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Selection among Synthetics

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Summary. The effect of the number of parents and their level of inbreeding on the mean and the variance of synthetic varieties was studied for diploids and autotetraploids. The number of parents and their level of inbreeding act in opposing ways. Maximum mean requires a high number of parents and no inbreeding. Maximum variance requires a small number of highly inbred and unrelated parents. When the number of parents increases ($k \geq 2$) the coefficients of the components of variance decrease, and the decrease is more rapid for variances associated with increasing order of interactions between genes. The coefficients of components of variance increase as the level of inbreeding of the parents increases and the increase is greater for components associated with increasing order of interactions between genes.

Consequently, according to the values of inbreeding depression and the components of genetic variance and heritability, an optimum genetic base may exist, i.e., an ideal combination of the number of parents and the level of their inbreeding. With no inbreeding, selection among synthetics uses mainly additive variance. By increasing the level of inbreeding of the parents, the effects of dominance and of additive × additive variances on genetic advance when selecting among synthetics increase. One cycle of selection among synthetics appears more efficient than individual selection within populations. The problem of population improvement before selecting among synthetics is discussed.

Introduction

For diploids, the selection theory of hybrid varieties is now well known (Cockerham, 1961), but for synthetic varieties, this is not so. In spite of recent work, theoretical problems such as the number of parents, their level of inbreeding, the way to use genetic effects etc., are not satisfactorily resolved for synthetics. For autotetraploids, and other autopolyploids, we do not know enough about the selection of hybrid or synthetic varieties. The problem for the breeder is to select combinations of individuals which give the best varieties, hybrids or synthetics. This is a problem of "group selection", as introduced by Griffing (1966). When we consider selection among all combinations of individuals from one source population, we can write, according to the general principles of linear prediction (Kempthorne, 1957):

$$ {}_GV = E(V) + \frac{{}_G\sigma^2}{{}_P\sigma^2}\left({}_PV - E(V)\right) \qquad (1) $$

${}_GV$, ${}_PV$	genotypic, phenotypic value of the combinations,
$E(V)$	expected value of all combinations,
${}_G\sigma^2$, ${}_P\sigma^2$	genotypic, phenotypic variance among combinations.

Clearly, the breeder must consider both the factors influencing the mean of all combinations and the factors influencing the variance between combinations. Hill (1971) has approached this problem for synthetics in the case of biallelism with non-inbred parents. We present a general method taking into account multiallelism and inbreeding of the parents.

We shall define the synthetic variety as a population produced by random mating over a limited number of generations of the offspring from natural crossing of the selected parents. We shall call the population from which the parents came the source population; it can be inbred or not. The reference population will be the random mating population in panmictic and linkage equilibria, from which the source population can be derived by inbreeding without selection.

Factors Influencing Mean: a Synthesis from Literature

For diploids, the expected value of all hybrid combinations of individuals is the mean of the reference population.

For synthetics, the problem is more complex because the mating system leads to inbreeding in advanced generations. Applying the results of Kempthorne (1957), we have shown (1967a, 1970a) that the expected value of diploid synthetics with a given number of parents, inbred or not, and without epistasis is:

$$ E(S) = \mu + F\,E(\beta_{ii})\,, \qquad (2) $$

and with epistasis limited to two loci (1971c):

$$ E(S) = \mu + F\,\{E(\beta_{i_1i_1}) + E(\beta_{k_2k_2})\} + F_{11}\,E(\delta_{i_1i_1k_2k_2}) \qquad (3) $$

μ = mean of the reference population,
$E(\beta_{ii})$ = expected value of dominance effects,
$E(\delta_{i_1i_1k_2k_2})$ = expected value of dominance × dominance effects,

F = coefficient of inbreeding,
F_{11} = probability of having identical genes at the two loci.

As pointed out by Kempthorne (1957), if there are no dominance × dominance effects, the vigour will be linearly related to F in spite of the fact that epistasis may be present.

For autotetraploïds, hybrids between inbred parents are also partly inbred. We have described (1967b, 1968a, b) the expected value of hybrids or synthetics, without epistasis:

$$E(V) = \mu + 6\,F\,E(\beta_{ii}) + 4\,(P_0 + 1/4\,P_1)\,E(\gamma_{iii}) + \\ + P_0\,E(\delta_{iiii}) + P_2\,E(\delta_{iijj}) \qquad (4)$$

$E(\beta_{ii})$, $E(\gamma_{iii})$, $E(\delta_{iiii})$, $E(\delta_{iijj})$ are expected values of digenic, trigenic and tetragenic interactions,

and P_0, P_1 and P_2 are coefficients of identity by descent of four alleles, i, j, k, l (1967b). If we consider four genes, i, j, k, l, at one locus, then:

$$P_0 = Pr\,(i \equiv j \equiv k \equiv l)$$

probability of having four identical genes,

$$P_1 = Pr\,(i \equiv j \equiv k \not\equiv l)\,,$$

$$P_2 = Pr\,(i \equiv j \not\equiv k \equiv l)\,.$$

For hybrid varieties from unrelated inbred parents $P_0 = P_1 = 0$.

When $E(\gamma_{iii}) = E(\delta_{iiii}) = E(\delta_{iijj}) = 0$, the vigour will be linearly related to F, in spite of the fact that interactions between more than two alleles may be present.

It must be mentioned that for diploids, without epistasis, the vigour of one particular synthetic in equilibrium S_{eq}, can be related to the mean $\overline{C}$ of all crosses between the k parents and to the mean $\overline{P}_s$ of selfed parents (Corkill, 1956; Gallais, 1967a), according to an expression which has the same structure as Wright's formula (1922):

$$S_{eq} = \overline{C} - \frac{1}{k}\,(\overline{C} - \overline{P}_s)\,. \qquad (5)$$

For autotetraploids, assuming that the vigour is linearly related to the coefficient of inbreeding, Busbice (1970) has given a generalization of this formula.

In order to fully discuss factors influencing the mean, it would be necessary to compute the coefficients of identity (F, F_{11}, P_0, P_1, P_2, . . .) for the several types of varieties. Such computations are sometimes tedious and we refer to the computation of inbreeding coefficient by Busbice (1969) and to work by Gallais (1967a; 1968a, b; 1970a; 1971a, b, c).

Formulae 2, 3, and 4 define genetic factors that control the expected vigour of a synthetic variety, i.e., its genotypic structure and the genetic effects. We summarize the main conclusions, partly given in Busbice (1969), Gallais (1967–1971) and Hill (1971). Increasing the number of parents at a given level of inbreeding increases heterozygosity and the expected vigour of the synthetics. With a given number of parents, increasing their level of inbreeding results in a decrease in expected vigour. For autopolyploids, the effect of varying the number of parents and their level of inbreeding will be stronger as the higher order interactions among alleles become greater.

The studies on means give a genetic base for the prediction formulae introduced *a priori* by Busbice (1970). More general prediction equations can be built by using other parameters of genotypic structure than F, even if the genetic hypotheses are not satisfied. Genetic hypotheses are necessary for the genetical interpretation of parameters, not for prediction which is a statistical problem. For example, the vigour of one or several varieties can be linearly related to F, F_{11} for diploids and to P_0, P_1, P_2, P_3, P_4 for tetraploids, or to linear combinations of these parameters (Dessureaux *et al.*, 1971; Gallais, 1971c). We think it is possible and necessary to extend these prediction formulae for one particular variety. This will be very useful for synthetic varieties, where advanced generations are necessary before final tests.

Variance among Means of Varieties. New Results

1. *First approach for diploids*

Cockerham (1961) has described the genetic variance for hybrid varieties. We shall consider here only synthetic varieties.

From formula (5) the variance between synthetic diploid varieties in equilibrium, without epistasis, is:

$$\sigma_S^2 = \frac{1}{k^2}\,var\,\overline{P}_s + \frac{2\,(k-1)}{k^2}\,cov\,\overline{P}_s\,\overline{C} + \frac{(k-1)^2}{k^2}\,var\,\overline{C}\,. \qquad (6)$$

When k increases, σ_S^2 tends towards var $\overline{C}$;

var $\overline{C}$ can be related to general and specific combining ability variances

$$var\,\overline{C} = \frac{4}{k}\,\sigma_g^2 + \frac{2}{k\,(k-1)}\,\sigma_s^2$$

and we know that without epistasis (Kempthorne, 1957):

$$\sigma_g^2 = \frac{1 + F_0}{4}\,\sigma_A^2$$

$$\sigma_s^2 = \left(\frac{1 + F_0}{2}\right)^2 \sigma_D^2$$

(F_0 is the coefficient of inbreeding of the parents).

Then if σ_S^2 is mainly determined by *var* $\overline{C}$ we can study the effect of the number of parents and of their inbreeding. Before discussing some consequences, we shall first give a general approach for diploids and tetraploids.

2. *General approach*

Variance between independent synthetics is equal to the covariance within synthetics. For diploids, Gillois (1964) and Harris (1964) have given independently the expression of covariance between inbred relatives:

$$Cov\,(X\,Y) \doteq 4\,\varphi_{XY}(i|i)\,E(\alpha_i^2) + 4\,\varphi_{XY}(ii|i)\,E(a_i\,\beta_{ii}) + \\ + \varphi_{XY}(ij|ij)\,E(\beta_{ij}^2) + \varphi_{XY}(ii|ii)\,E(\beta_{ii}^2) + \\ + \{\varphi_{XY}\,(ii|jj) - F_X\,F_Y\}\{E(\beta_{ii})\}^2\,. \quad (7)$$

$\varphi_{XY}\,(i|i) = r_{XY}$ is the coefficient of parentage (Malécot, 1948).

The other coefficients $\varphi_{XY}(|)$ are the new coefficients of parentage defined by Gillois and Harris; between brackets the vertical line separates the genes drawn from each zygote X and Y, and the letters represent classes of identity by descent of the genes drawn (Gallais, 1970b).

$$\varphi_{XY}(ii|i) \;= s_{XY}\,,$$

probability of having three identical genes, 2 in one zygote, 1 in the other zygote,

$$\varphi_{XY}(ii|ii) = t_{XY}\,,$$
$$\varphi_{XY}(ij|ij) = u_{XY}\,,$$
$$\varphi_{XY}(ii|jj) = v_{XY}\,.$$

Then we have to calculate these different coefficients of parentage:

$$\varphi(i|i) = \frac{1 + F_0}{2\,k}\ (F_0\text{, coefficient of inbreeding of the parents}).$$

$$\varphi(ii|i) = \frac{1 + 3\,F_0}{4\,k^2}\,,$$

$$\varphi(ij|ij) = 1/k^3 \left\{\frac{1 - F_0}{4} + 2\,(k-1)\left(\frac{1 + F_0}{2}\right)^2\right\},$$

$$\varphi(ii|ii) = 1/k^3\ \{F_0 + 1/8\,(1 - F_0)\}\,,$$

$$\varphi(ii|jj) = 1/k^3 \left\{\frac{1 - F_0}{8} + (k-1)\left(\frac{1 + F_0}{2}\right)^2\right\}.$$

For autotetraploids, Bouffette (1966) has given a general expression for covariance between inbred relatives without any assumptions on the genetic effects at one locus. This general expression contains 61 terms. We will retain here only the contributions of:

$$\sigma_A^2 = 4\,E(\alpha_i^2)\,,\quad \sigma_D^2 = 6\,E(\beta_{ij}^2)\,,\quad \sigma_T^2 = 4\,E(\gamma_{ijk}^2)\,,$$
$$\sigma_F^2 = E(\delta_{ijkl}^2)\,.$$

According to our previous notation (1969), the corresponding coefficients of these components for k parent synthetics in equilibrium will be: (see annexe):

$$\text{for } \sigma_A^2,\ 4\,\varphi_{XY}(i|i) = \frac{1 + 3\,F_0}{k}\,,$$

$$\text{for } \sigma_D^2,\ 6\,\varphi_{XY}\left(\begin{array}{c|c} i & i \\ j & j \end{array}\right) = \frac{6}{k^3}\,\{\pi + (k-1)\,\Delta^2\}\,,$$

$$\text{for } \sigma_T^2,\ 4\,\varphi_{XY}\left(\begin{array}{c|c} i & i \\ j & j \\ k & k \end{array}\right) = \frac{4}{k^5}\,\{(1/4)^5\,(P_3 + P_4) + \\ + (k-1)\,\pi\,\Delta + (k-1)\,(k-2)\,\Delta^3\}\,,$$

$$\text{for } \sigma_F^2,\ \varphi_{XY}\left(\begin{array}{c|c} i & i \\ j & j \\ k & k \\ l & l \end{array}\right) = \frac{1}{k^7}\,\{(1/4)^8\,P_4 + (1/4)^4\,(k-1) \times \\ \times\,(P_3 + P_4) + 3\,(k-1)\,\pi^2 + 6\,(k-1) \times \\ \times\,(k-2)\,\pi\,\Delta^2 + (k-1)\,(k-2)\,(k-3)\,\Delta^4\}\,,$$

with

$$\Delta = \frac{1 + 3\,F_0}{4}$$

and

$$\pi = 5/8\,P_1 + 1/2\,P_2 + 9/256\,P_3 + 3/128\,P_4\,,$$

and P_0, P_1, P_2, P_3 and P_4, the probability attached to the five situations of identity for one zygote (Gallais, 1967b).

For the case of ploidy of degree ν, we can give only one general result for the coefficient of σ_A^2 which is:

$$\nu\,\varphi_{XY}(i|i) = \frac{1 + (\nu - 1)\,F_0}{k}\,.$$

Obviously, at equilibrium, the coefficient of parentage $\varphi_{XY}(i|i)$ is equal to the coefficient of inbreeding F.

3. Discussion

In order to study the contribution of some components to the variance between synthetics, we have computed the corresponding coefficients of parentage for some particular cases (table 1). We note that the coefficients of σ_T^2 and σ_F^2 are always very small whatever the number of parents and their inbreeding.

For a given level of inbreeding of the parents, when k increases (from 2 to k), the coefficient of each component (σ_A^2, σ_D^2 for diploids, σ_A^2, σ_D^2, σ_T^2, σ_F^2 for tetraploids) decreases. The decrease is more rapid

Table 1. *Coefficients of σ_A^2 and σ_D^2 in the variance between synthetics according to the value of k and the level of inbreeding realized by n generations of selfing*

Diploids

k	$n = 0$ $(F_0 = 0)$		$n = 1$ $(F = 0.5)$		$n = \infty$ $(F = 1)$	
	$1/2\,\sigma_A^2$	σ_D^2	$1/2\,\sigma_A^2$	σ_D^2	$1/2\,\sigma_A^2$	σ_D^2
1	0.5000	0.2500	0.7500	0.1250	1.0000	0.0000
2	0.2500	0.0937	0.3750	0.1562	0.5000	0.2500
3	0.1667	0.0463	0.2500	0.0880	0.3333	0.1481
4	0.1250	0.0273	0.1875	0.0547	0.2500	0.0937
5	0.1000	0.0180	0.1500	0.0370	0.2000	0.0640
6	0.0833	0.0127	0.1250	0.0266	0.1667	0.0463
7	0.0714	0.0095	0.1071	0.0200	0.1428	0.0349
8	0.0625	0.0073	0.0937	0.0156	0.1250	0,0273

Tetraploids

k	$n = 0$ $(F_0 = 0)$		$n = 4$ $(F_0 = 0.5177)$		$n = \infty$ $(F = 1)$	
	$1/4\,\sigma_A^2$	$1/6\,\sigma_D^2$	$1/4\,\sigma_A^2$	$1/6\,\sigma_D^2$	$1/4\,\sigma_A^2$	$1/6\,\sigma_D^2$
1	0.2500	0.0234	0.6383	0.3778	1.0000	0.0000
2	0.1250	0.0107	0.3191	0.0982	0.5000	0.1250
3	0.0833	0.0055	0.2127	0.0442	0.3333	0,0741
4	0.0625	0,0033	0.1596	0.0250	0,2500	0,0469

for variances associated with increasing order of interactions among genes. This conclusion is also reached by Hill (1971) using another approach.

For a given number of parents ($k \geq 1$) increasing their level of inbreeding increases the coefficients of the previous components. The coefficient of σ_A^2 is linearly related to F. The increase is greater for components associated with increasing order of interactions between genes (digenic, trigenic, tetragenic,... interactions).

As in the first approach for diploids, the general approach shows that specific combining ability contributes less than general combining ability to the variance between synthetics, and even less as k becomes greater. As k increases, the variance between synthetics decreases. As inbreeding increases, the contribution of components of specific combining ability increases.

Consider the case where $k = 1$. With no inbreeding, the coefficients of σ_A^2 and σ_D^2 are maximum. The coefficient of σ_A^2 increases with inbreeding, whatever the level of ploidy. In diploids, the inbreeding of parents reduces the coefficient of σ_D^2. For tetraploids this coefficient reaches a maximum with four generations of selfing of the parents.

With multiallelism, without any information about the sign and magnitude of covariance terms such as $cov\ \overline{P}_s \overline{C}$ in (6) or $E\,(\alpha_i\,\beta_{ii})$, $E\,(\alpha_i\,\gamma_{iii})$, $E\,(\alpha_i\,\delta_{iiii})$, $E\,(\beta_{ii}\,\gamma_{iii})$, etc. ..., it is difficult to deduce precise rules on the effects of the number of parents and their level of inbreeding on the variance between synthetics. With biallelism ($A, a; p, q$) in diploids we can solve the problem because (Gallais, 1970b):

$$E(\alpha_i^2) = p\,q\,\{d - (p - q)\,h\}^2$$

(d and h from Mather, 1949).

$$E(\alpha_i\,\beta_{ii}) = 2\,p\,q\,(p - q)\,\{d - (p - q)\,h\}\,h\,,$$
$$E(\beta_{ii}^2) = 4\,p\,q\,(p^2 - p\,q + q^2)\,h^2\,,$$
$$E(\beta_{ij}^2) = \{E(\beta_{ii})\}^2 = 4\,p^2\,q^2\,h^2\,.$$

In this case, with no inbreeding, our exact treatment does not lead strictly to Hill's formula for the coefficient of σ_D^2. By numerical application, giving particular values to p and h/d, we can compute one quantity proportional to σ_S^2. Results show that when k increases from 2 to k, variance between synthetics decreases, whatever the level of inbreeding and value of p and h/d. For given $k > 1$, inbreeding increases σ_S^2. For $k = 1$, σ_S^2 is not always maximum, according to the level of inbreeding and the values of p and h/d. With overdominance and a low value for p, inbreeding can decrease σ_S^2. With inbreeding, overdominance, $h/d > 1$, and a low value for p, σ_S^2 can increase when k increases from 1 to 2 and then decrease.

Consequences

By combining the studies on means and variances according to formula (1) it is possible to determine an optimal genetic base for one particular type of variety. Indeed, to obtain the maximum mean, if there is inbreeding depression in the material, the genetic base must be broad (i.e.: a large number of parents, no inbreeding, no relationship between parents). For variance, in order to have high selection intensity, it appears that the genetic base must be narrow (i.e. small number of parents with high inbreeding). If mainly additive, variance will be maximum for one parent synthetics with maximum inbreeding; if there is mainly dominance, according to the level of inbreeding, variance between synthetics is maximum for $k = 1$ or $k = 2$. The results show that for autotetraploids it will be difficult to use the part of variance due to interaction between more than two alleles. By induction the same conclusions can be drawn about the use of variance of epistatic effects other than first order. Consequently, selection between synthetics for moderate value for k (2 to 4) will use mainly additive variance, part of dominance variance and part of epistatic variance (additive × additive). Use of dominance and epistatic variance increases with the level of inbreeding.

It appears that the effects of the number of parents and their level of inbreeding, i.e. the factors of genetic base, on the mean are in opposition to those on the variance. These effects are synthesized in formula (1) from which we can write for the expected value of selected synthetic varieties (Gallais *et al.*, 1970):

$${}_G\bar{S} = E(S) + i\,h\,{}_G\sigma_{Syn}$$

with

$$h = \frac{{}_G\sigma_{Syn}}{{}_P\sigma_{Syn}}$$

$$i = \frac{{}_P\bar{S} - E\,(S)}{{}_P\sigma_{Syn}}$$

(= intensity of selection between synthetics).

In order to study the optimal genetic base, it is necessary to know the importance of parameters such as inbreeding depression, variance and covariance of genetic effects.

For diploids, without epistasis, it is necessary to know the mean of selfed parents, the covariance between selfed parents and their crosses and the variance between crosses and its components, i.e. general and specific combining ability variances. If inbreeding depression is strong relative to ($i\,h\,{}_G\sigma_{Syn}$) it will be essential to increase the mean. If the genetic variance between synthetics is great in comparison with inbreeding depression, with large heritability it will be essential to use a small number of inbred parents. If the situation is intermediate, an optimum for the number of parents and their level of inbreeding may exist. There can be an ideal combination of inbreeding and number of parents (Gallais *et al.*, 1970). Remember here that a special case with both mainly additive variance and inbreeding depression can occur. From experimental values for genetic parameters of one population with some genetic hypotheses, it will be possible to compute this optimum genetic base. For diploids in the case of biallelism without epistasis, situations where there is an optimum genetic base can be studied by computation like simulation, from a theoretical population.

There are several experimental results which show that small numbers of parents are as good as, or better than, large numbers (see references in Corkill, 1956; Kehr et al., 1961; Kinman, 1945 for breeding synthetic varieties). Sometimes an optimum number is found. We do not know of any results on the influence of inbreeding of the parents. We know that for diploid hybrid varieties inbreeding increases genetic progress. Theoretically it appears that inbreeding may allow better synthetic varieties to be built. This effect will be greater when dominance variance is larger than additive variance. In this case there can be a possible additional gain by selection between groups of parents (i.e. between synthetics) instead of selection between parents.

Table 2. *Some illustrative results of computation of variance between diploid one locus synthetics with biallelism* (A, a; p, q)

k	$a = 0$			$a = 1$			$a = 2$		
	$F = 0$	$F = 1/2$	$F = 1$	$F = 0$	$F = 1/2$	$F = 1$	$F = 0$	$F = 1/2$	$F = 1$
				$p = 0.125$					
1	.4677	.5728	.6614	.6523	.6546	.6614	.8472	.7521	.6614
2	.3307	.4050	.4677	.5210	.5900	.6523	.7154	.7832	.8472
3	.2700	.3307	.3818	.4413	.5144	.5789	.6148	.7025	.7820
4	.2338	.2864	.3307	.3890	.4595	.5210	.5456	.6355	.7154
5	.2091	.2561	.2958	.3515	.4185	.4765	.4950	.5828	.6601
6	.1909	.2338	.2700	.3231	.3865	.4413	.4561	.5407	.6147
7	.1767	.2161	.2500	.3006	.3609	.4128	.4251	.5065	.5773
8	.1653	.2024	.2338	.2822	.3395	.3890	.3996	.4776	.5456
				$p = 0.5$					
1	.7071	.8660	1.0000	.7500	.8750	1.0000	.8660	.9013	1.0000
2	.5000	.6123	.7071	.5229	.6449	.7500	.5862	.7341	.8660
3	.4082	.5000	.5773	.4221	.5220	.6085	.4614	.5832	.6938
4	.3535	.4330	.5000	.3630	.4487	.5229	.3903	.4929	.5862
5	.3162	.3872	.4472	.3232	.3992	.4647	.3435	.4330	.5138
6	.2886	.3535	.4082	.2941	.3629	.4221	.3099	.3897	.4614
7	.2672	.3272	.3780	.2716	.3348	.3894	.2844	.3567	.4217
8	.2500	.3061	.3535	.2536	.3124	.3630	.2642	.3307	.3903
				$p = 0.875$					
1	.4677	.5728	.6614	.3121	.5142	.6614	.2480	.4873	.6614
2	.3307	.4050	.4677	.1594	.2470	.3121	.1401	.1977	.2480
3	.2700	.3307	.3818	.1116	.1663	.2086	.1158	.1397	.1682
4	.2338	.2864	.3307	.0881	.1277	.1594	.1028	.1187	.1401
5	.2091	.2561	.2958	.0740	.1053	.1306	.0937	.1077	.1254
6	.1909	.2338	.2700	.0645	.0905	.1116	.0869	.0998	.1158
7	.1767	.2164	.2500	.0577	.0798	.0981	.0814	.0939	.1086
8	.1653	.2024	.2338	.0525	.0720	.0881	.0768	.0889	.1028

Formula (1) can also be extended to selection between hybrids. For diploids, Cockerham (1961) has given formulae and in this case the expected value $E(V)$ of crosses is the mean of the reference population. Also, the best genetic base is the narrowest (2 highly inbred unrelated parents). For autotetraploids the mean of crosses depends on the level of inbreeding of the parents (Gallais, 1968b), as in synthetics. Then, for autopolyploids, it is not obvious that single crosses will be better for the efficiency of selection. As in synthetics, an optimum genetic base (number of parents, inbreeding) can exist for autopolyploid hybrid varieties, i.e., single or three way or double crosses . . .

A third conclusion can be drawn from our present study. With synthetics or with autopolyploid hybrids the expected value $E(V)$ of one variety is equal to the mean of the reference population plus an inbreeding effect so that a third level of breeding appears: population improvement. The population improvement which can be useful for synthetics is the within population selection procedure (or recurrent selection for general combining ability). There are two levels in an ideal scheme of breeding synthetics, firstly population improvement, and secondly the use of residual genetic variability in the improved population by selection among synthetics. However, if the within population selection is strong, or with repeated cycles, genetic variability decreases and little or none can be expected from using this reduced genetic variability in the optimum genetic base. A decrease in variability in the reference population increases the optimum genetic base, in order to avoid inbreeding depression not compensated for by selection. For one locus situation, it appears that the two methods of individual selection, within population and selection between synthetics, have the same potential. This can be seen in the expression of the population mean in the case of biallelism

$$\mu = (p - q)\, d + 2\, p\, q\, h$$

which, for given h/d, is maximum for

$$p = \frac{1 + h/d}{2\, h/d} = \frac{1 + a}{2\, a}$$

$h/d = a$ average degree of dominance (Comstock et al., 1948).

This value of p corresponds to the value for which the additive variance is zero (Griffing, 1963). By sampling groups of parents, this maximum mean can be approached more quickly by selection among synthetics than by individual within population selection. The variance between synthetics tends to be maximum for p values of about 1/2, for $0 \leq a < 1$. For $a = 1$ or nearly 1, the variance between synthetics is maximum for p values of about 1/2 with low values of k, $(2 - 4)$; with higher values of k, $(4 - 8)$, the variance tends to be maximum for low values of p. In the case of overdominance ($a = 2$ in our numerical application), the variance is maximum with low values of p. Therefore, differential selection among synthetics, for a given intensity of selection (i), is influenced by the variation of p due to the within population selection. The efficiency of population improvement before building synthetics depends upon the initial frequency of p and the value of the degree of dominance a. If we compare several biallelic populations with the same frequency of alleles, but with different degrees of dominance, it appears that for p between 0 and 1/2, increasing the value of a increases the variance between synthetics, but between 1/2 and 1, increasing the value of a tends to decrease the variance (table 2). This underlines the fact that breeding rules or results can differ from one material to another, according to the genetic effects. These results have to be extended for a polygenic situation.

If selection among synthetics can be more efficient than individual selection, there remains the problem of practical application. It is easier for the plant breeder to select individuals than to select groups of individuals with good combining ability in synthetics. A better theoretical and experimental knowledge of the relationships between parental characteristics (clonal value, value under inbreeding, general and specific combining ability . . .) and the value of synthetics at equilibrium should allow the best synthetics to be built without testing all combinations.

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Annexe

Computation of coefficients of parentage in the expression of variance between diploid k parent synthetics

Let F_0 coefficient of inbreeding of the parents.

$\varDelta = \frac{1 + F_0}{2}$ classical coefficient of parentage of one individual with itself.

$\varphi(i|i) = \frac{1}{k}\varDelta$ (Probability of having two identical genes from one parent).

$\varphi(i|ii) = \frac{1}{k^2}\{F_0 + 1/4\,(1 - F_0)\}$ (Probability of having three identical genes from one parent).

$\varphi\left(\begin{array}{c|c} i & i \\ j & j \end{array}\right) =$ Probability of having two genes i, j in one genotype, and 2 genes k, l in another genotype, such $i \equiv k$, $j \equiv l$. This is possible with genes from one parent or from two parents:

- from one parent with probability $(1/k^3)\,(1/4)\,(1 - F_0)$
- from two parents with probability $\frac{2\,(k-1)}{k^3}\,\Delta^2$

$\varphi\left(\begin{array}{c|c} i & i \\ i & i \end{array}\right) =$ Probability $(i \equiv j \equiv k \equiv l)$. This is only possible with genes from one parent:
  - homozygous by descent, with probability $(1/k^3)\,F_0$,
  - not homozygous by descent, with probability $(1/k^3)\,(1/8)(1 - F_0)$.

$\varphi\left(\begin{array}{c|c} i & j \\ i & j \end{array}\right) =$ Probability $(i \equiv j \not\equiv k \equiv l)$. This is possible with genes from one parent, or from two parents:

- from one parent (not homozygous by descent) with probability $(1/k^3)\,(1/8)\,(1 - F_0)$,
- from two parents with probability $\frac{k-1}{k^3}\,\Delta^2$.

For coefficient $\varphi\left(\begin{array}{c|c} i & i \\ j & j \end{array}\right)$, $\varphi\left(\begin{array}{c|c} i & i \\ j & j \\ k & k \end{array}\right)$, $\varphi\left(\begin{array}{c|c} i & i \\ j & j \\ k & k \\ l & l \end{array}\right)$

in autotetraploïds, we have used a similar process of computation, taking into account the facts that:

- any parent with genotype $i\,j\,k\,l$ can have five states of identity at one locus $(i \equiv j \equiv k \equiv l$, $i \equiv j \equiv k \not\equiv l$, $i \equiv j \not\equiv k \equiv l$, $i \equiv j \not\equiv k \not\equiv l$, $i \not\equiv j \not\equiv k \not\equiv l)$,
- drawings can be made from one or two parents for $\varphi\left(\begin{array}{c|c} i & i \\ j & j \end{array}\right)$, from one, two or three parents for $\varphi\left(\begin{array}{c|c} i & i \\ j & j \\ k & k \end{array}\right)$ and from one, two, three or four parents for $\varphi\left(\begin{array}{c|c} i & i \\ j & j \\ k & k \\ l & l \end{array}\right)$.

With these remarks the use of elementary laws of probability leads to the results given in the text.

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