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# A general approach for the study of a population of testcross progenies and consequences for recurrent selection

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**Summary.** A model to study genetic effects at the level of a population of testcross progenies is presented. As there is no dominance for the testcross value, with the restriction of epistasis to pairs of loci, only additive × additive epistasis can contribute to the variance among progenies. To estimate the variance among progenies due to epistasis, it is necessary to have the population structured in families of full sibs, half sibs or $S_1$, with only a few plants per family tested in combination with the tester. Using a two-way mating design to produce the families, it is possible to estimate the variance due to additive × additive epistasis. The consequence of the presence of epistasis is studied at the level of recurrent selection for combining ability with the tester. It seems that epistasis itself does not change the efficiency of the breeding methods considered. However, when the population from intercrossing is structured in families, it could be efficient to use a combined selection when the heritability is very low. In this case it would be efficient to produce full-sib families (by single-pair matings) at the level of intercrossing. The best procedure is to produce such families at the same time as crossing with the tester. In comparison to the classical scheme of selection for combining ability with a tester, such a modification increases the efficiency of selection 41.1% if an off-season generation can be used.

**Key words:** Combining ability – Additive × additive epistasis – Combined selection – Tester

## Introduction

Selection with the use of a tester is very common in the breeding of cross-fertilized plants and in particular in maize, *Zea mays* L. (Hallauer and Miranda 1981). The tester is a unit (genotype or population) to which the members of a population are crossed. The aim is to improve either the random-mating population itself or its combining ability with the tester. Only the latter aim will be considered in this paper. The theory of such a breeding method is already well developed. However, it has not considered that after intercrossing, the population is organized in families. If several plants are taken from a family and crossed to the tester, some progenies are "related." It is expected that the consideration of the kinship between the progenies will increase the efficiency of selection for traits with low heritabilities (Lush 1943). One of the objectives of this paper will be to include kinship information to increase efficiency of selection. Some consequences of the intercrossing method to increase the efficiency of selection will be considered. To solve such a problem, it is first necessary to develop a general approach to describe genetic effects at the level of a population of testcross progenies. It will be shown that the use of related testcross progenies can be an efficient tool to study the presence of some types of epistasis.

## The genetic effects

### *At one locus or in the absence of epistasis*

Consider a random-mating population with alleles $A_1$, $A_2, \ldots A_i, A_j \ldots$, and a tester with allelic composition denoted by $A_x$; regardless of the nature of the tester, $A_x$ can be an allele or a set of alleles. Let $A_i A_j$ be a genotype of the population, and $Y_{ix}$ the value of a "genotype" $A_i A_x$ ($A_i A_x$ is a genotype in the classical sense only if $A_x$ is one allele).

Then for the value $T(ij)$ of the genotype $A_i A_j$ in combination with the tester, it is possible to write:

$$T(ij)=1/2(Y_{ix}+Y_{jx}) \text{ or } T(ij)=\mu_T+{}_T\alpha_i+{}_T\alpha_j, \quad (1)$$

with $\mu_T = E(Y_{ix})$ the mean of all testcross progenies and ${}_T\alpha_i = 1/2(Y_{ix} - \mu_T)$.

${}_T\alpha_i$ can be defined as the additive effect for topcross value (or test value). Indeed, it can be easily verified that it is the average value in topcross of genotypes with allele $A_i$:

$${}_T\alpha_i = E_j[T(ij)] - \mu_T$$

because

$$E_j[T(ij)] = 1/2\ Y_{ix} + 1/2\ \mu_T .$$

Expression (1) shows that there are no dominance effects for the value of testcross, which was expected because the general combining ability contains only additive effects. If the tester is the population itself, the value in test of a genotype will be its general combining ability, and ${}_T\alpha_i = 1/2\ \alpha_i$ ($\alpha_i$ being the classical additive effects with the notation of Kempthorne 1957).

In the absence of epistasis, the total genotypic variance among testcross progenies can be written:

$$\sigma^2_{G_T} = \sigma^2_{A_T} = 2 \sum_l \underset{i}{E} ({}_T\alpha^2_{i,l}),$$

$l$ being the index for the locus.

*With two loci and epistasis*

With a two-loci genotype $i_1 j_1\ k_2 l_2$, with genes $i_1, j_1$ at locus 1 and genes $k_2, l_2$ at locus 2, it is possible to write its value in testcross, in the absence of linkage:

$$T(i_1 j_1, k_2 l_2) = 1/4\ (Y_{i_1 k_2 x_1 x_2} + Y_{i_1 l_2 x_1 x_2} + Y_{j_1 k_2 x_1 x_2} + Y_{j_1 l_2 x_1 x_2}).$$

This value depends only on the structure of the gametic array, so only additive × additive type of epistasis will exist, and it is possible to write:

$$T(i_1 j_1\ k_2 l_2) = \mu_T + {}_T\alpha_{i_1} + {}_T\alpha_{j_1} + {}_T\alpha_{k_2} + {}_T\alpha_{l_2} + {}_T(\alpha\alpha)_{i_1 k_2} + {}_T(\alpha\alpha)_{i_1 l_2} + {}_T(\alpha\alpha)_{j_1 k_2} + {}_T(\alpha\alpha)_{j_1 l_2} \quad (2)$$

with

$${}_T(\alpha\alpha)_{i_1 k_2} = T(i_1 ., k_2 .) - {}_T\alpha_{i_1} - {}_T\alpha_{k_2} - \mu_T$$

and

$$T(i_1 ., k_2 .) = \underset{j_1, l_2}{E} [T(i_1 j_1, k_2 l_2)] = 1/4\ Y_{i_1 k_2 x_1 x_2} .$$

Therefore, the total genotypic variance for value of testcross will be, after summation of all pairs of involved loci:

$$\sigma^2_{G_T} = \sigma^2_{A_T} + \sigma^2_{AA_T}.$$

Considering the epistasis between three loci, the formula can be extended directly.

$$\sigma^2_{G_T} = \sigma^2_{A_T} + \sigma^2_{AA_T} + \sigma^2_{AAA_T} .$$

Note that in the case where the tester is the population itself, ${}_T(\alpha\alpha)_{i_1 k_2} = 1/4(\alpha\alpha)_{i_1 k_2}$, the classical additive × additive epistatic effect. Then the value of testcross can be written:

$$T(i_1 j_1 k_2 l_2) = \mu_T + 1/2(\alpha_{i_1} + \alpha_{j_1} + \alpha_{k_2} + \alpha_{l_2}) + 1/4[(\alpha\alpha)_{i_1 k_2} + (\alpha\alpha)_{i_1 l_2} + (\alpha\alpha)_{j_1 k_2} + (\alpha\alpha)_{j_1 l_2}].$$

This is the expression of the general combining ability, and

$$\sigma^2_{G_T} = 1/4\ \sigma^2_A + 1/16\ \sigma^2_{AA}$$

is the general combining ability (GCA) variance, that is the covariance among half sibs.

*Covariances between related progenies*

To estimate the components of variance from mating designs, it is necessary to know the general expression of the covariance between relatives. Some components of variance could be translated in covariances between relatives.

The general expression of the covariances between relatives in a random-mating population can be used by replacing the individuals by the testcross progenies. The kinship is for the testcross progenies; then for two testcross progenies $(X_T, Y_T)$, it is possible to write directly:

$$\mathrm{cov}(X_T, Y_T) = 2\ \varphi\ \sigma^2_{A_T} + 4\ \varphi^2\ \sigma^2_{AA_T} + \ldots, \quad (3)$$

$\varphi$ being the classical coefficient of kinship, where

$\varphi = 1/4$ for full-sib progenies, and
$= 1/8$ for half-sib progenies.

It is also possible to consider the parent-offspring kinship, i.e., the kinship between the testcross progeny of the parent and the testcross progeny of offsprings; in this case $\varphi = 1/4$. The covariance parent-offspring will be the same as the covariance between full sibs.

The total genotypic variance can be derived from Eq. 2, but it is straightforward from Eq. 3. We have only to consider the covariance of a testcross family with itself; in this case $\varphi = 1/2$.

## Mating designs to estimate the variance components

*One-way mating designs*

In this type of mating design, a set of independent families is considered, with $n$ plants per family crossed to the tester. Two levels of variation can be considered (within and between families), and the experiment becomes a two-way mating design. An analysis of variance between and within families can be performed (Table 1).

Let $G_{ij}$ be the genotypic value of the progeny of a plant $j$ belonging to family $i$:

$$G_{ij} = \mu_T + B_i + W_{ij},$$

**Table 1.** Expected mean squares in an analysis of variance of a "one-way" mating design. $n$ plants per family are crossed with the tester, and the progenies are evaluated in an experimental design with $b$ repetitions

| Source variation | Expected mean square |
|---|---|
| Between families | $\sigma_e^2 + b\,\sigma_{GW}^2 + b\,n\,\sigma_{GB}^2$ |
| Plants within families | $\sigma_e^2 + b\,\sigma_{GW}^2$ |
| Residual | $\sigma_e^2$ |

where $B_i$ is the effect of family $i$, with variance $\sigma_{GB}^2$, and $W_{ij}$ is the effect of the progeny $ij$ within $i$, with variance $\sigma_{GW}^2$.

It is clear that

$$\text{cov}\, G_{ij}\, G_{ij'} = \sigma_{GB}^2$$

and

$$\text{cov}\, G_{ij}\, G_{ij} = \sigma_{GB}^2 + \sigma_{GW}^2 .$$

$\sigma_{GB}^2$ and $\sigma_{GW}^2$ are directly estimated from the analysis of variance. From such estimations it will be possible to derive the estimation of the two covariances between relatives: $\text{cov}\,(G_{ij}, G_{ij'})$ and $\text{cov}\,(G_{ij}, G_{ij}) = \sigma_{GT}^2$. Then it is possible to estimate the two components ($\sigma_{A_T}^2$ and $\sigma_{AA_T}^2$) of the genetic variance of testcross values.

The families can be full sibs, half sibs, $S_1$ full sibs, and $S_n$ full sibs. Consider each of these four types of families that are commonly used in plant breeding.

*Full-sib families.* The variance among full-sib families can be written as the covariance within families:

$$\sigma_{GB}^2 = \text{cov}\,(\text{FS})_T = 1/2\,\sigma_{A_T}^2 + 1/4\,\sigma_{AA_T}^2 .$$

Then the within component of variance is:

$$\sigma_{GW}^2 = \sigma_{GT}^2 - \text{cov}\,(\text{FS})_T$$
$$\sigma_{GW}^2 = 1/2\,\sigma_{A_T}^2 + 3/4\,\sigma_{AA_T}^2 .$$

*Half-sib families.* According to the previous results:

$$\text{cov}\,(\text{HS})_T = 1/4\,\sigma_{A_T}^2 + 1/16\,\sigma_{AA_T}^2 ,$$

where the contribution of epistasis to the covariance is only 1/16. Nearly all the epistasis will be within-family components:

$$\sigma_{GW}^2 = 3/4\,\sigma_{A_T}^2 + 15/16\,\sigma_{AA_T}^2 .$$

*$S_1$ families (or $S_n$ families).* The variance among $S_1$ families is equal to the variance among $S_0$ plants, because it is equivalent to a cross of a $S_0$ plant or its $S_1$ family to the tester. Then

$$\sigma_{GB\,S_1}^2 = \sigma_{A_T}^2 + \sigma_{AA_T}^2 .$$

The total genotypic variance at the level of the $S_1$ plant can be deduced from Eq. 3 by the consideration of the covariance of an individual progeny with itself, with $\varphi = 3/4$:

$$\sigma_{GT\,S_1}^2 = 3/2\,\sigma_{A_T}^2 + 9/4\,\sigma_{AA_T}^2 .$$

Then

$$\sigma_{GW\,S_1}^2 = 1/2\,\sigma_{A_T}^2 + 5/4\,\sigma_{AA_T}^2 .$$

If inbred plants (F = 1) are used [derived by single-seed descent (SSD) or by haplodiploidization], the total variance among testcross families will be:

$$\sigma_{GTL}^2 = 2\,\sigma_{A_T}^2 + 4\,\sigma_{AA_T}^2 .$$

Considering the general case of the study of inbred plants in testcross, the variance "between" families is the variance among $S_{n-1}$ plants:

$$\sigma_{GB\,S_n}^2 = 2\,\varphi_{n-1}\sigma_{A_T}^2 + 4\,\varphi_{n-1}^2\sigma_{AA_T}^2 , \qquad (n \geq 2)$$

with

$$\varphi_{n-1} = \frac{1 + \text{F}_{n-1}}{2}, \quad \text{F}_{n-1} = 1 - (1/2)^{n-1}$$

$$\varphi_{n-1} = 1 - (1/2)^n ,$$

and

$$\sigma_{GT\,S_n}^2 = 2\,{}_{xx}\varphi_n\,\sigma_{A_T}^2 + 4\,{}_{xx}\varphi_n^2\,\sigma_{AA_T}^2 ,$$

with ${}_{xx}\varphi_n$ being the covariance of an individual with itself, and

$${}_{xx}\varphi_n = \frac{1 + \text{F}_n}{2} = 1 - (1/2)^{n+1} .$$

Then,

$$\sigma_{GW\,S_n}^2 = \sigma_{GT\,S_n}^2 - \sigma_{GB\,S_n}$$
$$\sigma_{GW\,S_n}^2 = (1/2)^n\,\sigma_{A_T}^2 + 4\,(1/2)^n\,[1 - (3/4)(1/2)^n]\,\sigma_{AA_T}^2 .$$

*Two-factor mating design*

In the case of a two-factor mating design, three variances can be estimated: variances among halb-sib families ($\text{cov}\,(\text{HS})_T$), or variance of GCA for testcross value; variances of specific combining ability ($\text{cov}\,(\text{FS})_T - 2\,\text{cov}\,(\text{HS})_T$); and variance among plants within a full-sib family, or

$$\sigma_{GW}^2 = \sigma_{G_T}^2 - \text{cov}\,(\text{FS})_T .$$

Then it is possible to estimate three components of variance between testcross progenies and three components of the genotypic variance: $\sigma_{A_T}^2$, $\sigma_{AA_T}^2$, $\sigma_{AAA_T}^2$.

The three equations are

$$\begin{aligned} \text{cov}(\text{FS})_T &= 1/2\,\sigma_{A_T}^2 + 1/4\,\sigma_{AA_T}^2 + 1/8\,\sigma_{AAA_T}^2 \\ \text{cov}(\text{HS})_T &= 1/4\,\sigma_{A_T}^2 + 1/16\,\sigma_{AA_T}^2 + 1/64\,\sigma_{AAA_T}^2 \\ \sigma_{GW}^2 &= 1/2\,\sigma_{A_T}^2 + 3/4\,\sigma_{AA_T}^2 + 7/8\,\sigma_{AAA_T}^2 \end{aligned} \qquad (4)$$

and

$\sigma_{g_T}^2 = \text{cov}\,(\text{HS})_T$, the variance of "general combining ability" for testcross value;

$\sigma^2_{s_T} = \text{cov}\,(\text{FS})_T - 2\,\text{cov}\,(\text{HS})_T$, the variance of "specific combining ability" for testcross value; and

$\sigma^2_{s_T} = 1/8\ \sigma^2_{AA_T} + 3/32\ \sigma^2_{AAA_T}$.

With no epistasis, the variance of the specific combining ability for testcross value will be zero and it provides a test for the presence of epistasis. This result is similar to that established by Choo (1981) and Choo et al. (1986) for a diallel among lines where the $F_1$ values are replaced by their line value, a result generalized by Gallais (1990) for any two-way mating designs with inbred or noninbred parents. The analogy is clear, because haplodiploidization can be considered as a particular system of testing for which there also are no dominance effects.

The adaptation of the process of estimation according to the mating design is straightforward. In Tables 2–4 are given the analysis of variance for three mating designs: hierarchical plan (design I, N.C.), factorial plan (design II, N.C.), and the diallel, with an experimental design with $b$ repetitions and $n$ testcross progenies per full-sib family.

**Table 2.** Expected mean squares in an analysis of variance of testcross progenies from a nested A/B (N.C.I) mating design. There are $f$ plants crossed to each common parent

| Source of variation | Expected mean square |
|---|---|
| Common parent | $\sigma^2_e + b\,\sigma^2_{GW} + bn\,\sigma^2_{\text{F/M}} + bnf\,\sigma^2_{\text{M}}$ |
| Variable parent | $\sigma^2_e + b\,\sigma^2_{GW} + bn\,\sigma^2_{\text{F/M}}$ |
| Plant/family | $\sigma^2_e + b\,\sigma^2_{GW}$ |
| Residual | $\sigma^2_e$ |

$\sigma^2_{\text{F/M}} = \text{cov}(\text{FS})_T - \text{cov}(\text{HS})_T$, $\sigma^2_{\text{M}} = \text{cov}(\text{HS})_T = \sigma^2_{g_T}$)

**Table 3.** Expected mean squares in an analysis of variance of testcross progenies from a factorial design AB (N.C. II), with $m$ plants A, and $f$ plants B

| Source of variation | Expected mean square |
|---|---|
| Plant A | $\sigma^2_e + b\,\sigma^2_{GW} + bn\,\sigma^2_{\text{AB}} + bnf\,\sigma^2_{\text{A}}$ |
| Plant B | $\sigma^2_e + b\,\sigma^2_{GW} + bn\,\sigma^2_{AB} + bnm\,\sigma^2_{\text{B}}$ |
| Interaction A × B | $\sigma^2_e + b\,\sigma^2_{GW} + bn\,\sigma^2_{\text{AB}}$ |
| Plant/family | $\sigma^2_e + b\,\sigma^2_{GW}$ |
| Residual | $\sigma^2_e$ |

$\sigma^2_{\text{AB}} = \text{cov}(\text{FS})_T - 2\,\text{cov}(\text{HS})_T = \sigma^2_{s_T}$
$\sigma^2_{\text{A}} = \sigma^2_{\text{B}} = \text{cov}(\text{HS})_T = \sigma^2_{g_T}$

**Table 4.** Expected mean squares in an analysis of variance of testcross progenies from a diallel among $p$ plants [Griffing's Model 2 (1956), method 4]

| Source of variation | Expected mean square |
|---|---|
| GCA | $\sigma^2_e + b\,\sigma^2_{GW} + bn\,\sigma^2_{s_T} + bn(p-2)\,\sigma^2_{g_T}$ |
| SCA | $\sigma^2_e + b\,\sigma^2_{GW} + bn\,\sigma^2_{s_T}$ |
| Plant/family | $\sigma^2_e + b\,\sigma^2_{GW}$ |
| Residual | $\sigma^2_e$ |

## Application to recurrent selection

*Genetic advance in one cycle of recurrent selection*

The classical scheme of recurrent selection for combining ability with a tester (method 1) has three phases: the production of testcross progenies, the evaluation of testcross progenies, and intercrossing of the parents of the best testcross progenies. The mother plants can be maintained by vegetative propagation, if possible, or by self-fertilization. The general formulation of the genetic advance for the combining ability with the tester is (Gallais 1979a):

$$\Delta G = i\,\theta\,\frac{\text{cov}\ P_T\ O_T}{\sqrt{\text{var}\ P_T}}, \tag{5}$$

where $i$ is the selection intensity, $\theta$ is the degree of control of selection on both sexes, cov $P_T\ O_T$ is a covariance parent offspring, with parent and offspring evaluated according to the testing system $T$, and var $P_T$ is the phenotypic variance among tested units.

In the method considered:

$\theta = 2$, and $\text{cov}\ P_T\ O_T = 1/2\ \sigma^2_{A_T}$, (without epistasis)

therefore

$$\Delta G_1 = i\,\frac{\sigma^2_{A_T}}{\sqrt{\text{var}\ P_T}} = K. \tag{6}$$

The cycle takes three generations.

The parameter $\theta$ can be equal to 1 (method 2), and selection is only maternal. This will be the case if the intercrossing, by production of half-sib families, is developed at the same time as crossing with the tester. The length of the cycle is of only two generations, but the genetic advance per cycle is reduced 50%.

In the other two methods (methods 3 and 4), intercrossing is also developed at the same time as crossing with the tester, but it is performed by pair-crossing, which leads to full-sib families. With method 3 the selection is independent for each plant of a pair; it is, in fact, a kind of mixture of methods 1 and 2. Let $p$ be the percentage of selection among testcross progenies. For a fraction $\frac{2(1-p)}{2-p}$ of the pairs, only one plant is selected and the genetic advance is $1/2\ K$, and for a fraction $\frac{p}{2-p}$ of the pairs the genetic advance is $K$. Then the expected genetic advance per cycle is:

$$\Delta G_3 = \frac{1}{2-p}\,K. \tag{7}$$

The length of the cycle for method 3 is of two generations.

With method 4 (Fig. 1), the unit of selection is the pair of progenies. A pair will be selected and thereafter its two plants, according to the average value of the two testcross progenies. For the same number of intercrossed plants,

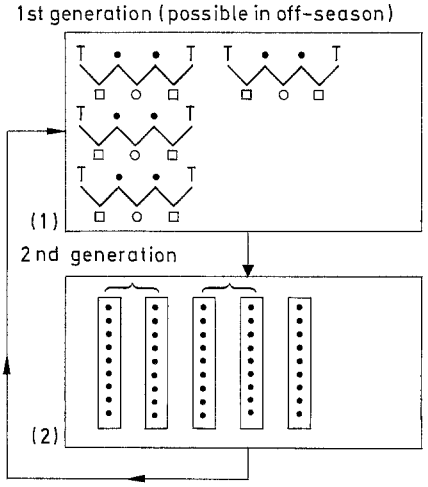


**Fig. 1.** A modification of the testcross progeny test to have intercrossing simultaneously to testcross with the tester. This shortens the length of the cycle and allows the production of full-sib family to develop combined selection with testcross progenies. (1) Crossing by pairs of unrelated plants and simultaneously crossing of the member of a pair to the tester ($T$).
(2) Test of testcross progenies with separate test of each plant of a pair. Identification of the best pairs. The next generation is constituted by the mixture of the full-sib [from (1)] associated to the best pairs

the selection intensity will be the same as previously, and the expected genetic advance in one cycle can be written:

$$\Delta G_4 = i \frac{\text{cov } \bar{P}_T \bar{O}_T}{\sqrt{\text{var } \bar{P}_T}}, \tag{8}$$

where $\bar{P}_T$ is the average value of the two testcross progenies of a pair, and $\bar{O}_T$ is the value in test (combining ability with the tester) of the full sibs from the crossing of the two plants.

For two plants $i$ and $j$ of a pair:

$\bar{P}_T = 1/2\ (P_{T_i} + P_{T_j})$, and $\bar{O}_{ij} = O_i + O_j$;

then

$\text{cov } \bar{P}_T \bar{O}_T = \text{cov } P_T O_T = 1/2\ \sigma^2_{A_T}$ as previously,

and

$\text{var } \bar{P}_T = 1/2 \text{ var } P_T$;

finally:

$$\Delta G_4 = i \sqrt{2}/2 \frac{\sigma^2_{A_T}}{\sqrt{\text{var } P_T}} = \sqrt{2}/2\ K. \tag{9}$$

A variant (method 4′) of this method consists in mixing the two progenies from a pair to produce only one "progeny." A pair will be selected according to the value of this artificial progeny. With the same amount of plots, this allows testing twice the number of plants. For selecting the same number of plants, the selection intensity among pairs will be greater. For example, if 200 progenies are studied with method 1, with a percentage of selection ($p$) of 20%, 40 plants are selected. With method 3, 100 pairs will be evaluated, and 20 pairs are selected ($p = 20\%$), leading to the intercrossing of 40 plants. With the modification (mixture of the two progenies of a pair), 200 pairs can be evaluated; to intercross 40 plants, it is necessary to select 20 pairs as previously, but in this case $p = 10\%$. The ratio of the selection intensities $i_{4'}/i_4$ will be $1.755/1.40 = 1.25$. This ratio will decrease with an increasing selection intensity. (Example: if $p_4 = 10\%$, $i_4 = 1.755$ and $p_{4'} = 5\%$, $i_{4'} = 2.063$, $i_{4'}/i_4 = 1.17$.)

The expected genetic advance of method 4′ can be written:

$$\Delta G_{4'} = i' \frac{\text{cov } \bar{P}'_T \bar{O}_T}{\sqrt{\text{var } \bar{P}'_T}},$$

where $P'_T$ represents the value of the artificial progeny from the two plants of a pair; then:

$\text{cov } \bar{P}'_T / \bar{O}_T = 1/2\ \sigma^2_{A_T}$ as for method 4,

$\text{var } \bar{P}'_T = 1/2\ \sigma^2_{A_T} + \sigma^2_{e'}$

with $\sigma^2_{e'}$ representing the residual variance in the test.

To simplify, this residual variance will be considered as equivalent to the residual variance ($\sigma^2_e$) in the previous methods, and in particular in method 3:

$\text{var } \bar{P}'_T = 1/2\ \sigma^2_{A_T} + 1/2\ \sigma^2_e$.

The assumption $\sigma^2_{e'} \sim \sigma^2_e$ is acceptable if the number ($n$) of plants per progeny is sufficiently great. Indeed:

$\sigma^2_e = 1/b\ [\sigma^2_p + (\sigma^2_{GW} + \sigma^2_{eW})/n]$,

where $b$ is the number of repetitions, $\sigma^2_p$ is the environmental variance at the plot level, $\sigma^2_{GW}$ is the within-plot genetic variance, and $\sigma^2_{eW}$ is the within-plot environmental variance. With $n$ sufficiently large, the contribution of $\sigma^2_{GW}$ will be very low; the contribution of $\sigma^2_{eW}$ is the same in both residuals.

In this case, with

$$h^2_T = \frac{\sigma^2_{A_T}}{\sigma^2_{A_T} + \sigma^2_e},$$

the heritability for the test values, it is possible to write:

$\text{var } \bar{P}_{T_{ij}} = 1/2\ (\sigma^2_{A_T}/h^2_T)$

$\text{var } \bar{P}'_{T_{ij}} \approx \frac{2 - h^2_T}{2\ h^2_T} \sigma^2_{A_T}$;

then

$$\frac{\text{var } \bar{P}'_{T_{ij}}}{\text{var } \bar{P}_{T_{ij}}} \sim 2 - h^2_T.$$

Method 4′ will be more efficient than method 4 if:

$$\frac{i'}{i} > \sqrt{2-h_T^2}\,.$$

For a ratio $i'/i$ of 1.25, it is necessary to have $h_T^2 > 0.4$; with $i'/i = 1.18$ it is necessary to have $h_T^2 > 0.6$. As expected, method 4′ is more efficient for a highly heritable character. However, as $h_T^2$ is defined at the level of means, a value between 0.4 and 0.6 corresponds to a relatively low value at the individual level. Therefore, it is possible to have method 4′ more efficient than method 4 in a realistic range of parameters of genetic advance.

Table 5 summarizes the expressions of expected genetic advance for methods 1 (taken as reference), 2, 3, and 4, which can be compared directly because considering the same selection intensities is justified.

The genetic advance is expressed per cycle ($A$), per generation ($B$), with three generations per cycle for methods 1 and two generations for the others, and per year ($C$) for an annual plant species, assuming one off-season generation for each scheme.

On a per cycle basis,

method 1 (100) > method 4 (70) > method 3 (55 for $p=0.20$) > method 2 (50).

On a per generation basis,

method 4 (106) ≥ method 1 (100) > method 3 (83.3 for $p=0.20$) > method 2 (75).

On a per year basis for an annual plant species with one off-season generation,

method 4 (141) > method 3 (111) > method 1 (100) = method 2 (100).

The relative efficiency of each method is included in parenthesis. On a per cycle basis, method 1 is the more efficient, but on a per year basis with one off-season generation, method 4 is 30% more efficient, regardless of the heritability. With low selection intensity and relatively high heritability, ($h_T^2 = \sigma_{A_T}^2/(\sigma_{A_T}^2+\sigma_e^2)$, $h_T^2 > 0.40$), method 4′, by mixture of the two progenies from a pair, can be more efficient than method 4, with separate test of the two progenies.

**Table 5.** Genetic advance for different breeding methods using testcross progenies. Method 1: classical method; method 2: maternal selection only; methods 3 and 4: simultaneous pair-crossing and testcross, with independent tests in 3 and selection of pairs in 4

| Scheme | $\Delta G$/cycle | $\Delta G$/generation | $\Delta G$/year[a] |
|---|---|---|---|
| Method 1 | $K$ | $1/3\,K$ | $1/2\,K$ |
| Method 2 | $1/2\,K$ | $1/4\,K$ | $1/2\,K$ |
| Method 3 | $[1/(2-p)]\,K$ | $[1/2(2-p)]\,K$ | $[1/(2-p)]\,K$ |
| Method 4 | $\sqrt{2}/2\,K$ | $\sqrt{2}/4\,K$ | $\sqrt{2}/2\,K$ |

[a] For an annual plant species with off-season generation

*The use of combined selection*

After intercrossing, the new population can be structured in half-sib families with methods 1 and 2 and in full-sib families with methods 3 and 4. Full-sib families can be also produced in method 1 if intercrossing among selected plants is developed by pair-crossing.

When crossed with the tester, the testcross progenies of the plants can be grouped in families. This generates a one-way mating design, as previously described, which can be used to estimate additive and epistatic variances for test values. Such a structuring can be used to predict with greater accuracy the genotypic value of the testcross progenies. It is possible to perform a combined selection with an index between family and within family. For example, with a family $i$ and a plant $j$ within the family, denoting by $T_{ij}$ the phenotypic value in testcross of a plant $ij$, the index predicting the testcross value of offspring from that plant is:

$$\hat{I} = \beta_1(T_{i\cdot} - T_{\cdot\cdot}) + \beta_2(T_{ij} - T_{i\cdot})\,. \tag{10}$$

To simplify, a constant number of tested plants ($n$) per family will be considered. The situation is analogous to the classical situation of selection on phenotypic values of individuals with a family structure. The results of Lush (1943) can be directly extrapolated by changing the notation:

$$\beta_1 = \frac{1+(n-1)\,r}{1+(n-1)\,t} \quad \text{and} \quad \beta_2 = \frac{1-r}{1-t},$$

with

$$t = \frac{\sigma_B^2}{\sigma_{P_T}^2} = \frac{\mathrm{cov(HS)}_T}{\sigma_{P_T}^2}, \quad \text{the intra-class correlation,}$$

and

$$r = \frac{\mathrm{cov(HUN)}_T}{\mathrm{cov(PO)}_T},$$

where $\mathrm{cov\,(HS)}_T$ is the variance among half-sib families of topcross progenies (if the intercrossing generates half-sib families; in the case of pair-crossing, $\mathrm{cov(HS)}_T$ will be replaced by $\mathrm{cov(FS)}_T$, the covariance among full-sib families). $\sigma_{P_T}^2$ is the total phenotypic variance among testcross progenies, which is the sum of the variance between family ($\sigma_B^2$), of the within-family variance ($\sigma_W^2$), and of the residual variance $\sigma_e^2$:

$$\sigma_{P_T}^2 = \sigma_B^2 + \sigma_W^2 + \sigma_e^2\,,$$

with

$$\sigma_B^2 = \mathrm{cov(HS)}_T\,.$$

$\mathrm{cov\,(HUN)}_T$ is the half uncle-nephew covariance for test value and $\mathrm{cov(PO)}_T$ the parent-offspring covariance for test value. The structure of the residual $\sigma_e^2$ is complex; it includes the variance of the environmental effects at the

level of the plot and the variance of specific effects (genetic and environmental) affecting an individual in a testcross progeny, divided by the number of plants per plot.

In the absence of epistasis:

$\mathrm{cov(HS)}_T = 1/4\,\sigma^2_{A_T}$; $\mathrm{cov(FS)}_T = 1/2\,\sigma^2_{A_T}$;
$\mathrm{cov(HUN)}_T = 1/8\,\sigma^2_{A_T}$; $\mathrm{cov(PO)}_T = 1/2\,\sigma^2_{A_T}$; and
$\mathrm{cov(UN)}_T = 1/4\,\sigma^2_{A_T}$ (covariance uncle-nephew).

Then

$$t_{HS} = 1/4\,\frac{\sigma^2_{A_T}}{\sigma^2_{P_T}} = 1/4\,h^2_T \quad \text{and} \quad t_{FS} = 1/2\,h^2_T,$$

$h^2_T$ being the heritability for test values, and

$r_{HS} = 1/4$ and $r_{FS} = 1/2$.

The genetic advance in one cycle of combined selection is:

$$\Delta G_{comb} = i\,\sigma_{P_T}\,h^2_T\,\sqrt{1+\frac{(r-t)^2}{1-t}\,\frac{(n-1)}{1+(n-1)\,t}}, \tag{11}$$

where $i$ is the selection intensity.

With individual testcross progeny selection, the genetic advance will be

$$\Delta G_{ind} = i\,\sigma_{P_T}\,h^2_T.$$

The relative efficiency of combined selection will be

$$E = \sqrt{1+\frac{(r-t)^2}{(1-t)}\,\frac{(n-1)}{1+(n-1)t}}.$$

With epistasis, formula 11 can always be used. Indeed, the variance of the predicted values can always be written:

$$\sigma^2_{\hat{I}_T} = \frac{[\mathrm{cov(PO)}_T]^2}{\sigma^2_{P_T}}\left\{1+\frac{(r-t)^2\,(n-1)}{(1-t)\,[1+(n-1)\,t]}\right\}.$$

Then,

$\Delta G_{comb} = i\theta\beta_T\,\sigma_{P_T}E$ ($\theta = 2$, if selection is on both sexes)

with

$$\beta_T = \frac{\mathrm{cov(PO)}_T}{\sigma^2_{P_T}},$$

and

$$\Delta G_{ind} = i\theta\beta_T\,\sigma_{P_T}.$$

Hence, $\Delta G_{comb}/\Delta G_{ind}$ is always equal to $E$, but it is necessary to adapt the values of $r$ and $t$:

$$t_{HS} = \frac{1/4\,\sigma^2_{A_T} + 1/16\,\sigma^2_{AA_T}}{\sigma^2_{P_T}}, \quad t_{FS} = \frac{1/2\,\sigma^2_{A_T} + 1/4\,\sigma^2_{AA_T}}{\sigma^2_{P_T}},$$

$$r_{HS} = \frac{1/8\,\sigma^2_{A_T} + 1/64\,\sigma^2_{AA_T}}{1/2\,\sigma^2_{A_T} + 1/4\,\sigma^2_{AA_T}}$$

and

$$r_{FS} = \frac{1/4\,\sigma^2_{A_T} + 1/16\,\sigma^2_{AA_T 2}}{1/2\,\sigma^2_{A_T} + 1/4\,\sigma^2_{AA_T}}.$$

Denoting by $a^2$ the ratio $\sigma^2_{AA_T}/\sigma^2_{A_T}$,

$$r_{HS} = \frac{1/4 + 1/32\,a^2}{1+1/2\,a^2}, \quad r_{FS} = \frac{1/2 + 1/8\,a^2}{1+1/2\,a^2}.$$

The general expression of $t$ and $r$ are

$$t = 2\varphi\,\frac{1+2\varphi\,a^2}{1+a^2}\,h^2_T \quad \text{with} \quad h^2_T = \frac{\sigma^2_{A_T} + \sigma^2_{AA_T}}{\sigma^2_{P_T}},$$

and

$$r = 2\varphi\,\frac{1+\varphi\,a^2}{1+1/2\,a^2}.$$

The relative efficiency of combined selection depends only on $r$, $t$, $h^2$, $n$, and $a^2$, which are determined by the material and the experimental structure: $r = 1/2$ or $1/4$ and $t = 1/2\,h^2_T$ or $1/4\,h^2_T$, according to the methods of intercrossing. The number of tested plants per family will be generally low (between 4 and 10). By numerical application, it is then possible to determine the relative efficiency of combined selection, noting that $h^2_T$ will be generally high because it is heritability at the level of the experimental design: $h^2_T = 0.30$ will correspond to low heritability at the individual level.

Some results of the numerical application are shown Table 6. Obviously some of these are predictable from previously known results: selection with full-sib families is more efficient than selection with half-sib families; relative efficiency of the combined selection is greater for low heritability and, in this case, it increases with the number of progenies included per family; the presence of epistasis tends to decrease the relative efficiency of the combined selection, but it does not affect the previous conclusions.

Considering a realistic example for the plant breeder with $n = 5$, and HS families, the relative efficiency is of 1.09 for very low heritability ($h^2_T = 0.10$) and 1.025 for a heritability of 0.50, which can be considered as an average heritability (at the level of means) for yield in maize. With FS families, the relative efficiency is 1.30 with $h^2_T = 0.10$ and 1.08 for $h^2_T = 0.50$. For $h^2_T$ greater than 0.40, the combined selection will not be justified. It is more justified for $h^2 < 0.30$ and mainly with full-sib families.

Assuming epistasis is ignored, the coefficients $\beta_1$ and $\beta_2$ in Eq. 10 will be wrong. Ignoring epistasis is equivalent to assuming $\mathrm{cov(PO)}_T = 2\,\mathrm{cov(HS)}_T$, $\mathrm{cov(HUN)}_T = 1/2\,\mathrm{cov(HS)}_T$ and $\mathrm{cov(UN)}_T = \mathrm{cov(HS)}_T$. The general expressions of $\beta_1$ and $\beta_2$ are, for half-sib families:

$$\beta_1 = \frac{1/n\,\mathrm{cov(PO)}_T + (n-1)/n\,\mathrm{cov(HUN)}_T}{\sigma^2_B + 1/n\,\sigma^2_W}$$

$$= \frac{\mathrm{cov(PO)}_T\,[1+(n-1)\,r]/n}{\sigma^2_{P_T}[1+(n-1)\,t]/n} = \frac{\mathrm{cov(PO)}_T}{\sigma^2_{P_T}}\,\frac{A}{B}$$

**Table 6.** Relative efficiency ($E$) of combined selection (A) and effect of ignoring epistasis (B). $n$ is the number of progenies per family. Values in A give the efficiency of combined selection relative to individual progeny selection. Values in B give the ratio $\Delta G_o/\Delta G_e$ of the genetic advance of combined selection ignoring epistasis to the genetic advance of combined selection considering epistasis (for $n=1$, it is the ratio for individual progeny selection). N.B.: considering the value of $a^2$, it can be shown that with intrapopulation testcross, a value of 1 corresponds to the case where the variance additive × additive epistasis is four times the additive variance. Therefore, values greater than 1 must be exceptional.

| | | | | | E according to n | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | (A) | | | | | (B) | | | | |
| φ | $h_T^2$ | $a^2$ | r | t | 1 | 3 | 5 | 7 | 9 | 1 | 3 | 5 | 7 | 9 |
| 0.125 | 0.100 | 0.00 | 0.250 | 0.025 | 1.000 | 1.048 | 1.090 | 1.127 | 1.160 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| 0.125 | 0.100 | 0.20 | 0.233 | 0.022 | 1.000 | 1.043 | 1.081 | 1.114 | 1.145 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| 0.125 | 0.100 | 0.50 | 0.207 | 0.016 | 1.000 | 1.034 | 1.066 | 1.094 | 1.120 | 1.000 | 0.998 | 0.997 | 0.997 | 0.996 |
| 0.125 | 0.100 | 1.80 | 0.161 | 0.013 | 1.000 | 1.021 | 1.041 | 1.060 | 1.078 | 1.000 | 0.993 | 0.988 | 0.985 | 0.982 |
| 0.125 | 0.100 | 5.40 | 0.113 | 0.009 | 1.000 | 1.011 | 1.021 | 1.31 | 1.040 | 1.000 | 0.984 | 0.971 | 0.961 | 0.954 |
| 0.125 | 0.200 | 0.00 | 0.250 | 0.050 | 1.000 | 1.038 | 1.068 | 1.093 | 1.114 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| 0.125 | 0.200 | 0.20 | 0.233 | 0.044 | 1.000 | 1.034 | 1.062 | 1.085 | 1.105 | 1.000 | 1.000 | 1.000 | 0.999 | 0.999 |
| 0.125 | 0.200 | 0.60 | 0.207 | 0.036 | 1.000 | 1.028 | 1.052 | 1.072 | 1.090 | 1.000 | 0.998 | 0.997 | 0.997 | 0.996 |
| 0.125 | 0.200 | 1.80 | 0.161 | 0.026 | 1.000 | 1.018 | 1.033 | 1.048 | 1.060 | 1.000 | 0.993 | 0.988 | 0.995 | 0.962 |
| 0.125 | 0.200 | 5.40 | 0.113 | 1.018 | 1.000 | 1.009 | 1.017 | 1.024 | 1.031 | 1.000 | 0.984 | 0.971 | 0.961 | 0.954 |
| 0.125 | 0.300 | 0.00 | 0.250 | 0.075 | 1.000 | 1.029 | 1.050 | 1.066 | 1.080 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| 0.125 | 0.300 | 0.20 | 0.233 | 0.066 | 1.000 | 1.026 | 1.046 | 1.063 | 1.076 | 1.000 | 1.000 | 1.000 | 0.999 | 0.999 |
| 0.125 | 0.300 | 0.60 | 0.207 | 0.054 | 1.000 | 1.022 | 1.040 | 1.054 | 1.067 | 1.000 | 0.998 | 0.997 | 0.997 | 0.996 |
| 0.125 | 0.300 | 1.80 | 0.161 | 0.039 | 1.000 | 1.014 | 1.027 | 1.037 | 1.046 | 1.000 | 0.993 | 0.988 | 0.925 | 0.982 |
| 0.125 | 0.300 | 5.40 | 0.113 | 0.028 | 1.000 | 1.007 | 1.013 | 1.019 | 1.024 | 1.000 | 0.983 | 0.971 | 0.961 | 0.954 |
| 0.125 | 0.400 | 0.00 | 0.250 | 0.100 | 1.000 | 1.021 | 1.035 | 1.046 | 1.054 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| 0.125 | 0.400 | 0.20 | 0.233 | 0.087 | 1.000 | 1.020 | 1.034 | 1.045 | 1.053 | 1.000 | 1.000 | 1.000 | 0.999 | 0.999 |
| 0.125 | 0.400 | 0.60 | 0.207 | 0.072 | 1.000 | 1.017 | 1.030 | 1.040 | 1.049 | 1.000 | 0.998 | 0.997 | 0.997 | 0.996 |
| 0.125 | 0.400 | 1.80 | 0.161 | 0.052 | 1.000 | 1.011 | 0.021 | 1.028 | 1.035 | 1.000 | 0.993 | 0.988 | 0.985 | 0.982 |
| 0.125 | 0.400 | 5.40 | 0.113 | 0.037 | 1.000 | 1.006 | 1.011 | 1.015 | 1.019 | 1.000 | 0.983 | 0.71 | 0.962 | 0.954 |
| 0.125 | 0.500 | 0.00 | 0.250 | 0.150 | 1.000 | 1.009 | 1.015 | 1.018 | 1.021 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| 0.125 | 0.600 | 0.20 | 0.233 | 0.131 | 1.000 | 1.009 | 1.015 | 1.020 | 1.023 | 1.000 | 1.000 | 1.000 | 0.999 | 0.999 |
| 0.125 | 0.600 | 0.60 | 0.207 | 0.108 | 1.000 | 1.009 | 1.015 | 1.020 | 1.023 | 1.000 | 0.998 | 0.997 | 0.997 | 0.996 |
| 0.125 | 0.600 | 1.80 | 0.161 | 0.078 | 1.000 | 1.007 | 1.011 | 1.015 | 1.018 | 1.000 | 0.993 | 0.988 | 0.985 | 0.982 |
| 0.125 | 0.600 | 5.40 | 0.113 | 0.055 | 1.000 | 1.003 | 1.005 | 1.005 | 1.010 | 1.000 | 0.983 | 0.971 | 0.962 | 0.955 |
| 0.250 | 0.100 | 0.00 | 0.500 | 0.050 | 1.000 | 1.178 | 1.308 | 1.408 | 1.489 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| 0.250 | 0.100 | 0.20 | 0.477 | 0.046 | 1.000 | 1.155 | 1.288 | 1.385 | 1.464 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| 0.250 | 0.100 | 0.60 | 0.442 | 0.041 | 1.000 | 1.145 | 1.356 | 1.346 | 1.420 | 1.000 | 0.998 | 0.998 | 0.998 | 0.998 |
| 0.250 | 0.100 | 1.80 | 0.382 | 0.034 | 1.000 | 1.111 | 1.200 | 1.274 | 1.337 | 1.000 | 0.992 | 0.990 | 0.969 | 0.969 |
| 0.250 | 1.100 | 5.40 | 0.318 | 0.029 | 1.000 | 1.078 | 1.144 | 1.199 | 1.242 | 1.000 | 0.980 | 0.974 | 0.972 | 0.971 |
| 0.250 | 0.200 | 0.00 | 0.500 | 0.100 | 1.000 | 1.139 | 1.228 | 1.291 | 1.338 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| 0.250 | 0.200 | 0.20 | 0.477 | 0.092 | 1.000 | 1.130 | 1.216 | 1.278 | 1.325 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| 0.250 | 0.200 | 0.60 | 0.442 | 0.081 | 1.000 | 1.115 | 1.195 | 1.254 | 1.299 | 1.000 | 0.998 | 0.998 | 0.997 | 0.997 |
| 0.250 | 0.200 | 1.80 | 0.382 | 0.068 | 1.000 | 1.089 | 1.154 | 1.204 | 1.244 | 1.000 | 0.992 | 0.989 | 0.988 | 0.988 |
| 0.250 | 0.200 | 5.40 | 0.318 | 0.58 | 1.000 | 1.062 | 1.110 | 1.148 | 1.180 | 1.000 | 0.979 | 0.972 | 0.969 | 0.967 |
| 0.250 | 0.300 | 0.00 | 0.500 | 0.150 | 1.000 | 1.105 | 1.166 | 1.206 | 1.235 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| 0.250 | 0.300 | 0.20 | 0.477 | 0.138 | 1.000 | 1.100 | 1.150 | 1.200 | 1.229 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| 0.250 | 0.300 | 0.60 | 0.442 | 0.122 | 1.000 | 1.090 | 1.146 | 1.185 | 1.214 | 1.000 | 0.998 | 0.997 | 0.997 | 0.997 |
| 0.250 | 0.300 | 1.80 | 0.392 | 0.102 | 1.000 | 1.070 | 1.117 | 1.151 | 1.177 | 1.000 | 0.991 | 0.989 | 0.987 | 0.986 |
| 0.250 | 0.300 | 5.40 | 0.318 | 0.087 | 1.000 | 1.049 | 1.083 | 1.109 | 1.129 | 1.000 | 0.978 | 0.970 | 0.966 | 0.964 |
| 0.250 | 0.400 | 0.00 | 0.500 | 0.200 | 1.000 | 1.077 | 1.118 | 1.143 | 1.160 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| 0.250 | 0.400 | 0.20 | 0.477 | 0.183 | 1.000 | 1.075 | 1.115 | 1.141 | 1.159 | 1.000 | 1.000 | 1.000 | 0.999 | 0.999 |
| 0.250 | 0.400 | 0.60 | 0.442 | 0.162 | 1.000 | 1.068 | 1.108 | 1.133 | 1.151 | 1.000 | 0.995 | 0.997 | 0.997 | 0.996 |

**Table 6.** (continued)

| φ | $h^2_T$ | a² | r | t | E according to n (A) 1 | 3 | 5 | 7 | 9 | (B) 1 | 3 | 5 | 7 | 9 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0.250 | 0.400 | 1.80 | 0.382 | 0.136 | 1.000 | 1.054 | 1.087 | 1.110 | 1.126 | 1.000 | 0.991 | 0.987 | 0.925 | 0.984 |
| 0.250 | 0.400 | 5.40 | 0.318 | 0.116 | 1.000 | 1.037 | 1.061 | 1.079 | 1.092 | 1.000 | 0.977 | 0.986 | 0.963 | 0.960 |
| 0.250 | 0.600 | 0.00 | 0.500 | 0.300 | 1.000 | 1.035 | 1.051 | 1.059 | 1.065 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| 0.250 | 0.600 | 0.20 | 0.477 | 0.275 | 1.000 | 1.036 | 1.052 | 1.062 | 1.068 | 1.000 | 1.000 | 0.999 | 0.999 | 0.999 |
| 0.250 | 0.600 | 0.60 | 0.442 | 0.244 | 1.000 | 1.034 | 1.051 | 1.062 | 1.068 | 1.000 | 0.998 | 0.997 | 0.996 | 0.996 |
| 0.250 | 0.600 | 1.80 | 0.352 | 0.204 | 1.000 | 1.029 | 1.043 | 1.052 | 1.059 | 1.000 | 0.990 | 0.956 | 0.983 | 0.982 |
| 0.250 | 0.600 | 5.40 | 0.318 | 0.173 | 1.000 | 1.018 | 1.029 | 1.036 | 1.041 | 1.000 | 0.976 | 0.965 | 0.959 | 0.956 |

and

$$\beta_2=\frac{[\mathrm{cov(PO)}_T-\mathrm{cov(HUN)}_T]}{\sigma^2_W}=\frac{\mathrm{cov(PO)}_T}{\sigma^2_{P_T}}\frac{1-r}{1-t}$$

$$=\frac{\mathrm{cov(PO)}_T}{\sigma^2_{P_T}}\frac{1-A}{1-B}\,.$$

The estimated coefficients will be

$$\beta'_1=\frac{1/n\,2\,\mathrm{cov(HS)}_T}{\sigma^2_{P_T}}\frac{[1+(n-1)r_0]/n}{[1+(n-1)t]/n}=\frac{2\,\mathrm{cov(HS)}_T}{\sigma^2_{P_T}}\frac{A_0}{B}$$

with

$$r_0=\frac{1/2\,\mathrm{cov(HS)}_T}{2\,\mathrm{cov(HS)}_T}=\frac{1}{4}$$

and

$$\beta'_2=\frac{2\,\mathrm{cov(HS)}_T}{\sigma^2_{P_T}}\frac{1-r_0}{1-t}=\frac{2\,\mathrm{cov(HS)}_T}{\sigma^2_{P_T}}\frac{1-A}{1-B}\,.$$

The value of $t$ is always the same. With FS families, it will be only necessary to change the value of $r_0$ ($r_0=1/2$). The selection is then performed from a linear combination $I'$ of the family effect and of the plant/family effect:

$$\hat{I}'_{0\,(ij)}=\beta'_1(T_{i\cdot}-\mu)+\beta'_2(T_{ij}-T_{i\cdot})\,. \tag{12}$$

The genetic advance in one cycle of recurrent selection will be:

$$\Delta G'=i\frac{\mathrm{cov}(\hat{I}'_0\,G)}{\sigma_{\hat{I}'_0}}\,,$$

with $\mathrm{cov}(\hat{I}'\,G)$ being the covariance between the value of an individual according to the index of combined selection with the wrong coefficient and the true genotypic value of the offspring.

When $\beta'_1=\beta_1$, and $\beta'_2=\beta_2$, then

$$\mathrm{cov}(\hat{I}'_0\,G)=\sigma^2_I\,,\quad\text{and}\quad \Delta G'=i\,\sigma_{\hat{I}_0}.$$

With half-sib families:

$$\mathrm{cov}\,\hat{I}'_0\,G=\beta'_1[1/n\,\mathrm{cov(PO)}_T+(n-1)n\,\mathrm{cov(HUN)}_T]$$
$$+\beta'_2(n-1)/n\,[\mathrm{cov(PO)}_T-\mathrm{cov(HUN)}_T]$$
$$=\beta'_1[1+(n-1)r]/n+\beta'_2(n-1)\,(1-r)/n$$

and

$$\sigma^2_{\hat{I}'_0}=\beta'^2_1\,E(T_{i\cdot}-\mu)^2+\beta'^2\,E(T_{ij}-T_{i\cdot})^2\,,$$

$$=\frac{[2\,\mathrm{cov\,HS}_T]^2}{\sigma^2_{P_T}}\left[\frac{A_0^2}{B}\frac{(1-A_0)^2}{1-B}\right].$$

After simplification it results that:

$$\sigma^2_{I_0}=\frac{[2\,\mathrm{cov\,(HS)}_T]^2}{\sigma^2_{P_T}}\left\{1+\frac{(r_0-t)^2\,(n-1)}{(1-t)\,[1+(n-1)\,t]}\right\}$$

$$=\frac{(2\,\mathrm{cov(HS)}_T)^2}{\sigma^2_{P_T}}C_o$$

and

$$\mathrm{cov}\,\hat{I}'_0\,G=\frac{2\,\mathrm{cov(PO)}_T\,\mathrm{cov(HS)}_T}{\sigma^2_{P_T}}\left\{1+\frac{(r-t)(r_0-t)(n-1)}{(1-t)[1+(n-1)t]}\right\}$$

$$=\frac{2\,\mathrm{cov(PO)}_T\,\mathrm{cov(HS)}_T}{\sigma^2_{P_T}}\,C_o$$

$$\Delta G'_0=i\frac{\mathrm{cov(PO)}_T}{\sigma_{P_T}}\frac{C_{oe}}{\sqrt{C_o}}\,.$$

If $n=1$, this gives the classical result for individual selection. The comparison of the genetic advance to the one ($\Delta G_e$) with consideration of epistasis becomes

$$\Delta G_e=i\frac{\mathrm{cov(PO)}_T}{\sigma_{P_T}}\sqrt{C_e}$$

with

$$C_e=1+\frac{(r-t)^2\,(n-1)}{(n-1)[1+(n-1)]}\,,$$

and

$$\frac{\Delta G'_0}{\Delta G_e} = \frac{C_{oe}}{\sqrt{C_e C_o}},$$

which is the correlation coefficient between the predicted value of offspring by ignoring the presence of epistasis and their predicted values taking into account the presence of epistasis.

Indeed: $\Delta G_0 = i \operatorname{cov} \hat{G}_0 G/\sigma_{\hat{G}_0}$, and

$$\Delta G_e = i\, \sigma_{\hat{G}_e}.$$

Then $$\frac{\Delta G_0}{\Delta G_e} = \operatorname{cov} \hat{G}_0 G/(\sigma_{\hat{G}_0}\, \sigma_{\hat{G}_e})$$

$$\operatorname{cov} G_0\, G = \operatorname{cov} \hat{G}_0\, \hat{G}_e$$

$$\frac{\Delta G_o}{\Delta G_e} = \varrho_{(\hat{G}_0\, \hat{G}_e)}.$$

By a numerical application, this formulation allows a very simple approach to the relative efficiency of the selection ignoring the epistasis. It seems (Table 6) that the ratio is nearly independent of the type of progenies (full-sib or half-sib) and of the value of heritability. It tends to be affected by the size of the progeny and by the amount of epistasis. Within reasonable range of variation of such parameters, however, their combined effect is no more than 5%. With the considered situation, epistasis does not disturb the prediction very much. This was expected from the consideration of the lower coefficients of epistasis in the expressions of covariances between relatives.

When selection is relaxed, only additive variance contributes to genetic advance (Griffing 1962; Gallais 1979 a, b). Then it is also interesting to consider the prediction of the testcross value of offsprings due only to additive effects. According to previous results, the index is as follows:

$$\hat{I}''_e = \beta''_1 (T_i. - \mu) + \beta''_2 (T_{ij} - T_i.), \tag{13}$$

with

$$\beta''_1 = \frac{(1/2\, \sigma^2_{A_T})}{\sigma^2_{P_T}} \frac{1+(n-1)\, r_0}{1+(n-1)\, t}$$

and $r_0 = 1/4$ or $1/2$ for half-sib or full-sib families, and:

$$\beta''_2 = \frac{(1/2\, \sigma^2_{A_T})}{\sigma^2_{P_T}} \frac{1-r_0}{1-t}.$$

By ignoring the epistasis, the index will be that one considered previously (Eq. 12). It is clear that index 13 is equivalent to index 12 because it can be deduced from it by multiplying by $\frac{2\, \mathrm{covHS}}{1/2\, \sigma^2_A}$. It results that the correlation between the two indexes is one. The predicted genetic advance by ignoring the epistasis is the genetic advance after relaxation of selection.

For the application of combined selection to method 4, the pairs are selected from the predicted value of the progenies of the full-sib family, which is given by the sum of the predicted value in testing each of the two plants of the pair. Comparison of the efficiency of combined selection method 4 to the efficiency of combined selection method 1 (with pair-crossing) for the expected genetic advance per unit of time with the use of an off-season generation leads to the same advantage for method 4 (+41%) as for individual progeny selection.

## Conclusions

The development of the concept of test value leads to simple and classical mating designs, which appear to be powerful for the detection of epistasis at the population level by the use of second-degree statistics. Indeed, with only a family structure it will be possible to estimate two variance components and, with a two-way mating design, it will be possible to estimate two variance components due to epistasis (additive × additive and additive × additive × additive). Such designs partially avoid the difficulties emphasized by Chi et al. (1969) for simultaneously estimating components due to epistasis and components due to additivity an dominance. The relative simplicity of estimating epistatic components is due to the absence of dominance. The situation is similar to that for line value (Gallais 1990). However, in this latter case, it is the epistasis homozygote × homozygote that is considered. These two approaches of epistasis will be very powerful in investigating the nature of epistasis either in autogamous or in allogamous plants. It will be very fruitful to apply these two approaches to the same populations within a species. It will be possible to have accurate estimates of additive × additive epistasis for testcrosss value (through $\sigma^2_{AA}$, if the population itself is taken as tester, or $\sigma^2_{AA_T}$ with an arbitrary tester) and of homozygote × homozygote epistasis. Such information would emphasize the organization of the genetic variation according to the system of mating.

For the application of recurrent selection, two major conclusions seem evident. First, considering the genetic advance per unit of time with the use of an off-season generation, it seems appropriate to include pair-crossing at the same time as crossing with the tester, considering the pair as unit of selection (method 4). Such a method is more efficient (+41%) than the classical method (method 1). The conclusion is also at the level of the use of combined selection. In methods with half-sib families, there is no gain with combined selection. The organization of the population in full-sib families allows a more efficient combined selection, but mainly for traits with relatively low heritability. This increases the interest of pair-crossing as in method 4.

Another advantage of pair-crossing is the possibility to control the development of inbreeding at the population level. To attain this goal, it will be necessary to control the pedigree of each plant to avoid crossing related plants. The use of circular pair mating or related plans as those discussed by Kimura and Crow (1963) and Cockerham (1970) must be considered. Their disadvantage is that they will not allow beween-family but only within-family selection. However, to avoid a too rapid loss of variability in recurrent selection programs, the breeder applies a very low selection intensity between families.

The effect of the presence of epistasis on relative efficiency of combined selection is relatively low. Such a conclusion can be extrapolated for any situation where there is only additive × additive epistasis at the level of the value according to the system of testing. This applies particularly for the selection on line value by the use of haplodiploidization with several lines per haplodiploidized plants and low heritability. The combined selection will increase the genetic advance (Gallais 1989), and more significantly for the cases considered in this study, because the coefficient of kinship between lines of the same plant is of 1/2. However, it is possible to predict that the presence of epistasis will not change the conclusions. This is an argument for ignoring epistasis in the development of the theory of recurrent selection when only one cycle is considered. However, with a long-term recurrent selection as with varietal development, it will be necessary to consider epistasis. Analogous developments and breeding schemes can be proposed for selection with $S_1$ progeny test or for any other types of selection with progeny test or analogous procedures, including clonal evaluation.

## References


Chi RK, Eberhart SA, Penny LH (1969) Covariances among relatives in a maize variety. Genetics 63:511–520

Choo TM (1981) Doubled haploid for studying the inheritance of quantitative characters. Genetics 99:525–540

Choo TM, Kotecha A, Reinbergs E, Song LSP, Fejer SO (1986) Diallel analysis of grain yield in barley using doubled haploid lines. Plant Breed 97:129–137

Cockerham CC (1970) Avoidance and rate of inbreeding. In Kojima K (ed) Mathematical topics in population genetics. Springer, New York, pp 104–127

Gallais A (1979a) Is Fisher's model necessary for the theory of population improvement? Theor Appl Genet 58:117–180

Gallais A (1979b) Application du concept de valeur variétale à la théorie de la sélection de variétés hybrides. Ann Amel Plant 29:23–41

Gallais A (1989) Optimization of recurrent selection on the phenotypic value of doubled haploid lines. Theor Appl Genet 79:501–504

Gallais A (1990) The quantitative genetics of doubled haploid populations. Application to selection for line value. Genetics 77:501–504

Griffing B (1956) Concept of general and specific combining ability in relation to diallel crossing systems. Aust J Biol Sci 9:463–493

Griffing B (1962) Prediction formulae for general combining ability selection methods utilizing one or two random-mating populations. Aust J Biol Sci 15:650–665

Hallauer AR, Miranda JB (1981) Quantitative genetics in maize breeding. Iowa State University Press, Ames, 468 pp

Kempthorne O (1957) Introduction to quantitative genetics. Wiley and Sons, New York

Kimura M, Crow JF (1963) On the maximum avoidance of inbreeding. Genet Res Camb, pp 399–415

Lush JG (1943) Family merit and individual merit as bases for selection. Part I Am Nat 81:241–261. Part II Am Nat 81:362–379