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SELECTION FOR YIELD IN EARLY GENERATIONS OF SELF-FERTILIZING CROPS

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SUMMARY

If a breeder is to apply selection to a cross-population of a self-fertilizing crop and wishes to maximize his chances of finding a productive genotype, he will have to introduce yield tests in the F_3 lines. Should he not do so because of his intention to work on many populations simultaneously, his tests would be considerably less accurate and the finding of a favourable combination more or less a matter of mere chance.

Bulk breeding will result in genetic drift or numbers of plants too large to manage, or in a combination of both.

Application of the Single Seed Descent for quantitative characteristics causes such a genetic drift, that the method is not to be recommended.

Multiple crosses (double-crosses) to improve quantitative characteristics require populations of a size, that cannot be realized and/or selected. This type of crosses is more suited for cases in which qualitative characteristics form the breeding goals and when it is impossible to obtain the favourable combination using only two varieties.

Genic recessive male sterility may be a means to raise large progenies. In the F_3 it confuses the issue of yield of fruits or seeds, which is highly vulnerable in any case. In the F_2 its significance for finding the proper recombinant is very low.

INTRODUCTION

It is and always will be the primary task of plant breeding to create genotypes with high yielding ability. This character is based on polygenes. In wheat, for instance, it is sure that each chromosome carries yield-controlling genes.

Proceeding on the, probably, too simple assumption that there are at least 21 independent loci for yield in a cross between two rather different varieties, the following situation will arise.

1. The F_2 of the smallest complete population must consist of 4398×10^9 plants. Such numbers cannot be realized. Even if it could be done, it would be impossible to find immediately the best-yielding individual.
2. In the F_2, however, one in every 421 plants may still carry all the desired alleles, whether homozygously or heterozygously. We can be practically certain that a random 1684 F_2 plants have not yet suffered an irreparable loss of desired alleles.
3. With further generations these numbers increase considerably. When there are 21 independent gene pairs, the chances of having one plant with all the desired alleles (either homozygous or heterozygous) are:

for the F_2: 1 on every 421 plants;
for the F_3: 1 on every 19343 plants;
for the F_4: 1 on every 176778 plants;
for the F_∞: 1 on every 2097152 plants.

Although the percentages of homozygous genotypes increase considerably with further generations, the number of plants that are necessarily involved in the selection becomes so large that the size of the population grows beyond manageable proportions. The discovery of a plant with all the desired alleles would then become just an illusion.

Nor does the decrease of a possible non-additive (overdominant) genotypic variation in later generations outweigh the disadvantages that are inherent to the large numbers of plants needed in these generations.

SINGLE SEED DESCENT (SSD) METHOD

To avoid being encumbered with the large numbers of plants that must be selected in a sofar uninvestigated advanced generation, the SSD method is sometimes followed (see, among others, BRIM, 1966). It consists of reaping one seed from every F_2 plant and all these seeds in bulk. The procedure is repeated in the F_3, etc. Line selection is taken up from about the F_5, as soon as the progeny has become sufficiently homozygous. In certain instances this method will offer practical advantages.

However, with SSD the breeder is faced with the insurmountable problems of genetic drift in the F_3 and the F_4, since the number of F_4 plants has remained equal to that of the F_2 individuals. Starting with 21 gene pairs, the F_4 population would represent only 0.24% of the smallest appropriate population (see Introduction). The result is a great loss of desirable alleles.

We may conclude therefore that the SSD method cannot be the proper way to select populations originating from parents which differ for many gene pairs.

SELECTION IN THE F_2

Selection of individual plants for yield by eye is an unreliable method (SHEBESKI, 1967; KNOTT, 1972; DE PAUW & SHEBESKI, 1973). Selection by weighing does not help much either, because soil irregularities may be considerable even when short distances are concerned. Besides, the plants are in competition with unknown genotypes. Broad sowing is no solution as in that case the soil heterogeneity starts to play up again, while selection takes place for performance under conditions that differ from those of a dense growing crop.

The honeycomb method of selection of individual plants as proposed by FASOULAS (1973) could make the mentioned problems less difficult. However, the method does not present a proper solution either on the point of competition and is very laborious. It may be a good thing to experiment with this method for its use in practice.

Another objection to applying selection in the F_2 is the relative extent of the non-additive variation.

Concluding, we cannot carry out a reliable plant-selection for quantitative characters as yield in the F_2.

SELECTION AMONG F_3 LINES

The problem can partly be solved by seeing that in the F_2 there are at least 1684 plants that can be selected for yield, i.e. the number of plants which must remain after selection for qualitative characters has been applied. If these plants grow in a wide stand, the yield per plant will be high enough
1. to obtain F_3 lines of a sufficiently large size;
2. to sow 3 rows per line in a normally dense stand.

Ad 1. To avoid irreparable losses of desired alleles in the F_3, each line must consist of a certain minimum number of plants. The F_2 plant which still possessed all desired alleles, must have been most likely homozygous for 7 loci and heterozygous for 14 loci. On the strength of this we conclude that the F_3 line from the respective individual must consist of at least 57 plants so as to warrant the one chance of obtaining again a plant without irreparable loss. To play safe, one should see that there are 228 plants per F_3 line. Many breeders, however, take less plants per F_3 line (SHEBESKI, 1967).

Ad 2. The selection for yield must be carried out in competition with similar types. What eventually counts is not the performance of each individual, but the performance of the crop in a dense stand. For this reason, of the 3 rows only the middle one must be harvested for yield determination. Selection by eye is not reliable (BRIGGS & SHEBESKI, 1970; STUTHMAN & STEIDL, 1976). The other rows may be kept to grow the F_4. With yield determination they only serve as guard rows for the middle row. This way of harvesting trial plots requires a new type of equipment.

Determination of yield without using replications is a very unreliable method. For that reason quite a number of standard plots must be sown among the lines. A 1:1 ratio would be ideal, but one could try a 1:3 ratio.

In the hope that no interactions take place, the yields of the middle rows of the F_3 lines may be expressed as percentages of the nearest standards.

MULTIPLE CROSSES

When the two partners of a cross are F_1's, their product is often called a double-cross, though designating it multiple cross might be better for self-fertilizing crops when the aim is to obtain a homozygous variety.

Variety A × Variety B   Variety C × Variety D
↓   ↓
F_1(AB)   × F_1(CD)
↓
double-cross = multiple cross

Segregation will take place, and in that respect the multiple cross can be compared to a 'normal' F_2 from crossing two varieties. However, the greater heterozygosity in a multiple cross is an aspect which makes the two products differ considerably.

Supposing each of the four varieties possesses specific alleles which are not present in the others, the multiple cross will then be heterozygous for all loci of the desired combination.

In case of 21 such specific alleles – excluding multiple alleles –, distributed over the 4 parent varieties, the chance of finding the heterozygote with all the desired alleles would be 1:2097152. True, the supposition is one of an extreme case, but it clearly shows that the creation of the smallest complete population of the self-fertilizing crops is a mere illusion when many factors are to be combined.

COULD MALE STERILITY BE A HELP?

One might argue that genic recessive male sterility could solve some of the problems. It would also further a recombination, especially so when 2 varieties are crossed and the seed is harvested on the male sterile F_2 plants.

However, this method would only increase the number of plants needed for selection; the relatively frequent male sterility in the F_3 and F_4 would confuse the yield (for fruits and seeds) trials. As reliable yield trials in the F_3 and F_4 are very important we cannot use genic male sterility although its frequency will diminish very quickly with later generations.

Cytoplasmic male sterility, which needs a restorer line as a male parent, would affect the F_3 and F_4 in the same way.

Perhaps chemical emasculation would be a better help.

Further, the significance of intensive (spontaneous) mating in the F_2 and the F_3 for recombination is negligeable (Bos, 1977; Stam, 1977). We can but conclude that male sterility will be of little use when intermating varieties of self-fertilizing crops.

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