ_E^2 is the error variance from the analysis of variance, σ_{GE}^2 is the variance of interaction effects of genotypes with environments, σ_G^2 the genetic variance expressed among testcross families of S_n individuals given in Table 1, and R and L are the numbers of replications and locations used in evaluation of testcross families, respectively.

Another situation encountered in recurrent selection with a tester is where an S_0 individual is self pollinated, and a single S_1 progeny is crossed to the tester with remnant S_1 seed being used to recombine selected families (Dr. K. Lamkey, USDA-ARS, Iowa State University, personal communication). Under these circumstances the selection response equation takes the form:

$$(\bar{X}_{STC} - \bar{X})\frac{\left[\frac{1}{2}\left[\frac{1}{4}\sigma_A^2 + \mathrm{Cov}(AD_T) + \frac{1}{2}V(D_T)\right]\right]}{\frac{1}{2}\mathrm{Var}(\bar{X}_{TC})_{S_1}},$$

where all terms are defined as above and $\mathrm{Var}(\bar{X}_{TC})_{S_1}$ is the phenotypic variance of the mean of a testcross family resulting from crossing an S_1 individual to the tester.

Comparison of the predicted selection response, where a single S_1 individual is crossed to the tester and remnant S_1 seed is used in intermating, with the response predicted when numerous individuals are sampled within the S_1 line and remnant S_1 seed is used in intermating, is of interest to breeders. The numerators of the two response equations are identical. The denominator of the equation for the situation where several S_1 individuals are crossed to the tester is smaller than the denominator where a single S_1 individual within the line is crossed to the tester. The genetic component of the phenotypic variance is 1.5 times as large for the latter situation as it is for the former. Thus, given the same selection differential, which may or may not occur, predicted response will be larger where several individuals are sampled within the S_1 line. Similar results are obtained with a population as a tester, with $\mathrm{Cov}(A\,\bar{\delta})$ and $V(\bar{\delta})$ substituting for $\mathrm{Cov}(AD_T)$ and $V(D_T)$ in the prediction formulae.

Other covariances of interest

Not only are breeders interested in predicting response to selection or the change in the mean of testcrosses from cycle to cycle, but they may also be interested in the relationships between testcross performance and the performance of either non-inbred or inbred progenies within the population. Consider the situation where an S_0 individual is crossed to an inbred tester and is also self-pollinated. Breeders are interested in the genetic relationships between the testcross family and either the S_0 individual or the corresponding S_1 line both in the same cycle of selection and in the following cycle. Because the reference population used to define all the effects is the non-inbred, equilibrium population, these relationships can be defined (see Smith 1986 for an alternate derivation). Two additional quadratic components need first to be defined, the first of these is the covariance of additive and homozygous dominance deviations (Cockerham 1983):

$$\mathrm{Cov}(AD_H) = \sum_i r_i \alpha_i \delta_{ii};$$

the second is the covariance of homozygous and testcross dominance deviations:

$$\mathrm{Cov}(D_H D_T) = \sum_i p_i \delta_{ik} \delta_{ii}.$$

The covariance of S_0 and testcross mean performance within the same cycle is

$$\mathrm{Cov}(S_0^t, TC^t) = \tfrac{1}{2}\sum_i\sum_j p_i p_j (\alpha_i + \alpha_j + \delta_{ij}) \cdot (\alpha_i + \alpha_j + 2\alpha_k + \delta_{ik} + \delta_{jk}) = \tfrac{1}{2}\sigma_A^2 + \mathrm{Cov}(AD_T)$$

where the superscript denotes the cycle. The covariance of S_1 and testcross mean performance within the same cycle is:

$$\begin{aligned}\mathrm{Cov}(S_1^t, TC^t) &= \tfrac{1}{2}\sum_i\sum_j p_i p_j (\alpha_i + \alpha_j + \tfrac{1}{4}(\delta_{ii} + \delta_{jj} + 2\delta_{ij})) \cdot (\alpha_i + \alpha_j + 2\alpha_k + \delta_{ik} + \delta_{jk}) - \tfrac{1}{2}\alpha_k \sum_i p_i \delta_{ii} \\ &= \sum_i p_i \alpha_i^2 + \tfrac{1}{4}\sum_i p_i \alpha_i \delta_{ii} + \tfrac{1}{2}\alpha_k \sum_i p_i \delta_{ii} + \sum_i p_i \alpha_i \delta_{ik} + \tfrac{1}{4}\sum_i p_i \delta_{ik} \delta_{ii} - \tfrac{1}{2}\alpha_k \sum_i p_i \delta_{ii} \\ &= \tfrac{1}{2}\sigma_A^2 + \tfrac{1}{4}\mathrm{Cov}(AD_H) + \mathrm{Cov}(AD_T) + \tfrac{1}{4}\mathrm{Cov}(D_H D_T).\end{aligned}$$

The covariance of testcross mean performance with S_0 progeny mean performance in the following cycle is:

$$\mathrm{Cov}(S_0^{t+1}, TC^t) = \tfrac{1}{4}\sum_i\sum_j p_i p_j (\alpha_i + \alpha_j) \cdot (\alpha_i + \alpha_j + 2\alpha_k + \delta_{ik} + \delta_{jk}) = \tfrac{1}{4}\sigma_A^2 + \tfrac{1}{2}\mathrm{Cov}(AD_T).$$

The covariance of testcross mean performance with S_1 progeny mean performance in the following cycle is:

$$\begin{aligned}\mathrm{Cov}(S_1^{t+1}, TC^t) &= 1/16 \sum_i\sum_j p_i p_j \cdot \left(4\alpha_i + 4\alpha_j + \delta_{ii} + \delta_{jj} + 2\sum_l p_l \delta_{ll}\right) \\ &\cdot (\alpha_i + \alpha_j + 2\alpha_k + \delta_{ik} + \delta_{jk}) - \tfrac{1}{2}\alpha_k \sum_i p_i \delta_{ii} \\ &= \tfrac{1}{4}\sigma_A^2 + 1/8\,\mathrm{Cov}(AD_H) + \tfrac{1}{2}\mathrm{Cov}(AD_T) + 1/8\,\mathrm{Cov}(D_H D_T).\end{aligned}$$

In both instances the covariance of progenies within cycles is exactly twice the covariance of progenies separated by a cycle of recombination. Similar quadratic terms can be defined with a population as a tester leading to a similar set of equations for the covariances of these progenies. The quadratic components are $\mathrm{Cov}(A\,\bar{\delta})$, which replaces $\mathrm{Cov}(AD_T)$ in the equations, and

$$\mathrm{Cov}(D_H\,\bar{\delta}) = \sum_i p_i \delta_{ii} \bar{\delta}_{i.};$$

which substitutes for $\mathrm{Cov}(D_H D_T)$ in the equations.

Predicted changes in heterosis and inbreeding depression

Prior to specifying exact equations for the changes in heterosis in testcross (the deviation of the mean of all testcross families from the population mean) and inbreeding depression within the population, the predicted changes in the noninbred and selfed population need to be specified. The predicted change in the noninbred population from testcross selection is:

$$(\bar{X}_{STC} - \bar{X})\,\frac{[\mathrm{Cov}(S_0^{t+1}, TC^t)]}{\frac{1}{2}\mathrm{Var}(TC)_{S_0}}$$

$$= (\bar{X}_{STC} - \bar{X}) \cdot \left\{\frac{[\frac{1}{4}\sigma_A^2 + \frac{1}{2}\mathrm{Cov}(AD_T)]}{\frac{1}{2}\left(\frac{\sigma_E^2}{RL} + \frac{\sigma_{GE}^2}{L} + \frac{1}{4}\sigma_A^2 + \mathrm{Cov}(AD_T) + \frac{1}{2}V(D_T)\right)}\right\}$$

for an inbred tester, and

$$(\bar{X}_{STC} - \bar{X})\,\frac{[\frac{1}{4}\sigma_A^2 + \frac{1}{2}\mathrm{Cov}(A\,\bar{\delta})]}{\frac{1}{2}\left(\frac{\sigma_E^2}{RL} + \frac{\sigma_{GE}^2}{L} + \frac{1}{4}\sigma_A^2 + \mathrm{Cov}(A\,\bar{\delta}) + \frac{1}{2}V(\bar{\delta})\right)}$$

for a population tester, where all terms are defined as previously. The predicted change from testcross selection in the population selfed is:

$$(\bar{X}_{STC} - \bar{X}) \frac{[\mathrm{Cov}(S_1^{t+1}, TC^t)]}{\frac{1}{2}\mathrm{Var}(TC)_{S_0}} = (\bar{X}_{STC} - \bar{X}) \frac{[\frac{1}{4}\sigma_A^2 + 1/8\,\mathrm{Cov}(AD_H) + \frac{1}{2}\mathrm{Cov}(AD_T) + 1/8\,\mathrm{Cov}(D_H D_T)]}{\frac{1}{2}\left(\frac{\sigma_E^2}{RL} + \frac{\sigma_{GE}^2}{L} + \frac{1}{4}\sigma_A^2 + \mathrm{Cov}(AD_T) + \frac{1}{2}V(D_T)\right)}$$

for an inbred tester, and

$$(\bar{X}_{STC} - \bar{X}) \frac{[\frac{1}{4}\sigma_A^2 + 1/8\,\mathrm{Cov}(AD_H) + \frac{1}{2}\mathrm{Cov}(A\,\bar{\delta}) + 1/8\,\mathrm{Cov}(D_H\,\bar{\delta})]}{\frac{1}{2}\left(\frac{\sigma_E^2}{RL} + \frac{\sigma_{GE}^2}{L} + \frac{1}{4}\sigma_A^2 + \mathrm{Cov}(A\,\bar{\delta}) + \frac{1}{2}V(\bar{\delta})\right)}$$

for a population tester. The predicted testcross heterosis for cycle t + 1 can be obtained as the observed heterosis in cycle t plus the difference between the predicted changes in testcross and S_0 performance with an inbred tester:

$$(\bar{X}_{TC} - \bar{X}_{S_0})_t + (\bar{X}_{STC} - \bar{X}) \frac{[(1/8\,\sigma_A^2 + \frac{1}{2}\mathrm{Cov}(AD_T) + \frac{1}{4}V(D_T)) - (\frac{1}{4}\sigma_A^2 + \frac{1}{2}\mathrm{Cov}(AD_T))]}{\frac{1}{2}\left(\frac{\sigma_E^2}{RL} + \frac{\sigma_{GE}^2}{L} + \frac{1}{4}\sigma_A^2 + \mathrm{Cov}(AD_T) + \frac{1}{2}V(D_T)\right)}$$

$$= \alpha_k + (\tfrac{1}{4}V(D_T) - 1/8\,\sigma_A^2) \frac{[\bar{X}_{STC} - \bar{X}]}{\frac{1}{2}\mathrm{Var}(TC)_{S_0}},$$

where $(\bar{X}_{TC} - \bar{X}_{S_0})_t$ is the expected difference between testcross and populations means in cycle t and is equal to α_k. Testcross heterosis will increase if $V(D_T) > 2\,\sigma_A^2$ and otherwise will decrease since the term within the bracket is strictly nonnegative. The equation for a population tester is similar with $\bar{\alpha}$., $\mathrm{Cov}(A\,\bar{\delta})$, and $V(\bar{\delta})$ substituting for α_k, $\mathrm{Cov}(AD_T)$ and $V(D_T)$ respectively.

The predicted change in inbreeding depression within the population can be obtained as the observed inbreeding depression plus the difference in the predicted changes in S_0 and S_1 performance; i.e.

$$(\bar{X}_{S_0} - \bar{X}_{S_1})_t + (\bar{X}_{STC} - \bar{X}) \frac{[(\frac{1}{4}\sigma_A^2 + \frac{1}{2}\mathrm{Cov}(AD_T)) - (\frac{1}{4}\sigma_A^2 + 1/8\,\mathrm{Cov}(AD_H) + \frac{1}{2}\mathrm{Cov}(AD_T + 1/8\,\mathrm{Cov}(D_H D_T)]}{\frac{1}{2}\left(\frac{\sigma_E^2}{RL} + \frac{\sigma_{GE}^2}{L} + \frac{1}{4}\sigma_A^2 + \mathrm{Cov}(AD_T) + \frac{1}{2}V(D_T)\right)}$$

$$= \tfrac{1}{2}\sum p_i\,\delta_{ii} - 1/8\,(\mathrm{Cov}(AD_H) + \mathrm{Cov}(D_H D_T)) \frac{[\bar{X}_{STC} - \bar{X}]}{\frac{1}{2}\mathrm{Var}(TC)_{S_0}}$$

where $(\bar{X}_{S_0} - \bar{X}_{S_1})_t$ is the expected difference in mean performance of S_0 and S_1 generation in cycle t, and is equal to $\frac{1}{2}\sum_i p_i\,\delta_{ii}$.

Inbreeding depression in the population will be less severe in cycle t + 1 than in cycle t if $\mathrm{Cov}(AD_H) + \mathrm{Cov}(D_H D_T)$ is positive. Both terms are covariances and thus may be negative.

Estimation

The mean differences $(\bar{X}_{S_0} - \bar{X}_{S_1})_t$ and $(\bar{X}_{TC} - \bar{X}_{S_0})_t$ can be estimated directly from the observe means for the corresponding generations in cycle t. The means, of course, should both be expressed on the same basis, i.e. on an individual plant or plot basis. The variances of the differences are simply the sum of the variances of the corresponding generations means. The predicted change in testcross performance is estimated by the product of the observed selectional differential and the heritability expressed on an entry-mean basis estimated from the analysis of testcross performance. Table 2 is a standard analysis of variance table for a randomized complete block design with T testcrosses, L locations, and R replicates per location. Based on the analysis of variance in Table 2 predicted selection response in testcross performance is equal to:

$$\widehat{(\bar{X}_{STC} - \bar{X})} \frac{[\frac{1}{2}(MS_3 - MS_4)/LR)]}{\frac{1}{2}MS_3/LR}$$

$$= \widehat{(\bar{X}_{STC} - \bar{X})}\left[1 - \frac{MS_4}{MS_3}\right],$$

where $\widehat{(\bar{X}_{STC} - \bar{X})}$ is the observed selection differential and MS_3 and MS_4 are the mean squares for testcrosses and testcrosses × location, respectively.

The estimation of predicted changes in the non-inbred and selfed populations can proceed once the S_0 individual plant mean data has been adjusted to the corresponding plot values, assuming a perfect stand. With S_0, S_1, and testcross data from cycle t all expressed on a plot basis the covariances of S_0 and testcross, and S_1 and testcross means may be estimated. Attention should be paid, in the estimation of these two covariances, to the assumption of no environmental covariances of relatives (see Casler 1982). The predicted response to testcross selection in the non-

Table 2. Analysis of variance for a randomized complete block design replicated at L locations, including the expectations of mean squares (E(MS)) for Testcross, Testcrosses x Location and Error

Source of variation	df	SS	MS	E(MS)[a]
Locations	L−1	SS_1	MS_1	
Replicate (locations)	L(R−1)	SS_2	MS_2	
Testcrosses	T−1	SS_3	MS_3	$\sigma^2_E + R\,\sigma^2_{TL} + R\,L\,\sigma^2_G$
Testcrosses x locations	(T−1)(L−1)	SS_4	MS_4	$\sigma^2_E + R\,\sigma^2_{TL}$
Error	(T−1)(R−1)L	SS_5	MS_5	σ^2_E

[a] σ^2_E is the error variance, σ^2_{TL} is the variance component for testcrosses x location and σ^2_G is the genetic comparent of variance expressed among families

inbred population is estimated as:

$$\frac{\widehat{[\bar{X}_{STC} - \bar{X}]}}{MS_3/LR} \times \widehat{Cov(S_0^t, TC^t)},$$

where $\widehat{\bar{X}_{STC} - \bar{X}}$ is the observed selection differential and $Cov(S_0^t, TC^t)$ is the estimated covariance of S_0 and testcross means in cycle t. The predicted response to testcross selection in the population selfed is estimated as:

$$\frac{\widehat{[\bar{X}_{STC} - \bar{X}]}}{MS_3/LR} \times \widehat{Cov(S_1^t, TC^t)},$$

where $\widehat{Cov(S_1^t, TC^t)}$ is the estimated covariance of S_1 and testcross family means in cycle t. There two formulae are used for both inbred and population testers. All other predicted changes are functions of the estimates described above.

Approximate confidence intervals on selection response

Approximate confidence intervals for regressions, or heritabilities which are linear functions of ratios of mean squares with known distribution, have been defined (Knapp et al. 1985). An appropriate $(1-\alpha)$ confidence interval on the regression function used in predicting selection response is obtained as:

$1 - [(M_3/M_4)\, F_{1-\alpha/2:\,df_3,df_4}]^{-1}$ and

$1 - [(M_3/M_4)\, F_{\alpha/2:\,df_3,df_4}]^{-1}$

which are the lower and upper confidence limits. In order to obtain an approximate $1-\alpha$ confidence interval on selection response, the further assumption, that the selection differential is a constant, needs to be made. This, of course, is not strictly true. The variance of the selection differential can be shown to be different from zero. However, there is no population parameter measured with greater precision than the selection differential with the single exception of the grand mean. Given the assumption that the selection differential is a constant, an appropriate $1-\alpha$ confidence interval on predicted selection response is obtained by multiplying the upper and lower confidence limits by the selection differential.

Conclusions

The proportion of the additive genetic variance expressed among testcross families or involved in covariances of testcross means is independent of the choice of tester, but is dependent on the inbreeding level in the population prior to crossing to the tester. The tester which maximizes the response to selection maximizes the variance expressed among testcrosses, i.e. maximizes $Cov(AD_T) + \frac{1}{2}V(D_T)$ or $Cov(A\bar{\delta}) + \frac{1}{2}V(\bar{\delta})$. These are independent of α_K or $\bar{\alpha}_.$, hence, the tester which maximizes the selection response may not express the greatest heterosis. An inbred tester will not be inherently better unless $Cov(AD_T) + \frac{1}{2}V(D_T)$ is consistently greater than $Cov(A\bar{\delta}) + \frac{1}{2}V(\bar{\delta})$. As indicated previously testcross heterosis will increase over cycles only if $V(D_T) > 2\sigma^2_A$ or $V(\bar{\delta}) > 2\sigma^2_A$ which is not likely to be consistently true. Inbreeding depression will be less severe with cycles of selection if either $Cov(DH_H) + Cov(D_H D_T)$ or $Cov(AD_H) + Cov(D_H\bar{\delta})$ is positive, a situation which may not occur, since all of these quadratic components may be negative. The actual values for population parameters and size of confidence intervals are best examined in real rather than hypothetical populations. This will be dealt with in an article currently in preparation.

References

Casler MD (1982) Genotype x environment interestion bias to parent-offspring regression heritability estimates. Crop Sci 22:540–542

Cockerham CC (1983) Covariances of relatives from self fertilization. Crop Sci 23:1177–1180

Hallauer AR, Miranda JB, Fo (1981) Quantitative genetics in maize breeding. Iowa State University Press, Ames, Iowa

Horner ES, Cundy HW, Lutrick MC, Chapman WH (1973) Comparison of three methods of recurrent selection in maize. Crop Sci 13:485–488

Horner ES, Lutrick MC, Chapman WH, Martin FG (1976) Effect of recurrent selection for combining ability with a single-cross tester in maize. Science 16:5–8

Knapp SJ, Stroup WW, Ross WM (1985) Exact confidence intervals for heritability on a progeny mean basis. Crop Sci 25(1):192–194

Rawlings JO, Thompson DL (1962) Performance level as criterion for the choice of maize testers. Crop Sci 2:217–220

Russell WA, Eberhart SA, Vega UH, O (1973) Recurrent selection for specific combining ability for yield in two maize populations. Crop Sci 13:257–261

Smith OS (1986) Covariance between line per se and testcross performance. Crop Sci 26:540–543