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The Selection of Parents for Synthetic Varieties of Outbreeding Diploid Crops

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Summary. As a criterion for the selection from a population of individuals with a high potential as parents of synthetic varieties, the general varietal ability of an individual is defined as the mean expression of all possible synthetics of a given size(s) having this plant as a common parent. Using known expressions for the prediction of the performance of advanced generations of diploid synthetic varieties, general varietal ability is expressed in terms of the F_1 and I_1 progenies of the plants under test, and is found to be a simple function of the polycross (g.c.a.) and inbred progeny means, where the contribution of the inbred progeny varies according to n and s. The implications and use of such a progeny test in the breeding of out-pollinating crops is discussed.

Introduction

In an outbreeding crop, the attribute of the individual which is of importance to the breeder is that portion of the genotype which is transmitted to its random bred progeny. This attribute is known as breeding value, and is a property not only of the individual, but depends also on the population to which it belongs (Falconer, 1960). The concept of breeding value is central to theories of selection and response in random mating populations, and can be defined as the mean genotype of offspring derived from all possible combinations of gametes produced by an individual with those from the population at large. In practice, breeding value is estimated as the mean of crosses made between an individual and a random sample of individuals drawn from the reference population. This term is therefore synonymous with general combining ability (g.c.a.), although the latter stems essentially from the different concept of the identification of consistently good parents of single cross hybrids.

In most outbreeding crops, the chief aim of selection is not only the change of population mean by mass or other selection, but ultimately the production of a synthetic variety, the novel feature of which is the severely restricted number of parents employed. This paper examines the role of the progeny test in the choice of potential parents for synthetic varieties.

The Prediction of Synthetic Performance in Diploid Heterozygous Material

It is well known that changes in mean population expression may accompany multiplication of a synthetic variety. The limited number of parents of the *Syn* 1 generation leads to inbreeding, resulting, in a self sterile species, in depression of vigour in the *Syn* 2 and subsequent generations (Corkill 1956). In diploids, no further change is expected following *Syn* 2, if strong epistatic effects are assumed absent, and no gene immigration or natural selection occurs during multiplication. As pointed out by Busbice (1970), the prediction of the performance of the commercial generations of a synthetic variety depends on a knowledge of the performance and average coefficients of inbreeding (F) of any two generations and the inbreeding coefficient of the synthetic variety. Assuming that no selection or gene immigration occurs during multiplication, and that the relationship between population mean and heterozygosity and hence inbreeding coefficient is linear, i.e. no genic interactions of the heterozygote × heterozygote type, then the mean of the second and subsequent generations of the synthetic is easily found as the single unknown in the system. Apart from the first synthetic generation, prediction is usually based on the completely homozygous, real or imaginary, ancestral generation ($F = 1$). More readily available to the breeder is the first inbred generation (I_1). Using the formulae given by Busbice (1969); for the first synthetic generation, $F = r_0$, for the first inbred generation, $F = 1/2\ (1 + F_0)$, and for the synthetic at equilibrium, $F = 1/2\ (1 + F_0)/s + ((s - 1)/s)\ r_0$, where s is the number of parents to be used in the formation of the synthetic, r_0 is their mean coefficient of parentage, and F_0 their mean coefficient of inbreeding. It is then readily found that:

$Syn_n = Syn_1\ ((s - 1)/s) + I_1(1/s)$, independently of F_0 and r_0, and hence of the breeding history of the parents.

The first generation crosses and inbreds used in the above prediction make up the complete diallel set among these s parents, since the inbreds (leading diagonal) constitute $1/s$th part of the table. Hence, the expected mean of any specified synthetic based on s parents can be found as the mean of the $s \times s$ diallel table which can be extracted from a larger

($n \times n$) diallel. This conclusion was to be expected in view of the equilibrium gene frequencies generated by a diallel crossing scheme, and has been used by Rogers and Thomson (1970) for the prediction of performance of some small synthetics in perennial ryegrass.

However, while it may be possible to identify useful synthetics in this way, it is a less efficient procedure than concentrating on the choice of superior parents (Hill, 1971). This is frequently achieved by the use of a progeny test which aims at the direct estimation of g.c.a., notable the polycross as used in the self-sterile grasses (Frandsen 1940). While g.c.a. is relevant to the selection of individuals for the improvement of an indefinitely large population, it takes no account of the effects of limitations of population size in the parental generation prior to the formation of the synthetic. The above consideration of the constitution of the synthetic variety implies that some measure of the performance of the inbred progeny of a potential parent can be included to give a more pertinent evaluation.

The Progeny Test in the Construction of a Synthetic

For convenience, the potential of an individual as a constituent of a synthetic variety will be referred to as its general varietal ability (g.v.a.). It will be seen that this quantity is specific to the size of the synthetic which is to be formed as well as to the individual and the population from which the remaining varietal constituents are to be drawn. The general varietal ability of the ith individual for synthetics of size s can be defined as the mean of all synthetics which have the ith as one of s parents chosen from n.

Table 1. *Frequencies and types of entry in the diallel table with respect to the general varietal ability of the ith parent (see text)*

Type of progeny	No. of entries per type	Total occurrences per type	No. of occurrences per individual entry
a_{ii}	1	x	x
a_{kk}	$(n-1)$	$x(s-1)$	$x(s-1)/(n-1)$
a_{ik}	$2(n-1)$	$2x(s-1)$	$x(s-1)/(n-1)$
a_{kl}	$(n-1)(n-2)$	$x(s-1)(s-2)$	$\frac{x(s-1)(s-2)}{(n-1)(n-2)}$
Total	n^2	$x s^2$	

Considering the crosses and inbreds involved in the prediction of synthetic performance as a complete diallel table as before, the entries specifying the general varietal ability of the ith individual for synthetics of size s can be allocated to one of four groups or types, each member of one of which will occur the same number of times in the prediction (see Table 1). Type a_{ii} is simply the ith diagonal (inbred) entry which occurs once in every synthetic involving the ith parent. This number need only be represented by x since, as will be shown later, its actual value is not relevant to the present problem. Type a_{kk} includes all other diagonal entries. Since $(s-1)$ of these occur in each synthetic, the $x(s-1)$ possible occurrences are shared among $(n-1)$ entries. Type a_{ik} includes all crosses involving the ith parent, that is, all off-diagonal entries in the ith array. Since a_{ik} must occur whenever a_{kk} occurs, then the number of occurrences of each entry of types a_{ik} and a_{kk} are the same (column 2 of Table 1). Knowing that the total number of occurrences must be $s^2 x$ (s^2 entries in each of x possible synthetics), then the number of occurrences for the fourth type of entry, a_{kl}, representing the remaining off-diagonal entries, can most easily be found by difference, and shared among the $(n-1)(n-2)$ entries of this type.

Table 2. *Simplified vectors for the derivation of difference in general varietal ability of the ith and jth parents after cancellation of common entries (see text)*

	a	b
Type of entry	Vector i minus vector j	Column a × $(n-1)(n-2)/(n-s)(s-1)$
a_{ii}	$(n-s)/(n-1)$	$(n-2)/(s-1)$
a_{jj}	$(s-n)/(n-1)$	$-(n-2)/(s-1)$
a_{kk}	0	0
a_{ik}	$\frac{(n-s)(s-1)}{(n-1)(n-2)}$	1
a_{jk}	$\frac{(s-n)(s-1)}{(n-1)(n-2)}$	-1
a_{kl}	0	0

The vector thus produced in column 2 of Table 1 gives a weighting which must be applied to the observed value of each cross or inbred family to give an unbiased estimate of general varietal ability. The essential purpose of this derived quantity is that it should be used to compare the values of available individuals for the purpose of choosing superior varietal parents. This involves the comparison of any two g.v.a. values (i.e. the ith and jth), and it is clear that certain elements of the two vectors will be equal, and can be removed by subtraction of one from the other. Furthermore, the factor x is common throughout, and can be ignored.

Table 2 shows the result of the subtraction of the jth parental vector from the ith (column a), while column b shows the resultant vector scaled to give unit weight to off-diagonal entries. It is clear from the table that, since all entries occurring in neither the ith nor the jth arrays of the diallel table disappear in this comparison, the g.v.a. for each parent can be effectively represented by a weighted combination of array members only. A comparison of the ith and jth g.v.a. values is simply the difference between the ith and jth array totals but with the diagonal entries weighted by the factor $(n-2)/(s-1)$.

It is worthwhile considering the effects on this final term of changes in the number of parents under assessment (n), and the size of synthetic under consideration (s). If s is very large, as would be the case with an indefinitely large selected population, then the diagonal, inbred, term disappears. This conforms to the definition of breeding value referred to earlier, and to Griffing's (1956) use of the 'modified' diallel. If n is reduced to two, then the term again disappears since no effective contrast is meaningful, both parents occurring in the only possible synthetic where $s > 1$.

The equality of weighting for all crosses within an array is important, because the mean array value, a direct estimate of g.c.a., can be used in conjunction with the inbred progeny. The mean of crosses within an array is in fact equivalent to the polycross progeny mean as used in the assessment of grasses, where complete self sterility of the constituent clones in the presence of foreign pollen can be assumed. The modification of such a progeny mean can therefore be achieved simply by the addition of the mean of selfed progeny, weighted by a factor of $(n-2)/(2(n-1)(s-1))$, since there are $2(n-1)$ non-diagonal entries in an array of the full diallel table so far considered. This is approximated by $1/(2(s-1))$ when n is large, or as a proportion of the total of $1/(2s-1)$.

Discussion

Formulae given by Busbice (1970) include the prediction of the performance of synthetic varieties from parents with polysomic inheritance. However, the assumption upon which all predictions are based, namely linearity of the relationship between performance and inbreeding coefficient, can only in general hold under disomic inheritance. Furthermore, the progeny test is of only limited value in polyploids since it fails to separate all non-additive from additive genetic variation. The foregoing arguments are therefore confined to diploid crops and alloploids showing diploid inheritance.

In a cross-fertilised crop, the progeny test may be used as an alternative to mass phenotypic selection for the improvement of a random mating population. It is more frequently used, however, as a means of choosing from this improved population a group of individuals with a high potential as parents of synthetic varieties, usually as a preliminary to the production and early generation testing of such varieties. The suggested modification of the progeny testing procedure to allow for the effects of inbreeding offers a sound basis for the isolation of potential mother plants. It does not, however, imply the automatic choice of those parents which will produce the best possible synthetic of a given size. Specific varietal effects arise from the fact that any selected group may have a higher or lower coefficient of parentage than the population as a whole, and necessitate the testing of all varieties produced.

The extent to which this proposed modification of the progeny test materially alters the ranking of genotypes depends both on the existence of variation among inbred family means, and the extent to which this is correlated with g.c.a. values. Since g.c.a. depends on the number of favourable alleles carried, irrespective of whether these are in the homozygous or heterozygous phase, while inbreeding depression in part, at least, depends on precisely this latter condition, there seem to be grounds for expecting the two attributes to show some measure of independence. One method of analysis of the complete diallel cross, given by Hayman (1954), allows the estimation of heterogeneity of the mean cross (g.c.a.) by self comparison over arrays (item b2). Little use has been made of this analysis in the assessment of outbreeding crops, although in the context of synthetic variety production it has especial value. A high level of significance for the b2 item was reported by Lewis (1970) for seed production characters in S23 perennial ryegrass. Similarly, Thomas and Frakes (1967) found low correlations between the rankings of tall fescue genotypes for various characters using inbred and polycross progeny.

Typical numbers of parents for synthetic varieties lie in the range four to eight (Kinman and Sprague, 1945). If inbreds are included in the progeny test according to the proportion $1/(2s-1)$, they will represent between one-seventh and one-fifteenth part of the total. In crops which are normally assessed at low densities, sufficient I_1 plants can probably be raised to represent this proportion. In the grasses, however, assessment of productivity characters is normally carried out under sward conditions, the value of the polycross lying essentially in its ability to provide adequate seed for this purpose. The production of about one-tenth of the total seed required by means of selfing (e.g. about 10 g from each clone in a typical ryegrass trial) is impossible, and the probable reduced vigour of the inbreds would in any case prejudice their establishment in competition with the polycross seed with which they were mixed. In these species, therefore, the use of inbreds would be confined to spaced plants or small simulated sward plots, and therefore to characters easily assessed at low densities. Where the number of parents to be included in the synthetic is greater than about ten, then the potential bias involved in ignoring the performance of inbred progeny will be negligible, and full confidence can be placed in the direct estimation of general combining ability.

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