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Covariances of relatives and selection response in generations of selfing from an outcrossed base population

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Summary. The covariances of relatives arising under selfing from a general outbred base population in linkage equilibrium and without epistasis given by Cockerham (1983) are expressed in an alternative form which is an extension of the treatment by Mather and Jinks (1982) of the more restricted population descended from a single F_1 family. Whereas no more than two quadratic components are required to describe any covariance in the case of F_1 descendants, this more general case calls for a total of four, three of which are needed for any particular covariance. The estimation of covariances and their use for the prediction of selection response is described for breeding programs initiated by one or more cycles of intermating among a number of parental lines, as advocated by Hansel (1964) and Jensen (1970). It is pointed out that the homozygous lines descended from such a population will have up to twice as much variance as those from an F_1 between a randomly chosen pair from the same population of parents. The selection method is especially recommended for undeveloped species in which the parental lines are not well characterized and large selection responses are needed.

Key words: Covariances of relatives – Selection response – Selfing – Outbred base population – Intercrossing

Introduction

Selection programs in self-pollinating species commonly concentrate a large proportion of their resources on comparisons among the descendants of particular crosses, selection between the crosses depending either on the choice of pairs of parents according to their known agricultural merits and deficiences, or on the assessment of their F_1's. Such a system reduces the potential of the program by subdivision of the gene pool, as the particular pair of alleles available at any locus is determined at the outset by the choice of parents.

The inclusion of a larger number of parental lines has been advocated (Hanson 1959; Hansel 1964; Jensen 1970) as a means of increasing the variability available in the segregating generations during selfing.

The analysis of the variation arising among the descendants of a single F_1 family for the purpose of predicting the response to selection in particular generations (Gates et al. 1957) or the distribution of the final inbred lines (Jinks and Perkins 1972; Snape and Riggs 1975; Jinks and Pooni 1976) is based on a genetical model which assumes no more than two alleles at a locus and is therefore inappropriate for the analysis of the generations descended from the more complex parentage considered above. The model used by Weir and Cockerham (1977) carries no assumptions about allele numbers or frequencies and is completely general with respect to additive and dominance effects as well as breeding systems, but leads to cumbersome expressions when applied to selfing series (Cockerham 1983).

This paper introduces a model which is in many respects a combination of the two described above and develops formulae for the covariances of relatives and expected selection response for the generations of selfing initiated from an outbred base population.

The two models

The terms included in the model used by Cockerham (1983) are expressed as deviations from the mean of an outbred base population, such that the single-locus genotype with alleles i and j is

$$\alpha_i + \alpha_j + \delta_{ij},$$

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where the α terms are the additive effects of alleles in the population and δ_{ij} is the dominance effect of the ijth combination. All effects are defined as least squares parameters in a random mating population. Mather and Jinks' (1982) model, on the other hand, uses two parameters to describe the three genotypes possible with two alleles, putting 2 d equal to the difference between the homozygotes and h equal to the deviation of the heterozygote from the homozygote mean, so that the effects are contrasts among genotypes without reference to any population.

The quadratic functions which arise from the two models are given in Table 1. When there are two equally frequent alleles, $D_R = 2\sigma_A^2 = \sum d^2 = D$, $H_R = 4\sigma_D^2 = \sum h^2 = H$, and $\mathscr{f} = D_1 = D_2^* = 0$. For the two-allele model, there are evident equivalences between the two sets of functions, and, apart from illuminating the relationships between models based on outbred and inbred reference populations, this suggests that the components D_R, H_R and $\mathscr{f}$ could be redefined in a form sufficiently general to accommodate multiple alleles. Apart from the direct equivalence evident between H_R and $4\sigma_D^2$, the following definitions are made:

$$\sigma_M^2 = 2\sigma_A^2 + 4D_1 + D_2^* = 4\sum_i\sum p_i \alpha_i^2 + 4\sum_i\sum p_i \alpha_i \delta_{ii} + \sum_i\sum p_i \delta_{ii}^2 = \sum_i\sum p_i (2\alpha_i + \delta_{ii})^2$$

$$\sigma_{MH} = 2D_1 + D_2^* = 2\sum_i\sum p_i \alpha_i \delta_{ii} + \sum_i\sum p_i \delta_{ii}^2 = \sum_i\sum p_i (2\alpha_i + \delta_{ii})\,\delta_{ii}$$

where summation is over loci and alleles. Like D_R, σ_M^2 is the variance of homozygotes but defined for a population with an arbitrary number of alleles. The covariance of homozygous genotypes with the homozygous dominance deviations of the same allele, σ_{MH}, is an extension of Mather and Jinks' $\mathscr{f}$ (1982).

Covariances of relatives

Weir and Cockerham (1977) gave a general expression for a covariance between relatives which uses various identity by descent measures, and this covariance can be expressed in terms of the new components following a simple rearrangement of these coefficients. However, for the present purpose the covariance of relatives under selfing which was given by Cockerham (1983) will be translated directly. In the absence of epistasis and linkage, the covariance of members of the gth and g′th generations of selfing from an outbred (zeroth generation) population in linkage equilibrium, and whose last common ancestor occurred in the tth generation, is

$$C_{tgg'} = (1 + F_t)\,\sigma_A^2 + (F_g + F_{g'} + 2F_t)\,D_1 + \left[F_t + \frac{(F_g - F_t)(F_{g'} - F_t)}{2(1 - F_t)}\right] D_2^* + \frac{(1 - F_g)(1 - F_{g'})}{(1 - F_t)}\,(\sigma_D^2 + F_t H^*)$$

$$= \frac{1}{2}\left\{(1 + F_t)\,\sigma_M^2 + (F_g + F_{g'} - 2)\,\sigma_{MH} + \frac{(1 - F_g)(1 - F_{g'})}{(1 - F_t)}\,[D_2^* + 2\sigma_D^2 + 2F_t H^*]\right\}$$

where F denotes an inbreeding coefficient, F_n being that of the nth generation, $F_n = 1 - (1/2)^n$, and with $t \leqq g$ and $t \leqq g'$. Here $g \leqq g'$, and the variances for a single generation are given when $g' = g$.

The first outcome of this new system is that the original five components are reduced to four, since D_2^* and $2\sigma_D^2$ have the same coefficient and can be combined. For future convenience, the definition

$$\sigma_H^2 = D_2^* + 2\sigma_D^2$$

Table 1. Quadratic functions for the two models [a]

	Description	General case	Two-allele case
σ_A^2	Additive variance of outbreds	$2\sum_i\sum p_i \alpha_i^2$	$2\sum p(1-p)[d + h(1-2p)]^2$
σ_D^2	Dominance variance of outbreds	$\sum_i\sum p_i p_j \delta_{ij}^2$	$4\sum p^2(1-p)^2 h^2$
D_1	Covariance of additive and homozygous dominance effects	$\sum_i\sum p_i \alpha_i \delta_{ii}$	$-2\sum p(1-p)[d + h(1-2p)](1-2p)\,h$
D_2^*	Variance of homozygous dominance effects	$\sum_i\sum p_i \delta_{ii}^2 - \sum(\sum_i p_i \delta_{ii})^2$	$4\sum p(1-p)(1-2p)^2 h^2$
H^*	Squared inbreeding effects summed over loci	$\sum(\sum_i p_i \delta_{ii})^2$	$4\sum p^2(1-p)^2 h^2$
D_R	Homozygote variance	–	$4\sum p(1-p)\,d^2$
H_R	Dominance variance	–	$16\sum p^2(1-p)^2 h^2$
$\mathscr{f}$	Covariance of homozygote and homozygous dominance effects	–	$-8\sum p(1-p)(1-2p)\,dh$

[a] Summation is over loci for the two-allele model, and over both loci and alleles (at frequencies p_i) for the general case

is made. This covariance can therefore be expressed in the more explicit form

$$C_{tgg'} = [1 - (\tfrac{1}{2})^{t+1}]\,\sigma^2_M - [(\tfrac{1}{2})^{g+1} + (\tfrac{1}{2})^{g'+1}]\,\sigma_{MH} + (\tfrac{1}{2})^{g+g'-t+1}\,\sigma^2_H + [(\tfrac{1}{2})^{g+g'-t} - (\tfrac{1}{2})^{g+g'}]\,H^*.$$

Subdivision of total covariances

The above notation can be extended to allow a subdivision of the covariances arising from the hierarchy of families generated by the selfing scheme, as was done by Horner (1952). The component of covariance for families in the gth and g'th generations with a common ancestor in the tth but belonging to a subpopulation descended from a common ancestor in the kth generation will be written as $C_{ktgg'}$. It should be noted that this alters the sequence of indexing used by Horner (1952), Gates (1954) and Gates et al. (1957) but has the merit that now $k < t \leqq g \leqq g'$. Following Gates (1954), the hierarchical nature of these covariances implies that

$$C_{ktgg'} = C_{tgg'} - C_{kgg'}$$

for any values of $k < t$. $C_{ktgg'}$ can also be regarded as the covariance among families bulk-selfed from the tth to the gth and g'th generations belonging to subpopulations originating from distinct members of the kth. Further, $C_{ktgg'}$ is a component of covariance in the hierarchical analysis of covariance, and when $g = g'$ it is a component of variance in the analysis of variance. Putting $k = t - 1$ gives the complete hierarchical breakdown of the covariance of individuals in the gth and g'th generations into the components arising between families in the tth generation within families in the $t-1$th:

$$C_{tgg'} = C_{0gg'} + \sum_{j=1} C_{j-1jgg'},$$

in which the first term is already a component of covariance, as any covariance for $t < 0$ involves no common ancestor and is zero. Then, for $t = 0$,

$$C_{0gg'} = (\tfrac{1}{2})\,\{\sigma^2_M + (F_g + F_{g'} - 2)\,\sigma_{MH} + (1 - F_g)\,(1 - F_{g'})\,\sigma^2_H\},$$

and for $t > 0$

$$C_{t-1tgg'} = (\tfrac{1}{2})\,(F_t - F_{t-1}) \cdot \left\{\sigma^2_M + \frac{(1 - F_g)\,(1 - F_{g'})}{(1 - F_t)\,(1 - F_{t-1})}\,[\sigma^2_H + 2H^*]\right\}.$$

These can be reduced to

$$C_{0gg'} = (\tfrac{1}{2})\,\sigma^2_M - [(\tfrac{1}{2})^{g+1} + (\tfrac{1}{2})^{g'+1}]\,\sigma_{MH} + (\tfrac{1}{2})^{g+g'+1}\,\sigma^2_H$$

and

$$C_{t-1tgg'} = (\tfrac{1}{2})^{t+1}\,\sigma^2_M + (\tfrac{1}{2})^{g+g'-t+2}\,[\sigma^2_H + 2H^*].$$

It may be noted at this point that for a single F_2 family, there are two equally frequent alleles, so that $D^*_2 = \sigma_{MH} = 0$, $H^* = \sigma^2_D = H/4$, $\sigma^2_M = D$, and the above expressions reduce to

$$C_{0gg'} = (\tfrac{1}{2})\,D + (\tfrac{1}{2})^{g+g'+2}\,H = W_{1Fg+2g'+2}$$

$$C_{t-1tgg'} = (\tfrac{1}{2})^{t+1}\,D + (\tfrac{1}{2})^{g+g'-t+2}\,H = W_{t+1Fg+2g'+2}$$

in the notation of Mather and Jinks (1982).

The main features which distinguish the general formulae from those appropriate to a single F_2 are that all covariances involve three instead of just two components, and that the σ_{MH} term in covariances with $t = 0$ is replaced by a term in H^* when $t > 0$. This cancellation of the covariance of additive and dominance effects was also noted by Gates et al. (1957) for a model with two alleles per locus. It occurs because these covariances relate back to single individuals in the base population or later generations and are therefore free from the effects of unequal allele frequency, but H^* is involved because there is additional variation due to the random distribution of pairs of identical alleles.

Although it was noted that H^* and σ^2_D are equal when there are just two alleles, this need not apply otherwise because there is then more than one heterozygous genotype at a locus. As an example, consider the case when the heterozygotes and homozygotes vary so as to generate a large σ^2_D, but H^* is small because some heterozygotes have an advantage over the respective homozygotes and others a disadvantage. In general, either of the two components may be the larger. When just the components of covariance for $t > 0$ are considered, then $[\sigma^2_H + 2H^*]$ can be regarded as a single component because there are only two alleles within a pedigree, but in general, the terms have to be kept distinct. It may also be noted that, with two alleles, $\sigma^2_H + 2H^* = D^*_2 + 2\sigma^2_D + 2H^* = 4\sum p\,(1-p)\,h^2$, which is a function used by Gates et al. (1957) and by Mather and Jinks (1982).

Kempthorne (1957) derived some covariances under selfing in a similar form to those used here by the direct method of expressing a random genotypic value in each generation as the mean value of the homozygotes to which it would give rise under continued selfing and a deviation which represents the consequent inbreeding depression. Covariances were then obtained by expansion of the product of these compounds.

Selection response

The response of the mean of the g'th generation to selection among large families selfed as bulks from the

tth to the gth generation is given by

$$\Delta_{tgg'} = i\, C_{tgg'}/\sigma_{tgg} = i\, C_{tgg'}/(C_{tgg} + \sigma_e^2)^{1/2}$$

where i is the standardized selection differential, σ_{tgg} is the phenotypic standard deviation of these selection units, and σ_e^2 is the appropriate error variance. When t = g, selection is among individuals; more commonly, t = g − 1 or g − 2 for families of sibs or grand-sibs, and the difference is even greater when bulk selfing is employed over several generations.

If selection is confined to individuals or families descended from a common individual in the kth generation, then $C_{tgg'}$ and C_{tgg} in the above are replaced by $C_{ktgg'}$ and C_{ktgg}, respectively. In this case,

$$C_{ktgg'} = [(\tfrac{1}{2})^{k+1} - (\tfrac{1}{2})^{t+1}]\,\sigma_M^2 + [1 - (\tfrac{1}{2})^{t-k}]\,(\tfrac{1}{2})^{g+g'-t+1}\,[\sigma_H^2 + 2H^*].$$

A case of special interest is for k = 0 when selection is among the descendants of a single outbred individual, as such an individual is equivalent to an F_1 between a random pair of parents. This is the most commonly used base population for selection programs in self-pollinating species. The responses of the final homozygous lines when selection is among descendants of an outbred population created by intercrossing a large number of parental lines and from a single random F_1 depend on the covariances $C_{tg\infty}$ and $C_{0tg\infty}$, respectively:

$$C_{tg\infty} = [1 - (\tfrac{1}{2})^{t+1}]\,\sigma_M^2 - (\tfrac{1}{2})^{g+1}\,\sigma_{MH}$$

and

$$C_{0tg\infty} = (\tfrac{1}{2})\,[1 - (\tfrac{1}{2})^{t}]\,\sigma_M^2.$$

If selection is deferred until homozygosity, usually preceded by several generations of single-seed descent, then the covariances are $C_{\infty\infty\infty} = 2C_{0\infty\infty\infty} = \sigma_M^2$. Thus, in the absence of epistasis, the final lines from the whole base population have twice the variance of those descended from a single random F_1. If selection is among homozygous bulks, each of which is descended from a distinct individual in the tth generation, then this ratio is even greater. Since they are not individually in equilibrium, there may be differences among individual F_1's with respect to their descendant line variances, but these are not predictable and with many loci are expected to be small.

Estimation of components

Estimation of quadratic components from certain measured covariances, generally those in the earlier generations, allows the prediction of other covariances which determine selection responses. Since the performance of the final homozygous lines is of most interest, the important components are σ_M^2 and σ_{MH}, the latter being needed to predict the relative value of selection between and within lines of descent from individual outbred ancestors.

As pointed out by Cockerham (1983), covariances $C_{tgg'}$ for which t = g involve the measurement of single individuals, and are probably difficult to estimate in many species. Table 2 gives the coefficients of quadratic components for the statistics available from the growth and measurement of families arising from three generations of selfing, equivalent to the F_3, F_4, and F_5 when a single F_2 is involved.

The estimation of the four quadratic components can be carried out using a hierarchical analysis of variance (Horner and Weber 1956) or by a weighted least squares analysis as described by Mather and Jinks (1982). Unfortunately, from the point of view of estimation, the coefficients of σ_M^2, σ_{MH}, and σ_H^2 are highly mutually correlated in these statistics although those of H* are almost independent, and this problem remains even if more generations are grown. Mather and Jinks (1982) show that families produces by sib mating at different generations help to break these correlations in the case of F_2 descendants, but their use is not considered further here. For selection in the generations which are used for estimation, the standard deviations of observations can be measured directly, so that independent estimates only of σ_M^2 and σ_{MH} are necessary, but if predictions of the value of selection in later generations are required, then at least three of the four components are needed, in addition to the appropriate error variances. When only within-pedigree selection is of interest, then only within-pedigree statistics need be measured in order to estimate two genetic parameters, σ_M^2 and $(\sigma_H^2 + 2H^*)$, as in the case of a single F_2.

Table 2. Coefficients of quadratic components in statistics estimable from families following three generations of selfing

	σ_M^2	σ_{MH}	σ_H^2	H*
C_{011}	$\frac{1}{2}$	$-\frac{1}{2}$	$\frac{1}{8}$	0
C_{012}	$\frac{1}{2}$	$-\frac{3}{8}$	$\frac{1}{16}$	0
C_{022}	$\frac{1}{2}$	$-\frac{1}{4}$	$\frac{1}{32}$	0
$C_{0122} = C_{122} - C_{022}$	$\frac{1}{4}$	0	$\frac{1}{32}$	$\frac{1}{16}$
C_{013}	$\frac{1}{2}$	$-\frac{5}{16}$	$\frac{1}{32}$	0
C_{023}	$\frac{1}{2}$	$-\frac{3}{16}$	$\frac{1}{64}$	0
C_{033}	$\frac{1}{2}$	$-\frac{1}{4}$	$\frac{1}{128}$	0
$C_{0123} = C_{123} - C_{023}$	$\frac{1}{4}$	0	$\frac{1}{64}$	$\frac{1}{32}$
$C_{0133} = C_{133} - C_{033}$	$\frac{1}{4}$	0	$\frac{1}{128}$	$\frac{1}{64}$
$C_{1233} = C_{233} - C_{133}$	$\frac{1}{8}$	0	$\frac{1}{64}$	$\frac{1}{32}$

Epistasis and linkage

The general formulae have assumed linkage equilibrium in the outbred base population and absence of linkage and epistasis.

Although the genotypic model has been shown to be convenient when just additive and dominance effects are included, and can accommodate epistasis when there are two equally frequent alleles at each locus (Mather and Jinks 1982), an attempt at further generality meets with difficulties. The inclusion of additive by additive epistasis in $C_{tgg'}$ requires the addition of variance and covariance terms whose coefficients are functions of allele frequency as well as of generations of selfing. In the model defined by least squares, the only new term is $(1+F_t)^2\,\sigma^2_{AA}$, because the method of successive fitting leads to the absorption of the remaining variance and the covariance into the additive variance. This additive and additive by additive least squares model is an alternative to the additive-dominance model, and the two can be compared for goodness-of-fit (Cockerham 1983). The complete description of epistasis with inbreeding requires the separation of the interactions involving dominance effects of identical and non-identical allele pairs (Gallais 1974; Weir and Cockerham 1977) and leads to a large number of components.

It is only the variances or components of variance of homozygous lines that can be written explicitly in terms of the single locus homozygote variance (σ^2_M) and interactions of homozygous genotypes at two or more loci (σ^2_{MM}, σ^2_{MMM}, etc.). The variances of final lines from the outbred base and from a single F_1, with epistasis of any type, are

$$C_{\infty\infty\infty} = \sigma^2_M + \sigma^2_{MM} + \ldots$$

and

$$C_{0\infty\infty\infty} = \tfrac{1}{2}\,\sigma^2_M + \tfrac{3}{4}\,\sigma^2_{MM} + \ldots,$$

the nth term in $C_{0\infty\infty\infty}$ having a coefficient of $1-(\tfrac{1}{2})^n$. Epistasis therefore reduces the ratio of $C_{\infty\infty\infty}$ to $C_{0\infty\infty\infty}$.

Linkage leads to linkage disequilibrium in a single F_2, and disequilibrium can exist in the more general base population even in the absence of linkage. For a model with two alleles at arbitrary frequencies, Gates et al. (1957) showed that cross products of additive and dominance effects at different loci enter the covariances. Their decay with selfing when linkage is incomplete causes bias in the prediction of unknown covariances from those which can be measured, but also allows tests for linkage to be devised (Gates 1954; Mather and Jinks 1982). For the more general model with two alleles, Gates et al. (1957) showed that the component of covariances $C_{t-1tgg'}$ includes the extra terms:

$$(\tfrac{1}{2})^{t-2}\sum_i\sum_{j>i} d_i\,d_j\,\Pi_{ij}\,\lambda^t + (\tfrac{1}{2})^{g+g'-2}\sum_i\sum_{j>i} h_i\,h_j\,x_{ij}\,\lambda^2\,(1+\lambda^2)^{t-1}$$

where Π_{ij} is the linkage disequilibrium between loci i and j in the base population, $c_{ij}=(1-\lambda_{ij})/2$ their recombination rate, and x_{ij} the frequency of double heterozygotes. Whereas these terms disappear when there is no linkage, the covariances $C_{tgg'}$ contain joint contributions of the dominance effects of pairs of loci in disequilibrium regardless of whether they are linked or not.

Although Jinks and Pooni (1982) have shown that the linkage bias involved in the prediction of the variance of homozygotes from an F_2 using estimates of covariances from earlier generations is not expected to be large, that for covariances involved in response to selection in earlier generations remains. However, for a population of intercrosses, the individual Π_{ij}'s may be smaller than in the case of a single F_2 as well as variable in sign, so that there is no consistent bias and the errors may be small. This is particularly likely when more than one generation of intercrossing precedes selfing (Gates 1954).

Discussion

In his examination of the value of a system of intermating prior to the commencement of selfing, Hanson (1959) emphasized that an increase in the number of parents used would not only have a beneficial effect on the rate of breakup of linkage blocks, but would also provide the breeding program with a wider genetic base. With the exception of work by Hansel (1964) and Jensen (1970), subsequent consideration of this means of increasing available variation has largely disappeared and emphasis has been placed on investigation of the value of intermating among the progeny of a single cross (Baker 1968; Pederson 1974; Bos 1977). Jensen (1970) suggested that a diallel scheme of intercrossed F_1's should be used as the base population from which selfing is initiated. This single generation of intercrossing, in addition to that among the parents, allows the inclusion of alleles from up to four parents in any single genotype before the commencement of selfing. In general, a total of n cycles allows 2^n parents to contribute. In many naturally self-fertilised species, intercrossing may be facilitated by the chemical induction of male sterility and the use of markers to detect the progeny of chance selfings.

Apart from showing how the expected response to selection of any type can be predicted and the parameters necessary estimated from available statistics, the covariances among relatives given here allow some comparisons to be made between different selection strategies. The variance of lines descended from a complex base population might be expected to be larger than for any specific F_2 because more alleles are present at each locus, and a higher proportion of loci is expected to be initially heterozygous. It has now been confirmed that such lines show 100% more variance due to single loci and 33% more due to interactions of pairs of loci because an F_1 samples just two alleles from the population of alleles at each locus and four

from any pair. In general, the variance among the descendant lines from a population derived from k parental lines as a proportion of that from an infinite base is $(k-1)/k$ and $(2k-1)/2k$ for σ^2_M and σ^2_{MM}, respectively. The proportions appearing within F_1 pedigrees from a base population initiated by k parents are therefore $k/(2(k-1))$ and $6k/[4(2k-1)]$, respectively. If several generations of intercrossing are used before selfing, then k represents an effective population size which depends on the numbers used at each generation.

These variances give only part of the information necessary for comparison of selection programs based on the two types of base population, as in practice an F_1 will be the result of crossing two selected rather than random parents. The formal question now posed by the consideration of broad-based source populations is analogous to a comparison between single- and multistage selection procedures; whether it is efficient to select among the parents and then among the final lines, or to defer all selection until the latter stage. In the absence of epistasis, the mean value of descendant lines equals that of their parents and any gain from parental selection is transmitted in full to the lines. However, realistic formulations of the total gain cannot easily be made, as if earlier selection has brought about negative linkage disequilibrium the variance is reduced and the effectiveness of selection is impaired. Furthermore, the choice of parents has not always been explicitly recognized as a selection process, and they are usually selected as a complementary pair with the idea of raising the variance as well as the mean of the resultant lines. Although this may sometimes be reasonable for two traits, there is no means of predicting for any single trait the variance of lines descended from a parental combination without information from descendant generations. If the major emphasis is placed on this criterion, the choice of parental lines may be little better than random.

It may be concluded that schemes of selection based on populations of intercrosses among parental lines could be advantageous in many species, but especially those whose agricultural potential is relatively undeveloped and whose parental lines are therefore not well characterized. These are also likely to be those in which a wide spectrum of environmental conditions are met, so that a single selection program has multiple objectives and a "fine tuning" approach is inappropriate.

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