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Analysis of variance components of testcross progenies in an autotetraploid species and consequences for recurrent selection with a tester

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Summary. For autotetraploid species the development of the concept of test value (value in testcross) leads to a simple description of the variance among testcross progenies. When defining directly genetic effects at the level of the value of the progenies, there is no contribution of tri- and tetragenic interactions. To estimate additive and dominance variances it is only necessary to have the population of progenies structured in half-sib or full-sib families; it is then possible to determine the presence of epistasis using a two-way mating design. When the theory of recurrent selection is applied dominance variance can be neglected for the prediction of genetic advance in one cycle as well for the development of combined selection when progenies are structured in families. The results are similar to those for diploids with two-locus epistasis. The more efficient scheme consists of the development of pair-crossing in off-season generations (for intercrossing) and simultaneous crossing of each plant to the tester. In comparison to the classical scheme, the relative efficiency of such a scheme is 41%. The use of combined selection will further increase this superiority.

Key words: Autotetraploidy – Combining ability – Tester – Combined selection

Introduction

Variance components in a random mating autotetraploid populations are difficult to explore because of possible interactions between more than two alleles. Without epistasis and without restrictions on interactions between alleles, there are four components to describe genotypic variance of a complex character. Hence, it is impossible to explore the presence of epistasis by the use of complex designs such as the three or four-way mating designs described by Cockerham (1963) and the one applied by Gallais (1977, 1984). It is also difficult to obtain a reliable estimate of the epistatic components of the genotypic variance in diploid species because of the number of parameters (five) and the interdependance of their coefficients (Chi et al. 1969).

The use of testcross progenies has been presented as a means to determine the presence of epistasis in diploids (Gallais 1990). Direct definition of genetic effects for the value of testcross progenies suppresses the component of variance due to dominance and all epistatic components involving dominance (additive × dominance, dominance × dominance ...). By restricting epistasis to pairs of loci, there remains only additive and additive × additive components for the variance among testcross progenies.

A similar approach can be extended to autotetraploids. Because the gametes are diploid, the variance among testcross progenies in the absence of epistasis will be described by the additive and the dominance variances. If the plant breeder or the geneticist wishes to test for the presence of epistasis for pairs of loci, five components will be necessary to describe the variance among progenies: additive, dominance, additive × additive, additive × dominance, and dominance × dominance components. However, it will be impossible to have an accurate estimate of these five components. It is possible, for example, to restrict epistasis to the additive × additive epistasis, without any restriction on the interactions between alleles. In this paper I will consider this situation. Some consequences for recurrent selection will be also considered.

Definition of genetic effects

1. Without epistasis

Consider a random mating population with alleles A_1, $A_2, \ldots A_i$, A_j and a tester with an allelic composition denoted by A_x. Whatever the nature of the tester, A_x can be an allele or a set of alleles, gametes of the tester will be denoted A_xA_x. Let $A_iA_jA_kA_l$ be a genotype of the population, and Y_{ijxx} the value of a "genotype" $A_iA_jA_xA_x$ from a progeny with the tester ($A_iA_jA_xA_x$ will be a genotype if A_xA_x represents only one type of gamete from the tester). For the value $T_{(ijkl)}$ of the genotype $A_iA_jA_kA_l$ in combination with the tester, it is possible to write:

$$T_{(ijkl)} = 1/6\,(Y_{ijxx} + Y_{ikxx} + Y_{ilxx} + Y_{jkxx} + Y_{jlxx} + Y_{klxx}) \tag{1}$$

The value of Y_{ijxx} is broken down according to the following model:

$$Y_{ijxx} = \mu_T + {}_T\alpha'_i + {}_T\alpha'_i + {}_T\beta'_{ij} \tag{2}$$

where ${}_T\alpha'_i$ is defined as the additive effect in test and ${}_T\beta'_{ij}$ as the dominance effect in test:

$${}_T\alpha'_i = E_j\,(Y_{ijxx}) - \mu_T$$

$${}_T\beta'_{ij} = Y_{ijxx} - {}_T\alpha'_i - {}_T\alpha'_j - \mu_T$$

with $E_j\,(Y_{ijxx}) = \Sigma_j\, p_j\, Y_{ijxx}$, p_j being the frequency of the allele A_j in the random mating population. From equations (1) and (2) it is possible to write:

$$T_{(ijkl)} = \mu_T + 1/2\,({}_T\alpha'_i + {}_T\alpha'_j + {}_T\alpha'_k + {}_T\alpha'_l) + 1/6\,({}_T\beta'_{ij} + {}_T\beta'_{ik} + {}_T\beta'_{il} + {}_T\beta'_{jk} + {}_T\beta'_{jl} + {}_T\beta'_{kl}) \tag{3}$$

To simplify the notation, additive effect and dominance effect are redefined as follows:

$${}_T\alpha_i = 1/2\ {}_T\alpha'_i \quad \text{and} \quad {}_T\beta_{ij} = 1/6\ {}_T\beta'_{ij}\ , \tag{4}$$

then

$$T_{(ijkl)} = \mu_T + {}_T\alpha_i + {}_T\alpha_j + {}_T\alpha_k + {}_T\alpha_l + {}_T\beta_{ij} + {}_T\beta_{ik} + {}_T\beta_{il} + {}_T\beta_{jk} + {}_T\beta_{jl} + {}_T\beta_{kl}\ .$$

Clearly, trigenic and tetragenic effects cannot contribute to the value in test. Obviously, if the tester is the random mating population itself ${}_T\alpha'_i = \alpha_i$ and ${}_T\beta'_{ij} = \beta_{ij}$, and expression (3) gives the expression of the general combining ability in terms of genetic effects.

A variance is defined for each parameter:

$\sigma^2_{A_T} = 4\,E\,({}_T\alpha_i^2)$ is the additive variance in test,

$\sigma^2_{D_T} = 6\,E\,({}_T\beta_{ij}^2)$ is the dominance variance in test,

and

$\sigma^2_{G_T} = \sigma^2_{A_T} + \sigma^2_{D_T}$ is the "genotypic" variance in test;

that is, the variance among testcross progenies of unrelated plants from a random mating population. If the tester is the population itself:

$$\sigma^2_{G_T} = \sigma^2_g = 1/4\ \sigma^2_A + 1/36\ \sigma^2_D \tag{5}$$

which is also the variance among half-sibs.

2. With additive × additive epistasis

To solve this problem it is necessary to consider a two-locus genotype with genes i_1, j_1, k_1, l_1 at locus 1 and i_2, j_2, k_2, l_2 at locus 2. Assuming no linkage the value in the test of a genotype $G_{i_1j_1k_1l_1,i_2j_2k_2l_2}$ can be written

$$T_{(i_1j_1k_1l_1,i_2k_2l_2)} = 1/36\,[{}_TY_{i_1j_1i_2j_2} + {}_TY_{i_1j_1i_2k_2} + \ldots + Y_{k_1l_1k_2l_2}]\,,$$

where ${}_TY_{i_1j_1i_2j_2}$ is the value of the "genotype" given by the gamete $i_1j_1i_2j_2$ with the tester. There are 36 such "genotypes". With the same approach as previously, it is possible to write:

$${}_TY_{i_1j_1k_2l_2} = \mu_T + {}_T\alpha'_{i_1} + {}_T\alpha'_{j_1} + {}_T\alpha'_{k_2} + {}_T\alpha'_{l_2} + {}_T\beta'_{i_1j_1} + {}_T\beta'_{k_2l_2} + {}_T(\alpha\alpha)'_{i_1k_2} + {}_T(\alpha\alpha)'_{i_1l_2} + {}_T(\alpha\alpha)'_{j_1k_2} + {}_T(\alpha\alpha)'_{j_1l_2}$$

and

$$T_{(i_1j_1k_1l_1,i_2j_2k_2l_2)} = \mu_T + {}_T\alpha_{i_1} + \ldots + {}_T\alpha_{k_2} + \ldots + {}_T\beta_{i_1j_1} + \ldots + {}_T\beta_{i_2j_2} + \ldots + {}_T(\alpha\alpha)_{i_1i_2} + {}_T(\alpha\alpha)_{i_1j_2} + \ldots {}_T(\alpha\alpha)_{l_1l_1}\ .$$

Obviously there are 16 terms of the type ${}_T(\alpha\alpha)_{i_1i_2}$ and ${}_T(\alpha\alpha)_{i_1i_2} = 1/4\ {}_T(\alpha\alpha)'_{i_1i_2}$.

The epistatic effects can be defined directly from the value of the testcross progenies:

$${}_T(\alpha\alpha)_{i_1i_2} = E_{i_1i_2}\,[T_{(i_1j_1k_1l_1,i_2j_2k_2l_2)}] - {}_T\alpha_{i_1} - {}_T\alpha_{i_2} - \mu_T\,,$$

where $E_{i_1i_2}$ is the expectation on all indices ($i_1, j_1, k_1, l_1, i_2, j_2, k_2, l_2$) except i_1 and i_2.

Let $\sigma^2_{AA_T}$ be the additive × additive variance in test:

$$\sigma^2_{AA_T} = 16\,E\,[{}_T(\alpha\alpha)^2_{i_1i_2}]\,,$$

and the total variance among testcross progenies will be:

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

if the tester is the population itself,

$$\sigma^2_{G_T} = \sigma^2_g = 1/4\ \sigma^2_A + 1/36\ \sigma^2_D + 1/16\ \sigma^2_{AA}\ , \tag{6}$$

which is the covariance among half-sibs.

The covariances between related progenies

Related progenies are testcross progenies derived from related plants. For example, from a family of full-sib plants it is possible to develop what can be called full-sib

progenies. Then, the classical expression of the covariances between relatives in a random mating population (Kempthorne 1957, Gallais 1989 a) can be extended to the covariances between related progenies. For two related testcross progenies X_T and Y_T (from the plants X and Y), it is possible to write in the absence of linkage:

$$\text{cov}(X_T, Y_T) = 4\,\varphi_A\,\sigma^2_{A_T} + 6\,\varphi_D\,\sigma^2_{D_T} + 16\,\varphi^2_A\,\sigma^2_{AA_T}\,, \qquad (7)$$

where φ_A is the classical coefficient of kinship, φ_D is the "double" coefficient of kinship or the probability that the two genes drawn in Y are identical by descent to the two genes drawn in X. For half-sibs: $\varphi_A = 1/16$ and $\varphi_D = 1/216$. When these values are put in expression (7), we have expression (6), which was established by another way for the covariance among half-sibs:

$$\text{cov}(HS)_T = 1/4\,\sigma^2_{A_T} + 1/36\,\sigma^2_{AA_T}\,.$$

For full-sibs: $\varphi_A = 1/8$ and $\varphi_D = 1/27$, and the covariance among full-sib progenies is:

$$\text{cov}(FS)_T = 1/2\,\sigma^2_{A_T} + 2/9\,\sigma^2_{D_T} + 1/4\,\sigma^2_{AA_T}\,. \qquad (8)$$

Obviously, the results can be extended for more complex types of epistasis.

Designs to estimate the variance components

1. 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 among families), and the experiment becomes a two-way mating design. An analysis of variance among and within families can be performed as developed by Gallais (1990). The variances among families ($\sigma^2_{GB_T}$) and within families ($\sigma^2_{GW_T}$) can be estimated. Two covariances are available, and, consequently, only the additive and dominance variances components of the genetic variance among progenies can be estimated. The families can be half-sibs or full-sibs. S_1 full-sibs cannot be considered unlike in diploids because the progenies are inbred.

Case of half-sib families. According to previous results the variance among half-sib families is:

$$\text{cov}(HS)_T = 1/4\,\sigma^2_{A_T} + 1/36\,\sigma^2_{D_T}.$$

The contribution of dominance is very low, and nearly all of the dominance variance will be in the variation within families:

$$\sigma^2_{GW_T} = 3/4\,\sigma^2_{A_T} + 35/36\,\sigma^2_{D_T}\,. \qquad (9)$$

It is then essential to have an accurate estimate of the variance among families.

Case of full-sib families. The variance among full-sib families is the covariance among full-sib families, and:

$$\text{cov}(FS)_T = 1/2\,\sigma^2_{A_T} + 2/9\,\sigma^2_{D_T}\,.$$

The within full-sib variance component is:

$$\sigma^2_{GW_T} = \sigma^2_{G_T} - \text{cov}(FS)_T = 1/2\,\sigma^2_{A_T} + 7/9\,\sigma^2_{D_T}\,. \qquad (10)$$

2. Two-way mating designs

Three two-way mating designs can be considered (nested design or design I NC, factorial design or design II NC, and diallel).

In the case of these two-way mating designs, three variances can be estimated:

- variance among half-sib families ($\text{cov}(HS)_T$) or variance of GCA for value in test;
- the variance of specific combining ability [$\text{cov}(FS)_T - 2\,\text{cov}(HS)_T$]
- the variance among plants within a full-sib family or: $\sigma^2_{GW_T} = \sigma^2_{G_T} - \text{cov}(FS)_T$.

The analysis of variance has been given by Gallais (1990).

It is possible to estimate three components of the genotypic variance: $\sigma^2_{A_T}$, $\sigma^2_{D_T}$, $\sigma^2_{AA_T}$. The three equations are:

$$\text{cov}(FS)_T = 1/2\,\sigma^2_{A_T} + 2/9\,\sigma^2_{D_T} + 1/4\,\sigma^2_{AA_T}$$

$$\text{cov}(HS)_T = 1/4\,\sigma^2_{A_T} + 1/36\,\sigma^2_{D_T} + 1/16\,\sigma^2_{AA_T}\,.$$

$$\sigma^2_{GW_T} = 1/2\,\sigma^2_{A_T} + 7/9\,\sigma^2_{D_T} + 3/4\,\sigma^2_{AA_T}\,. \qquad (11)$$

In the absence of epistasis the specific combining ability variance for test values is not zero unlike in the case of diploids:

$$\sigma^2_s = \text{cov}(FS)_T - 2\,\text{cov}(HS)_T = 1/16\,\sigma^2_{D_T}\,. \qquad (12)$$

There is no simple test for the presence of epistasis. The presence of epistasis could be evaluated only through the estimation of the components of variance among testcross progenies. If the estimates are more coherent assuming epistasis than assuming no epistasis, it can be concluded that epistasis is present. However, this requires accurate estimation of the three variances or covariances: $\text{cov}(HS)_T$, $\text{cov}(FS)_T$ and $\sigma^2_{GW_T}$.

Application to selection with a tester

1. Genetic advance according various schemes

In the classical breeding scheme of recurrent selection with a tester, the three phases of seed production for test, testing, and intercrossing are separated (method 1). To maintain the mother plant it will be better to use vegetative propagation instead of selfing because selfing will

generate inbreeding at the level of the population after one generation of intercrossing. If self-fertilization is used in order to suppress a great part of inbreeding, it will be possible to develop another generation of intercrossing during the off-season.

Ignoring the effect of the panmictic disequilibrium, and assuming vegetative propagation of the mother plant, the genetic gain per cycle will be

$$\Delta G_1 = i\, 2\, \mathrm{cov}\, P_T O_T \sqrt{\mathrm{var}\, P_T},$$

$$\Delta G_1 = i\, 2\, (1/2\, \sigma^2_{A_T} + 1/6\, \sigma^2_D)/\sqrt{\mathrm{var}\, P_T},$$

$$\Delta G_1 = i\, (\sigma^2_{A_T} + 1/3\, \sigma^2_{D_T})/\sqrt{\mathrm{var}\, P_T}. \qquad (13)$$

This will be performed in three generations. In another possible scheme (method 2) to reduce the length of the cycle, the intercrossing is developed at the same time as crossing with the tester. Then the selection will be only maternal. This suppresses one generation, but the genetic advance will be half of the previous. Even with per generation or per unit of time if off-season generations are used in both schemes, the second scheme will be at the best equal to the first.

A third scheme (method 3) proposed by Gallais (1990) for diploids can also be applied. In this scheme, as in the previous, intercrossing is developed simultaneously to crossing with the tester. The difference is in the modality of intercrossing and of selection. To develop intercrossing pairs of plants are constituted, and the two plants are crossed to produce a full-sib family and at the same time crossed with the tester. For selection, the unit will be a pair of plants, and it will be selected on the basis of the average of the two associated testcrosses. The length of the cycle is two generations. The genetic advance in one cycle will be

$$\Delta G_3 = i\, \mathrm{cov}\, \bar{P}_T \bar{O}_T / \sqrt{\mathrm{var}\, \bar{P}_T},$$

where $\mathrm{cov}\, \bar{P}_T \bar{O}_T$ is the covariance between the average $\bar{P}_T$ of the two testcross progenies of a pair and the values ($\bar{O}_T$) in testcross of the full-sibs from the two plants. Then:

$$\mathrm{cov}\, \bar{P}_T \bar{O}_T = \mathrm{cov}\, 1/2\, (P_{i_T} + P_{j_T})\, (O_{i_T} + O_{i_T})$$

$$= \mathrm{cov}\, P_T O_T$$

$$= 1/2\, \sigma^2_{A_T} + 1/6\, \sigma^2_{D_T},$$

and

$$\mathrm{var}\, P_T = 1/2\, \mathrm{var}\, P_T.$$

Consequently,

$$\Delta G_3 = i \sqrt{2}/2\, (\sigma^2_A + 1/3\, \sigma^2_{D_T}) \sqrt{\mathrm{var}\, P_T}. \qquad (14)$$

N.B. Expressions (13) and (14) give the genetic effect of selection in one cycle. For the total change in mean in one cycle of selection, it would also be necessary to take into account the effect of random mating, in presence of gametic disequilibrium. However, as shown, by Gallais (1989 b) this effect is expected to be low

This quantity is less than the quantity (13), and the ratio of the two genetic advances ($\Delta G_3/\Delta G_1$) is 0.707. Considering the genetic advance per generation, the ratio takes the value $3\sqrt{2}/4 = 1.06$, and if for each breeding schemes there is an off-season generation, the ratio is 1.414: method 3 is 41% more efficient than method 1, as for diploids.

2. Combined selection

In recurrent selection with a tester the best progenies are identified and the mother plants of the selected progenies are intercrossed. Intercrossing gives the new population for the next cycle of recurrent selection. This new population is generally structured in families, half-sib families if there is a "polycross" of the selected plants, or full-sib families if the intercrossing is developed by crossing pairs of plants by hand. This structure is generally ignored, and the genetic advance is predicted by ignoring the effect of dominance. In progeny test selection, the effects of dominance are not very important because the coefficient of dominance is always very low in comparison to that of additive variance (Gallais 1989 a).

2.1. Ignoring the effect of dominance. In this case, the same result as for diploids without epistasis can be extrapolated for autopolyploids.

With half-sib families the expected gain will be relatively low except for very low heritability (Gallais 1990). For example, with five progenies per half-sib family and a heritability of 0.10 at the level of mean, the gain due to combined selection is 9% and only 2.5% with a more realistic heritability of 0.50.

With full-sib families, five progenies per family, and a heritability of 0.10, the expected gain due to combined selection will be 30%, and 8% for a heritability of 0.50. Thus, it could be very efficient to consider structuring of the population in full-sib families when heritability is low. Clearly, with very low heritability (as for yield in perennial forage crops) it would be interesting to use two-way mating designs to develop intercrosses. This will allow the use of three predictors (half-sib family, full-sib family, and progeny within full-sib family), and the efficiency will be further increased in comparison to the use of information from only full-sib families. With perennial plants the development of such plans will not be more expensive than the development of only crossing pairs to produce full-sib families. A series of small disconnected 4×4 diallels can be used (Gallais 1989 a) or a series of small disconnected factorials.

With annual plants where vegetative propagation can be difficult, it is possible to develop pair-crossing at the same time as top-crossing as in method 3 (Gallais 1990). This will be advantageous in comparison to classical

intercrossing after selection only if pair-crossing and intercrossing can be developed in the off-season.

The use of combined selection will increase the efficiency of method 3 to a much greater extent because it is based upon full-sib families. Note that even without an off-season generation, method 3 with the use of combined selection will be more efficient than method 1.

2.2. Considering the effect of dominance. In this case the theory of combined selection must be redeveloped. With a family i and a plant j within the family, with T_{ij} denoting the phenotypic value in the testcross of the plant ij, the maximum genetic advance will be by the use of the following index:

$$I = \beta_1 (T_{i\,.} - T_{..}) + \beta_2 (T_{ij} - T_{i\,.}) . \qquad (15)$$

To simplify, a constant number of tested plants (n) per family will be considered. As shown by Gallais (1990), the result of Lush (1943) can be directly extended to the considered situation by changing the notation:

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

with $t = \dfrac{\text{cov}\,(HS)_T}{\sigma^2_{P_T}}$ the intra-class correlation for half-sib families (for full-sib families $\text{cov}\,(FS)_T$ will replace $\text{cov}\,(HS)_T$) and $r = \dfrac{\text{cov}\,(HUN)_T}{\text{cov}\,(PO)}$ with half-sib families. $\text{Cov}\,(HUN)_T$ is the covariance half-uncle-nephew; for full-sib families, $\text{Cov}\,(UN)_T$ (covariance uncle-nephew) will replace $\text{cov}\,(HUN)_T$. $\sigma^2_{P_T}$ is the total phenotypic variance among testcross progenies, which is the sum of the among family variance and the within family variance and of the residual without epistasis. It is possible to write:

$$\begin{aligned}
\text{cov}\,(HS)_T &= 1/4\,\sigma^2_{A_T} + 1/36\,\sigma^2_{D_T} \\
\text{cov}\,(FS)_T &= 1/2\,\sigma^2_{A} + 2/9\,\sigma^2_{D_T} \\
\text{cov}\,(HUN)_T &= 1/8\,\sigma^2_{A_T} + 1/216\,\sigma^2_{D_T} \\
\text{cov}\,(UN)_T &= 1/4\,\sigma^2_{A_T} + 1/27\,\sigma^2_{D_T} \\
\text{cov}\,(PO)_T &= 1/2\,\sigma^2_{A_T} + 1/6\,\sigma^2_{A_T} .
\end{aligned}$$

Then:

$$t_{HS} = \frac{1/4\,\sigma^2_{A_T} + 1/36\,\sigma^2_{D_T}}{\sigma^2_{A_T} + \sigma^2_{D_T} + \sigma^2_e} \qquad t_{FS} = \frac{1/2\,\sigma^2_{A_T} + 2/9\,\sigma^2_{D_T}}{\sigma^2_{A_T} + \sigma^2_{A_T} + \sigma^2_e} \qquad (16)$$

In $\text{cov}\,(FS)_T$ and $\text{cov}\,(PO)_T$ the coefficient of the dominance variance appears to be non negligible. However, consider the expressions (4): ${}_T\alpha_i = 1/2\ {}_T\alpha'_i$, and ${}_T\beta_{ij} = 1/6\ {}_T\beta'_{ij}$. The effects α' and β' are defined at the level of a genotype, and α and β are defined at the level of a mixture of genotypes (the testcross progeny). If dominance effects exist, they will be more affected by a dilution effect than additive effects:

$$\sigma^2_{A_T} = 1/4\ \sigma^2_{A'_T} \qquad \sigma^2_{A'_T} = 4\ E\,({}_T\alpha'_i)^2$$

$$\sigma^2_{D_T} = 1/36\ \sigma^2_{D'_T} \qquad \sigma^2_{D'_T} = 6\ E\,({}_T\beta'_{ij})^2 .$$

Assuming $\sigma^2_{A'_T} = \sigma^2_{D'_T}$ the ratio $\sigma^2_{D_T}/\sigma^2_{A_T} = 1/9$. As in $\text{cov}\,(FS)_T$ and $\text{cov}\,(PO)_T$, the coefficient of $\sigma^2_{D_T}$ is always lower than the coefficient of $\sigma^2_{A_T}$, in many cases the effect of dominance is expected to be low.

To transform the formulae for a numerical application, the ratio $a^2 = \sigma^2_{A_T}/(\sigma^2_{A_T} + \sigma^2_{D_T})$ and the heritability for the testing system $h^2 = (\sigma^2_{A_T} + \sigma^2_{D_T})/\sigma^2_{P_T}$ are introduced. Then

$$\begin{aligned}
t_{HS} &= [1/4\,a^2 + 1/36\,(1-a^2)]\,h^2 , \\
t_{FS} &= [1/2\,a^2 + 2/9\,(1-a^2)\,h^2 , \qquad (18) \\
r_{HS} &= \frac{1/8\,a^2 + 1/216\,(1-a^2)}{1/2\,a^2 + 1/6\,(1-a^2)}, \qquad r_{FS} = \frac{1/4\,a^2 + 1/27\,(1-a^2)}{1/2\,a^2 + 1/6\,(1-a^2)}
\end{aligned}$$

If φ is the classical coefficient of kinship and φ' the coefficient of "double" kinship, t and r can be rewritten as follows:

$$t = [4\,\varphi\,a^2 + 6\,\varphi'\,(1-a^2)]\,h^2$$

and (19)

$$r = \frac{2\,\varphi\,a + \varphi'\,(1-a^2)}{1/2\,a^2 + 1/6\,(1-a^2)} .$$

If $a^2 = 1$, this gives the diploid results without epistasis.

Numerical application has been developed with different h^2 values ranging from 0.10 (h^2 being defined at the level of trial mean, this value is very low) to 0.50, which is more realistic (such values are common for yield in corn). For ratio $\sigma^2_{A_T}/\sigma^2_{G_T}$ (a^2) six values have been considered: 0.10, 0.20, 0.30, 0.50, 0.70, and 1.

Some results are given in Table 1. As classically, combined selection is more efficient when the kinship between members of a family is high, as in full-sibs in comparison with half-sibs, and when heritability is low. In this latter case it increases with an increasing number of progenies per family.

The presence of dominance decreases the efficiency of combined selection. However, it is necessary to have a very high level of dominance to have a significant effect on the variance. If $a^2 = 0.50$, $\sigma^2_{A_T} = \sigma^2_{D_T}$ or on an individual basis:

$$1/4\ \sigma^2_{A'_T} = 1/36\ \sigma^2_{D'_T} ,$$

or

$$\sigma^2_{A'_T} = 1/9\ \sigma^2_{D'_T} \quad \text{and} \quad \sigma^2_{D'_T} = 9\ \sigma^2_{A'_T} ,$$

which corresponds to a very high proportion of dominance variance. Values of a^2 less than 0.50 will be the

Table 1. Relative efficiency (E) of combined selection (A) and effect of ignoring dominance (B). n is the number of progenies per family. Values in A give the efficiency of combined selection relatively to individual progeny selection. Values in B give the ratio $\Delta G_o/\Delta G_d$ of the genetic advance of combined selection ignoring dominance (for $n=1$ it is the ratio for individual progeny selection)

Half-sib families										Full-sib families								
				E according to n								E according to n						
				A			B					A			B			
h_T^2	a^2	r_{HS}	t_{HS}	3	5	10	3	5	10	r_{FS}	t_{HS}	3	5	10	3	5	10	
0.0500	0.10	0.063	0.002	1.006	1.013	1.029	0.975	0.956	0.922	0.291	0.012	1.074	1.140	1.290	0.974	0.966	0.962	
0.0500	0.20	0.123	0.004	1.014	1.028	1.060	0.986	0.975	0.952	0.341	0.014	1.101	1.188	1.367	0.986	0.982	0.981	
0.0500	0.40	0.175	0.006	1.028	1.055	1.117	0.995	0.992	0.987	0.407	0.017	1.140	1.258	1.489	0.996	0.995	0.995	
0.0500	0.70	0.222	0.009	1.044	1.085	1.175	0.999	0.999	0.998	1.465	0.021	1.178	1.321	1.590	0.999	0.999	0.999	
0.0500	1.00	0.250	0.012	1.054	1.103	1.209	1.000	1.000	1.000	0.500	0.025	1.200	1.357	1.643	1.000	1.000	1.000	
0.1000	0.10	0.083	0.005	1.006	1.012	1.026	0.975	0.956	0.922	0.291	0.025	1.067	1.125	1.239	0.974	0.965	0.960	
0.1000	0.20	0.123	0.007	1.013	1.026	1.055	0.986	0.975	0.959	0.341	0.029	1.092	1.168	1.314	0.986	0.981	0.979	
0.1000	0.40	0.176	0.012	1.026	1.051	1.106	0.995	0.992	0.987	0.407	0.033	1.128	1.229	1.415	0.995	0.994	0.994	
0.1000	0.70	0.222	0.018	1.040	1.076	1.152	0.999	0.999	0.998	0.465	0.042	1.160	1.281	1.492	0.999	0.999	0.999	
0.1000	1.00	0.250	0.025	1.048	1.090	1.175	1.000	1.000	1.000	0.500	0.050	1.178	1.308	1.524	1.000	1.000	1.000	
0.2000	0.10	0.083	0.010	1.005	1.010	1.022	0.975	0.956	0.922	0.291	0.050	1.054	1.098	1.175	0.973	0.962	0.955	
0.2000	0.20	0.123	0.014	1.012	1.022	1.045	0.986	0.975	0.958	0.341	0.056	1.075	1.133	1.232	0.985	0.980	0.976	
0.2000	0.40	0.176	0.023	1.023	1.043	1.085	0.995	0.992	0.987	0.407	0.067	1.104	1.180	1.304	0.995	0.994	0.993	
0.2000	0.70	0.222	0.037	1.033	1.061	1.114	0.999	0.999	0.998	0.465	0.083	1.128	1.215	1.348	0.999	0.999	0.999	
0.2000	1.00	0.250	0.050	1.038	1.068	1.123	1.000	1.000	1.000	0.500	0.100	1.139	1.228	1.357	1.000	1.000	1.000	
0.3000	0.10	0.083	0.015	1.005	1.009	1.019	0.975	0.956	0.922	0.291	0.075	1.043	1.075	1.129	0.972	0.960	0.950	
0.3000	0.20	0.123	0.022	1.010	1.019	1.039	0.986	0.975	0.952	0.341	0.083	1.060	1.103	1.172	0.984	0.978	0.974	
0.3000	0.40	0.176	0.035	1.109	1.035	1.069	0.995	0.992	0.987	0.407	0.100	1.084	1.140	1.224	0.995	0.993	0.992	
0.3000	0.70	0.222	0.055	1.026	1.047	1.085	0.999	0.999	0.998	0.465	0.125	1.101	1.163	1.240	0.999	0.999	0.999	
0.3000	1.00	0.250	0.075	1.028	1.050	1.085	1.000	1.000	1.000	0.500	0.150	1.105	1.166	1.246	1.000	1.000	1.000	
0.4000	0.10	0.083	0.020	1.004	1.008	1.015	0.975	0.956	0.923	0.291	0.100	1.033	1.057	1.092	0.970	0.958	0.947	
0.4000	0.20	0.123	0.029	1.009	1.016	1.032	0.986	0.975	0.958	0.341	0.111	1.049	1.079	1.126	0.983	0.977	0.971	
0.4000	0.40	0.176	0.047	1.016	1.029	1.054	0.995	0.992	0.987	0.407	0.133	1.066	1.107	1.164	0.994	0.992	0.991	
0.4000	0.70	0.222	0.073	1.021	1.036	1.063	0.999	0.999	0.998	0.465	0.157	1.077	1.121	1.177	0.999	0.999	0.999	
0.4000	1.00	0.250	0.100	1.021	1.035	1.058	1.000	1.000	1.000	0.500	0.200	1.077	1.118	1.167	1.000	1.000	1.000	

exception. If we consider values of a^2 between 0.6 to 0.9 there is little or no effect of dominance.

It can be verified that for the same experimental parameters the results of Table 1 for autotetraploids are similar to those derived from diploids (Gallais 1990). With realistic contributions of dominance, it is not expected that the presence of dominance will affect selection based on the diploid formulae. To verify such a prediction, it is possible to predict the genetic advance ignoring the dominance and to compare predicted genetic advance to the true one. In this case, the coefficients β_1 and β_2 in expression (15) are wrong. Ignoring dominance is equivalent to assuming no epistasis in diploids:

$$\text{cov}(PO)_T = 2\,\text{cov}(HS)_T\,; \quad \text{cov}(HUN)_T = 1/2\,\text{cov}(HS)_T\,;$$

and

$$\text{cov}(UN)_T = \text{cov}(HS)_T.$$

As the general expressions of β_1 and β_2 are (Gallais 1990):

$$\beta_1 = \frac{\text{cov}(PO)_T}{\sigma^2_{P_T}} \frac{A}{B} \qquad A = [1+(n-1)\,r]/n\,,$$
$$\beta_2 = \frac{\text{cov}(PO)_T}{\sigma^2_{P_T}} \frac{1-A}{1-B} \qquad B = [1+(n-1)\,t]/n\,, \tag{20}$$

the coefficients that will be estimated for half-sib families are

$$\beta' = \frac{2\,\text{cov}(HS)_T}{\sigma^2_{P_T}} \frac{A_0}{B} \quad \text{with} \quad A_0 = [1+(n-1)\,r_0]/n$$
$$\beta'_2 = \frac{2\,\text{cov}(HS)_T}{\sigma^2_{P_T}} \frac{1-A_0}{1-B} \quad \text{and} \quad r_0 = \frac{1/2\,\text{cov}(HS)_T}{2\,\text{cov}(HS)_T} = 1/4. \tag{21}$$

The values of t do not change. With FS families it is only necessary to change the value of r_0.

The formulation of the problem is exactly as for diploids and the established results can be extrapolated. If $\Delta G'_0$ is the genetic advance using combined selection by ignoring dominance and ΔG_d the genetic advance when dominance is taken into account, the ratio $\Delta G'_0/\Delta G_d$ will be equal to the correlation coefficient between the predicted value of offspring when the presence of dominance is ignored and the predicted value when the presence of dominance is considered. Numerical application shows that the correlation coefficient is not greatly affected by the amount of dominance within a large range of variation. This is as expected from the consideration of the low coefficient of the components due to dominance in the expressions of covariances between relatives. Furthermore, with the analogy between epistasis in diploids and dominance in autotetraploids, it can be extrapolated that the genetic advance due to additive variance when dominance is ignored, is in fact the genetic advance due to additive advance; that is, the genetic advance after relaxation of the selection.

Conclusion

At the population level the development of the concept of test value and the definition of genetic effects for this value lead to simple and classical mating designs for the detection of dominance, and eventually of additive × additive epistasis, at the population level, by the use of second-degree statistics. With progenies in a family structure, it will be possible to estimate two variance components (additive variance and dominance variance), and with a two-way mating design it will be possible to explore the epistasis components. Such designs avoid, at least partially, the difficulties in estimating simultaneously more than two variance components with classical designs (see Chi et al. 1969; Gallais 1976, 1977). The simplification is due to the absence of tri- and tetragenic interactions for the values in test.

Considering the application to recurrent selection, the same results as for diploids remain because the effects of dominance can be generally neglected for the prediction of genetic advance. As for diploids, the combined selection appears efficient relative to individual progeny selection if the kinship between members of the family is sufficiently strong. There is nothing to gain with combined selection using half-sib families, but full-sib families can increase significantly the efficiency of combined selection if heritability is relatively low (at the level of the individual). However, when the experimental structure needed to test progenies with realistic ranges of heritabilities is taken into consideration, as well as the number of progenies per family, the gain in efficiency will be only between 10% and 30%.

The development of intercrossing by pair-crossing will be very efficient for combined selection. Scheme 3 of recurrent selection, with pair-crossing at the same time as crossing with the tester with one off-season generation, will be favoured. Without combined selection, the superiority of scheme 3 is expected to be 41%. In diploids another breeding scheme was very competitive with scheme 3: it includes testcross progenies of S_1 plants with 3–5 progenies per S_1 and the intercrossing of S_2 families of the best S_1 plants. With an annual plant and two off-season generations (one for crossing with the tester and the other for intercrossing) the gain in comparison with method 1 with intercrossing in off-season is greater than 40% and can reach 100% by the use of combined selection for low to moderate heritabilities. However, for autopolyploids it is not possible to use such a scheme because the intercrossing of the S_1 plants does not completely remove the inbreeding, or it will be necessary to use one more generation of intercrossing. The greater length of the cycle will decrease the advantage of this method. However, in both situations, (i.e., with the intercrossing of the S_1 plants with one or two generations of intercrossing), it would be interesting to consider the genetic advance per unit of time: it could be greater than with the test of S_0 plants. Unfortunately, inbreeding generates new parameters (the components of covariance between inbred relatives), which are difficult to estimate (Gallais 1976). Then a priori predictions are difficult.

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