Selection Strategy in Breeding of Self-fertilizing Crops. II. On the Use of Selection among F_2 Populations by the Presence and Absence of Promising Phenotypes

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Breeders seldom have enough time and labour to estimate the amount and nature of the genetic variation of segregating populations. Cross combinations therefore are assessed by the presence and absence of the promising phenotypes which appear to meet the breeding objective concerned. The application of this type of cross selection in F_2 is investigated to the conclusion that the breeding efficiency for a given breeding cost is increased by this selection; F_2 populations should be entirely discarded if no promising phenotype is found regarding qualitative characters and some continuous characters which are easily assessed and as heritable as regularly show significant correlations between F_2 plants and F_3 progenies. This holds even with a relatively small population size as 500~1,000 and in the presence of a negative but not very close genetic association between these characters and the ones which also are concerned with the breeding objective but not assessed in F_2 . With a large F_2 population, the selection among and within crosses is useful even when the characters are negatively and closely associated. The direct measurement of yield in F_2 as still proposed by some workers is not expected to be rewarding.

Introduction

It is known empirically that the frequency of cross combinations which lead to new varieties is extremely small even with carefully chosen parents; some workers have suggested that in highly improved crops such as rice and wheat, only one out of hundreds of crosses has the potentiality of leading to a new variety (PALMER 1953, ISHIZUMI 1976). Reflecting this, breeders usually make many cross combinations, either simultaneously or sequentially, for one breeding objective.

With such a small frequency of desirable cross combinations, discarding undesirable crosses in F_2 generation would be of great practical merit, since by this procedure the cost for keeping and testing undesirable crosses can be saved, or, used for increasing selection efficiency for desirable ones.

Methodology for selection among cross combinations has been discussed by many authors. SAKAI (1954) and JINKS and POONI (1978) have suggested that the genetical potentiality of a cross can be predicted using estimates of some genetic statistics of the first and second degrees. WHITEHOUSE et al. (1958) have applied the diallel crosses among parents. In these methods, some special designs of crossing and a large scale of field experiment are needed to obtain reliable estimates of the various genetic parameters. And in addition, interpretation of the estimates depends on a number of assumptions which are difficult to confirm for agronomic characters. Some workers have suggested that mean and variance for yield may be predictive of yielding potentiality of F_2 populations (FUKUOKA and KIRIYAMA 1970, SKORDA 1973). This method also assume yield measurement of single plants. In

practical breeding programmes with limited time and labour, any method which requires laborious and time-consuming measurement has not come into a wide use. Breeding cost has not properly been appreciated in the above studies.

HAMBLIN and EVANS (1976) and NASS (1979) have tried a more simplified assessment where yields of parental, F_1 and F_2 populations are bulk-measured under a fairly large scale of experiment. In this method, crosses may be rejected even if some very promising plants are segregating. Besides, single plant selection may not be operational in F_2 generation, or, has to be operated duplicatedly with the bulk-measurement of yield. This method would be rewarding only in comparing crosses with largely different genetic potentialities.

It has been previously shown that F_2 single plant selection is advantageous for the various characters which are visually or easily assessed (YONEZAWA and YAMAGATA 1981). Application of the cross selection by the presence and absence of promising phenotypes for these characters will be examined in this paper.

Mathematical Formulation

It is assumed that F_2 plants are evaluated and selected for a character, say selective character, selection for other characters, say non-selective characters, being operated in later generations. In this type of selection, two attitudes can be taken towards the F_2 populations which lack promising phenotypes for the selective character; first, these populations are entirely discarded in F_2 , and secondly, maintained to F_3 generation to re-examine the genetic segregation. Selection among F_2 populations is operated in the former, but not in the latter. These two attitudes, which are referred to as selection systems CS and NCS respectively, will be compared in this paper based on the probability that one or more promising genotypes (desirable homozygotes and promising heterozygotes) are included in overall F_3 populations. The practical implication of this probability has been explained in the previous paper (YONEZAWA and YAMAGATA 1981).

With the selection criterion in F_2 as above mentioned, any cross combination belongs to one of the following three states, whether or not identified by breeders,

A : having the potentiality of releasing desirable genotypes for both selective and non-selective characters,

B : having the potentiality for the selective character but not for non-selective characters,

C : the reverse of state B, or, lacking the potentiality for both of the characters.

Crosses of state A are desirable since they have the potentiality of releasing new varieties. Crosses of states B and C are undesirable.

For F_2 populations of state A, the probability that one or more promising phenotypes for the selective character are recognised is formulated as

$$F_A = 1 - \sum_{i_1+i_2+i_3=N_2} \frac{N_2!}{i_1!i_2!i_3!} f_{1A}^{i_1} f_{2A}^{i_2} f_{3A}^{i_3} (1-\theta_1)^{i_1} (1-\theta_2)^{i_2} (1-\theta_3)^{i_3} \\ = 1 - (1-\theta_A)^{N_2}, \quad (1)$$

where

N_2 = F_2 population size ($i_1+i_2+i_3=N_2$),

f_{1A} = the expected frequency of desirable homozygotes for the selective character,

f_{2A} = that of promising heterozygotes which have the potentiality of segregating the desirable

homozygotes in their progeny lines or families,

f_{3A} = that of unpromising genotypes, ($f_{1A} + f_{2A} + f_{3A} = 1$),

θ_1 = the proportion with which the desirable homozygotes fall in the critical phenotypic range for F_2 selection,

θ_2 = that for the promising heterozygotes,

θ_3 = that for the unpromising genotypes,

$\theta_A = f_{1A}\theta_1 + f_{2A}\theta_2 + f_{3A}\theta_3$, i.e. mean of the above three proportions, which is equal to the selection intensity (fraction) averaged over the F_2 populations of state A.

Assuming disomic and independent inheritance of the genes concerned, the genotype frequencies f_{1A} and f_{2A} are formulated as

$$f_{1A} = \sum_{i=k_0}^k \binom{k}{i} \left(\frac{1}{4}\right)^i \left(\frac{3}{4}\right)^{k-i}, \quad (2)$$

$$f_{2A} = \sum_i \binom{k}{i} \left(\frac{3}{4}\right)^i \left(\frac{1}{4}\right)^{k-i} - f_{1A}, \quad (3)$$

giving the aggregate frequency of the promising genotypes

$$f_A = f_{1A} + f_{2A} = \left(\frac{1}{4}\right)^k \sum_i \binom{k}{i} 3^i, \quad (4)$$

where

k = the total number of segregating genes affecting the selective character,

k_0 = the minimum number of the genes (among the k genes) for which a new variety should be fixed for some particular allele, say desirable allele.

Linkage among the genes makes the frequency f_{1A} take larger and smaller values than the above formulated one, depending on the coupling and repulsion linkage among desirable alleles respectively. The reversed relationship holds between f_{2A} and the states of linkage, to the estimation that the sum f_A is much less affected by linkage than each of the two component frequencies. The probabilities θ 's have been fully described in the previous paper (YONEZAWA and YAMAGATA 1981).

Similar definitions and formulations can be made for the populations of state B, the subscript A of the corresponding parameters being substituted by B. The values of the parameters may vary with the states of populations; the frequency of the promising genotypes in the populations of state B, f_B , should be smaller than f_A in the presence of a desirable and consistent (taking the same sign over all or most of the available crosses) genetic association between the selective and non-selective characters, and should be larger than f_A with an undesirable or negative genetic association. The parameters for the populations of state C are similarly obtained by the substitution of the subscripts, and in this case, $f_{1C} = f_{2C} = f_C = 0$, $f_{3C} = 1$, and therefore $\theta_C = \theta_3$.

Introducing the relative frequencies α, β and γ ($= 1 - \alpha - \beta$) of the three different states of F_2 populations, the overall frequency of the crosses which include one or more promising phenotypes for the selective character is presented by

$$\bar{F} = \alpha F_A + \beta F_B + \gamma F_C, \quad (5)$$

and the average selection intensity over all F_2 populations is

$$\bar{\theta} = \alpha \theta_A + \beta \theta_B + \gamma \theta_C. \quad (6)$$

Now, the probability that promising genotypes (regarding both selective and non-selective characters) are maintained in F_3 generation in system CS is formulated by

$$\begin{aligned}\Phi_{CS} &= 1 - \sum_{i_1+i_2+i_3=M} \frac{M!}{i_1!i_2!i_3!} \alpha^{i_1} \beta^{i_2} \gamma^{i_3} \sum_{0 \leq i \leq i_1} \binom{i_1}{i} F_A^i (1-F_A)^{i_1-i} \cdot (1-\phi_s)^i \\ &= 1 - (1 - \alpha F_A \phi_s)^M \doteq \alpha M F_A \phi_s,\end{aligned}\quad (7)$$

where M stands for the total number of available crosses. The symbol ϕ_s means the probability that the promising genotypes are included in the F_3 progenies of the F_2 plants which are selected from the populations of state A. The probability is formulated as

$$\phi_s \doteq n N_2 (f_{1A} \theta_1 p \bar{r} + f_{2A} \theta_2 q \bar{s}), \quad (8)$$

where

n = the number of F_3 offsprings per plant selected in F_2 ,

p = the F_2 frequency of promising genotypes for non-selective characters, which is calculated for the sub-population of desirable homozygotes for the selective character (cf. Table 1 in YONEZAWA and YAMAGATA 1981),

q = similarly defined frequency for the sub-population of promising heterozygotes for the selective character,

$\bar{r}$ = mean segregation ratio of the promising genotypes (regarding both selective and non-selective characters) in a progeny of a desirable homozygote for the selective character,

$\bar{s}$ = similarly defined segregation ratio for a progeny of a promising heterozygote for the selective character.

The corresponding probability for selection system NCS is presented by

$$\begin{aligned}\Phi_{NCS} &= 1 - \sum_{i_1+i_2+i_3=M} \frac{M!}{i_1!i_2!i_3!} \sum_{0 \leq i \leq i_1} \binom{i_1}{i} F_A^i (1-F_A)^{i_1-i} \cdot (1-\phi_s')^i (1-\phi_{ns})^{i_1-i} \\ &\doteq \alpha M (F_A \phi_s' + (1-F_A) \phi_{ns}),\end{aligned}\quad (9)$$

where ϕ_s' is similarly defined as ϕ_s excepting that as explained below n now takes a smaller value, say n' , than in system CS. ϕ_{ns} shows the probability of the promising genotypes being contained in an F_3 population which is derived from an F_2 population of state A but lacking promising phenotypes in F_2 . Assuming that n'' offsprings are taken from each of randomly selected $N_2' (\leq N_2)$ plants, this probability is given by

$$\phi_{ns} \doteq n'' N_2' (f_{1A} p \bar{r} + f_{2A} q \bar{s}). \quad (10)$$

Adopting the symbols,

N_3 = the number of F_3 plants to be grown for a cross in system NCS,

n_0 = the average offspring number per selected F_2 plants in the case $N_2 = N_3$, which by definition is equal to $\bar{F}/\bar{\theta}$,

the plant numbers n' and n'' are equal to $n_0 N_3/N_2$ and N_3/N_2' respectively. With the same total number of F_2 and F_3 plants summed over all of the crosses, in other words, with the same breeding cost in F_2 and F_3 , the plant number n in system CS should be $1/\bar{F}$ times larger than n' , since only $\bar{F}$ of all crosses are taken up and leave progenies to F_3 .

The condition for system CS to be superior to NCS is presented by

$$\Phi_{CS} > \Phi_{NCS}$$

which is rewritten as

$$\frac{\bar{F}}{1-\bar{F}} \cdot \frac{F_A}{1-F_A} > g \quad (11)$$

where $g = n_0 (f_{1A} \theta_1 p \bar{r} + f_{2A} \theta_2 q \bar{s}) / (f_{1A} p \bar{r} + f_{2A} q \bar{s})$.

The discussion in the previous paper corresponds to the comparison between system *NCS* and the delayed selection system (*DS* system) where neither plant nor cross selection are operated in F_2 generation. By the present terminology, the condition for system *NCS* to be superior to *DS* is presented by $\alpha M(F_A \phi_s' + (1-F_A) \phi_{ns}) > \alpha M \phi_{ns}$ which is equivalent to $\phi_s' > \phi_{ns}$. The conclusion was that system *NCS* is advantageous when $g > 1$. So, the relation

$$\frac{\bar{F}}{1-\bar{F}} \cdot \frac{1-F_A}{F_A} < 1, \quad \therefore F_A > \bar{F} \quad (12)$$

defines a sufficient condition for system *CS* to be superior to both *NCS* and *DS*. With a sufficiently large value of F_A compared to $\bar{F}$, inequality (11) holds even when $g < 1$, indicating that F_2 plant selection in system *CS* can be useful even when not useful in *NCS*. This supports our previous suggestion that the efficiency of F_2 plant selection is increased by incorporating selection among F_2 populations (YONEZAWA and YAMAGATA 1981).

Using formulae (1) and (5) and the approximation $(1-f_A u_A)^{N_2} \doteq \exp(-N_2 f_A u_A)$, the condition (12) is rewritten to the form

$$\frac{1 - \exp(-N_2 f_A u_A)}{1 - \exp(-N_2 f_B u_B)} > \frac{\beta}{1-\alpha} \quad (13)$$

where u_A equals $\left\{ f_{1A} \left(1 - \frac{1-\theta_1}{1-\theta_3} \right) + f_{2A} \left(1 - \frac{1-\theta_2}{1-\theta_3} \right) \right\} / f_A$. The parameter u_A may roughly be approximated by the correlation between F_2 plants and their F_3 progenies. Although u_A and the correlation are defined on different logical grounds, a fairly good correspondence exists between the two; both of them are close to unity for the characters where genotypes are well identified and regulated by additive gene effects, zero when genotypes are hardly identified, and take a negative value when some particular types of epistatic gene interactions are prevalent to cause phenotypic inferiority of promising F_2 genotypes. The parameter u_B is similarly defined for the populations of state *B*.

Inequality (13) is always satisfied when

$$f_A u_A > \ln \left(1 - \frac{\beta}{1-\alpha} \right)^{-1} / N_2. \quad (14)$$

In this situation, the selection is effective unless the selective and non-selective characters are negatively and completely associated. The right side of this inequality will be denoted by v_0 for simplicity. Otherwise, the relation

$$\frac{f_B u_B}{f_A u_A} < \frac{1}{N_2 f_A u_A} \cdot \ln \left\{ 1 - \frac{1-\alpha}{\beta} (1 - \exp(-N_2 f_A u_A)) \right\}^{-1} \quad (15)$$

has to hold for effective selection among crosses. The ratio $f_B u_B / f_A u_A$ is zero when the selective character is desirably and fully associated with non-selective ones, unity when independently inherited, and positive infinite when negatively and fully associated. The parameter $\rho_{CR} = (f_A u_A - f_B u_B) / (f_A u_A + f_B u_B)$ would be convenient to measure the direction and strength of the genetic association, taking 1, 0 and -1 according to the above three situations. Using this parameter, inequality (15) is expressed as

$$\rho_{CR} > \frac{1-w_0}{1+w_0}, \quad (16)$$

where w_0 stands for the right side of inequality (15). The right side of inequality (16) gives the lower limit of the genetic association for effective selection among populations,

and will be denoted by ρ_{CO} in the following discussion. The value of w_0 is equal to or larger than unity, indicating that ρ_{CO} is zero or negative, i.e. cross selection is useful for any character which is not associated or desirably associated with non-selective characters.

The parameters $f's$, $\theta's$, p , q , $\bar{r}$ and $\bar{s}$ may vary with populations even within the same state of populations, but were taken as constants in the above formulations. This simplification causes no inconvenience in deriving the relative efficiencies of the different selection systems.

Numerical Computations and Conclusion

Numerical computations of the parameters v_0 , w_0 and ρ_{CO} were made for some probable values of the constituent parameters, and were presented in Tables 1 and 2. The genotype frequency f_A were also calculated using formula (4), and the results were shown in Table 3.

As seen by formulae (14), and (16), the efficiency of cross selection is the larger with the smaller values of v_0 and ρ_{CO} , or with the larger value of w_0 . Bearing this, it is known from Table 1 and 2 that the frequency of populations of state B has the largest influence on the efficiency of cross selection. The frequency of populations of state A and the frequency (f_A) and identification (u_A) of promising genotypes cause only a little influence in the range of the computations presented in these tables. As intuitively expected, the efficiency of the selection is increased with population size.

For simply inherited characters as affected by a single or two genes with large genetic effects, the genotype frequency f_A is $3/4$ for the case of $k=k_0=1$, and $(3/4)^2$ for the case of $k=k_0=2$ with independent inheritance of the genes, and the parameter u_A takes some value between $1/3$ and 1 for the former case and between $1/9$ and 1 for the latter case, depending on the degree and type of dominance and epistatic interactions between the genes. For such a character, the left side of inequality (14), $f_A u_A$, is in the range of

Table 1. Computations of the right side of inequality (14), v_0

α	β	N_2			
		200	500	1,000	5,000
10^{-3}	0.1	0.0005	0.0002	0.0001	0.0000
	0.3	0.0018	0.0007	0.0004	0.0001
	0.5	0.0035	0.0014	0.0007	0.0001
	0.7	0.0060	0.0024	0.0012	0.0002
10^{-2}	0.1	0.0005	0.0002	0.0001	0.0000
	0.3	0.0018	0.0007	0.0004	0.0001
	0.5	0.0035	0.0014	0.0007	0.0001
	0.7	0.0061	0.0025	0.0012	0.0002
10^{-1}	0.1	0.0006	0.0002	0.0001	0.0001
	0.3	0.0020	0.0008	0.0004	0.0001
	0.5	0.0041	0.0016	0.0008	0.0002
	0.7	0.0075	0.0030	0.0015	0.0003

α =the frequency of the promising cross combinations which have the potentiality of releasing a new variety,

β =the frequency of the crosses which have the potentiality of segregating promising genotypes for the characters assessed in F_2 but not for other characters,

N_2 = F_2 population size.

Table 2. Computations of the parameters w_0 and ρ_{co} which are equal to the right side of inequalities (15) and (16) respectively

α	β	$f_A u_A$		N_2			
				200	500	1,000	5,000
10^{-3}	0.1	10^{-4}	w_0	11.02	13.36	30.09	*
			ρ_{co}	-0.83	-0.86	-0.94	
		10^{-6}		10.00	10.01	10.04	10.22
				-0.82	-0.82	-0.82	-0.82
	0.3	10^{-4}		3.41	3.54	3.81	*
				-0.55	-0.56	-0.58	
		10^{-6}		3.33	3.33	3.33	3.35
				-0.54	-0.54	-0.54	-0.54
	0.5	10^{-4}		2.02	2.05	2.11	3.09
				-0.34	-0.34	-0.36	-0.51
		10^{-6}		2.00	2.00	2.00	2.00
				-0.33	-0.33	-0.33	-0.33
	0.7	10^{-4}		1.43	1.44	1.46	1.65
				-0.18	-0.18	-0.19	-0.25
		10^{-6}		1.43	1.43	1.43	1.43
				-0.18	-0.18	-0.18	-0.18
10^{-1}	0.1	10^{-4}		9.81	11.56	19.41	*
				-0.82	-0.84	-0.90	
		10^{-6}		9.01	9.02	9.04	9.19
				-0.80	-0.80	-0.80	-0.80
	7.0	10^{-4}		1.29	1.30	1.31	1.41
				-0.13	-0.13	-0.13	-0.17
		10^{-6}		1.29	1.29	1.29	1.29
				-0.13	-0.13	-0.13	-0.13

* Inequality (14) holds.

Table 3. Computations of the frequency (f_A) of promising genotypes in F_2

k		2		3		4		5	
k_0		k_0		k_0		k_0		k_0	
1	0.75	1	0.94	1	0.98	1	0.99	1	0.99
		2	0.56	2	0.84	2	0.95	2	0.98
				3	0.42	3	0.74	3	0.90
						4	0.32	4	0.63
								5	0.24
10		20		30		40		50	
k_0		k_0		k_0		k_0		k_0	
5	0.98	10	0.99	15	0.99	20	0.99	25	0.99
6	0.92	12	0.96	18	0.98	24	0.99	30	0.99
7	0.78	14	0.79	21	0.80	28	0.82	35	0.84
8	0.53	16	0.41	24	0.35	32	0.30	40	0.26
9	0.24	18	0.09	27	0.03	36	0.02	45	0.01
10	0.06	20	0.00	30	0.00	40	0.00	50	0.00

0.25~0.75 and 0.66~0.56 for the respective cases. Values in these ranges are about ten or more times larger than the values of v_0 shown in Table 1, leading to the conclusion that F_2 populations which include no promising phenotype for these character should be discarded.

As seen from the formulation of u_A in the previous section, $f_A u_A$ may take a smaller

value than v_0 when desirable alleles are recessive and very closely linked with undesirable ones concerned with the selective character. Formula (16) shows that cross selection is advantageous also in this case unless this character is undesirably and closely associated with non-selective characters. Computations of ρ_{C0} in Table 2 further indicate that even a close negative association between the characters does not invalidate the cross selection when the expected frequency of promising crosses is relatively small and/or the size of F_2 population is sufficiently large.

For continuous characters, not enough information is available to estimate precisely the parameters f_A and u_A . But, rough estimates or ranges of the parameters can be obtained from experiments undertaken hitherto. In cereal crops such as rice, wheat and barley, F_2 and later segregations of relatively highly heritable characters such as heading date and plant height have been shown to be explained by a relatively small number of genes (e.g., SYAKUDO *et al.* 1952, FUKU 1954, LEONARD *et al.* 1956), unless the parents are genetically much diverse as in a cross between alien varieties. Table 3 shows that f_A is around or larger than 0.25 when k is around or less than 5, and even when $k=10$ as far as $k_0 \leq 9$.

As already mentioned, the parameter u_A could be approximated by the correlation between F_2 plants and their F_3 progenies. The correlations for the above characters are mostly if not always significant and very rarely less than 0.2 (e.g., ISHIKAWA and KARIYA 1952, NEI 1960, MATSUO *et al.* 1960). So, there would be no serious overestimation in assuming that $f_A u_A$ is around or larger than 0.05 (0.25×0.2), which far exceeds most of the values of v_0 presented in Table 1. Inequality (14) may not be satisfied when desirable alleles are recessive and closely linked with undesirable ones. As seen from formula (16) and Table 2, selection is useful also in this case unless the characters are negatively and closely associated with non-selective characters and the population size is limited. Cross selection would be useful also for some other length characters such as panicle length, which appear to be affected by a small number of genes (TAKEZAKI 1927, SYAKUDO 1950) and are not much less heritable than plant height.

Even more genes may be segregating for yield and some yield component characters such as panicle weight and number, and F_2 — F_3 correlations for these characters are not significant in many cases, or, extremely small even if statistically significant (GOTOH 1959, MATSUO *et al.* 1960). In practice, even negative correlations have not rarely been obtained (NEI 1960, HORIE *et al.* 1964). There is therefore no positive reason of believing that yield measurement of F_2 plants is efficient enough to cancel out such a large amount of labour and time required for that.

It is noted in this context that the condition represented by inequality (14) is always satisfied when $F_A > F_B$ or $f_A u_A > f_B u_B$, which holds for any character that is not undesirably correlated with non-selective characters. Numerous experiments have shown that some visually assessed characters with relatively high heritabilities such as plant type, spike size and flag leaf area are associated with yielding potentiality (GOTOH 1963, YAP and HARVEY 1972, NASS 1963, McNEAL *et al.* 1978). This suggests that visual assessment of yield potentiality may effectively be made based on some morpho-physiological traits which themselves may not be the objective characters of breeding. At the present state of our understanding of the relationship between yield and its component characters, however, this

visual selection should not be too intensive. Visual selection for high yield has not always been effective (FUTSUHARA *et al.* 1965, STUTHAN and STEIDL 1976, HANSON *et al.* 1979). A handy and reliable indicator for yielding potentiality remains to be established.

In conclusion, breeding efficiency can be much increased by incorporating selection among F_2 populations. F_2 populations should be entirely rejected when no promising phenotypes are found for the characters which are easy to assess and regularly show significant F_2 — F_3 correlations. This type of selection is useful even when the population size is relatively small, safely say around 500, and the selective characters are negatively but not very closely associated with other characters which are not assessed in F_2 . The direct measurement of yield is not considered to be rewarding.

Discussion

Breeders may consider several or more characters *en masse* in assessing F_2 plants and populations; plants with promising phenotypes regarding all of these characters together are taken up. In this case, the various parameters f 's, θ 's etc. are to be defined on the 'aggregate' genotypes covering all of these selective characters. In general, the genotype frequency f_A gets small with the number of the characters to be assessed together, and so does u_A if selection criteria for the characters are inappropriate. Formulae and numerical computations in the previous sections show that selection is useful even with very small values of the product $f_A u_A$ if a sufficiently large F_2 population is available. To achieve the largest efficiency of a breeding programme as a whole, however, F_2 population size should be within some limit. Population sizes and selective characters in early generations should be determined considering not only F_2 but also F_3 and later selection manipulations. This problem will be discussed elsewhere.

It has been suggested that the genetic potentiality of crosses is determined essentially in F_2 and F_3 generations (YONEZAWA and YAMAGATA 1978). The efficiency of breeding therefore largely depends on the selection system in early generations. The efficiency of early selection in turn is much increased if yielding potentiality of plants is visually or easily assessed.

As already mentioned, many experiments have shown that some morpho-physiological traits are predictive of yielding capacity of plants and lines. The contribution of each component character to yield, however, is not consistent; not only the degree but also the manner of the contribution appear to vary with the genetical and environmental factors which can be neither foreseen nor controlled. The measures to cope effectively with this difficulty remain to be established, and will be investigated in a later paper of this series.

It once has been suggested by the senior author that cross selection may not be useful for continuous characters (YONEZAWA 1978). This makes an oversimplification. The detailed discussion of the present paper shows that the selection is advantageous for the continuous characters which are as heritable as regularly show significant correlations between F_2 plants and F_3 progenies.

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自殖性作物の育種選抜方策に関する研究
II. F_2 集団内の有望表現型個体の有無に
よる交配組合せ選抜の効果について

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育種の実際場面では通常、個々の分離集団の遺伝的変異の大きさや性質を推定するための時間的労力の余裕がないため、交配組合せ間の選抜は、育種目標にそうと思われる有望表現型個体の有無によって行わざるを得ない。本報では、このような基準による F_2 集団間選抜の可否を理論的な立場から検討した。

2つの選抜モデル、すなわち、ある選抜対象形質について有望と思われる表現型個体が認められない組合せは F_2 の時点で完全に棄却する（有望表現型個体を含む組合せについては、その個体を選抜する）方法と、 F_3 まで維持する（有望個体を含む組合せについては上記と同様）方法を想定し、供試組合せ全体としての育種コストあるいは個体数が同一の条件下で、育種目標に関与する全形質について有望な遺伝子型が F_3 集団に保有される確率を比較した。

式の数値計算および従来のデータに基づき、質的形質あるいは表現型の評価が容易でかつ、 F_2 — F_3 相関が有意な正の値を示すような連続形質について有望表現型個体が認められない組合せは、 F_2 で棄却した方が一般に有利であることが示された。このことは、 F_2 集団が比較的小さく（500~1,000 個体）、かつ F_2 での選抜対象形質と F_2 で評価の対象とされない他形質との間に負の遺伝相関がある場合でも、その相関があまり強くなければなりたつ。 F_2 集団が大きい場合は、上記負の遺伝相関が1に近い場合でも組合せ内および間の選抜は有利である。 F_2 での収量実測は、最近においても一部研究者の提唱するところであるが、効果的な方法であるとは思われない。