PROGRESSIVE IMPROVEMENT IN SELF-FERTILISED CROPS

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WHEN breeding for increases in quantitative characters by hybridisation, the objective is usually to produce varieties surpassing any available as parents. Akerman and MacKey (1948) aptly call this transgressive breeding. With this sort of breeding any parental combination may be useful, but with crops which have been cultivated and selected over a long period, most are of no value. For instance, at the New Zealand Wheat Research Institute, where increase in yield is one of the main objectives, of some 300 crosses which have been grown sufficiently long for their worth to be estimated, only three have produced new varieties, one of them producing two, while only 24 have produced lines of merit sufficient to warrant test in extensive field trials. Good crosses are obviously rare, and should therefore be utilised to the fullest extent possible.

All the evidence indicates that a large number of genes determines the expression of most quantitative characters, and that a large number of genes determining these characters is segregating in most crosses. Where a large number of genes is segregating, the frequency of any one genotype in the segregating population is low. The homozygous genotype with the maximum character expression will be present with the frequency of $1/4^n$ in F_2 and $1/2^n$ when segregation is complete. (n = the number of segregating gene pairs). Where many genes are segregating, the chances of producing or finding this genotype are remote. But this, the "ideal", will not be the only useful genotype in the hybrid population. If both parents of the cross contribute a substantial number of segregating plus genes to the cross, there will be numerous homozygous genotypes in the population with a higher character expression than either parent. Assuming, for instance, that each parent contributes ten independently segregating plus genes, individuals homozygous for more than (say) 15 plus genes would be valuable.

The relative frequencies of homozygous individuals with more than 15 unlinked plus genes when segregation is complete are set out below.

Number of plus genes	.	.	.	16	17	18	19	20
Frequency (all over 2^{20})	.	.	.	4845	1140	190	20	1

These frequencies show that valuable genotypes will occur in reasonable numbers in moderately large populations. They also

suggest that the successful selections from any hybrid population probably do not represent the genotypes with the highest expression which can possibly occur in that population. Crosses which have yielded valuable lines are therefore promising sources for breeding or selecting still further improved lines.

This may be done in two ways. The first is to grow large F_2 populations of the desired crosses and select from them, or from later generation populations derived from them. The likelihood of producing lines with the highest possible expression by this method is remote. For instance, lines with yield equal to that of F_1 are still an objective, not an achievement, in most plant breeding schemes (Ellerton, 1944).

The second, suggested here, is based on the following considerations. If several high-yielding lines are isolated from a cross it is unlikely that they will all contain the same plus genes. Those missing from one line will probably be present in another. In the hypothetical case quoted above, there are $4845/2^{20}$ homozygous lines with 16 plus genes. If any two such lines are crossed, in $1820/4845$ of the cases each parent will contain four different plus genes; in $2240/4845$ of the cases they will have one gene pair in common and hence will contain three different plus genes; in $720/4845$ cases they will both lack two particular plus genes; in $64/4845$ cases they will both lack three particular plus genes, and in $1/9690$ cases they will be identical. The probable results of such a crossing scheme are tabulated below, each cross being carried without selection until segregation is complete.

Number of genes by which parents differ	Probability of their being crossed	Number of homozygous geno- types according to numbers of plus genes					Total population
		16	17	18	19	20	
8	$1820/4845$	70	56	28	8	1	256
6	$2240/4845$	20	15	6	1		64
4	$720/4845$	6	4	1			16
2	$64/4845$	2	1				4
0	$1/9690$	1					1

The chances are heavily weighted in favour of producing populations with relatively high frequencies of the highest, or near highest, yielding genotypes. They will be much more common than in the original F_2 or unselected populations derived from it, so that smaller segregating populations can be used with greater prospects of success.

This, then, appears to be a much surer and more economical method of utilising the potential advantages of a successful cross than selection from the original hybrid population. Two or three cycles of such selection and crossing should assemble the major linkage groups determining maximum expression of a character in

one or a few homozygous lines. Comparison of character expression in such a line with that in F_1 will show whether or not further cycles to disrupt these linkage groups would be warranted.

The most obvious disadvantage of the method is that it is slow. Each cycle could hardly take less than six years ; it would probably take ten. It is not suggested that all the facilities of a breeding institution be devoted to this intensive treatment of a few crosses. As the amount of ultimate progress is restricted by the genic constitution of the original parents of the cross, such a course would be unwise ; as good results can be expected with relatively small populations, it is unnecessary. Rather, one would suggest that when they are found outstanding parental combinations be treated in this manner, while the search for such crosses continues.

SUMMARY

In transgressive breeding for quantitative characters valuable crosses are rare. Therefore, when found, they should be utilised fully. If many genes are segregating in any particular cross the ideal combination occurs but rarely, but other combinations short of perfection will be useful and relatively common. Lines selected from crosses therefore probably belong in this latter category. Crossing together high yielding lines isolated from the same cross will give populations with a relatively high frequency of the higher yielding genotypes, and will be the surest and most economical method of producing the highest yielding genotype. Such a programme would be a useful adjunct to normal breeding programmes.

REFERENCES

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