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A General Approach to the Concept of Varietal Ability for Synthetic Varieties*

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Summary. Genetic effects for varietal value are defined at the level of the population of k-parent synthetic varieties. A simple expression for the total variance among synthetics arises directly from these definitions. A general expression for the covariance among related synthetics is given. Genetic effects are also defined in a completely general way so as to allow for any system of testing and used to derive an expression for the genetic advance in recurrent selection for varietal value. Covariances between relatives evaluated in the system of testing and in varietal combination are introduced, allowing a direct expression of the genetic advance in varietal development when parents are selected either individually or in groups. Some general implications for plant breeding are outlined.

Key words: Varietal ability – Synthesising ability – Synthetic varieties – Breeding methods

1 Introduction

Hill (1966, 1972) has proposed, from an empirical point of view, the analysis of the value of a synthetic variety in terms of main effects of parents and interactions of all possible order among them. He called such effects 'combining abilities'. However, the concept of varietal ability and its importance in synthetic variety development was emphasised by Wright (1973, 1974). In analogy with general combining ability as used in hybrid variety production, the general synthesising ability of an individual (G.S.A.) was defined as the expected value of all k-parent synthetics from a given population with this as a common parent. Gallais (1975) extended this concept at the population level, and included specific synthesising abilities (S.S.A.) of different orders, defined as the interactions between 2, 3..., k-parents. Clearly, such a complete set of definitions can be made for synthetics of different sizes, and from a fixed or random point of view, allowing the formulation of a general theory of varietal development (Gallais 1977, 1978).

Wright (1974) studied the expected advance of varietal value during both the population improvement and varietal construction phases of a breeding programme for different methods of testing, but used a simple model which excluded multiple allelism and epistasis. The aim of this paper is to give a completely general approach to the breeding theory of synthetic varieties in diploid crops through the definition of genetic effects for varietal value and for the criterion of testing.

2 Population Parameters

The analysis of genetic variance in a random mating population developed by Kempthorne (1957) and others is based on a model for gene effects which uses the individual genotype as its fundamental unit. The expectations of various covariances among relatives are deduced according to their degree of relationship. Such a model can be extended to examine statistics which involve synthetic varieties (Wright 1974; Gallais 1974b). However, an alternative procedure is to use the synthetic variety itself as the basic unit and to redefine all genetic effects with respect to a population of such synthetics. This approach is very similar to that used by Griffing (1967) in the study of group selection, and in fact the selection of synthetics can be regarded as a particular case of group selection.

From a non-inbred population the population of synthetics of size k is obtained from the k-way combinatorial product involving the base population genotype array. For diploids reduced to one locus:

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$$(\Sigma\, p_{i_1} p_{j_1} (A_{i_1} A_{j_1}))(\Sigma\, p_{i_2} p_{j_2} (A_{i_2} A_{j_2})) \ldots$$
$$(\Sigma\, p_{i_k} p_{j_k} (A_{i_k} A_{j_k}))$$
$$= \Sigma\, p_{i_1} p_{j_2} \ldots p_{i_k} p_{j_k} (A_{i_1} A_{j_1}, A_{i_2} A_{j_2} \ldots A_{i_k} A_{j_k}$$

where p_{i_k} is the frequency of allele A_{i_k}.

The genotypic value of a particular k-parent synthetic drawn from such a population can be expanded according to a factorial model (without epistasis).

$$S_{i_1 j_1 i_2 j_2 \ldots i_k j_k} = \mu_S + \sum_{n=1}^{n=k} ({}_S\alpha_{i_n} + {}_S\alpha_{j_n}) + \sum_{n=1}^{n=k} {}_S\beta_{i_n j_n} + \sum_{m<n} \sum ({}_S\beta_{i_m i_n} + {}_S\beta_{i_m j_n} + {}_S\beta_{j_m i_n} + {}_S\beta_{j_m j_n})$$

μ_S is the mean of all varieties with k parents, equal to the varietal value of the population;

${}_S\alpha_{i_1}$ is the additive effect of gene A_{i_1} in synthetic combination:

$${}_S\alpha_{i_1} = \Sigma\, p_{j_1} p_{i_2} p_{j_2} \ldots S_{i_1 j_1 i_2 j_2 \ldots} - \mu_S$$

${}_S\beta_{i_1 j_1}$ is the dominance effect:

$${}_S\beta_{i_1 j_1} = \Sigma\, p_{i_2} p_{j_2} \ldots S_{i_1 j_1 i_2 j_2 \ldots} - {}_S\alpha_{i_1} - {}_S\alpha_{j_1} - \mu_S$$

${}_S\alpha_i$ and ${}_S\beta_{ij}$ are related to the classical parameters as follows (Gallais 1978)

$${}_S\alpha_i = (1/k)\{\alpha_i + (1/4k)(\beta_{ii} - E(\beta_{ii}))\}$$

$${}_S\beta_{ij} = (1/2k^2)\beta_{ij}$$

Epistatic effects could be defined in the same manner.

Each parameter of the factorial model has an expectation of zero and is independent of the others. Additive and dominance variances for varietal value can be defined:

$$\sigma^2_{A_S} = 2\, E({}_S\alpha_i^2)$$

$$\sigma^2_{D_S} = E({}_S\beta_{ij}^2)$$

Noting the occurrence of independent ${}_S\alpha_i$ and ${}_S\beta_{ij}$ terms in the expectation of the mean value of a synthetic, the total genetic variance among synthetics is

$$\sigma^2_{G_S} = k\,\sigma^2_{A_S} + k(2k-1)\,\sigma^2_{D_S}$$

which is a simple derivation of a formula given by Hill (1971).

3 Covariances Between Related Synthetics

By considering a k-parent synthetic as the fundamental unit of analysis, it is possible to study the covariance among related synthetics in the same way as classical analysis considers that among related individuals. According to a general theory of covariances among relatives (Gallais 1974a, 1976) we can write the covariance between two synthetics S_x and S_y as:

$$\begin{aligned}\operatorname{cov} S_x S_y &= 4\,\psi_S(i\,|\,i)\,k^2 E({}_S\alpha^2_{i_1}) \\ &\quad + \psi_S(ij\,|\,ij)\,k^2(2k-1)^2\, E({}_S\beta^2_{i_1 j_1}) \\ &= 2\,\psi_S(i\,|\,i)\,k^2\sigma^2_{A_S} \\ &\quad + \psi_S(ij\,|\,ij)\,k^2(2k-1)^2\sigma^2_{D_S}\end{aligned}$$

because there are altogether k^2 terms of the form $E({}_S\alpha_i\, {}_S\alpha_{i'})$ and $k^2(2k\text{-}1)^2$ of the form $E({}_S\beta_{ij}\, {}_S\beta_{i'j'})$. Here ψ_S (i|i) is equivalent to the classical coefficient of kinship, and ψ_S(ij|ij) to the coefficient of kinship for two alleles drawn from the parental population. This is the same expression as the covariance between relatives in a random mating population except that σ^2_A and σ^2_D are respectively replaced by $k^2\sigma^2_{A_S}$ and $k^2(2k\text{-}1)^2\sigma^2_{D_S}$.

This general formula can be applied to the study of the variance among synthetics by putting $S_x = S_y$, and in this case ψ_S(i|i) and ψ_S(ij|ij) are the coefficients of kinship of a synthetic with itself:

$$\psi_S(i|i) = 1/(2k), \quad \psi_S(ij|ij) = 1/(k(2k-1))$$

If we consider the covariance between synthetics having one parent in common, this gives the variance of general synthesising ability $\sigma^2_{G_S}$ with

$$\psi_{G_S}(i|i) = 1/(2k^2) \quad \psi_{G_S}(ij|ij) = 1/(k^2(2k-1)^2)$$
$$\sigma^2_{G_S} = \sigma^2_{A_S} + \sigma^2_{D_S}$$

Similar reasoning can be used to lead to the covariance between synthetics with n parents in common:

$$\operatorname{cov} S_x S_y = n\sigma^2_{A_S} + n(2n-1)\,\sigma^2_{D_S}$$

4 Some Applications to the Theory of Selection of Synthetics

4.1 Within Population Improvement of Varietal Value

Applying the general principles of linear prediction, the genetic advance in population varietal value following one cycle of selection is (Gallais 1977)

$$\mu_{V_{n+1}} - \mu_{V_n} = (\mu_{V_{n,1}} - \mu_{V_n}) + i\,\theta\, k \frac{\operatorname{cov}[\mathscr{T}_P(G), \mathscr{M}_{PV}(G)]}{\sqrt{\operatorname{var}[\mathscr{T}_P(G)]}}$$

where $\mu_{V_{n+1}}$ is the varietal value of the population at generation (n+1) after selection at generation n, and

$\mu_{V_{n,1}}$ is the varietal value at (n+1) without selection. The term in brackets therefore represents changes which can occur during one cycle of relaxation of selection during a recurrent selection scheme. $\underline{i}$ is the selection intensity in standard deviation units, θ expresses the control of selection on the two sexes ($\theta = 1$ or 2), and k is the number of parents. cov $[\mathscr{T}_P(G), \mathscr{M}_{PV}(G)]$ is the covariance of the value of a genotype (G) under a particular system of testing $\mathscr{T}_P(G)$ and the varietal value of its progeny following random mating $\mathscr{M}_{PV}(G)$. While cov$[\mathscr{T}_P(G), \mathscr{M}_{PV}(G)]$ represents the relationship of one individual or predictor to varietal value, θk is the number of such predictors.

Consideration is confined here to the expression of the covariance cov $[\mathscr{T}_P(G), \mathscr{M}_{PV}(G)]$. The value of genotype A_iA_j according to a particular system of testing $\mathscr{T}$ can be expanded as follows

$$\mathscr{T}_P(A_iA_j) = \mu_T + {}_T\alpha_i + {}_T\alpha_j + {}_T\beta_{ij}$$

An equivalence can now be established between these parameters and those defined for any particular system of testing. For example, with selection based on general combining ability

$$\mathscr{T}_P(A_iA_j) = \mu + (1/2)(\alpha_i + \alpha_j)$$

so that

$${}_T\alpha_i = (1/2)\alpha_i \quad \text{and} \quad {}_T\beta_{ij} = 0;$$

In general, any system of testing can be evaluated by substitution of parameters of one of three types. For those systems which do not involve inbreeding (e.g. mass selection, selection for general combining ability [G.C.A.]), the classical random mating parameters α_i and β_{ij} can be used. The use of S1 families require the definition of new parameters $({}_T\alpha_i = \alpha_i + 1/4\ \beta_{ii})$ while for selection based on general synthesising ability (G.S.A.) the varietal effects ${}_S\alpha_i$ and ${}_S\beta_{ij}$ are appropriate and thus lead to covariances which can be written as variances. Table 1 summarises the equivalences of the parameters for some breeding methods.

The covariance cov$[\mathscr{T}_P(G), \mathscr{M}_{PV}(G)]$ can be expressed as a covariance between relatives. Including additive, dominance, and additive x additive interactions, this is

$$\begin{aligned}\text{cov}[\mathscr{T}_P(G), \mathscr{M}_{PV}(G)] &= 4\,\psi(i|i)\,E({}_T\alpha_i\ {}_S\alpha_i) \\ &\quad + \psi(ij|ij)\,E({}_T\beta_{ij}\ {}_S\beta_{ij}) \\ &\quad + 16\,\psi(ik|ik) \\ &\qquad E({}_T(\alpha\alpha)_{ik}\ {}_S(\alpha\alpha)_{ik}) \\ &= 2\,\psi(i|i)\,\sigma_{A_TA_S} \\ &\quad + \psi(ij|ij)\,\sigma_{D_TD_S} \\ &\quad + 4\,\psi(ik|ik)\,\sigma_{AA_TAA_S},\end{aligned}$$

where

$$\sigma_{A_TA_S} = 2\,E({}_T\alpha_i\ {}_S\alpha_i),\ \sigma_{D_TD_S} = E({}_T\beta_{ij}\ {}_S\beta_{ij}),$$

and

$$\sigma_{AA_TAA_S} = 4\,E({}_T(\alpha\alpha)_{ik}\ {}_S(\alpha\alpha)_{ik})$$

In most selection schemes, one generation of intercrossing is allowed before reselection. In this case, the covariance is that of parent and offspring, so that $\psi(i|i) = 1/4$ and $\psi(ij|ij) = 0$. In the absence of linkage $\psi(ik|ik) = [\psi(i|i)]^2 = 1/16$, while the coefficients for other epistatic effects are zero. Thus

$$\text{cov}[\mathscr{T}_P(G), \mathscr{M}_{PV}(G)] = (1/2)\sigma_{A_TA_S} + (1/4)\sigma_{AA_TAA_S}$$

The expectation of the covariance for any testing method is then derived by substitution of the appropriate parameters from Table 1. Some breeding methods in common use involve more than one generation of intercrossing between selection cycles: for example, selected half-sib families may be allowed to intercross to reconstitute the population. In this case, cov$[\mathscr{T}_P(G), \mathscr{M}_{PV}(G)]$ is a covariance of grand-parent and grand-offspring, with $\psi(i|i) = 1/8$ and $\psi(ik|ik) = 1/64$, so that

Table 1. Equivalence of ${}_T\alpha_i$ and ${}_T\beta_{ij}$ parameters to classical and varietal parameters for various population improvement methods

Method of assessment	$\mathscr{T}_P(G)$	${}_T\alpha_i$	${}_T\beta_{ij}$
Phenotype	$\mu + \alpha_i + \alpha_j + \beta_{ij}$	α_i	β_{ij}
G.C.A.	$\mu + (1/2)(\alpha_i + \alpha_j)$	$(1/2)\alpha_i$	0
S_1	$\mu_I + \alpha_i + \alpha_j + (1/4)(\beta_{ii} + \beta_{jj}) + (1/2)\beta_{ij}$	${}_I\alpha_i = \alpha_i + (1/4)\beta_{ii}$	$(1/2)\beta_{ij}$
G.S.A.	$\mu_S + {}_S\alpha_i + {}_S\alpha_j + {}_S\beta_{ij}$	${}_S\alpha_i$	${}_S\beta_{ij}$
G.S.A. of offspring	$\mu_S + (1/2)({}_S\alpha_i + {}_S\alpha_j)$	$(1/2)_S\alpha_i$	0

Table 2. Covariance between the value of a genotype according to the value of test $\mathcal{T}_P$, which defines the breeding method, and the varietal value of its offspring $\mathcal{M}_{PV}$ following one generation of intercrossing

Breeding method	Cov $\mathcal{T}_P, \mathcal{M}_{PV}$
Individual Selection	
Mass selection	$(1/2)\sigma_{A.A_S} + (1/4)\sigma_{AA.AA_S}$
Selection on G.C.A.	$(1/4)\sigma_{A.A_S} + (1/16)\sigma_{AA.AA_S}$
Selection on S_1	$(1/2)\sigma_{A_IA_S} + (1/4)\sigma_{AA_IAA_S}$
Selection on parental G.S.A.	$(1/2)\sigma^2_{A_S} + (1/4)\sigma^2_{AA_S}$
Selection on G.S.A. of offspring	$(1/4)\sigma^2_{A_S} + (1/16)\sigma^2_{AA_S}$
Selection on parental G.S.A. in n-syn	$(1/2)\sigma_{A_{S_n}A_{S_k}} + (1/4)\sigma_{(AA)_{S_n}(AA)_{S_k}}$
Family selection	
HS families	$(1/8)\sigma_{A.A_S} + (1/64)\sigma_{AA.AA_S}$

$$\mathrm{cov}[\mathcal{T}_P(G), \mathcal{M}_{PV}(G)] = (1/4)\sigma_{A_TA_S} + (1/16)\sigma_{AA_TAA_S}$$

A simpler method can be used to derive the covariance for those methods which involve only classical parameters in the testing system $\mathcal{T}_P$. The coefficients of kinship appropriate to the type of relationship are used to give the covariance with direct reference to the random mating population. For selection according to G.C.A. for example:

$$\psi(i|i) = 1/8, \quad \psi(ij|ij) = 0, \text{ and } \psi(ik|ik) = 1/64,$$

to give

$$\mathrm{cov}[\mathcal{T}_P(G), \mathcal{M}_{PV}(G)] = (1/4)\sigma_{A.A_S} + (1/16)\sigma_{AA.AA_S}$$

which is the same result as that obtained using the parent-offspring covariance approach, because ${}_T\alpha_i = (1/2)\alpha_i$ and ${}_T(\alpha\alpha)_{ik} = (1/4)(\alpha\alpha)_{ik}$.

Expressions for $\mathrm{cov}[\mathcal{T}_P, \mathcal{M}_{PV}]$ for various selection methods are given in Table 2. In the absence of epistasis there are nominally the same as those given by Wright (1974), but are in fact k times smaller, a discrepancy balanced in the formula for selection advance by the multiplier k. The formula for selection advance is now sufficiently general to allow for selection in either one or both sexes, and for the case where n parents have already been chosen and are regarded as fixed, and selection is aimed at the improvement of varietal ability of the residue of the population, so that the covariance is multiplied by (k-n) rather than k.

In practice, selection for G.S.A. may be based on predictors which remove the necessity for its direct estimation by assessment of synthetics in equilibrium (Wright 1973; Gallais 1974c, 1975). The expression for genetic advance after n cycles of selection according to any method can be deduced from the results of Gallais (1979) as the advance after relaxation of selection.

4.2 Genetic Advance During Varietal Development

Varietal development involves the selection of genotypes for immediate use as varietal parents. These can be selected either independently or in groups, so that both general and specific synthesising abilities can be utilised.

4.2.1 Individual Selection

Expected genetic advance can be expressed in a way analogous to that for population improvement:

$$\mu^*_{V_n} - \mu_{V_n} = ik \frac{\mathrm{cov}[\mathcal{T}_V(G), \mathcal{M}_V(G)]}{\sqrt{\mathrm{var}[\mathcal{T}_V(G)]}}$$

where $\mu^*_{V_n}$ is the expected value of varieties produced from selected individuals, μ_{V_n} the expected value of all synthetics, and $\mathrm{cov}[\mathcal{T}_V(G), \mathcal{M}_V(G)]$ is the covariance of individual genotypic varietal values with their values under a particular testing system. Thus, if epistasis is restricted to the additive x additive type:

$$\text{cov}[\mathcal{T}_V(G), \mathcal{M}_V(G)] = 2\,\psi(i|i)\,\sigma_{A_T A_S} + \psi(ij|ij)\,\sigma_{D_T D_S} + 4\,\psi(ik|ik)\,\sigma_{AA_T AA_S}$$

and because the relationship is between two different attributes of the same individual: $\psi(i|i) = 1/2$, $\psi(ij|ij) = 1$ and $\psi(ik|ik) = 1/4$
So, in general:

$$\text{cov}[\mathcal{T}_V(G), \mathcal{M}_V(G)] = \sigma_{A_T A_S} + \sigma_{D_T D_S} + \sigma_{AA_T AA_S} \ldots \text{etc.}$$

As in the case of population improvement, the covariance for any specific testing scheme is found by substitution of classical, synthetic or S1 parameters where appropriate (Table 1). Table 3 gives some results for different selection methods in the presence of additive x additive epistasis. It is clear that the contribution of additive and dominance effects are the same as those for population improvement with $\theta = 2$, whereas, in the absence of linkage, the coefficient for the epistatic component is twice that for population improvement. In addition, the complete expression would include contributions from additive x dominance and dominance x dominance epistasis.

4.2.2 Group Selection

Group selection is a method where the parents are evaluated in groups of size n, with $n < k$, where the groups might involve hybrid or synthetic combination. Two methods of arrangement of these groups can be envisaged, firstly where all possible combinations of n are produced from a group of size k, and secondly where the combinations have no common members so that there are b independent groups, with $k = bn$.

The expression for advance under individual selection is not appropriate for group selection, as the test criterion is now the mean value of a group. It can be expressed as

$$\mu^*_{V_n} - \mu_{V_n} = i\,\frac{\text{cov}[\mathcal{T}_V, \mathcal{M}_V]}{\sqrt{\text{var}[\mathcal{T}_V]}}$$

Table 3. Covariance between the value of a genotype according to the system of testing $\mathcal{T}_V$, which defines the selection method, and its general synthesising ability

Breeding method	cov $\mathcal{T}_V, \mathcal{M}_V$
Phenotypic selection	$\sigma_{A.A_S} + \sigma_{D.D_S} + \sigma_{AA.AA_S}$
Selection on G.C.A.	$(1/2)\sigma_{A.A_S} + (1/4)\sigma_{AA.AA_S}$
Selection on S_1	$\sigma_{A_I A_S} + \sigma_{D_I D_S} + \sigma_{AA_I AA_S}$
Selection on G.S.A.	$\sigma^2_{A_S} + \sigma^2_{D_S} + \sigma^2_{AA_S}$

where $\mu^*_{V_n}$ and μ_{V_n} have the same meaning as before, but cov $[\mathcal{T}_V, \mathcal{M}_V]$ is the covariance between the predicted values according to the testing system $\mathcal{T}_V$ and the true values $\mathcal{M}_V$, and var $[\mathcal{T}_V]$ is the phenotypic variance of these predicted values. $\mathcal{T}_V$ can also be defined as the predictor of the varietal value.

The value of a particular synthetic can be expanded in terms of a factorial model:

$$S_{IJK\ldots} = \mu_S + \sum_I {}_S a_I + \sum_{I,J} {}_S d_{IJ} + \sum_{I,J,K} {}_S t_{IJK} + \ldots$$

where ${}_S a_I$ is the G.S.A. of the genotype I, ${}_S d_{IJ}$ is the S.S.A. of genotypes I and J...

Similarly the value of a group of parents according to a system of testing can be written:

$$T_{IJK\ldots} = \mu_T + \sum_I {}_T a_I + \sum_{I,J} {}_T d_{IJ} + \sum_{I,J,K} {}_T t_{IJK\ldots}$$

Then cov$[\mathcal{T}_V, \mathcal{M}_V]$ can be expanded as follows:

$$\text{cov}[\mathcal{T}_V, \mathcal{M}_V] = K_1\,\text{cov}\,{}_T a_I\,{}_S a_I + K_2\,\text{cov}\,{}_T d_{IJ}\,{}_S d_{IJ} + \ldots$$

K_1, K_2 ... being a function of the size n of the group for evaluation.

In the absence of epistasis, the S.S.A. are limited to those of the first order. Thus:

$$\text{cov}[\mathcal{T}_V, \mathcal{M}_V] = k\,\text{cov}\,{}_T a_i\,{}_S a_i + [k(k-1)/2]\,\text{cov}\,{}_T d_{ij}\,{}_S d_{ij}$$

Such a covariance can be expressed in terms of the covariances between a set of individuals evaluated by $_V$ and a synthetic having one or two parents in common (cov 1 and cov 2).
Then cov 1 = cov ${}_T a_i\,{}_S a_i$

$$\text{cov } 2 = 2\,\text{cov}\,{}_T a_i\,{}_S a_i + \text{cov}\,{}_T d_{ij}\,{}_S d_{ij}$$

so cov$[\mathcal{T}_V, \mathcal{M}_V]$ = k cov 1 + (k(k-1)/2)(cov 2 – 2 cov 1)

Is is also possible to express this covariance in terms of the effects for the testing system and varietal abilities which have already been introduced. The value of a set of k parents $(i_1 j_1, i_2 j_2, \ldots, i_k j_k)$ according to the system of testing can be expanded according to an expression analogous to expression (1) by replacing the subscript S by T. Noting the fact that such an expansion is not necessarily symmetrical for all effects (e.g. for dominance effects in the absence of epistasis for some types of testing), it is necessary to take account of the parental origin of genes, i.e. two alleles can originate from either the same or different parents. Then the general expression for the covariance between a set (x) of k individuals evaluated according to system $\mathcal{T}_V$ in groups of size n and a k-parent synthetic S_y will be

Table 4. Covariance between the predicted value of a synthetic according to the system of testing $\mathscr{T}_V$ for different group selection methods and its true value, when all possible combinations of n are produced from a group of size k

Nature of the group	cov $\mathscr{T}_V \mathscr{M}_V$
1. Individual	$\sigma_{A.A_S} + \sigma_{D.D_S}$
2. of a single cross)	$2\,\sigma_{A_{SC}S_S} + 4\,\sigma_{D_{SC}D_S}$*
3. F_2 (from self-fertilisation of a single cross)	$2\,\sigma_{A_{F_2}A_S} + 4\,\sigma_{D_{F_2}D_S}$*
4. Double cross	$4\,\sigma_{A_{DC}A_S} + 24\,\sigma_{D_{DC}D_S}$*
5. n-Synthetics (n < k)	$n\,\sigma_{A_{S_n}A_{S_k}} + n(2n-1)\,\sigma_{D_{S_n}D_{S_k}}$
6. k-Synthetics	$k\,\sigma^2_{A_S} + k(2k-1)\,\sigma^2_{D_S}$

* We have choosen to define additive (A) and dominance (D) effects for each criterion of test to show the analogy with the selection in synthetic combinations. We have $A_{SC} = (1/2)A$, $D_{SC} = (1/4)D$, $A_{DC} = (1/4)A$, $D_{DC} = (1/16)D$. So cov $[\mathscr{T}_V, \mathscr{M}_V]$ is the same for methods 1 and 2 (and 4 for the situation with b independent double crosses, k = 4b)

$$\text{cov}\, T_x S_y = 2kn\,\psi(i_1|i_1)\,\sigma_{A_T A_S} + (kn\,\psi(i_1 i_1|i_1 j_1) + \frac{kn(k-1)(n-1)}{4}\,\psi(i_1 j_2|i_1 j_2))\,\sigma_{D_T D_S}$$

where $\psi(i_1 i_1|i_1 j_1)$ is the coefficient of kinship for two alleles drawn from the some parent, and $\psi(i_1 j_2|i_1 j_2)$ that for two alleles from different parents.

When the k parents in T_x and S_y are common, then cov $T_x S_y$ gives cov$[\mathscr{T}_V, \mathscr{M}_V]$ directly, and since

$$\psi(i_1|i_1) = 1/(2k), \quad \psi(i_1 j_1|i_1 j_1) = 1/k \text{ and}$$
$$\psi(i_1 j_2|i_1 j_2) = 8/(k(k-1))$$

a general expression is found to be:

$$\text{cov}[\mathscr{T}_V, \mathscr{M}_V] = n\,\sigma_{A_T A_S} + (\delta_1 n + 2\delta_2\, n(n-1))\,\sigma_{D_T D_S}$$

where the values taken by δ_1 and δ_2 depend on the type of group being evaluated. For individual selection, $\delta_1 = 1$ and $\delta_2 = 0$. For $n > 1$, δ_2 is always 1. For hybrids, where alleles from the same parent cannot occur together, δ_1 is 0, whereas it is 1 for synthetics. The expectations for cov $[\mathscr{T}_V, \mathscr{M}_V]$ for various testing systems are given in Table 4.

In the case where the k parents are evaluated in b independent groups where k = bn, the covariance is unchanged for methods 2, 3 and 5 (the problem being trivial in the case of methods 1 and 6), but with double cross evaluation (method 4):

$$\text{cov}[\mathscr{T}_V, \mathscr{M}_V] = 4\,\sigma_{A_{DC}A_S} + 16\,\sigma_{D_{SC}D_S}$$

It should be noted that the advance will not be expected to be the same for both types of group, whatever the system of testing, because $\sqrt{\text{var}\,[\mathscr{T}_V]}$ will alter.

4.3 Some Breeding Implications

The theory developed in this paper has been concerned only with the covariance in the numerator of the formulae for predicting the advance in varietal value under different types of selection. Although the expectation of the genetic portion of the denominator (var $\mathscr{T}_P$) can be obtained very simply, the environmental components may be complex, in particular for predictors of G.S.A. derived either directly as the mean of equilibrium synthetics, or, following Sewall Wright (1922), using a linear combination of the means of progeny obtained by crossing and selfing (Busbice 1970, 1976; Wright 1973; Gallais 1974, 1975). Furthermore, different methods will afford different selection intensities (i), different control of selection in the two sexes (θ), and different lengths of selection cycle.

However, similarities with existing theory for population improvement are apparent, and allow some general principles to emerge. Whereas advance from the varietal building phase of a breeding programme depends on the varietal value of the selection per se, that from one cycle of population improvement must be evaluated after the selections have been intercrossed to generate a new population, and hence depends on the varietal value of the random-bred offspring of these selections. Thus the fraction of the advance in varietal value due to non-additive effects (Table 3) is not maintained during population improvement (Table 2) (Wright 1974). This is exactly what happens to genotypic values during conventional selection and evaluation, and follows directly from the relationships between the parameters employed in the two models, so that varietal value is here a direct replacement for genotypic value.

The advance in varietal value for any method of population improvement can be cast in a more familiar form similar to that used for conventional selection (Falconer 1960). Hence

$$\mu_{V_{n+1}} - \mu_{V_{n,1}} = i\,\theta\, h\, r\, \sqrt{\text{var}[\mathscr{M}_{PV}(G)]}$$

where h^2 is the normal narrow-sense heritability of the criterion, and r is the additive genetic correlation between test values and varietal values of the progeny of tested plants ($\mathscr{M}_{PV}(G)$). (A similar formulation is possible for the varietal construction phase, involving broad-sense heritability and a genotypic correlation of test values and va-

rietal values). The superiority of one method (x) over an alternative (z) (ignoring i and θ) depends on

$$h_x r_x > h_z r_z$$

If criterion x is a direct estimator of G.S.A., then $r_x = 1$, but this does not necessarily imply a superiority for this method. In fact, all the formulae given here for the advance of varietal value during population improvement using the common selection procedures (mass, G.C.A., of family selection) are identical with the orthodox formulae for the advance of genotypic value (Gallais 1977), a part from the substitution of $\sigma_{A.A_S}$ for σ^2_A and $\sigma_{AA.AA_S}$ for σ^2_{AA}. Thus all existing information as to the relative merits of these methods can be applied directly to questions concerning synthetic variety production.

Discussion

The system of analysis of the genetic variation in randomly mating populations described by Kempthorne (1957) uses the individual genotype as the fundamental unit, and derives expectations for covariances among individuals according to their degree of relationship. This approach can be adapted to study the covariances necessary in the formulation of a theory of breeding for synthetic varieties (Gallais 1974b, Wright 1974). However, the method developed in this paper, recognising that variation among individual within varieties is not relevant to the problem, uses the synthetic variety itself as the unit of analysis, and redefines the various genetic parameters accordingly. This leads to a simpler treatment of all statistics involving varieties and their relationship to the various methods of parental assessment.

The cost of this redefinition is a loss of the obvious relationships between the new statistics and the old, and between the theory for one size of synthetic and that for another, (e.g. the variance among synthetics appears to increase with k, whereas in reality it must decrease). However, the new parameters can in fact be related to those in the classical theory.

Within this framework, a coherent theory is developed which provides a sound theoretical basis for the comparison of the expected efficiencies of different breeding methods in the development of synthetic varieties with a given number of parents, leading to results that are simpler than those from the classical theory, due to a reduction in the number of parameters. The definition of separate genetic effects for the criterion of test and varietal value with reference to the varietal unit allows a very general formulation of advance during population improvement and varietal development which can be applied to any type of variety, including composites and all types of hybrids (Gallais 1978).

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