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ON SOME ASPECTS OF RECIPROCAL RECURRENT SELECTION[1]

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ABSTRACT

Comments are given on several critical points regarding the merits of reciprocal recurrent selection as a method in hybrid breeding. A review of definitions reveals that the method utilizes general combining ability only. In simplified terms some theory of population genetics is presented and used in comparing the effectiveness of reciprocal recurrent selection with that of recurrent selection for specific combining ability to a single cross. It is found that the latter method need not be inferior if at loci exhibiting overdominance multiple alleles mutually interacting in this way may be assumed to exist. Further comments concern the use of a constant tester, the expected interactions of testcrosses with years and places, and the possibilities of an immediate utilization of testcrosses in commercial hybrids.

It is concluded that reciprocal recurrent selection should not be regarded as a short-cut but as a way to enhance the genetic diversity of breeding stocks for the future. Other methods may be preferable if one has the twofold need for an early output of better hybrids and a long-sighted improvement of the same material.

1. INTRODUCTION

Reciprocal recurrent selection was proposed by COMSTOCK, ROBINSON and HARVEY (3) as a breeding technique for improvement of commercial hybrids in diploid organisms. The authors concluded from theoretical considerations that the proposed procedure, while superior to recurrent selection for general combining ability for loci exhibiting overdominance, would be more effective than recurrent selection for specific combining ability with respect to loci at which there is partial dominance. Since in plant breeding practice each type of recurrent selection will require high investments of labour and time, any further information concerning the relative merits of the methods in question should be welcome. However, critical evidence from experimental comparisons between different schemes of recurrent selection is still lacking, at least in cultivated plants. Therefore it may be justified to add some points to the discussion. In the following we shall comment upon several theoretical and practical aspects of the reciprocal recurrent selection procedure, in part by comparing it to recurrent selection for specific combining ability. Our discussion will have a special view to the breeding of maize, but should apply also to other crops where commercial hybrids are feasible.

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2. General and specific combining ability in reciprocal selection

We may anticipate some remarks concerning the terminology to be used. **Sprague** and **Tatum** (13) introduced the term "general combining ability" to designate the average performance of a line in its crosses with a set of other lines. The term "specific combining ability" then refers to the cross of two lines, designating the deviation from the performance expected as the average of the general combining abilities of the two lines crossed. These definitions are substantially equal to those given by **Henderson** (7). Note that the lines (or individuals) involved need not be homozygous. The set of lines used as testers for general combining ability is usually regarded as a random sample of some population such as a variety, and can be replaced by the population itself. It is customary in population genetics (see **Kempthorne**, 10) to define the general combining ability of some genotype by means of its testcrosses to that particular population from which it had descended; also specific combining ability is then understood on an intra-population basis. In my opinion, general and specific combining ability might equally well be defined on an inter-population basis, i.e. with respect to the crosses of members of one population to some different tester population and its individual members, respectively. Both cases, although differing in their genetical consequences, would have in common the point stressed by **Cauderon** (1) that testing for general combining ability means using a tester having a much broader genetical base than a tester appropriate for evaluating specific combining ability.

Turning now to our subject we meet a somewhat paradoxical situation. With reciprocal recurrent selection, as is well known, desirable plants in a population A are selfed and outcrossed each to several plants of a population B. Selection is based on the performance of bulked testcrosses which apparently provide a measure of the general combining abilities of individual A-plants to population B. Also, on the other side, desirable plants of population B are selfed and tested for general combining ability to population A. Thus we see that in reciprocal recurrent selection, although it was explicitly designed to make maximum use of both general and specific combining ability, there is actually no utilization of specific combining ability, at least not in the earlier cycles when both populations are still heterogeneous. Despite of this, reciprocal recurrent selection may be very effective in enhancing the genetic diversity of two breeding stocks. However, such effectiveness will be due to the reciprocity of the testing scheme and not to selection of pairs of good specific combiners. On the other hand, one could well think of a reciprocal recurrent selection procedure modified in such a way as to base selection partly or entirely on specific combining ability; and the latter case is clearly involved in the recurrent selection plan proposed by **Hull** (8) in which an inbred line or a single cross is used as a constant tester throughout all cycles.

It might be objected against our point of view that nevertheless there is some kind of specifical testing in the method of reciprocal recurrent selection. Such a claim would probably be based on the idea that both populations involved may be regarded as individual members of some super-population comprising all existing varieties of the species in question. Undoubtedly, general and specific combining ability might be defined with respect to the populations forming the members of this super-population. However, specific combining ability operating on such a level of genetic breadth would hardly be comparable to that kind of specific combining ability which is utilized in HULL's method as well as in customary hybrids.

3. EFFECT OF CHANGING GENE FREQUENCIES ON COMBINING ABILITY

Going one step further we have to remind that the general combining ability of some genotype, even under specified environmental conditions, is not a stable property of that genotype but has an exact meaning only with respect to a given set of other genotypes serving as testers. Consequently, the general combining ability of a plant may change if the gene frequencies in the tester set change by selection or by other causes. For simplicity, we shall examine the situation for a random mating population derived from one segregating locus. It should be mentioned that in this case there is a direct correspondence of additive gene effects with general combining ability values. See GRIFFING (6) for the case when two or more loci are involved.

We assume a population segregating for two alleles, B and b, which occur with respective frequencies p and q adding to unity, as depicted in table 1. Using a notation similar to that employed by COMSTOCK and ROBINSON (2) we symbolize the expected phenotypic expressions of the two homozygotes, BB and bb, by $(c + u)$ (and $c - u$), respectively, and the expression of the heterozygote, Bb, by $(c + au)$. Thus c stands for a constant, and $2u$ is the difference between the two homozygotes, while a reflects the degree of dominance operating at this locus.

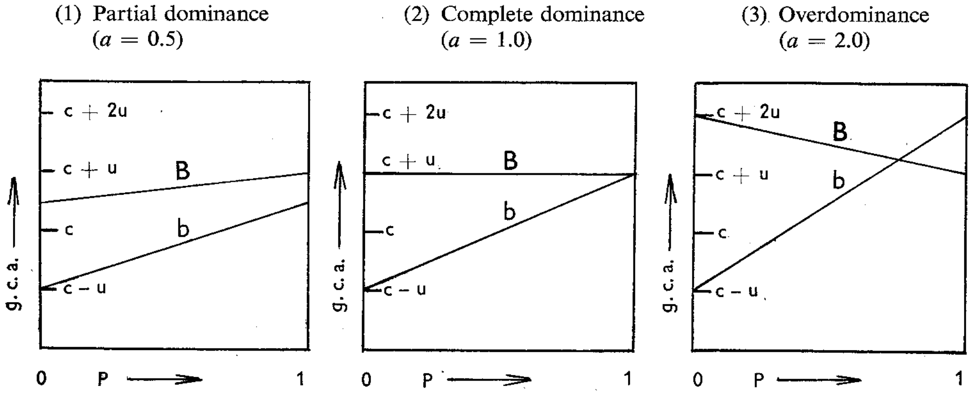
TABLE 1. GENOTYPIC VALUES IN A RANDOM MATING POPULATION DERIVED FROM ONE LOCUS SEGREGATING FOR TWO ALLELES (genotypic frequencies are the products of corresponding marginal frequencies)

		♂-Gametes B	♂-Gametes b	Marginal frequency
♀-Gametes	B . . .	$(c + u)$	$(c + au)$	p
	b . . .	$(c + au)$	$(c - u)$	q
Marginal frequency . .		p	q	1

Now consider the general combining abilities of two gametes (or inbred lines) one of which carries the allele B whereas the other one has allele b. The two gametes (or genotypes, respectively) are expected to differ in their general combining abilities by the amount of

$$[p(c + u) + q(c + au)] - [p(c + au) + q(c - u)] = u + (q - p)au,$$

which is half the difference between the two homozygotes plus the term $(q - p)au$ arising from the heterozygotes. This term, being positive or negative according to which allele is more frequent in the population, will affect the general combining ability difference proportionally to the value of a which specifies the level of dominance operative at the locus in question. The way in which the general combining ability expectations of B-gametes and b-gametes change with changing gene frequencies in the tester population is shown for three different levels of dominance in figs. 1–3. In all cases the superiority of the "more favourable" allele *B* over *b* is greatest when its frequency, *p*, is zero in the tester population. However, with *p* approaching unity, the superiority of *B*, while still extant for loci with only partial dominance, vanishes for loci with complete dominance, and is even converted to inferiority of *B* in relation to *b* if there is overdominance at the locus in question.


(1) Partial dominance ($a = 0.5$)

(2) Complete dominance ($a = 1.0$)

(3) Overdominance ($a = 2.0$)

FIGS. 1–3. GENE FREQUENCY AND EXPECTED GENERAL COMBINING ABILITY (*g.c.a.*) OF TWO GAMETES, *B* AND *b*, FOR THREE LEVELS OF DOMINANCE

The relations illustrated have obvious significance as to the effectiveness of reciprocal recurrent selection. In both populations under selection that part of genetic variability which can be utilized by the method consists of genotypic differences in general combining ability to the other population, and these differences are largely made up of "general combining ability"-differences between the alleles available at individual loci. In each cycle of selection such allelic differences, being reciprocally fixed in size by the momentary frequencies of corresponding alleles in the opposite population, will determine the speed of advance by selection regarding the respective loci. Non-allelic interactions may also be operating, but will probably not seriously modify the general outcome. However, loci linked in the repulsion phase could show "pseudo-overdominance" even though dominance were less than complete at individual loci. For a discussion of the latter points see COMSTOCK and ROBINSON (4).

4. COMPARISON BETWEEN TWO SCHEMES OF RECURRENT SELECTION

The theoretical grounds outlined above provide a suitable basis for a comparison between reciprocal recurrent selection and recurrent selection for specific combining ability. In the latter method the tester used can be an inbred line as was assumed in the comparison presented by COMSTOCK, *et al.* (3). However, a single cross tester could much easier be handled and utilized in a practical corn breeding program. Therefore it may be of interest to give some results of a comparison between reciprocal recurrent selection and recurrent selection for specific combining ability to a single cross tester.

For loci at which dominance is far less than complete, reciprocal selection will clearly be the better method with regard to the limit of improvement, since both populations could be changed so as to contain the more favourable allele only. On the other side, selection for specific combining ability does not provide for an improvement of the constant tester. If the tester is chosen so as to be a high yielding single cross, it would probably be heterozygous for the majority of the loci involved.

The matter should be different for loci at which dominance is complete or nearly so. At the outset, both methods might be about equally effective. However, as in later cycles of reciprocal selection the frequency of the dominant allele increases in one or both populations, the speed of advance will slow down more and more, as is evident from fig. 2. On the contrary, selection for specific combining ability should have high efficiency from the first to the last cycle, if the tester single cross carries the dominant allele only with frequency 0.5 at most loci. It would be ineffective, of course, as to such loci at which the tester is homozygous for the dominant allele. This, however, would be the same with the other method.

As regards loci at which there is overdominance, reciprocal selection tends to fix different alleles in the two populations involved. Which allele will be fixed in which of the two populations depends on the initial gene frequencies, and if the latter are about equal for both populations (i.e. if there is but little genetic diversity at the outset), selection may have poor or even zigzag effects, till finally a clear diversity of gene frequencies is reached in some way, thereby raising the efficiency of further selection. Here is one of the reasons why COMSTOCK, *et al.* (3) require that the two populations to start with should be as genetically different as possible.

Turning again to selection for specific combining ability, an interesting problem arises with respect to loci exhibiting overdominance. Apparently, space for improvement would be extremely limited concerning such overdominance loci at which there are only two alleles available both of which are present in the tester single cross. But improvement as to such loci would surely be possible if more than two alleles interacting with each other in the overdominance fashion were available. Thus it is an important question whether at certain loci multiple alleles mutually interacting in this way do exist or not. It may be mentioned that the same problem plays a critical role in the genetical theory of breeding synthetic varieties.

HULL (9), in commenting on the explanation of heterosis proposed by EAST (5), makes the following statement: "He apparently did not accept that heterozygote superiority might be general, with multiple alleles affecting vigor. I do not accept it either as a likely proposition." In opposition to this, I cannot see any reason why the ability of producing overdominance, if occurring at all, should be confined to only two alleles per locus. EAST's very idea of one allele developing by successive steps of mutation into another allele suggests to me that such step-by-step diverging from each other in function could well go in more than one direction at any given locus. Even with only one line of divergence, two alleles at hand must not necessarily represent the two extremes possible. Finally it is beyond all dispute that within a block of several linked loci there can occur more than two different gene constellations all of which would show "pseudo-overdominance" with each other.

After all, it does not seem to be a constraining expectation that recurrent selection for specific combining ability to a single cross would be inferior to reciprocal recurrent selection concerning loci at which the heterozygotes surpass the homozygotes. Of course, which of the two breeding methods is more efficient on the whole depends on what degree of dominance prevails in the material used. If for instance only partial dominance were the rule, reciprocal recurrent selection would offer greater potentialities.

5. PRACTICAL CONSIDERATIONS AND CONCLUSIONS

Incidentally some more practical aspects of the methods in question will be commented upon. As pointed out by SPRAGUE (14) recurrent selection for specific combining ability implies the assumption that the tester used will be equally valuable in commercial seed production at the end of the procedure as it is at the outset. After a period of years it might well happen that the constant tester is surpassed by new lines with respect to seed production qualities or disease resistance, etc. However, the same event could happen even more to the improved populations, in that method as well as in reciprocal recurrent selection. In order to prevent such an outcome, each cycle should include a special selection of the selfed strains concerning the desired characters, besides the evaluation of their corresponding testcrosses. In this respect the breeder has not only to make compromises in selecting the strains but also to overcome a difficulty which forms a common (though seldom discussed) problem in most inbreeding programs: in as far as the value in commercial seed production depends on characters which are partly subjected to heterosis but required to be on some desirable level also in the more or less homozygous condition, efficiency of selection may be poor owing to masking effects of different heterozygosity levels of the selfed families. Examples of such characters include germination ability, tolerance to adverse climatic conditions, resistance to various diseases, etc.

Another point raised by SPRAGUE (15) concerns the "hybrid × location" and "hybrid × year" interactions which are expected to be smaller with reciprocal selection, at least in earlier cycles, than with selection for specific combining ability. This may be regarded as a disadvantage of the latter method in as far as testing subjected to higher interactions must be extended over more locations and years in order to gain information of some desired degree of reliability. On the other hand, this disadvantage is perhaps partly balanced out by the fact that testing for specific combining ability furnishes that sort of information which is anyhow needed before the improved strains can be utilized in customary hybrids. In selection for specific combining ability to a single cross the testcrosses are equivalent to double crosses, and should therefore be subjected to interactions of similar size as to which double hybrids are subjected when grown in yield trials or in farming. If testing has been done on an adequate scale of environments, the very best testcrosses of each cycle could immediately be released for use as commercial hybrids, with the involved S_1-lines being propagated and maintained by sibbing, as described by WELLHAUSEN, WORTMAN, and PETERNIANI (16). In reciprocal recurrent selection a similar use of the best S_1-lines would at least require some additional evaluation of specific combinations which then also would be subjected to interactions as high as are usually connected with double crosses.

It can be reasoned, of course, that reciprocal recurrent selection is not intended for such an immediate use of selected strains in commercial hybrids. This argument confirms the point of view that reciprocal recurrent selection is not a short-cut method of breeding. Rather it should be regarded and used as a very promising way of enhancing the genetic diversity of the breeding stocks of to-morrow. However, reciprocal recurrent selection may not be the most suitable method for a breeding program in which restricted investments have to serve the twofold need for an early output of better hybrids and a long-sighted improvement of the same material. Where this is the task to be accomplished, recurrent selection for specific combining ability to a single cross may prove to be an efficient procedure over a certain number of cycles, depending on the desirability of the constant single cross used. Of course, still other methods are possible in such situations. Several modified schemes of reciprocal selection have been proposed, and are being practised, in the new breeding work for hybrid maize in European and Mediterranean countries. Some examples can be found in publications by CAUDERON (1) and LASCOLS (11). As concerns a recent proposal of this sort we may mention a breeding scheme named "alternating reciprocal improvement" (SCHNELL, 12) which, although entirely based on specific combining ability, provides for a continuous improvement of both components of a hybrid, and still permits an immediate commercial utilization in improved hybrids after each four-year-period forming a half cycle.

REFERENCES

1. CAUDERON, A., Hétérosis et sélection réciproque chez le maïs. In: Eucarpia, Zweiter Kongress der Europäischen Gesellschaft für Züchtungsforschung, Köln. 1959: 256–264.
2. COMSTOCK, R. E., and ROBINSON, H. F., The components of genetic variance in populations of biparental progenies and their use in estimating the average degree of dominance. Biometrics *4* (1948): 254–266.
3. COMSTOCK, R. E., ROBINSON, H. F., and HARVEY, P. H., A breeding procedure designed to make maximum use of both general and specific combining ability. Agron. J. *41* (1949): 360–367.
4. COMSTOCK, R. E., and ROBINSON, H. F., Estimation of average dominance of genes. In: Heterosis. Iowa State College Press, Ames. 1952: 494–516.
5. EAST, E. M., Heterosis. Genetics *21* (1936): 375–397.
6. GRIFFING, B., A generalised treatment of the use of diallel crosses in quantitative inheritance. Heredity *10* (1956): 31–50.
7. HENDERSON, C. R., Specific and general combining ability. In: Heterosis. Iowa State College Press, Ames. 1952: 352–370.
8. HULL, F. H., Recurrent selection and specific combining ability in corn. J. Amer. Soc. Agron. *37* (1945): 134–145.
9. HULL, F. H., Recurrent selection and overdominance. In: Heterosis. Iowa State College Press, Ames. 1952: 451–473.
10. KEMPTHORNE, O., An introduction to genetic statistics. Wiley, New York (1957), 545 pp.
11. LASCOLS, X., Sélection réciproque et maïs hybrides précoces franco-américains. Annales de l'Amélioration des Plantes *9* (1959): 377–401.
12. SCHNELL, F. W., Über Methoden zur reziproken Verbesserung der Kombinationseignung. Vorträge für Pflanzenzüchter *6* (1961), in press.
13. SPRAGUE, G. F., and TATUM, L. A., General vs. specific combining ability in single crosses of corn. J. Amer. Soc. Agron. *34* (1942): 923–932.
14. SPRAGUE, G. F., The experimental basis for hybrid maize. Biol. Rev. *21* (1946): 101–120.
15. ~~SPRAGUE, G. F., Problems in the estimation and utilization of genetic variability~~. Cold Spring Harbor Symposia Quant. Biol. *20* (1955): 87–92.
16. WELLHAUSEN, E. J., WORTMAN, S., and PETERNIANI, E., Comparison of original and third generation sibbed seed-stocks of S_1-lines of corn. Agron. J. *47* (1955): 136–138.