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Selection with Truncation in Autotetraploids Comparison with Diploids

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Summary. Using the general principle of linear prediction for autotetraploids in the absence of epistasis, we envisage different types of individual selection with truncation: mass selection, general combining ability selection, and selection on progenies from self fertilization. General expressions for the first cycle of selection are given. With the assumption that a locus effect can be neglected relative to the total variance, response to n cycles of selection can be predicted. Because of a dominance effect, the response will be curvilinear. The consequence of relaxation of selection is also envisaged. For all three selection procedures, after several cycles of random mating without selection, the genetic advance decreases rapidly towards an asymptotic value which is dependent only on the additive variance. Results for autotetraploids without epistasis are clearly analogous to Griffing's results for diploids with epistasis restricted to pairs of loci.

Prediction formulae for genetic advance and consequences of relaxation of selection for different selection methods with truncation in random mating diploid populations have been developed by Griffing (1960, 1962), taking into account the combined effect of linkage and of epistasis limited to pairs of loci.

In this paper, we use Griffing's approach to consider autotetraploid random mating populations assuming absence of epistasis. We envisage different types of individual selection: mass selection, general combining ability selection and selection on the basis of selfed progenies. The main objective of this paper is to show that the results for autotetraploids without epistasis can be compared with those obtained for diploids with epistasis restricted to pairs of loci. The theoretical approach is directly based on the principle of linear prediction and is more direct than the arguments used by Griffing.

Genetic Advance in one Cycle of Selection

In each cycle of an individual selection method, it is necessary to distinguish:

1. The system of testing, i.e. the way in which the selection value of an individual is evaluated. This can be the individual value itself in the case of mass selection, or its general combining ability, or its value under inbreeding ... and so on.

2. The system of mating of selected individuals in order to form a new population. This can be random mating, inbreeding, crossing etc ...

Let $\wp_x$ be one individual, $\wp^*_x$ be the value of $\wp_x$ under the system of testing, and $\mathcal{M}(\wp_x)$ the value of the offspring from $\wp_x$ under the system of mating $\mathcal{M}$.

Applying the principles of linear prediction (Kempthorne, 1960; Price, 1970), we immediately have for selection on one sex in the generation 0:

$$\mathcal{M}[{}_0\wp_x/{}_0\wp^*_x] = E\{\mathcal{M}({}_0\wp_x)\} + \frac{\operatorname{cov}_0 \wp^* \mathcal{M}({}_0\wp)}{\operatorname{var}_0 \wp^*}\{{}_0\wp^*_x - E({}_0\wp^*_x)\} \tag{1}$$

where $\mathcal{M}[{}_0\wp_x/{}_0\wp^*_x]$ is the expected value given ${}_0\wp^*_x$ of offspring from ${}_0\wp_x$ under the system of mating $\mathcal{M}$ and $E\{\mathcal{M}(\wp_x)\} = \mu$ is the mean of the population obtained from mating individuals such as $\wp_x$ without selection under the same system $\mathcal{M}$.

The mean of the population after one cycle of selection will then be:

$$\mu^*_1 = E\{\mathcal{M}_0\wp_x/{}_0\wp^*_x\} = \mu_1 + \frac{\operatorname{cov}_0 \wp^* \mathcal{M}({}_0\wp)}{\operatorname{var}_0 \wp^*} S \tag{2}$$

where S is the selection differential.

Formula (2) is valid whatever the system of testing, the system of mating, the genetic effects or the ploidy level. The linearity of response to selection requires only the assumption that conditional expectations (equation 1) are linear.

$\wp^*_x$ and $\mathcal{M}(\wp_x)$ can be phenotypic values if the new population is measured in one macro-environment different from that of the testing system. We shall not discuss this problem here; it has been discussed by Griffing (1968). In what follows, we suppose that the macro-environment conditions of the testing system and of the new population are the same, or that there is no genotype x environment interaction. Then the phenotypic value of $\wp_x$ may be regarded, conceptually, as the sum of the two classic independent components with normal distributions:

G = average phenotype for the genotype of the chosen individual

E = environmental effect

The expected value of $\mathcal{M}(P_x)$ is then $\mathcal{M}(G_x)$. So

$$\mu_1^* = \mu_1 + \frac{\mathrm{cov}_0 G^* \mathcal{M}({}_0G^*)}{\mathrm{var}_0 P^*} S \qquad (3)$$

$\mathrm{cov}_0 G^* \mathcal{M}({}_0G^*)$ is the covariance between genotypic values of relatives. With the assumptions of an infinite source population in random mating and linkage equilibria, such covariances have a known structure. In the application below, we give their values in the absence of epistasis for the methods of selection under consideration.

Application

The application of the previous general formulae gives some known results already established in other ways.

1. For random mating

a. Individuals selected on their phenotypic values This is mass selection:

$$\mu_1^* = \mu_0 + \frac{\mathrm{cov}\,P\,0}{\sigma_P^2} S_P \qquad \text{for selection on one sex}$$

$$\mu_1^* = \mu_0 + \frac{2\,\mathrm{cov}\,P\,0}{\sigma_P^2} S_P \qquad \text{for selection on both sexes}$$

Restriction of the level of ploidy is necessary only for the genetic interpretation of the covariance. For autotetraploids with our assumptions:

$$\mathrm{cov}\,P\,0 = 1/2\,\sigma_A^2 + 1/6\,\sigma_D^2$$

b. Individuals selected on their general combining ability

$$\mu_1^* = \mu_0 + \frac{\mathrm{cov}\,HS}{\sigma_{P(g)}^2} S_g \qquad \text{for selection on one sex}$$

$$\mu_1^* = \mu_0 + \frac{2\,\mathrm{cov}\,HS}{\sigma_{P(g)}^2} S_g \qquad \text{for selection on both sexes}$$

$$\mathrm{cov}\,HS = 1/4\,\sigma_A^2 + 1/36\,\sigma_D^2 \qquad \text{for autotetraploids}$$

c. Individuals selected on the performance of their self fertilization progenies

$$\mu_1^* = \mu_0 + \frac{2\,\mathrm{cov}\,S_1 0_R}{\sigma_{P(S1)}^2} S_{s1}$$

From the results of Gallais (1970) for diploids with linkage and those of Jacqueline Bouffette (1966) for autotetraploids, it is possible to give an expression for the covariance between the S_1 of an individual and its offspring under random mating, 0_R.

For diploids (two loci) with alleles i, j, at one locus and k, l, at the other, noting additive effect by (α), dominance effects by (β), additive x additive epistasis by (ξ), additive x dominance (γ), dominance x dominance (δ):

$$\begin{aligned}\mathrm{cov}\,S_1 0_R = {} & 4\varphi({}^{i}|{}^{i})\{E(\alpha_i^2)+E(\alpha_k^2)\}+4\varphi({}^{ii}|{}^{i})\{E(\alpha_i\beta_{ii})\\ & +E(\alpha_k\beta_{kk})\}+16\varphi(ik|ik)E(\xi_{ik}^2)\\ & +8\varphi\left(\frac{i}{kk}\middle|\frac{i}{-}\right)\{E(\gamma_{ikk}\alpha_i)+E(\gamma_{iik}\alpha_k)\}\\ & +16\varphi\left(\frac{ii}{k}\middle|\frac{i}{k}\right)\{E(\gamma_{ikk}\xi_{ik})+E(\gamma_{ikk}\xi_{ik})\}\\ & +4\varphi\left(\frac{ii}{kk}\middle|\frac{i}{-}\right)\{E(\delta_{iikk}\alpha_i)+E(\delta_{iikk}\alpha_k)\}\\ & +8\varphi\left(\frac{ii}{kk}\middle|\frac{i}{k}\right)E(\delta_{iikk}\xi_{ik})\end{aligned}$$

$\varphi(\,|\,)$ are generalized coefficients of relationship as introduced by Harris (1964) and Gillois (1964). The vertical line separates the genes taken from each of the two related zygotes S_1 and 0_R. Genes with the same letters are identical in descent. We give the value of such coefficients only for the case of absence of epistasis:

$$\varphi(i|i) = 1/4 \qquad \varphi(ii|i) = 1/16$$

Other coefficients will appear in the next part of this study. For tetraploïds with one locus and alleles i, j, k, l, we have similar results; with the same notation for the coefficients of relationship and for the states of identity between the alleles, noting additive effects (α), digenic effects (β), trigenic effects (γ), quadrigenic effects (δ):

$$\begin{aligned}\mathrm{Cov}\,S_1 0_R = {} & 16\varphi(i|i)E(\alpha_i^2)+48\varphi(ii|i)E(\alpha_i\beta_{ii})+\\ & +32\varphi(ii|i)E(\alpha_j\gamma_{iij})+8\varphi\left(\frac{ii}{jj}\middle|{}^{i}\right)E(\alpha_i\delta_{iijj})+\\ & +36\varphi(ij|ij)E(\beta_{ij}^2)+48\varphi\left(\frac{i}{jj}\middle|\frac{i}{j}\right)E\beta_{ij}\gamma_{ijj})+\\ & +12\varphi\left(\frac{ii}{jj}\middle|\frac{i}{j}\right)E(\beta_{ij}\delta_{iijj})+12\varphi\left(\frac{ii}{jk}\middle|{}_{jk}\right)E(\beta_{jk}\delta_{iijk})\end{aligned}$$

We give the coefficients corresponding to the absence of interaction between more than two alleles:

$$\varphi(i|i) = 1/8 \qquad \varphi(ii|i) = \frac{1}{48} \qquad \varphi(ij|ij) = \frac{5}{36}$$

The values of the other coefficients will appear in a later part of this study.

From these results it can be seen that the contribution of additive variance is greater with this procedure than with the general combining ability selection. It may thus be more efficient if variance is mainly additive, because phenotypic variance between families can be considered to be similar. But in general, the efficiency depends on the covariance terms such as $E(\alpha_i \beta_{ii})$...etc.

2. For self fertilization

Individuals selected on their phenotypic value.

$$\mu_1^* = \mu_1 + \frac{C(0,1)}{\sigma_{{}_0P}^2} S$$

where $C(0,1)$ is the covariance between an individual in the source population and its offspring under selfing.

This gives the result obtained by Pederson (1968). For autotetraploïds we know that the mean μ_n after n generations of selfing without selection is (Gallais, 1967):

$$\mu_n = \mu_0 + 6F_n E(\beta_{ii}) + 4(P_{0_n} + 1/4 P_{1_n}) E(\gamma_{iii}) +$$
$$+ P_{0_n} E(\delta_{iiii}) + P_{2_n} E(\delta_{iijj})$$

where F is the coefficient of inbreeding, and P_0, P_1, P_2 the probabilities of the nulliplex, simplex and duplex states of identity by descent. With the assumption of random mating equilibrium in the base population, the expression for covariance between inbred relatives was first given by Jacqueline Bouffette (1966). We give below this formulae limiting the interactions between alleles to the first order:

$$\mathrm{Cov}\, Z_I Z_J = 16\varphi(i|i) E(\alpha_i^2) + 48\varphi(i|ii) E(\alpha_i \beta_{ii}) +$$
$$+ 36\varphi\left(\begin{smallmatrix} i \\ j \end{smallmatrix}\middle|\begin{smallmatrix} i \\ j \end{smallmatrix}\right) E(\beta_{ij}^2) + 36\varphi(ii|ii) E(\beta_{ii}^2) +$$
$$+ 36\{\varphi(ii|jj) - F_I F_J\}\{E(\beta_{ii})\}^2$$

$\varphi(\,|\,)$ are generalized coefficients of relationship as above.

From these three examples, it can be seen that the general formula (1) can express directly the genetic advance in one cycle in terms of genetic parameters for any system of testing or mating. Extensions of this formula to the cases of combined selection (individual and family) and to the cases of different selection procedures according to sex are obviously possible.

Prediction of the Response to the n^{th} Cycle of Selection

For any cycle of selection the linearity of response requires the assumption that conditional expectations are linear as equation 4.

$$\mu_{n+1}^* = \mu_{n+1} + \frac{\mathrm{cov}\, {}_nG^* \mathcal{M}({}_nG)}{\mathrm{var}\, {}_n\wp^*} S \tag{4}$$

With this assumption for each cycle, it is possible to express the second cycle from characteristics of the first cycle and so on. However, the useful prediction of the n^{th} cycle of selection from genetic parameters of the source population, assumed to be infinite and in random mating equilibrium, needs more restrictive assumptions. It is possible to assume that $\mathrm{Cov}\, {}_nG^* \mathcal{M}({}_nG^*)$ can always be replaced by routeing expressions for covariances between relatives defined in the source infinite random mating population.

Restricting our study to the case where $\mathcal{M}$ is random mating, to relate one cycle (n+1) to the previous (n) we use the frequencies of the gametes. This approach will be valid for autotetraploids with one locus or for diploids with two loci. Let ${}_nf_{ik}^*$, ${}_nf_{jl}^*$ be the frequencies of gametes which unite to give the zygote i j k l of value G_{ijkl}. After n cycles of selection on the two sexes the mean of the new population will be:

$$\mu_{n+1}^* = \sum_{ik} \sum_{jl} {}_nf_{ik}^* \, {}_nf_{jl}^* \, G_{ijkl} \tag{5}$$

The problem is then to predict the frequencies ${}_nf_{ik}^*$ since selection induces non-random associations between genes. Assuming a linear relationship between the frequency f_{ijkl} of a genotype and its breeding value G_{ijkl}^*, its frequency f_{ijkl}^* after selection, but before random mating, will be:

$${}_nf_{ijkl}^* = {}_nf_{ijkl} + {}_nf_{ijkl} \frac{{}_nG_{ijkl}^* - E({}_nG_{ijkl}^*)}{\mathrm{var}\, {}_n\wp^*} S \tag{6}$$

where $\mathrm{var}\, {}_n\wp^*$ represents the phenotypic variance of the genotype (or subgenotype) ijkl, i.e. the environmental variance plus all genetic variance not due to the unit ijkl. Then according to the assumption that the effect of the subunit can be neglected relative to the total variance, $\mathrm{var}\,\wp^*$ represents the total phenotypic variance. To simplify the notation we put ${}_nG^*_{ijkl} - E({}_nG^*) = Y^*_{ijkl}$ and $\mathrm{var}\,\wp^* = \sigma^2$.

Following arguments introduced by Kimura (1958) and used by Griffing (1960, 1962), it can be shown that equation (6) is justified if quantities such as $(Y^*_{ijkl}/\sigma)^2$ and $(Y^*_{ijkl}/\sigma^2)^2$ may be neglected. However the equation (6) can be assumed a priori. From expression (6) we can deduce the frequency of gametes with genes i and k, and the frequency of one gene. For the genic frequency, we have immediately:

$$ {}_{n+1}p^*_i = {}_np_i + \frac{S}{\sigma^2} \sum_{jkl} {}_nf^*_{ijkl}\ {}_nY^*_{ijkl} \tag{7} $$

For the gametic frequency, we must note that according to the origin of genes i and k, there are two types of genotypes, (ik, jl) with genes ik contributed by the same gamete, and (il, jk) with gene i contributed by one gamete and k by the other. Genotype (ik, jl) reproduces gamete ik or jl with the probability Π, and genotypes (il, jk) give such types of gametes with the probability $(1-\Pi)$. Note that $\Pi = 1-c$ for diploids, with c the recombination value between two loci, and $\Pi = 1/3$ for autotetraploids with random segregation of the chromosomes. So the frequency of gametes ik after selection will be:

$$ \begin{aligned} {}_{n+1}f^*_{ik} &= \Pi \sum_{jl} f^*_{ik,jl} + (1-\Pi) \sum_{jl} f^*_{il,jk} = \\ &= {}_{n+1}f_{ik} + \frac{S}{\sigma^2} \{ \Pi\, {}_nf_{ik} \sum_{jl} {}_nf_{jl}\ Y^*_{ijkl} + \\ &+ (1-\Pi) \sum_{jl} {}_nf_{il}\ {}_nf_{jk}\ Y^*_{ijkl} \} \end{aligned} \tag{8} $$

with ${}_{n+1}f_{ik} = \Pi\, {}_nf_{ik} + (1-\Pi)p_ip_k$ the frequency of gamete ik without selection. This is a well known relation for diploids (Malecot, 1948) and for autotetraploids (Demarly, 1963).

Then, using the same arguments as Griffing (1960) with the assumptions that $\left[\dfrac{G^*_{ijkl} - E(G^*)}{\sigma}\right]^2$ and $\left[\dfrac{G^*_{ijkl} - E(G^*)}{\sigma^2}\right]^2$ may be neglected, recurrence equations (7) and (8) can be solved. Hence:

$$ {}_np_i = {}_0p_i \{1 + n(S/\sigma^2)\, {}_0Y^*_{i...}\} \text{ with } {}_0Y^*_{i...} = \sum_{jkl} p_jp_kp_l\, Y^*_{ijkl} $$

or ${}_np_i - {}_op_i = n({}_1p_i - {}_0p_i)$

The consequences of the linear approach and the simplifying assumptions on genetic effects is that the predicted changes in genic frequencies are the same in each cycle of selection. So it seems that the assumptions are acceptable only for the first cycles of selection, and with low values of the frequencies p_i. Putting:

$$ {}_0f_{ik} = {}_0p_i\ {}_0p_k $$

$$ \sum_{jl} {}_0p_j\ {}_0p_l\ Y^*_{ik,jl} = Y^*_{ik,..} \qquad \sum_k p_k\ Y^*_{ik,..} = Y^*_{i...} $$

$$ \sum_{jl} {}_0p_j\ {}_0p_l\ Y^*_{il,jk} = Y^*_{i.,.k} \qquad \sum_k p_k\ Y^*_{i.,.k} = Y^*_{i...} $$

It results in:

$$ \begin{aligned} {}_nf^*_{ik} &\simeq {}_0f_{ik} + n(S/\sigma^2)\, {}_0f_{ik} (Y^*_{i...} + Y^*_{.k..}) + \\ &+ (S/\sigma^2)\, \frac{1-\Pi^n}{1-\Pi}\, {}_0f_{ik} \{ \Pi\, Y^*_{ik,..} + (1-\Pi) Y^*_{i.,.k} - \\ &- (Y^*_{i...} + Y^*_{.k..}) \} \end{aligned} \tag{10} $$

For diploids, Griffing (1962) has given the values of $Y^*_{i...}$; $Y^*_{ik,..}$; $Y^*_{i.,.k}$, for mass selection and general combining ability selection. We recall these results in Tables 1 and 2, with results for autotetraploïds, and for individuals selected on the basis of their self-fertilization progenies.

From formulae (5) and (10) we obtain after simplification and approximation:

$$ \begin{aligned} \mu^*_n &= \mu_0 + n(S/\sigma^2)\, 2\{E(Y^*_{i...}\ \alpha_i) + E(Y^*_{.k..}\ \alpha_k)\} + \\ &+ (S/\sigma^2)\, \frac{1-\Pi^n}{1-\Pi}\, 2\{\Pi E(Y^*_{ik,..}\ \beta_{ik}) + \\ &+ (1-\Pi) E(Y^*_{i.,.k}\ \beta_{ik})\} \end{aligned} \tag{11} $$

This formula is valid for diploids with two loci or for autotetraploids with one locus. (For diploids, β must be replaced by ξ.) For the autotetraploid case we have, according to the values of the parameters:

- for mass selection:

$$ \mu^*_n = \mu_0 + n(S/\sigma^2)\sigma^2_A + 3/2\{1-(1/3)^n\}(S/\sigma^2)\, 1/3\, \sigma^2_D $$

- for general combining ability selection:

$$\mu_n^* = \mu_0 + n(S/\sigma^2)1/2\,\sigma_A^2 + 3/2\,\{1-(1/3)^n\}\,(S/\sigma^2)\,1/18\,\sigma_D^2$$

- for selection of individuals on the basis of their self-fertilization progenies:

$$\mu_n^* = \mu_0 + n(S/\sigma^2)2\,V_A + 3/2\,\{1-(1/3)^n\}\,(S/\sigma^2)2\,V_D$$

with

$$V_A = 2E(\alpha_i^2)+1/12\,E(\alpha_i\beta_{ii})+1/6\,E(\alpha_i\gamma_{ikk})+1/6\,E(\alpha_i\delta_{iikk})$$

$$V_D = 5/36\,E(\beta_{ik}^2)+1/18\,E(\beta_{ik}\gamma_{ikk})+1/36\,E(\beta_{ik}\delta_{iikk})+ + 1/9\,E(\beta_{ik}\delta_{ikll})$$

Table 1. Values of ${}_0Y^*_{i\ldots}$ according to three selection procedures. For procedures (1) and (2) values are the same whatever the level of ploïdy. For procedure (3), 2n results are for two loci, 4n for one locus. The notation $\underset{i}{E}$ means E with i fixed

Selection procedures	${}_0Y^*_{i\ldots}$
(1) Mass selection	α_i
(2) General combining ability	$1/2\,\alpha_i$
(3) Self-fertilization progeny 2n	$\alpha_i+1/4\,\beta_{ii}+1/4\,E(\beta_{ii})+1/2\,E(\beta_{kk})+1/2\,\underset{i}{E}\,(\gamma_{ikk})+\{\frac{(1-c)^2}{2}+(\frac{c}{2})^2\}\,\{\underset{i}{E}(\delta_{iikk})+E(\delta_{jjll})\}$
4n	$\alpha_i+1/24\,\beta_{ii}+1/8\,E(\beta_{ii})+1/12\,\underset{i}{E}\,(\gamma_{ikk})+1/12\,\underset{i}{E}\,(\delta_{iijj})+1/12\,E(\delta_{kkll})$

Table 2. Values of ${}_0Y^*_{ik,\ldots}$ according to three selection procedures and two levels of ploidy. For tetraploids with one locus, ${}_0Y^*_{i.,.k}$ values are identical to ${}_0Y^*_{ik,\ldots}$. For diploids with two loci, genes i,j at the one and k,l at the other, in order to obtain ${}_0Y^*_{i.,.k}$ from ${}_0Y^*_{ik,\ldots}$ it is only necessary to replace 1/2(1-c) by 1/2 c and vice-versa

Selection procedures	${}_0Y^*_{ik,\ldots}$
(1) Mass selection	$(\alpha_i+\alpha_k)+\beta_{ik}$ (ξ_{ik} replace β_{ik} for diploids)
(2) General combining ability 2n	$1/2(\alpha_i+\alpha_k)+\frac{1-c}{2}\,\xi_{ik}$
4n	$1/2(\alpha_i+\alpha_k)+1/6\,\beta_{ik}$
(3) Self-fertilization progeny 2n	$(\alpha_i+\alpha_k)+1/4(\beta_{ii}+\beta_{kk})+1/4\{E(\beta_{ii})+E(\beta_{kk})\}+1/2(1/4+\frac{1-c}{2})\xi_{ik}+\frac{1-c}{2}(\gamma_{iik}+\gamma_{ikk})+$ $+\frac{c}{2}\{\underset{k}{E}(\gamma_{jjk})+\underset{i}{E}(\gamma_{ill})\}+(\frac{1-c}{2})^2\{\delta_{iikk}+E(\delta_{jjll})\}+(\frac{c}{2})^2\{\underset{i}{E}(\delta_{iill})+\underset{k}{E}(\delta_{jjkk})\}$
4n	$(\alpha_i+\alpha_k)+1/24(\beta_{ii}+\beta_{kk})+1/12\,E(\beta_{ii})+5/36\,\beta_{ik}+1/36(\gamma_{iik}+\gamma_{ikk})+1/18\{E_k(\gamma_{jjk})+$ $+\underset{i}{E}\,(\gamma_{ill})\}+1/36\,\delta_{iikk}+1/9\,\underset{ik}{E}\,(\delta_{ikll})+1/18\{\underset{i}{E}(\delta_{iill})+\underset{k}{E}(\delta_{jjkk})\}+1/36\,E(\delta_{jjll})$

For diploids with two loci, results for the first two selection procedures have been given by Griffing (1962). For the third procedure we have from (11)

$$\mu^*_n = \mu_0 + n(S\sigma^2)2V_A + \frac{1-(1-c)^n}{c}(S/\sigma^2)2V_D$$

with

$$V_A = \{E(\alpha_i^2)+E(\alpha_k^2)\}+1/4\{E(\alpha_i\beta_{ii})+E(\alpha_k\beta_{kk})\}+$$
$$+1/2\{E(\alpha_i\gamma_{ikk})+E(\alpha_k\gamma_{iik})+\{(\tfrac{1-c}{c})^2+$$
$$+(\tfrac{c}{2})^2\}\{E(\alpha_i\delta_{iikk})+E(\alpha_k\delta_{iikk})\}$$

$$V_D = 1/4\{1/2+(1-c)^2+c^2\}E(\xi_{ik}^2)+1/2\{(1-c)^2+c^2\}\times$$
$$\times\{E(\xi_{ik}\gamma_{iik})+E(\xi_{ik}\gamma_{ikk})\}+1/4\{(1-c)^3+c^3\}E(\xi_{ik}\delta_{iikk})$$

In this way it is obvious that we find the value of the generalized coefficients of relationship φ(|), introduced in the first part of this study for the genetic advance in one cycle of selection.

For these three individual selection procedures, it appears that interaction between two genes (i.e. additive x additive epistasis for diploids, or dominance for tetraploids) causes a curvilinearity of the response of selection with time. The common cause is the dependence between genes. For the first two procedures, this influence diminishes as the number of cycles of selection increases. The same thing occurs for the third procedure if V_D is positive. However it is not certain that V_D is always positive. Clearly if there is only additivity, the response to selection will be linear with time. $\mu^*_n = \mu_0 + n(S/\sigma^2)2\{E(Y^*_{i...}\,\alpha_i)+E(Y^*_{.k..}\,\alpha_k)\}$. This is a well known result for diploids with the assumptions given above (7) - (Falconer, 1961).

The above results established for autotetraploids with one locus or for diploids with two loci, can be extended to several loci by summation over all independent loci, or pairs of loci.

Consequences of Relaxation of Selection

Suppose that after n generations of continuous selection there are m generations of random mating without selection. The selected population is in random mating disequilibrium. Then for autotetraploids (Demarly, 1963) and for diploids (Griffing, 1960):

$${}_{n,m}f_{ik} = {}_np_i\,{}_np_k + \Pi^m({}_{n,0}f_{ik} - {}_np_i\,{}_np_k)$$

From formulae (8) and (10) we know ${}_np_i$, ${}_np_k$ and ${}_{n,0}f_{ik}$ ($\mathcal{M}$ being random mating). Then:

$${}_{n,m}f_{ik} \simeq {}_0f_{ik} + n(S/\sigma^2)\,{}_0f_{ik}\,(Y^*_{j...} + Y^*_{.k..})+$$
$$+(S/\sigma^2)\Pi^m(\tfrac{1-\Pi^n}{1-\Pi})\{\Pi Y^*_{ik,..}+(1-\Pi)Y^*_{i.,.k}-(Y^*_{i...}+Y^*_{.k..})\}$$

Then the mean will be: (ξ replacing β for diploids)

$$\mu_{n,m} \simeq \mu_0 + 2n(S/\sigma^2)\{E(Y^*_{i...}\,\alpha_i) + E(Y^*_{.k..}\,\alpha_k)\}+$$
$$+2(S/\sigma^2)\Pi^m(\tfrac{1-\Pi^n}{1-\Pi})\{\Pi E(Y^*_{ik,..}\,\beta_{ik})+$$
$$+(1-\Pi)E(Y^*_{i.,.k}\,\beta_{ik})\} \qquad (12)$$

and according to the value of the parameters for autotetraploids

- for mass selection:

$$\mu_{n,m} \simeq \mu_0 + n(S/\sigma^2)\sigma_A^2+$$
$$+(3/2)(1/3)^m\{1-(1/3)^n\}(S/\sigma^2)1/3\,\sigma_D^2$$

- for general combining ability selection:

$$\mu_{n,m} = \mu_0 + n(S/\sigma^2)1/2\,\sigma_A^2+$$
$$+(3/2)(1/3)^m\{1-(1/3)^n\}(S/\sigma^2)1/18\,\sigma_D^2$$

- for selection of individuals on the basis of their selfed progenies:

$$\mu_{n,m} = \mu_0 + n(S/\sigma^2)2V_A + 3/2(1/3)^m\{1-(1/3)^n\}(S/\sigma^2)2V_D$$

The values of V_A and V_D have been given above.

From formula (12) and the previous results, it is easy to deduce the results for diploids.

For the three procedures of individual selection, and by induction for all procedures of selection, formula (12) states that after several cycles of random mating following selection the genetic advance remaining is only that due to additive variance. The mean of the selected population declines towards this asymptotic limit. Hill (1971) has also given this conclusion for autotetraploids, with biallelism, for different models of direct phenotypic selection (Models I, II, III).

By induction from Griffing's (1962) results and ours, it is clear that whatever the ploidy and epistasis, the mean for a selected population multiplied by random mating without selection decreases towards a limit which is that part of its genetic advance contributed by additive variance. Hill (1971) has shown in a particular model (IV, i.e. biallelism A, a, with duplex dominance and selection against aaaa and aaaA) that the change in mean can be in either direction, depending on the state of the population at the time of relaxation of selection, but will be small in most cases. This result is slightly different from ours. We suggest that this is due to the assumptions on gene effects underlined by Griffing. We recall them:

- absence of natural selection;
- the population of phenotypic values is considered to be unlimited;
- the gene effects are small relative to the phenotypic standard deviation; results are then not valid for genes of major effect, which may be important in plant breeding in selection for resistance to some diseases. The approach of Latter (1965) can help to solve this problem. However we think that for a complex character such as yield this assumption allows an approximation of the selection effect for the first cycles.

Conclusion

The linear prediction approach of selection theory leads to general results for one cycle of selection, whatever the level of ploidy. It gives directly change in mean, in gene, gamete and genotypic frequencies in one cycle of selection with the global assumption of linearity of the dependent variate on the independent variate, the genotypic value under the testing system used. This is a statistical problem first discussed by Kempthorne (1960). The assumptions of such linearity for genotypic frequencies and on genetic effects are strong. However they are justified for a polygenic character controlled by many loci (or combination of loci) of small effect relative to the phenotypic standard deviation. Moreover they allow consideration of the response to n cycles of selection in terms of classical parameters first and second degree statistics defined in the source infinite random mating population. Some of the restrictive assumptions can be lifted by using second degree in place of linear equations. The approaches of Latter (1965) and Price (1970) can take into account deviations from linearity in (6).

The results concerning selection in random mating populations for autotetraploids for one locus are strictly similar to those for diploids with two loci and epistasis. In both cases this results from the dependence relationship between genes due to the fact that a gamete necessarily transmits, two genes i.e., two non-homologous genes for diploids, two homologous genes for autotetraploids, so that parental gametic associations are maintained with certain probabilities in the following generation (Gallais, 1974a,b). In both cases, even with the restrictive assumptions, the response to selection can be curvilinear due to interactions between genes. After relaxation of selection the decrease in mean of the selected population toward the equilibrium, due only to the additive variance, will be more rapid for autotetraploids than for diploids.

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