

A Breeding Procedure Designed To Make Maximum Use of Both General and Specific Combining Ability¹

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UTILIZATION of heterosis between homozygous lines is best exemplified in corn breeding practice. Breeding programs directed at the development of improved commercial corn hybrids consist in general of two phases. The first involves the development of lines and choice of those to be tested in hybrid combinations; the second, the comparison of hybrids among the selected lines. In the development and selection of lines attention is commonly given to genetic diversity in origin, plant characters known to be important (including some attention to yield of inbreds), and general combining ability of the lines. In some programs general combining ability is measured only in the final stage prior to comparison of specific hybrids. However, selection among early generation inbreds on the basis of general combining ability was suggested by Jenkins (5)³ and has been used extensively by other workers. It is not until the second phase of the process that attention is given specific combining ability, except for that inherent in the development of lines from several genetically divergent sources.

Sprague and Tatum (7) have demonstrated the importance of specific combining ability as a source of variance among single-crosses. Their findings are a logical consequence of the sorts of gene action that could be responsible for heterosis. In view of the role of specific combining ability in determining the performance of hybrids, it obviously would be desirable if procedures were available for guiding the development of lines in such a way that their combining ability in predetermined combinations would be enhanced.

East (3) has postulated a hereditary mechanism in corn involving sets of multiple alleles in which certain of the heterozygous genotypes possible at a given locus are superior to any of the possible homozygous genotypes. Hull (4) advanced reasons for believing that genes conditioning corn yield exhibit over-dominance. While the two proposals are not the same, they have in common the concept of heterozygosity superior to homozygosity of the best genes in a population. It is this aspect of both proposals that has special significance relative to breeding methods. Hull pointed out

that with respect to loci at which over-dominance (heterozygote superior to best homozygote) is operative, improvement of hybrids resulting from selection among lines on the basis of either their own performance or their general combining ability will level off at a point below the potential maximum yield of hybrids. He proposed a procedure which he calls recurrent selection for specific combining ability that would be more effective with respect to improvement stemming from genes that exhibit over-dominance. He pointed out, however, that it would be inefficient relative to genes that are partially dominant.

Crow (2) concluded that heterosis much in excess of 5% of the mean of the random breeding population cannot be explained on the basis of simple dominance alone, but must rest on other sorts of genotype effects such as interactions of non-allelic genes or superiority of the heterozygote to either homozygote, i.e., over-dominance. Robinson *et al.* (6) reported an estimate of the average degree of dominance of genes conditioning grain yield in corn that was in the over-dominance range. The method which they employed for the estimate is described in detail by Comstock and Robinson (1). It is pointed out in both of these manuscripts that linkage could be responsible for genetic behaviour which on the basis of present evidence could not be distinguished from that which would result from over-dominance.

At present available evidence does not establish either the existence or nonexistence of over-dominance. Moreover, even though there were over-dominance at some loci, partial dominance could be the rule at others. In view of this situation the authors set out to discover a breeding and selection method that would be effective regardless of the level of dominance and which by giving attention to specific combining ability from the outset, might be more effective for genes showing complete or partial dominance than are current procedures. The authors are using the term recurrent reciprocal selection to designate the method described below. For brevity it will be referred to in what follows as simply reciprocal selection.

Description of the Reciprocal Selection Method

Foundation material from two sources is used. The hybrid or hybrids to be developed will involve crossing material descended from these two sources, hence the sources should be as genetically divergent as possible. Two varieties, two synthetics, or the F₂ generation plants of the two single crosses involved in a successful double cross can serve as the source material.

s₀ or s₁ plants from source A are self-pollinated and at the same time out-crossed to plants from source B. Selection is based on experimental comparison of test-cross progenies and selected plants are interbred the third year using their selfed seed produced the first year. The cycle is reinitiated the fourth year. Source B plants are tested against source A plants in the same way. Outlined in greater detail the procedure would be as indicated below. (The numbers of plants and progenies indicated were arbitrarily chosen and could of course be varied. Attention has not been given to the question of optima).

Year 1.—Out-cross each of about 200 plants from source A with four or five plants taken at random from source B, and each of about 200 plants from source B with four or five plants from source A. Self-pollinate all plants used as pollen parent in these out-crosses.

Year 2.—Conduct two field trial comparisons of the progeny of crosses made in year 1. The one would involve progenies of source A plants as pollen parent; the other, progenies of source B plants as pollen parent. All seed from each of the four or five crosses involving a single pollen parent would be bulked to produce a single progeny from that parent. Thus there would at most be 200 entries in each of the two trials. The actual number would depend on success of pollinations in year 1 and the design chosen for the progeny comparisons. Perhaps 169 progenies of each group would be compared in 13 by 13 lattice designs.

Year 3.—Plant seed produced by self-fertilization in year 1 using seed from only those plants in each of the source groups (A and B) whose progenies were superior in the field trials of year 2. Within each source group make all or a large number of the possible single crosses between plants from which seed was planted.

Years 4, 5, and 6.—Repeat the procedures of years 1, 2, and 3 using as a starting point the group A and B seed produced in year 3.

By testing source A plants in crosses with source B plants, selection pressure for those specific genes which contribute most to the cross of material from the two sources is insured. The criteria for evaluation of the test cross progenies should be those on which commercial hybrids are evaluated for the geographical area involved. For example, progenies that exhibit lodging or disease susceptibility should not be considered even though their yield is high. In years favorable to their measurement selection might well be based completely or in large part on such agronomic characters.

Sufficient plants should be selected in each generation to hold inbreeding within the two source material groups at a low level since otherwise the within-group variability on which selection operates will be lost. For the same reason the plants selected in any generation should not all trace to one or two matings made in an earlier cycle of the program. To insure this, controlled pollination accompanied by recording of pedigree information should be practiced in the interbreeding phase of the cycle.

Commercial seed would be produced by crosses between the A and B selection material groups; however, the amount of inbreeding done prior to making the seed production cross could vary. At the one extreme relatively pure lines could be developed for use in double crosses of the type (A₁ × A₂) × (B₁ × B₂) where A₁ and A₂ are lines developed from source A material and B₁ and B₂ are lines from source B material. The other extreme would involve crossing noninbred descendants of random matings among the selected plants within each of the two groups.

Comparison of the Potentialities of Reciprocal Selection with Those of Other Procedures

The two other breeding methods considered were the following:

Method 1: Selection based on general combining ability with a common tester series.—The tester series assumed was one consisting of at least two single crosses between pure lines. Use of double crosses or varieties would involve loss of efficiency due to genetic variation among tester parent plants involved in the top crosses. The idea of recurrent selection cycles is as applicable in this method as in that of reciprocal selection. It was therefore assumed that plants from two or more genetically divergent sources would be tested and that, as in the reciprocal selection method, selected plants of each source would be interbred and a new selection cycle initiated. Thus the only difference between the two methods is in the tester. In this method all selection material is tested against the same tester. In the reciprocal method source A plants are tested against source B plants and source B plants against source A plants.

Method 2: Recurrent selection for specific combining ability as proposed by Hull.—This involves one segregating pool of material from which plants are topcrossed to a tester. Selection is based on performance of the topcrossed progenies, selected plants are interbred using their selfed seed, and new topcrosses made for the next selection cycle using plants of the resulting population. The tester used is a pure line or single cross of pure lines and is one of the parents of the commercial hybrid, of which the improved selection material is the other parent. While there are practical objections to use of a pure line as the tester, it was chosen as the basis of this comparison since in the genetic situation for which this method was originated maximum potentialities for improvement in commercial hybrid performance would not be realized using a single cross tester.

Recurrent reciprocal selection, the procedure proposed in this manuscript, will be referred to as method 3.

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³Figures in parentheses refer to "Literature Cited", p. 367.

BASIS FOR THE COMPARISONS

The comparisons of the three methods were made subject to the following assumptions:

- No interactions of non-allelic genes.
- No more than two alleles per locus.
- Equilibrium state relative to the joint distribution of genotypes at linked loci.

It is highly improbable that any one of these assumptions is strictly valid for the general situation. However, the problem becomes more tractable when comparisons are made first for the simplified situation and the effects of non-validity of the assumptions are considered later. Some comments on these effects will be made later in the manuscript. It will suffice at this point to state that the general conclusions to be drawn concerning the methods are apparently not seriously affected as a consequence of basing the comparisons on a simplified genetic model.

COMPARISON OF IMPROVEMENT LIMITS

The methods were compared first with respect to the potential limit of improvement by each. It was sufficient to consider the response at a single locus since the findings for one will cover possibilities with respect to any other locus.

Three specific situations were considered with respect to dominance. If the value of the genotypes possible at the locus of a gene pair (B, b) are symbolized as follows:

Genotype	Value
BB	2u
Bb	u+au
bb	0

a is obviously a measure of the dominance involved in the action of the alleles, B and b.

If dominance is complete, $a=1.0$; if dominance is partial, $a<1.0$, and for over-dominance, $a>1.0$. Values of a considered were .5, 1.0, and 2.0.

Let B be a more favorable gene than its allele, b, p be the frequency⁴ of B in the material under selection and q be its frequency in the material used as the tester parent.

The algebraic sign of the regression of p on performance of test cross progenies indicates the direction of the selection effect on gene frequency. This regression is

$$\frac{\text{Cov. } pY}{V_Y}$$

where Y symbolizes the performance of test cross progenies; V_Y , the variance of progeny means; and

⁴The frequency of a gene refers to the number of that gene in a population as a fraction of the total number of loci occupied by it or an allele. For example, in a pure line all gene frequencies will be either 1.0 or zero depending on whether the line is homozygous for the gene in question or for an allele of that gene. In an F_1 between pure lines, gene frequencies will be 1.0, 0.5, or zero; in a tester composed of two such F_1 's they will be 1.0, .75, 0.5, .25, or zero, and in a variety they can vary from zero to 1.0.

$\text{Cov. } pY$, the covariance of p and Y. Since variances are always positive the sign of the regression is determined by its numerator. It can be shown that

$$\text{Cov. } pY = \frac{p(1-p)}{2} (1+f) [1+(1-2q)a] u \quad (1)$$

where f is inbreeding of the material under selection in terms of Wright's coefficient. Since neither $p(1-p)$, $1+f$, nor u can take a negative value, the sign of $\text{Cov. } pY$ is determined by the factor $[1+(1-2q)a]$. It will be positive when $q < (1+a)/2a$ and negative when $q > (1+a)/2a$. When $q = (1+a)/2a$ it will equal zero and selection will have no effect on gene frequency. Values of $(1+a)/2a$ are listed below for the a -values to be considered.

a	$(1+a)/2a$
.5	1.5
1.0	1.0
2.0	.75

It follows that with two exceptions the average effect of selection in the cases to be considered will be to increase the frequency of B. When $a=1.0$ and q , the frequency of B in the tester, $=1.0$, selection will have no effect. When $a=2.0$, selection will decrease p , the frequency of B in the selection material, whenever $q>.75$.

The comparison of limits of improvement for the three selection methods is summarized in Table 1. The tabled values can be verified by inspection keeping in mind the facts brought out above relative to the direction of the selection effect. For example, with method 1, $a=2.0$, tester genotype BB, and both alleles present in both groups of selection material; selection would carry the frequency of B toward zero in both groups. When this limit has been reached all lines developed from the material would be of the bb genotype, hybrids between them would be the same, and the limiting genotypic value approached through selection would be zero.

The upper portion of the table relates only to methods 1 and 3 and to those situations in which the material of both source groups is completely homozygous for one of the alleles. Obviously selection will be ineffective in these situations regardless of method. The lower portion of the table covers all other situations relative to methods 1 and 3 and all situations relative to method 2.

The important points brought out by Table 1 are:

- When $a<1.0$ the improvement limit is the same for methods 1 and 3 but lower for method 2. The value 2u will be reached by the latter method only when B is present in both the tester and the selection material whereas it will be attainable by the other two methods whenever B is present in both selection material groups, an occurrence to be expected more frequently.

TABLE 1.—Limit of improvement in genotype at a single locus of hybrids.

Original genotype in			$a = 0.5$			$a = 1.0$			$a = 2.0$		
			Method			Method			Method		
Tester	Selection material*		1	2	3	1	2	3	1	2	3
	BB	BB	2u		2u	2u		2u	2u		2u
	BB	bb	1.5u		1.5u	2u		2u	3u		3u
	bb	BB	1.5u		1.5u	2u		2u	3u		3u
	bb	bb	0		0	0		0	0		0
BB	B, b†	BB	2u	2u	2u	2u	2u	2u	3u	2u	3u
		B, b	2u	2u	2u	2u	2u	2u	0	3u	3u
		bb	1.5u	1.5u	1.5u	2u	2u	2u	0	3u	3u
B, b ($q<.75$)	B, b	BB	2u		2u	2u		2u	2u		3u
		B, b	2u		2u	2u		2u	2u		3u
		bb	1.5u		1.5u	2u		2u	0		3u
B, b ($q>.75$)	B, b	BB	2u		2u	2u		2u	0		3u
		B, b	2u		2u	2u		2u	0		3u
		bb	1.5u		1.5u	2u		2u	0		3u
bb	B, b	BB	2u	1.5u	2u	2u	2u	2u	2u	3u	3u
		B, b	2u	1.5u	2u	2u	2u	2u	2u	3u	3u
		bb	1.5u	0	1.5u	2u	0	2u	3u	0	3u

*With respect to methods 1 and 3, the two columns represent material from two genetically divergent sources; with respect to method 2, consider only the second column.

†B, b indicates that both alleles are present in the material, not that all individuals of the material are heterozygous.

‡Selection ineffective since all top-cross genotypes would have the same value.

- When $a>1.0$ the improvement limit will be essentially the same for methods 2 and 3 but much lower for method 1.
- When $a=1.0$ there would under no circumstances be much difference among the limits for the three methods. Method 1 would be somewhat less efficient if the tester involved were homozygous for the dominant allele at any considerable number of loci. Method 2 would suffer by comparison if there were insufficient genetic diversity represented in the selection material used.

COMPARISON OF RATES OF IMPROVEMENT

In view of what has been learned from consideration of improvement limits, interest in expected improvement rates centers on comparison of reciprocal selection with selection based on general combining ability in the case of complete or partial dominance, and on comparison of the reciprocal method with Hull's method in the over-dominance case. Good estimates of absolute rates of improvement would require experimental data that are not now available. However, comparisons are possible on a relative basis.

Genetic change resulting from selection is a consequence of changes in gene frequencies. When selection is based on the performance of test cross progenies, as

in all the methods under consideration, the regression of gene frequency in plants tested upon performance of their test cross progenies can, as indicated in the foregoing section, be shown to be

$$b_{pY} = \frac{p(1-p)(1+f)[1+a-2aq]u}{2V_Y} \quad (2)$$

The change in p resulting from selection will be the product of this regression coefficient and the selection differential, the difference between the mean of all progenies and that of the progenies of selected plants. The selection differential will be symbolized as $s\sqrt{V_Y}$ where s is the differential in units of the standard deviation of progeny means, $\sqrt{V_Y}$. Then the expected change in gene frequency as a consequence of selection is

$$\begin{aligned} \Delta p &= p(1-p)[1+a-2aq](1+f) \frac{su}{2\sqrt{V_Y}} \\ &= p(1-p)[1+a-2aq](1+f)c \end{aligned} \quad (3)$$

where

$$c = \frac{su}{2\sqrt{V_Y}}$$

It will be convenient for our purpose to consider c equal for all three methods. The only objection to so doing is the fact that $\sqrt{V_Y}$ will be a trifle larger for method 3 because of sampling variance among genotypes of tester plants. However, if each test cross progeny involves as many as three or four tester parent plants $\sqrt{V_Y}$ for method 3 would only under the most extreme conditions be more than 10% larger than for the other methods.⁵

⁵The basis for this conclusion was the following. The genotypic variance among progeny means was derived in terms of gene frequencies in the material under selection and in the tester. It was then evaluated relative to non-genetic variance on the basis of data available from the study reported by Robinson *et al.* and a liberal margin of safety allowed in arriving at the 10% figure indicated in the text. Space does not permit reporting on this in detail.

The mean genotypic value for a given locus in hybrids resulting from random crosses between two populations will be

$$\bar{X} = [p_1(1+a) + p_2(1+a) - 2ap_1p_2]u \quad (4)$$

where p_1 and p_2 are frequencies of the favorable allele in the two populations. After selection has increased p_1 to $p_1 + \Delta_1$ and p_2 to $p_2 + \Delta_2$ this mean performance will be

$$\bar{X}' = [(p_1 + \Delta_1)(1+a) + (p_2 + \Delta_2)(1+a) - 2a(p_1 + \Delta_1)(p_2 + \Delta_2)]u$$

The difference, $\bar{X}' - \bar{X}$, is the increase in hybrid performance resulting from the selection.

$$\bar{X}' - \bar{X} = [\Delta_1(1+a) + \Delta_2(1+a) - 2a\Delta_1p_2 - 2a\Delta_2p_1 - 2a\Delta_1\Delta_2]u \quad (5)$$

Since Δ_1 and Δ_2 resulting from one cycle of selection will be small fractions, the effect of ignoring the term involving their product will be inconsequential. Substituting in this expression on the basis of equation (3), and reducing, expressions for improvement in hybrid genotype resulting from one selection cycle are obtained for each of the selection methods. They are as follows:

$$\begin{aligned} \text{Method 1} \quad \Delta\bar{X} &= \bar{X}' - \bar{X} \\ 1 \quad [p_1(1-p_1)(1+a-2ap_2) + p_2(1-p_2)(1+a-2ap_1)] & \\ \quad (1+a-2aq)(1+f)cu & \quad (6) \\ 2 \quad p(1-p)(1+a-2aq)^2(1+f)cu & \quad (7) \\ 3 \quad [p_1(1-p_1)(1+a-2ap_2)^2 + p_2(1-p_2)(1+a-2ap_1)^2] & \\ \quad (1+f)cu & \quad (8) \end{aligned}$$

It is clear from the way f enters these expressions that comparisons based on them are valid regardless of the amount of inbreeding of the selection material that precedes the making of test crosses, so long as we assume it constant for all methods.

If the value of q which makes (6) and (8) equal is symbolized by q' , we have

$$q' = \frac{p_1p_2(1-p_1)(1+a-2ap_2) + p_1p_2(1-p_2)(1+a-2ap_1)}{p_1(1-p_1)(1+a-2ap_2) + p_2(1-p_2)(1+a-2ap_1)} \quad (9)$$

This result is obtained by equating (6) and (8) and solving for q . When $q = q'$ the expected improvement from one cycle of selection will be essentially⁶ the same for methods 1 and 3. When $q > q'$, improvement will be more rapid by method 3; when $q < q'$ more rapid improvement will be expected with method 1. Thus the ratio of expected improvement rates for the two methods is not a constant but varies as p_1 , p_2 , and q vary. Since (6) and (8) are equal when $q = q'$, (8) is equal to

$$[p_1(1-p_1)(1+a-2ap_2) + p_2(1-p_2)(1+a-2ap_1)](1+a-2aq')(1+f)cu \quad (10)$$

and the ratio of improvement rate by method 1 to that by method 3 is

$$(1+a-2aq) / (1+a-2aq') \quad (11)$$

⁶Not exactly since the term $2a\Delta_1\Delta_2$ was dropped in going from (5) to (6) and (8).

When $a = 1.0$, equation (9) reduces to

$$q' = \frac{2p_1p_2}{p_1 + p_2} \quad (12)$$

which is less than $(p_1 + p_2) / 2$, the mean of p_1 and p_2 , unless $p_1 = p_2$, in which case $q' = p_1 = p_2$. Thus when dominance is complete q must be less than $(p_1 + p_2) / 2$ if method 1 is to be as effective as method 3. When there is only partial dominance ($0 < a < 1.0$), q' will be less than $(p_1 + p_2) / 2$ when

$$p_1 + p_2 < 1 + \frac{1+a}{2a} p_1p_2 \quad (13)$$

and for those loci at which this condition does not hold, improvement by method 1 will be greater than by method 3 if $q = (p_1 + p_2) / 2$.

If the lines used in the method 1 tester are chosen at random, it can reasonably be assumed that q will, on the average for all loci, be about equal to the mean of the initial values of p_1 and p_2 . Further, since the source material groups are to be as genetically divergent as possible, p_1 and p_2 may be assumed unequal for almost all loci. With these two points in mind consider a numerical example. Suppose that dominance were complete and that at a given locus, $p_1 = .6$ and $p_2 = .9$. Then from (12), $q' = .72$ and if $q = (p_1 + p_2) / 2 = .75$, as expected on the average if lines for the method 1 tester are chosen at random, the progress expected with method 1 will, from (11), be 89% of that expected with method 3. Computations of this sort for a range of values of p_1 and p_2 and for both partial and complete dominance have led to the following general conclusions relative to methods 1 and 3:

- (1) In the case of complete or almost complete dominance, method 3 should at the outset yield a little more rapid improvement. However, as p_1 and p_2 are increased by the selection, a point is reached where on the average for all loci, they are sufficiently large relative to gene frequency in the method 1 tester so that improvement will be more rapid by method 1. It is unlikely that the initial advantage of method 3 would ever exceed 20 to 25%. The advantage possible in genotype improvement at a single locus approaches 100% as a limit, but for loci contributing most to total improvement it would be much less.
- (2) In case of partial dominance the initial advantage of method 3 would be less than in the case of complete dominance and conceivably there might be a slight advantage for method 1.
- (3) Choice of lines with low general combining ability, and hence presumably lower than average frequencies of favorable genes, for use in the method 1 tester might make method 1 equal to 2 even at the outset and would increase its superiority in later cycles.

The important point to be noted is that in the situation, *absence of over dominance*, to which selection for general combining ability is adapted, this method is at best not greatly superior to reciprocal selection. However, in the event that over-dominance prevails at any considerable number of loci selection for general combining ability will be unsatisfactory because of ineffectiveness with respect to improvement at the over-dominance loci. Reciprocal selection will then be the more effective of the two methods.

It should perhaps be pointed out here that equation (6) relates only to improvement in average performance of hybrids between lines of diverse origin expected to result from selection for general combining ability and not to that to be obtained by selection for specific combining ability among such hybrids. However, this does not invalidate the comparison since that source of final improvement is available no matter which of the two methods is used.

Comparison of methods 2 and 3, as noted earlier, need be made only under the assumption of over-dominance ($a > 1.0$). As a basis for the comparison it seems reasonable to assume that the same genetic material would be used regardless of the method employed; that if method 2 were to be used all this material would be pooled to establish the segregating population to which selection was to be applied; and that if method 3 were to be used two such populations would be established dividing the genetic material in the manner believed most likely to result in the greatest genetic divergence between the two populations. We can then consider that the frequency (p) of a specific gene in the method 2 selection material would be the average of its frequencies (p_1 and p_2) in the two groups of selection material that would be used in method 3. Symbolically, this amounts to the following:

$$p = (p_1 + p_2) / 2, p_1 \neq p_2$$

That in general $p_1 \neq p_2$ is assured if the two groups of selection material used in method 3 are genetically divergent. Now consider a group of loci for all of which p has the same value, and let r be the proportion of these loci at which q for the method 2 tester is 1.0. Then using equations (4), (7), and (8) it is possible to determine for any values of p and $(p_1 - p_2)$.

- a. The value of r necessary if initial hybrid performance is to be as good for the method 2 material as for the method 3 material.
- b. The value of r necessary if improvement per selection cycle is to be as rapid by method 2 as by method 3.

It turns out that

- a. When $p < \frac{1+a}{2a}$, r must be larger than p if initial

hybrid performance is to be as large for method 2 as for method 3. The required value of r increases

as the difference $(p_1 - p_2)$, i.e., the genetic divergence between the selection material groups of method 3, increases. However, as $p_1 - p_2$ is increased a point is reached where if r is large enough so that initial hybrid performance will be equal for the two methods, expected improvement will be less by method 2.

- b. When $p = \frac{1+a}{2a}$ initial hybrid performance will

always be less for method 2, but expected improvement rate will be greater by method 2.

- c. When $p > \frac{1+a}{2a}$, r must be less than p if initial

hybrid performance is to be as great for method 2. However, the expected improvement rate will always be larger for method 2.

The most reasonable value for r is the same as for p . On that basis, it is to be expected that initial hybrid performance would ordinarily be lower in method 2 than in method 3. If the method 2 tester line is chosen on the basis of its combining ability with the segregating selection material, the initial hybrid performance could be made better but improvement rate from selection

would suffer if in general $p < \frac{1+a}{2a}$. The difference to be

expected in improvement rate depends on the size of p relative to $\frac{1+a}{2a}$ and the magnitude of $(p_1 - p_2)$. If

$(p_1 + p_2) / 2 > \frac{1+a}{2a}$, improvement will almost certainly

be more rapid by method 2; if $p < \frac{1+a}{2a}$, improvement

can be more rapid by method 3 if $(p_1 - p_2)$ is large enough i.e., if the genetic divergence between the two groups of selection material is sufficient. Moreover, the above is based only on results expected in the first cycle of selection. Since rate of improvement by method 3 increases as $(p_1 - p_2)$ is increased and since this difference is in general increased by the selection, the comparison of the methods would become more favorable to method 3 in subsequent cycles of selection.

The important over-all conclusions relative to methods 2 and 3 for selection when $a > 1.0$ are as follows: If the two groups of selection material for the reciprocal selection method are well chosen (so that there is maximum genetic divergence between them) initial hybrid performance will tend to be better than for method 2. Which method will yield the most rapid improvement at the outset depends on gene frequencies, but in any event the ratio will become more favorable to the reciprocal method in later cycles of selection. Thus even assuming no partial dominance loci, it appears unlikely that the method proposed by Hull could

have, at the most, more than a slight advantage over reciprocal selection.

Nonvalidity of Assumptions

The assumptions (see Basis for Comparisons) under which the foregoing comparisons were made are in all probability not generally valid. The consequences of their being invalid upon the results of the comparisons must therefore be considered.

THE EFFECT OF INTERACTIONS OF NON-ALLELIC GENES

When there are interactions of non-allelic genes, the effects of some genes are conditioned by genes present at other loci. As a consequence, the importance of a gene to performance in a test cross, and therefore the intensity of selection for it, depends on genes present at certain other loci in the tester. Clearly, when such interactions are important in the genetic mechanism, the advantage of testing against the same material to be used as the opposite parent of the commercial hybrid is increased. Hence, if the assumption of no interactions of nonallelic genes is invalid, the method of selection for general combining ability suffers by comparison with the others.

THE EFFECT OF MULTIPLE ALLELES

The situation with multiple alleles is not greatly different from that with only two at each locus. It differs mainly in that at the outset of selection the frequencies of more than one allele of a series may be increased; though the ultimate effect of continued selection would be to increase the most favorable gene of a series and decrease the frequencies of all the others. The specific allele favored in all stages of continued selection will be the one having the best effect in the test crosses. Thus, if the genetic system were that proposed by East (3) it would again be advantageous to use the same material for tester that will later be used as the opposite parent of the commercial hybrid.

It would appear that multiple allelism would not seriously modify the comparison of the methods made subject to all three assumptions; that methods 1 and 3 would be superior to method 2 if the homozygote of one of the alleles were the best genotype possible at the locus; but that methods 2 and 3 would be superior to method 1 if the best genotype were (as postulated by East) the heterozygote involving two alleles of the series.

THE EFFECT OF DISEQUILIBRIUM IN THE RELATIVE FREQUENCIES OF GENOTYPES FOR LINKAGE GROUPS

If the chromosome segment involved in a linkage group is considered as a single "locus", the various possible gametic combinations of the individual genes involved become analogous to the genes of a multiple

allelic series. If the frequency distribution of these combinations, or "alleles", is that expected on the basis of random distribution of the individual genes the effect of selection is no different because of the linkage. However, if the genes for certain loci are associated predominantly in the repulsion phase, the situation is changed. Then among the "alleles" available in the population certain heterozygotes would very likely be superior to any homozygote (even though individual genes were no more than partially dominant to their alleles) and the situation is once more a less favorable one for method 1.

On the other hand, assuming that there is no over-dominance in the action of the individual genes and that some exhibit only partial dominance, method 2 would be deficient in not providing the means for taking advantage of recombinations in the improvement of both parents.

Discussion

The most important aspect of the comparisons made above is the fact that reciprocal selection appears about as effective as either of the other two methods in all of the genetic situations considered. Further, it is clearly superior to selection for general combining ability for loci at which there is over-dominance and to the method proposed by Hull for loci at which there is partial dominance. Hence, in the event of partial dominance at some loci and over-dominance at others reciprocal selection would be more effective than either of the other methods. In addition, assuming no over-dominance, there appears a strong possibility that reciprocal selection would be superior to selection for general combining ability as a consequence of either interactions of nonallelic genes or repulsion phase linkages between certain loci, or both.

There remain a few points relative to the application of reciprocal selection which deserve some discussion.

The authors feel that it offers potentialities for further improvement of good double crosses. It is known that advanced generations of the single crosses of a double cross combine as well as the singles themselves. It appears entirely possible that reciprocal selection applied to segregating generations of the single crosses would affect improvement in the hybrid between them. This would be an important application of the method since it would offer the possibility of working improvement from a starting point of already superior performance.

The importance of basing selection among test cross progenies on all agronomic characters in proportion to their importance and not on yield alone deserves re-emphasis. Since the test-crosses are between the same parent stocks as will be used in the commercial hybrid this would appear particularly pertinent and logical.

A problem that may well arise in application of the method is that of avoiding inbreeding within the two selection stocks. This was mentioned earlier, but the importance of controlled pollination and pedigree recording as an aid to avoiding a serious amount of inbreeding must definitely be recognized. If such inbreeding were allowed it would clearly result in decreased opportunity for effective selection. However, this same problem also arises with other methods.

Summary

A breeding and selection technique for improvement of commercial hybrids in diploid organisms has been outlined, and designated as recurrent reciprocal selection. Theoretical comparisons have been made of the limits of improvement and improvement rates to be expected of this method, selection for general combining ability, and the method proposed by Hull (4). They indicate that under no circumstances would reciprocal selection be more than slightly inferior to the better of the other two. However, it would be definitely superior to selection for general combining ability for loci at which there is over-dominance or if a situation analogous to that with over-dominance exists due to linkage;

and it would be definitely superior to the method proposed by Hull for loci at which there is partial dominance. In view of the reality of linkage and the improbability of partially dominant genes being of minor importance in real genetic situations, there is good reason to believe reciprocal selection will in practice be more effective than the other methods discussed in this paper.

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