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ON THE NUMBER AND SIZE OF CROSS COMBINATIONS IN A BREEDING PROGRAMME OF SELF-FERTILIZING CROPS

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SUMMARY

The number and size of crosses in a breeding programme were discussed to the conclusion that the number of crosses rather than the size of a cross should be increased with a given total population size. The advantage due to this manipulation, however, is relatively small when such genotypes as improved for many (twenty-five or more) loci are to be obtained, or when a high proportion (around 0.1 or more) of available combinations have the potentiality of releasing the objective genotypes. In such a case, the ease with which crossing and cultivation can be carried out becomes the decisive factor.

INTRODUCTION

Since the genetical capacity of parental material can not be well predicted in advance for most agronomic characters, breeders generally make many cross combinations for one breeding objective. So, the number of crosses and the size of individual crosses are first to be determined in actual breeding programmes. Unexpectedly, however, no consistent consideration seems to have been made regarding this aspect until now, while numerous studies have been undertaken on the selection methods after crossing (e.g. see FREY, 1975). Optimum number and size of crosses will be discussed in this report.

DEFINITIONS AND MATHEMATICAL FORMULATIONS

The number and size of crosses should be chosen in such a way that the risk (probability) of desirable or promising genotypes being excluded in the whole F_2 population should be minimized. This criterion is reasonable because all efforts of breeders for selection would be in vain if neither desirable nor promising genotypes exist in the first segregating population.

To formulate this risk, the following symbols are introduced:

N: total number of plants permissible in the F_2 generation for the breeding objective concerned;

n: number of F_2 plants per cross (size of a cross);

m: number of crosses (= N/n);

P: the probability that a cross is favorable, i.e. has the potence to segregate desirable (homozygous and fitting to the breeding objective) and promising (heterozygous and capable of transmitting the desirable genotype to the subsequent generations) genotypes;

p and q: the probabilities (expected frequencies) that the desirable and promising genotypes are segregated respectively in such a favourable cross (these probabilities vary with crosses, but will be treated as the same for all of those crosses, because there is no way of determining beforehand the values for individual crosses);

p′: p + q.

It has been empirically suggested in some published reports and records of practical breeding (e.g. PALMER, 1953; ISHIZUMI, 1976) that one among a hundred crosses as a rough estimate leaves a desirable variety in highly improved crops such as wheat and rice, indicating that the value of P is around the order of 10^{-2}. The range of $10^{-1} \sim 10^{-2}$ would cover most of the actual situations. With i unlinked genes affecting the breeding objective, the probabilities p and q are given by $(1/4)^i$ and $(3/4)^i$–$(1/4)^i$, respectively. Genetics of agronomic characters of cereal crops has shown that i is generally larger than ten, namely, p and q are around or below the orders of 10^{-6} and 10^{-2}, respectively (see Table 1). Linkage among the loci would greatly change the relative sizes of p and q, but not so much the aggregate frequency p′.

Using the above symbols, the risk (R) is presented by

$$R = \{(1-P) + P(1-p-q)^n\}^m.$$

With the ranges of P and p′ as above mentioned, this formula can be approximated by

$$R = \exp\left[-NP\frac{1-e^{-np'}}{n}\right],$$

which becomes

$$R = \begin{cases} \exp[-NPp'] & \ldots\ldots np' \ll 1 \\ \exp[-NP/n] \text{ or } \exp[-mP] & \ldots\ldots np' > 10. \end{cases}$$

The last two formulae indicate that with a relatively large value of p′, the risk gets small as n is decreased, or, as m is increased. With a sufficiently small value of p′, the risk is independent of m and n, that is, any crossing scheme is equally efficeint.

NUMERICAL COMPUTATIONS AND CONCLUSIONS

Numerical computations were made for some probable values of the parameters. To find the optimum crossing scheme, only the term $(1-e^{-np'})/n$ was calculated, which exclusively determines the relative size of the risk with given F_2 population size (N) and available parents (P); the larger the term, the smaller the risk. Results of the computations are illustrated in Fig. 1.

It is evident from this figure that the risk is reduced with the decrease in size of a cross, in other words, breeding efficiency increases with the number of crosses. This trend is sharp with relatively large values of p′, but rather unimportant with small values as 10^{-4} or lower orders. In the latter case which corresponds to the segregation

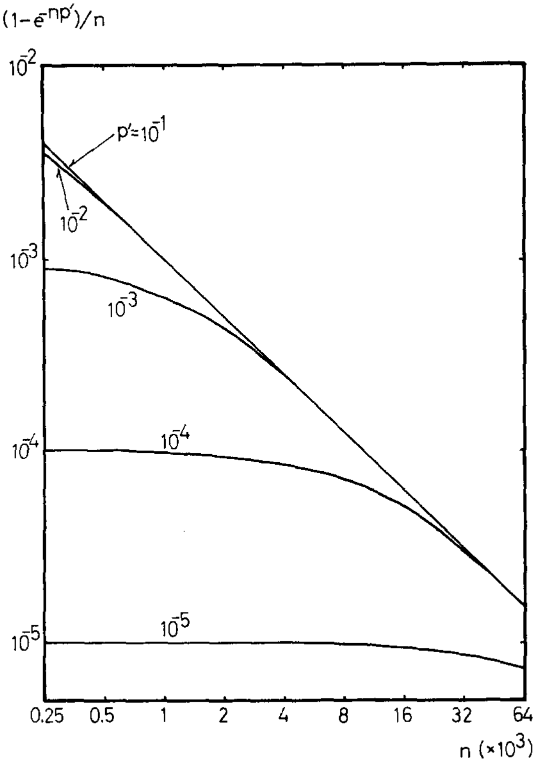

Fig. 1. Relative efficiencies of the crossing schemes with different sizes of a cross (n) and expected frequencies (p′) of the desirable and promising genotypes with given F_2 population size and available parents.

of twenty-five or more genes (Table 1), the cost and labour required for crossing or other manipulations may be the decisive factors of the crossing scheme.

The calculations shown in Table 2, however, explain that with such low genotypic frequencies (p′) as 10^{-4} or lower orders, the risk itself exceeds 0.5 for the range of $P \leq 50^{-1}$ and for any F_2 population sizes manageable in practice. Taking this and the failure of artificial selections in the F_2 and later generations, it could be said that in highly improved crops those genotypes as bettered simultaneously for 25 or more loci have little chance to be obtained in an ordinarily permissible scale of breeding (in Japan, for example, about 20–50 crosses and 500–3000 F_2 plants per cross seem to have been employed in the bulk breeding method of rice). The desirable genotypes obtainable through one cycle of crossing may be in most cases the ones that

Table 1. F_2 segregation ratios of the desirable homozygotes (p) and promising heterozygotes (q) in a favourable cross, assuming independent inheritance of the genes affecting the breeding objective.

	Number of genes				
	5	10	15	20	25
p	9.77×10^{-4}	9.54×10^{-7}	9.31×10^{-10}	9.09×10^{-13}	8.88×10^{-16}
q	2.36×10^{-1}	5.63×10^{-2}	1.34×10^{-2}	3.17×10^{-3}	7.53×10^{-4}
Order of p′	10^{-1}	$10^{-1} \sim 10^{-2}$	10^{-2}	10^{-3}	$10^{-3} \sim 10^{-4}$

Table 2. The probabilities of the desirable and promising genotypes being excluded in the whole F_2 population.

N	10^4			5×10^4			10^5			5×10^5		
P	10^{-1}	50^{-1}	10^{-2}	10^{-1}	50^{-1}	10^{-2}	10^{-1}	50^{-1}	10^{-2}	10^{-1}	50^{-1}	10^{-2}
$p'=10^{-1}$	0.135	0.670	0.819	0.000	0.135	0.368	0.000	0.019	0.135	0.000	0.000	0.000
	0.368	0.819	0.905	0.007	0.368	0.607	0.000	0.135	0.368	0.000	0.000	0.007
	0.607	0.905	0.951	0.082	0.607	0.779	0.007	0.368	0.607	0.000	0.007	0.082
10^{-2}	0.137	0.672	0.820	0.000	0.137	0.370	0.000	0.019	0.137	0.000	0.000	0.000
	0.368	0.819	0.905	0.007	0.368	0.607	0.000	0.135	0.368	0.000	0.000	0.007
	0.607	0.905	0.951	0.082	0.607	0.779	0.007	0.368	0.607	0.000	0.007	0.082
10^{-3}	0.455	0.854	0.924	0.020	0.455	0.675	0.000	0.207	0.455	0.000	0.000	0.020
	0.531	0.881	0.939	0.042	0.531	0.729	0.002	0.282	0.531	0.000	0.002	0.042
	0.649	0.917	0.958	0.115	0.649	0.806	0.013	0.421	0.649	0.000	0.013	0.115
10^{-4}	0.907	0.981	0.990	0.614	0.907	0.952	0.377	0.823	0.907	0.008	0.377	0.614
	0.909	0.981	0.991	0.621	0.909	0.954	0.386	0.827	0.909	0.009	0.386	0.621
	0.913	0.982	0.991	0.636	0.913	0.956	0.404	0.834	0.913	0.011	0.404	0.636
10^{-5}	0.990	0.998	0.999	0.951	0.990	0.995	0.905	0.980	0.990	0.607	0.905	0.951
	0.990	0.998	0.999	0.951	0.990	0.995	0.905	0.980	0.990	0.608	0.905	0.951
	0.990	0.998	0.999	0.952	0.990	0.995	0.906	0.980	0.990	0.610	0.906	0.952

$n = 500, 1{,}000$, and $2{,}000$, upper to lower ($m = N/n$).

segregate with the ratio (p') of 10^{-3} or higher, which correspond to the case of twenty or less genes' segregation (Table 1).

With sufficiently large values of P and N such as 10^{-1} and 50,000 respectively, the increase in cross number causes no substantial decrease in the risk, while it remains that the decreasing rate per se is larger with larger values op p'.

Summing up the above, it could be generally concluded that the number of crosses rather than the size of a cross should be increased if circumstances permit.

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