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Effects of Competition on Means, Variances and Covariances in Quantitative Genetics with an Application to General Combining Ability Selection

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Summary. General expressions are established for means, variances and covariances, taking into account the effect of interactions between individuals. For simplicity, only groups of size two are considered so that interactions are restricted to pairs of individuals; genetic effects are reduced to additivity and to additive × additive interaction between the direct effect of an allele and the associate effect of another. The effect of family structure is studied, and some consequences of interest to plant breeding are discussed by an application to general combining ability selection. From a population genetic point of view, this approach reveals a new application of coefficients of kinship.

Introduction

In classical plant breeding theory, it is assumed that individuals do not interact. Many experiments show that such an assumption is unrealistic and untenable. Griffing (1967) has proposed a model which takes into account the interactions between genotypes of unordered groups. He has considered the effect of interactions in the case of individual selection and of group selection in terms of parent-offspring covariances (1968). He has not, however, considered the effect of interaction on other types of selection, such as general combining ability, half-sib and full-sib family selection. To approach this problem, we give expressions of the means of different types of family and of the covariances between relatives according to their repartition in different unordered groups. An application is made to general combining ability selection. We restrict the development to groups of size two.

The Model

We use Griffing's (1967) model for unordered groups, with the same notation. Considering a group of size two (i_1j_1, i_2j_2), the genotype to be evaluated will be called "direct", and the other "associate", so the genes can also be direct or associate. Restricting, for simplicity, the interactions between genes to the first order, without dominance and epistasis, the genotypic value ${}_{i_1j_1}y_{i_2j_2}$ of i_1j_1 can be partitioned as:

$$
{}_{i_1j_1}y_{i_2j_2} = \mu_R + {}_d\alpha_{i_1} + {}_d\alpha_{j_1} + {}_a\alpha_{i_2} + {}_a\alpha_{j_2} + {}_{da}(\alpha\alpha)_{i_1i_2} + {}_{da}(\alpha\alpha)_{i_1j_2} + {}_{da}(\alpha\alpha)_{j_1i_2} + {}_{da}(\alpha\alpha)_{j_1j_2}
$$

μ_R is the general mean of the population in random mating equilibrium and with a random distribution of genotypes among the groups.

${}_d\alpha_{i_1} = \Sigma p_{i_1} p_{i_2} p_{j_2}\ {}_{i_1j_1}y_{i_2j_2} - \mu_R$: direct additive effect of allele i_1,

${}_a\alpha_{i_2} = \Sigma p_{i_1} p_{j_1} p_{j_2}\ {}_{i_1j_1}y_{i_2j_2} - \mu_R$: associate additive effect of allele i_2 as measured on genotype i_1j_1,

${}_{da}(\alpha\alpha)_{i_1i_2}$ = additive × additive interaction between direct allele i_1 and associate allele i_2.

There is an analogy between the parameter ${}_{da}(\alpha\alpha)$ and the parameter of dominance: both are first order interactions between genes at the same locus.

The parameters ${}_d\alpha, {}_a\alpha, {}_{da}(\alpha\alpha)$ are defined in reference to the population in random mating equilibrium and with a random distribution of individuals. So, using the symbol E for expectation:

$$
E({}_d\alpha_{i_1}) = E({}_a\alpha_{i_2}) = 0
$$

$E_{i_2}\{{}_{da}(\alpha\alpha)_{i_1 i_2}\} = E_{i_1}\{{}_{da}(\alpha\alpha)_{i_1 i_2}\} = 0$ (E_{i_1} being E with i_1 given).

Some experimental results show that direct × associate interactions can be reduced to a linear function of associate effect (Jacquard 1970, Breese 1973). We do not consider here the consequences of such decomposition which could be useful in further developments.

Effect on the Mean of a Population of the Repartition of Genotypes

When individuals are distributed according to a family structure, there are interactions between relatives which lead to interactions of an allele i_1 with itself as expressed in two related individuals. We consider that a family is represented by an infinite number of groups (of size two) in which the related genotypes are randomly distributed. The probability of 2 alleles identical by descent occurring one in a direct genotype and the other in an associate genotype will be the coefficient of kinship (Malécot 1948) of these two genotypes. We denote it ${}_{da}\varphi(i.i)$. Thus, we can write:

$$E\{{}_{da}(\alpha\alpha)_{i_1 i_2}\} = [1 - {}_{da}\varphi(i.i)]\, E_{C_1}\{{}_{da}(\alpha\alpha)_{i_1 i_2}\} + {}_{da}\varphi(i.i)\, E_{C_2}\{{}_{da}(\alpha\alpha)_{i_1 i_2}\}$$

E_{C_1} (E_{C_2}) is the expectation in the situation where i_1 and i_2 are not (are for E_{C_2}) identical by descent. Since in condition C_2, $i_1 \equiv i_2$, we replace i_1 and i_2 by i, and we write:

$$E\{{}_{da}(\alpha\alpha)_{i_1 i_2}\} = {}_{da}\varphi(i.i)E\{{}_{da}(\alpha\alpha)_{ii}\}$$

and the mean μ_F will be:

$$\mu_F = \mu_R + 4\,{}_{da}\varphi(i.i)\,E\{{}_{da}(\alpha\alpha)_{ii}\}. \tag{1}$$

With a group of size $n > 2$, restricting interactions between two individuals, we must also consider associate × associate interactions. In this case:

$$\mu_F = \mu_R + 4(n-1)\,{}_{da}\varphi(i.i)E\{{}_{da}(\alpha\alpha)_{ii}\} + 2(n-1)(n-2)\,{}_{aa}\varphi(i.i)E\{{}_{aa}(\alpha\alpha)_{ii}\}$$

${}_{aa}\varphi(i.i)$ is the probability of two alleles, taken one from each of two associate zygotes, being identical by descent.

For half-sib and full-sib families, we have respectively:

$${}_{da}\varphi(i.i) = {}_{aa}\varphi(i.i) = 1/8,\quad {}_{da}\varphi(i.i) = {}_{aa}\varphi(i.i) = 1/4\ ,$$

and such coefficients are zero with random distribution of individuals.

Covariances between Competing Arbitrary Relatives

As introduced by Griffing (1967), selection can be at the individual or at the group level. However, the response to selection is evaluated at the group level so, to predict the genetic advance according to the selection procedure, we have to consider two types of covariance: covariances between direct individuals and their related groups; and covariances between groups. Both types can be studied by the consideration of covariances between two random zygotes taken one from each of two different groups. We use a general method already developed by Gillois (1964), Bouffette (1966) and Gallais (1970, 1974). For the sake of simplicity, the genetic effects and the size of the groups will be restricted, as in the first part of this study. Our aim is only to show the general method of derivation of the covariance formula.

$$\mathrm{Cov}(Z_I, Z_J) = E(G_I - \mu_R)(G_J - \mu_R) - E(G_I - \mu_R)E(G_J - \mu_R)$$

$E(G_I - \mu_R)(G_J - \mu_R)$ can be written:

$$4E({}_d\alpha\,{}_d\alpha') + 4E({}_a\alpha\,{}_a\alpha') + 4[E({}_a\alpha\,{}_d\alpha') + E({}_d\alpha\,{}_a\alpha')] +$$
$$8[E\{{}_a\alpha\,{}_{da}(\alpha\alpha)'\} + E\{{}_a\alpha'\,{}_{da}(\alpha\alpha)\}] +$$
$$8[E\{{}_d\alpha\,{}_{da}(\alpha\alpha)'\} + E\{{}_d\alpha'\,{}_{da}(\alpha\alpha)\}] +$$
$$16[E\{{}_{ad}(\alpha\alpha)\,{}_{ad}(\alpha\alpha)'\}]$$

A prime denotes parameters involving genes from J; parameters without a prime involve genes from I. We have to compute each expectation applying the theorem of conditional expectations. Thus:

$$E\left({}_{d}\alpha\,{}_{d}\alpha'\right) = \left[1 - {}_{dd}\varphi(i|i)\right] E_{C_1}\left({}_{d}\alpha_i\,{}_{d}\alpha_i\right) + {}_{dd}\varphi(i|i)\,E\left({}_{d}\alpha_i^2\right) = {}_{dd}\varphi(i|i)\,E\left({}_{d}\alpha_i^2\right) \qquad (2)$$

$$E\left({}_{a}\alpha\,{}_{a}\alpha'\right) = \left[1 - {}_{\alpha\alpha}\varphi(i|i)\right] E_{C_1}\left({}_{a}\alpha_i\,{}_{a}\alpha_i\right) + {}_{aa}\varphi(i|i)\,E\left({}_{a}\alpha_i^2\right) = {}_{aa}\varphi(i|i)\,E\left({}_{a}\alpha_i^2\right) \qquad (3)$$

$$E\left({}_{a}\alpha\,{}_{d}\alpha'\right) = E\left({}_{a}\alpha'\alpha_{d}\right) = {}_{da}\varphi(i|i)\,E\left({}_{a}\alpha_i\,{}_{d}\alpha_i\right) \qquad (4)$$

where the ${}_{xy}\varphi(i|j)$ represent coefficients of kinship, i.e., the probability of two alleles identical by descent $(i = j)$, i from the zygote x of one group, j from the zygote y of another group, x and y being either associate (a) or direct (d). Similarly:

$$E\left\{{}_{d}\alpha\,{}_{da}(\alpha\alpha')\right\} = E\left\{{}_{d}\alpha'\,{}_{da}(\alpha\alpha)\right\} = {}_{d.da}\varphi(i|i.i)\,E\left\{{}_{d}\alpha_i\,{}_{da}(\alpha\alpha)_{i\,i}\right\} \qquad (5)$$

$$E\left\{{}_{a}\alpha\,{}_{da}(\alpha\alpha')\right\} = E\left\{{}_{d}\alpha'\,{}_{da}(\alpha\alpha)\right\} = {}_{a.da}\varphi(i|i.i)\,E\left\{{}_{a}\alpha_i\,{}_{da}(\alpha\alpha)_{i\,i}\right\} \qquad (6)$$

where $\varphi(i|i.i)$ is the probability of three genes identical by descent taken one from each of three zygotes I, J, K, I being a direct or associate zygote of one group, J and K respectively direct and associate zygotes of another. The expectations are zero for all other states of identity of the three genes. When four genes are involved:

$$\begin{aligned} E\left\{{}_{da}(\alpha\alpha)\,{}_{da}(\alpha\alpha)'\right\} = {} & {}_{da\cdot da}\varphi(i.j|i.j)\,E\left\{{}_{da}(\alpha\alpha)^2_{ij}\right\} + \\ & {}_{da\cdot da}\varphi(i.i|j.j)\,E\left\{{}_{da}(\alpha\alpha)_{ii}\,{}_{da}(\alpha\alpha)_{jj}\right\} + \\ & {}_{da\cdot da}\varphi(i.i|i.i)\,E\left\{{}_{da}(\alpha\alpha)^2_{ii}\right\} + \\ & {}_{da\cdot da}\varphi(i.j|j.i)\,E\left\{{}_{da}(\alpha\alpha)_{ij}\,{}_{da}(\alpha\alpha)_{ji}\right\} \end{aligned} \qquad (7)$$

$(i.j|i.j)$, $(i.i|j.j)$, $(i.i|i.i)$, $(i.j|j.i)$ represent the situations which lead to a non-zero associated expectation. The notation $(i.j|k.l)$ concerns genes i and k from different direct zygotes I and K, and genes j, l from their respective associates K and L. This separates genes from different zygotes of the same group. $\varphi(\,|\,)$ is the associate probability. Using the expressions 2 to 7 and those of the correction factor which result from the expression of the mean (1), we derive the covariance formula given in appendix 1.

As an application, Table 1 gives the values of the coefficients of kinship for covariances between individuals distributed in groups of half sib and full sib families. Such covariances are, respectively, the variances between half sib and independent full sib families, with a family distribution of individuals.

Table 1. Values of coefficients of kinship appearing in the expression of covariances between half sib and full sib families, with a family distribution of individuals and interactions between genes restricted to the first order without dominance and epistasis

Coefficient	Half sib	Full sib
${}_{dd}\varphi(i\|i) = {}_{da}\varphi(i\|i) = {}_{aa}\varphi(i\|i)$	1/8	1/4
${}_{d.da}\varphi(i\|i.i) = {}_{d.da}\varphi(i\|i.i)$	1/32	1/16
${}_{da.da}\varphi(i.j\|i.j)$	1/128	3/64
${}_{da.da}\varphi(i.j\|j.i)$	1/128	3/64
${}_{da.da}\varphi(i.i\|j.j)$	1/128	3/64
${}_{da.da}\varphi(i.i\|i.i)$	1/128	1/64

If individuals are randomly distributed among the groups the covariance formula is reduced to:

$$4\,{}_{dd}\varphi(i|i)E\left({}_{d}\alpha_i^2\right) + 4\,{}_{aa}\varphi(i|i)E\left({}_{a}\alpha_i^2\right) + 8\,{}_{da}\varphi(i|i)E\left({}_{d}\alpha_i\,{}_{a}\alpha_i\right)$$

because

$${}_{d.da}\varphi(i|i.i) = {}_{a.da}\varphi(i|i.i) = {}_{da.da}\varphi(i.j|i.j) = {}_{da.da}\varphi(i.j|j.i) = {}_{da.da}\varphi(i.i|j.j) = {}_{da.da}\varphi(i.i|i.i) = \varphi(i.i) = 0$$

and for the particular case of parent-offspring relationship as

$${}_{dd}\varphi(i|i) = 1/4, \qquad {}_{da}\varphi(i|i) = 1/8, \qquad {}_{aa}\varphi(i|i) = 0$$

$$\text{cov PO} = E\left({}_{d}\alpha_i^2\right) + E\left({}_{d}\alpha_i\,{}_{a}\alpha_i\right),$$

we find the result given by Griffing (1967).

The variance can be deduced directly from covariance by equating zygotes I and J in the formula. Coefficients $\varphi(\,|\,)$ thus become coefficients of relationship of an individual with itself. It is clear that the total genotypic variance will also depend on the family repartition.

Case of Covariances between Related Groups

Two groups I and J will be related if one or several members of group I are related to one or several members of group J. Covariances between related groups are necessary for the study of group selection introduced by Griffing (1967). Clearly, if the value of a group is evaluated by the average of the values of its members, the covariance between two groups will be equal to the covariance between two random members taken one from each group. However a direct approach to the covariance between groups lead to a reduction of the number of parameters. Indeed the performance of a group (ij,kl) of size two can be written with our simplifying restrictions:

$$2y_{ij,kl} = 2\mu_R + \alpha'_i + \alpha'_j + \alpha'_k + \alpha'_l + (\alpha'\alpha')_{ik} +$$

$$(\alpha'\alpha')_{il} + (\alpha'\alpha')_{jk} + (\alpha'\alpha')_{jl}$$

$$\text{with } \alpha'_i = {}_d\alpha_i + {}_a\alpha_i \qquad (8)$$

$$\text{and } (\alpha'\alpha')_{ik} = {}_{da}(\alpha\alpha)_{ik} + {}_{da}(\alpha\alpha)_{ki}$$

Using as above the properties of conditional expectations, it gives for the covariance:

$$4\varphi(i|i)E(\alpha'_i)^2 + 8\varphi(i|i.i)E\{\alpha'_i(\alpha'\alpha')_{ii}\} +$$

$$4\varphi(i.j|i.j)E(\alpha'\alpha')^2_{ij} + 4\varphi(i.i|i.i)E(\alpha'\alpha')^2_{ii} + \qquad (9)$$

$$4[\varphi(i.i|j.j) - \varphi_I(i.i)\varphi_J(i.i)][E(\alpha'\alpha')_{ii}]^2$$

Within a group, a genotype is at the same time direct and associate, so subscripts for $\varphi(\,|\,)$ are not necessary. As above, the notation (i.j|k.l) concerns genes i and j, respectively, from zygotes I and J of one group, and genes k and l from zygotes K and L of another.

It can be verified that the consideration of relations (8) in (9) leads to the covariance formula given in appendix 1, with the conditions that

$$\varphi(i|i) = {}_{d.d}\varphi(i|i) = {}_{a.a}\varphi(i|i) = {}_{d.a}\varphi(i|i)$$

$$\varphi(i.j|i.j) = 2\,{}_{da.da}\varphi(i.j|i.j) = 2\,{}_{da.da}\varphi(i.j|j.i)$$

$$\varphi(i|i.i) = {}_{d.da}\varphi(i|i.i) = {}_{a.da}\varphi(i|i.i)$$

$$\varphi(i.i|i.i) = {}_{da.da}\varphi(i.i|i.i),\ \varphi(i.i|j.j) = {}_{da.da}\varphi(i.i|j.j)$$

Indeed, there are such relations between the two kinds of coefficients. With a random distribution of individuals among the groups,

$$\varphi(i.i) = \varphi(i|i.i) = \varphi(i.j|i.j) = \varphi(i.i|i.i) = \varphi(i.i|j.j) = 0,$$

so the covariance is reduced to: $4\varphi(i|i)E(\alpha'_i)^2$ which is always positive. This a a generalization of Griffing's results.

Some Consequences of Interest to Plant Breeding: Application to General Combining Ability Selection

It is not the aim of this paper to give all implications of competition in plant breeding theory. Griffing (1967-1968) has considered the case of phenotypic (mass) selection with a random distribution of individuals. We only want to give here, as an example, the effect of interactions between individuals on the meaning of the combining abilities and on selection based on general combining ability.

1. Interpretation of the combining abilities

We consider mainly the case of the general combining ability (GCA). The GCA of a genotype with genes (i,j) can be evaluated according to four methods:

1st method: the half sib progenies are mixed and the individuals randomly distributed among the groups. The

GCA of a parent ij is the expected value of its half sib progeny:

$$g_1 = \mu_R + 1/2\,({}_{d}\alpha_{i} + {}_{d}\alpha_{j}) \qquad (10)$$

because all other effects have a zero expectation (they involved genes not related to i and j).

2nd method: with the same repartition as in the 1st method, the GCA is evaluated as the expectation of groups with one half-sib of the same family:

$$g_2 = \mu_R + 1/2\,({}_{d}\alpha_{i} + {}_{d}\alpha_{j} + {}_{a}\alpha_{i} + {}_{a}\alpha_{j}) =$$

$$g_1 + 1/2\,({}_{a}\alpha_{i} + {}_{a}\alpha_{j}) \qquad (11)$$

3rd method: the half-sib families are evaluated in groups with individuals of the same family ("pure stand" test)

$$g_3 = g_2 + 1/4\,[{}_{da}(\alpha\alpha)_{ij} + {}_{da}(\alpha\alpha)_{ji} + {}_{da}(\alpha\alpha)_{ii} + {}_{da}(\alpha\alpha)_{jj}] \qquad (12)$$

4th method: the individuals in a group are full-sib. In this case it can be shown (see appendix 2) that:

$$g_4 = g_3 + 1/2\,E\,({}_{da}(\alpha\alpha)_{ii}) \qquad (13)$$

This result has been established in the absence of dominance and with interactions between genes restricted to the first order. Lifting these restrictions leads to a similar result. Equation (13) in particular shows that the variance of GCA will be the same for the last two methods of evaluation.

The same approach can be developed for the specific combining ability, (SCA) considering the expectation of full sib families. All individuals can be randomly distributed among the groups and the performance of the full sib family can be evaluated as the expectation of the value of its members within a group (1st method), or as the expectation of the value of groups with one individual of the same full sib family (2nd method). In a 3rd method (the only one used by the plant breeder until now) the full sib families can be evaluated in a group with individuals of the same full-sib family ("pure stand" test). In this case, interactions between genes in different individuals mimic dominance and can induce specific combining ability in the absence of dominance.

2. Genetic advance according to the method of evaluation of GCA

We have shown above the influence of the experimental structure on the estimation of GCA. This will determine the expected genetic advance. Whatever the method of GCA evaluation, the genetic advance is relative to a population with a random distribution of individuals among the groups. We wish to predict the expected performance of groups. The expected contribution to the value of a group of the half sib from an individual with genotype ij will be:

$$g_2 = \mu_R + 1/2\,({}_{d}\alpha_{i} + {}_{d}\alpha_{j} + {}_{a}\alpha_{i} + {}_{a}\alpha_{j})$$

By selection on one sex only, the expected genetic advance for a given method of evaluation i, will be:

$$\Delta G_i = S\,\frac{\mathrm{cov}\ g_i g_2}{\mathrm{var}\ g_i} \qquad (14)$$

where S is the differential selection, and $\mathrm{var}\, g_i$ the phenotypic variance of half-sib families according to the method of evaluation i. Table 2 gives the expression of $\mathrm{cov}\, g_i g_2$ and in appendix 3 are the values of the associated coefficients φ for such covariances between half-sibs. It appears that only method 2 can assure a positive advance. In Griffing's terminology, method 2 is a group selection method. Method 1 can lead to no change or to a negative change when $E\,({}_{a}\alpha_{i}\,{}_{d}\alpha_{i})$ is negative and greater in absolute value than $E\,({}_{d}\alpha_{i}^{2})$. Indeed, experimental results show that at the genotypic level the correlation between direct and associate effects is negative (Jacquard 1970, Gallais 1972). These are the same results as those established by Griffing (1967) for phenotypic selection. Methods 3 and 4 classically used by the plant breeder can be better than method 1, because they consider both direct and associate effects of the genes involved in the selected parent. The problem for these methods is to know the sign and amplitude of parameters such as $E\,({}_{a}\alpha_{i}\,{}_{da}(\alpha\alpha)_{ii})$ or $E\,({}_{d}\alpha_{i}\,{}_{da}(\alpha\alpha)_{ii})$.

Clearly, in the absence of interactions direct × associate and of associate effects, all covariances $\mathrm{cov}\, g_i g_2$ are reduced to the classical result $1/2\,E\left(\alpha_i^2\right) = 1/4\,\sigma_A^2$.

Table 2. Expression of the covariance between value of half sibs individuals in method i and their contribution to the value of the group with a random distribution of individuals. Such covariance determines, the genetic advance (see formula 14)

Methods	cov $g_i\, g_2$	Sign
1	$1/2\ E\left({}_{d}\alpha_i^2\right) + 1/2\ E\left({}_{a}\alpha_i\ {}_{d}\alpha_i\right)$	$\lessgtr\ 0$
2	$1/2\ E\left({}_{d}\alpha_i^2\right) + 1/2\ E\left({}_{a}\alpha_i^2\right) + E\left({}_{a}\alpha_i\ {}_{d}\alpha_i\right) = \sigma^2_{g_2}$	$>\ 0$
3 or 4	$\sigma^2_{g_2} + 1/4\ E\left\{{}_{a}\alpha_i\ {}_{da}(\alpha\alpha)_{ii}\right\} + 1/4\ E\left\{{}_{d}\alpha_i\ {}_{da}(\alpha\alpha)_{ii}\right\}$	$\lessgtr\ 0$

Conclusion

The first extension of the Griffing theory given in this paper is a new step towards redeveloping all breeding theory to account for competition effects. Some important consequences for the plant breeder are expected from such developments. The application to GCA selection gives an example of this. From the point of view of population genetics, this extension reveals a new application for coefficients of kinship. The same approach may be extended to groups of arbitrary size and to admit dominance (direct and associate), direct dominance × associate dominance, inbreeding, and more complex situations.

Appendix 1 Covariances between competing arbitrary relatives. Groups of size two; genetic effects restricted to additivity and additive × associate interactions

$$4\,{}_{dd}\varphi(i|i)E\left({}_{d}\alpha_i^2\right) + 4\,{}_{aa}\varphi(i|i)E\left({}_{a}\alpha_i^2\right) +$$

$$8\,{}_{da}\varphi(i|i)E\left({}_{d}\alpha_i\,{}_{a}\alpha_i\right) + 16\,{}_{d.da}\varphi(i|i.i)E\left\{{}_{d}\alpha_i\,{}_{da}(\alpha\alpha)_{ii}\right\} +$$

$$16\,{}_{a.da}\varphi(i|i.i)E\left\{{}_{a}\alpha_i\ {}_{da}(\alpha\alpha)_{ii}\right\} +$$

$$16\,{}_{da.da}\varphi(i.j|i.j)E\left\{{}_{da}(\alpha\alpha)_{ij}^2\right\} +$$

$$16\left[{}_{da.da}\varphi(i.i|j.j) - \varphi_I(i.i)\varphi_J(i.i)\right]\left\{E\,{}_{da}(\alpha\alpha)_{ii}\right\}^2 +$$

$$16\,{}_{da.da}\varphi(i.i|i.i)E\left\{{}_{da}(\alpha\alpha)_{ii}^2\right\} +$$

$$16\,{}_{da.da}\varphi(i.j|j.i)E\left\{{}_{da}(\alpha\alpha)_{ij}\ {}_{da}(\alpha\alpha)_{ji}\right\}$$

Appendix 2 Relationship between GCA evaluated from separate (FS) or mixed (HS) full sib families. The value of a full sib family issued from the cross of two genotypes ij and kl and evaluated in competition with itself in a group of size two, will be:

$$\mu_R + 1/2\left({}_{d}\alpha_i + {}_{d}\alpha_j + {}_{d}\alpha_k + {}_{d}\alpha_l + {}_{a}\alpha_i + {}_{a}\alpha_j + {}_{a}\alpha_k + {}_{a}\alpha_l\right) +$$

$$1/4\left\{{}_{da}(\alpha\alpha)_{ii} + {}_{da}(\alpha\alpha)_{jj} + {}_{da}(\alpha\alpha)_{kk} + {}_{da}(\alpha\alpha)_{ll}\right\} +$$

$$1/4\left\{{}_{da}(\alpha\alpha)_{ij} + {}_{da}(\alpha\alpha)_{ji} + {}_{da}(\alpha\alpha)_{ik} + {}_{da}(\alpha\alpha)_{ki} +\right.$$

$${}_{da}(\alpha\alpha)_{il} + {}_{da}(\alpha\alpha)_{li} + {}_{da}(\alpha\alpha)_{jk} + {}_{da}(\alpha\alpha)_{kj} + {}_{da}(\alpha\alpha)_{jl} +$$

$$\left.{}_{da}(\alpha\alpha)_{lj} + {}_{da}(\alpha\alpha)_{kl} + {}_{da}(\alpha\alpha)_{lk}\right\}$$

Taking the expectation on k and l and following expression (12) gives the GCA evaluated with separate full sib families, as given in expression (13).

Appendix 3 Values of the coefficients $\varphi(\,|\,)$ for different types of covariances between half-sibs which determine the expected genetic advance according to the method of evaluation of GCA.

The other coefficients $\varphi(\,|\,)$ are zero except $\varphi(i|i)$ for methods 3 and 4 but, as $\varphi_J(i|i)$ for a random distribution of individuals is zero, the correction factor in the covariance is zero.

Method	${}_{dd}\varphi(i\|i)$	${}_{aa}\varphi(i\|i)$	${}_{da}\varphi(i\|i)$	${}_{d.da}\varphi(i\|i.i)$	${}_{a.da}\varphi(i\|i.i)$
1	1/8	0	1/16	0	0
2	1/8	1/8	1/8	0	0
3 or 4	1/8	1/8	1/8	1/64	1/64

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