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Comparison of Selection Based on Yield of Half Sib Progenies and of I_1 Lines *Per Se* in Rye (*Secale cereale* L.)

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Summary. Using the relation of genotype-location and error variances between half-sib families and I_1 lines in rye, the efficiency of selection based on I_1 lines *per se* in comparison with half sib family selection is investigated. It is concluded that selection on the performance of I_1 lines could be advantageous especially in cases of higher degrees of dominance and gene frequencies of the favourable genes higher than 0,5. The difficulties caused by the strong self-incompatibility in rye and possible ways of overcoming them are discussed.

In recent years two methods of selection for population improvement, viz. first generation inbred (I_1) and testcross (half sib family) evaluation, have been discussed intensively in maize breeding (e.g. Burton *et al.* 1971; Genter 1973). In this crop hybrids are released for commercial use. The thought behind population improvement therefore is that productive populations *per se* tend to lead to productive crosses, because selection which increases frequencies of favourable alleles in base populations should enhance the probability of extracting superior inbred genotypes.

In rye the common breeding methods aim at better panmictic varieties though there have been great efforts to use male sterility for breeding hybrid varieties in recent years (Geiger 1972). Yet, population improvement and, therefore, fixing a high number of favourable genes in those populations is important for breeding panmictic as well as hybrid varieties of rye.

In this paper the two methods of selection will be discussed with respect to breeding synthetic rye varieties. The main task in breeding better synthetic varieties rests on the evaluation of the general combining ability of the lines composing the synthetic variety. The simplest way is to choose single plants from a random mating population and to determine the performance of their progenies giving in this case an estimation of the covariance of half sib families and thus the variance of the general combining ability effects. With this method it is possible to double the gain of selection if selfed seeds of the plants can be used to compose the synthetic population, rather than remnant seeds of the selected half sib families. This can be done in the breeding of plants which bear more than one inflorescence, one being selfed simultaneously, as for example two-eared maize plants. Due to the strong incompatibility system in rye this procedure is impossible.

Another way of influencing the gain of selection is to increase the effective genetic variance. This is possible by using inbred lines in a top cross. For fully inbred lines the variance between top-cross progenies is doubled in comparison with half sib families of non inbred parents. Yet, in rye the difficulty again is its strong self-incompatibility; this leads to a yield of a few kernels after selfing, which is not sufficient to maintain the majority of lines.

In addition forced selfing causes strong selection for mutations to self-fertility. Thus the few lines which represent the final inbreeding generations would be self-fertile to a certain degree. Schnell and Geiger (1970) found, in a polycross of inbred lines with a high degree of inbreeding, an average of 46 % seed setting from selfing varying between 4 % and 86 %.

However, if full self-fertilily can be achieved by certain mutants, their systematic introduction into breeding populations offers the possibility of obtaining plants with full seed set after selfing. Thereby some of the difficulties mentioned above can be circumvented if selection is applicable to the performance of the inbred lines themselves. This should increase the exploitable genetic variance between lines considerably. The yield per single plant is sufficient to perform field trials with micro plots in two or three environments and to select on the performance of I_1 lines themselves. In this investigation a comparison with half sib testing is made.

The difficulty that remains is that, as a consequence of the introduced self-fertility gene, self-fertilization may occur in the selected population leading to some inbreeding, which in turn results in inbreeding depression and lower yield. How this problem could be solved will be dealt with in the discussion.

Theoretical Consideration

If there is no epistatic variance, equilibrium for synthetic populations is reached one generation past the Syn_1. In particular $Syn_2 = \overline{F}(k-1)/k + \overline{J}/k$, where k is the number of lines of the synthetic population and $\overline{J}$ the mean yield of selfed progenies of the lines (Gallais, 1967). The average F_1 yield ($\overline{F}$) as represented in the formula can be judged from the general combining ability of the lines composing the synthetic population.

If selection is to be based on the performance of inbred lines the first task is to determine that part of the genetic variance between I_1 lines which is exploitable for the breeding of synthetic varieties. This can be done by calculating the correlation between the general combining ability effects of the genotypes and their performance as I_1 lines. This correlation is known to be rather high. For r, the correlation coefficient, one gets a simple mathematical expression (Table 1).

The higher genetic variance between I_1 lines as compared with half sib families is demonstrated in Fig. 1. Calculations were done for one gene only, assuming no epistasis.

Yet, the high increase of K, the quotient of the variance of I_1 lines and half sib families, with higher gene frequencies is not full effective for selection. To calculate the higher portion of useful variance of I_1 lines we have to multiply Kr^2 times α/α^*, $\alpha[= a + d(q-p)]$ being the average effect of a gene substitution in a random mating population and $\alpha^*[= a + d(q-p)/2]$ the same of I_1 lines.

In addition, we have to concede, that inbreeding lines have inherently higher genotype-environmental variances and higher error variances so that the superiority of this form of selection is not quite as large as $Kr^2 \cdot \alpha/\alpha^*$. To account for this we used estimates for the genotypic and genotypic-environmental variances from field trials for half sib families and I_1 lines.

Table 1. Correlation between general combining ability and performance of I_1 lines

Genotype	Frequency	g.c.a.	Performance of I_1
B B	p^2	$q\,\alpha$	a
B b	$2pq$	$(q-p)/2 \cdot \alpha$	d/2
b b	q^2	$-p\,\alpha$	-a

$$r_{g.c.a./J_1} = \frac{a + d(q-p)/2}{\sqrt{[a + d(q-p)/2]^2 + \frac{1}{2}pqd^2}}$$

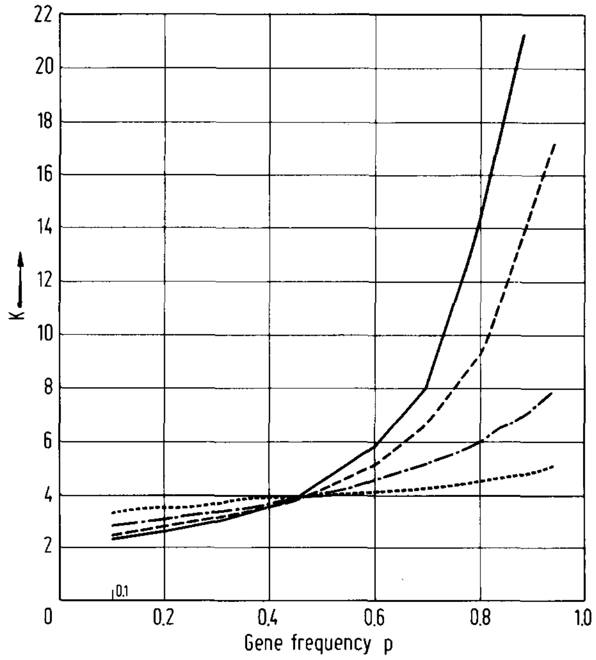

Fig. 1. Ratio between the variance of I_1 lines and half sib families (K) with various degrees of dominance. d = 0,2 .....; d = 0,5 -.-.-.-; d = 0,8 ------; d = 1 ———.

Material and Methods

Each experiment of half sib families contains lines from different populations, that is two German varieties (Petkuser Normalstrohroggen and Petkuser Kurzstrohroggen) and 3 synthetic populations. The I_1 lines can be traced back to a population in which the self-fertility factor of a self-fertile selection of the Canadian variety Dakold was introduced followed by several back-crosses with German varieties as described by Wricke (1973).

The plots consisted of 2 or 3 rows each, 50 cm long with a normal plant density resulting from a seed-rate of about 120 kg per ha; the number of replications varied between 2 and 4. All experiments were performed over 2 to 3 locations and analysed as a two-factor experiment (lines or families and locations) in randomized blocks.

Results and Discussion

In Table 2 the results of 5 experiments with half sib families[1] and 6 experiments with I_1 lines carrying the self-fertility gene are given. Apart from considerably higher genotypic variance of I_1 lines as compared with half sib families, the genotype-location interaction variance of I_1 lines is also higher, as expected.

Table 2. Variance components of half sib families (a) and I_1 lines (b)

	Year	Locations	n	V_G	$V_{G\times P}$	V_E
(a)	1961	3	32	19	63	389
	1961	3	32	108	125	482
	1963	2	39	61	77	510
	1963	2	40	143	26	766
	1963	2	31	78	69	454
			mean:	82	72	520
(b)	1971	2	20	1531	209	393
	1972	2	60	725	83	344
	1973	2	60	500	201	1347
	1973	2	60	358	287	740
	1974	2	97	324	57	684
	1974	2	97	312	241	604
			mean:	625	180	685

n = number of families and lines respectively
V_G = Genotypic variance
V_E = Environmental variance (plot basis)
$V_{G\times P}$ = Genotypic × location variance

If the estimates of $V_{G\times P}$ and V_E are expressed as a fraction of the variance of half sib families, i.e. 82, the following ratios are obtained from the averages in Table 2:

	$V_{G\times P}$	V_E
HS	0.88	6.34
I_1	2.20	8.35

The formula for the selection gain, G, for a trial in p environments (e.g. locations) with r replications each, is

$$G = i \cdot V_g \Big/ \sqrt{V_G + \frac{1}{p} V_{GP} + \frac{1}{r \cdot p} V_E},$$

where i is the selection intensity and V_g the usable portion of the genetic variance.

If all variance components are related to the genetic variance of half sib families the gain of selection for half sib families can be written as

$$x = \frac{i \cdot 1}{\sqrt{1 + \frac{1}{p} V_{G\times P} + \frac{1}{rp} V_E}},$$ and for I_1 lines

$$Y = \frac{i \cdot Kr^2 \cdot \alpha/\alpha^*}{\sqrt{K + \frac{1}{p} V_{G\times P} + \frac{1}{rp} V_E}}.$$ Using the above variance for genotypic-environmental and error variances and assuming the experiments are conducted in 3 environments and 2 replications each the quotient for selection of I_1 lines and for half sib families becomes

$$\frac{Y}{x} = \frac{Kr^2 \cdot \alpha/\alpha^* \sqrt{1 + \frac{1}{3}(0.88) + \frac{1}{6}(6.34)}}{\sqrt{K + \frac{1}{3}(2.20) + \frac{1}{6}(8.35)}},$$ or

$$\frac{Y}{x} = \frac{\sqrt{2.35}\, Kr^2 \alpha/\alpha^*}{\sqrt{2.125 + K}}.$$ This formula enables us to compare the efficiency of selection for the two selection procedures.

In Table 3 the value $\frac{Y}{x}$ is given for various degrees of dominance d and different gene frequencies p for the favourable allele. We observe that the effectivity is increased with increasing degrees of dominance and gene frequencies higher than 0.5. Especially in cases where both conditions hold, indirect selection via the performance of inbred lines should be more effective than that on half sib families using remnant seed of the selected half sib families to compose the synthetic population. The latter selection method which has so far been applied to rye may have indeed raised the frequency of favourable genes to 0.5 or above. If this assumption is correct, further selection on I_1 lines should give good results.

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Table 3. $\frac{y}{x}$ values for different gene frequencies, p and different levels of dominance, d

	d = 1	d = 0,8	d = 0,5
p = 0,1	2,22	2,26	2,33
p = 0,2	2,25	2,29	2,36
p = 0,3	2,29	2,33	2,38
p = 0,4	2,33	2,37	2,42
p = 0,5	2,38	2,42	2,45
p = 0,6	2,25	2,48	2,49
p = 0,7	2,53	2,55	2,54
p = 0,8	2,65	2,65	2,60
p = 0,9	2,82	2,79	2,67

In this connection it is interesting to discuss the case in which, with half sib family selection, it would be possible, as in other species, to make use of selfed seed for building up the synthetic population. Then the value $\frac{y}{x}$ (Table 3) is halved. If we assume that the relation of genotype-environmental and error variances between half sib families and I_1 lines holds as found in rye selection on the performance of I_1 lines would be equal or still slightly preferable to half sib family selection also in the case of low and medium gene frequencies with reasonable degrees of dominance from 0.5 to 1.0 (as seen from Table 3).

If we aim at the production of a synthetic population from a small number of lines then we require - as mentioned earlier - an estimation of the performance of the selfed parental lines of the synthetic population. One can obtain this from the selfed I_1 lines since it is well known that there is a high correlation between the performance of I_1 and I_2 lines.

As mentioned earlier on, a problem still remains to be solved if selection is done on the performance of inbred lines obtained with the aid of a self-fertility gene: the selected population contains the self-fertility gene which may cause a certain degree of self-fertility even under natural propagation of the selected parents. This would cause inbreeding and as a consequence inbreeding depression in the resulting population. To avoid this, the self-fertility allele has to be removed from the improved population by selection against the segregating self-fertile genotypes. Discriminations between self-fertile and self-sterile plants is possible either by bagging single plants and checking for seed setting or by microscopic inspection of pollen tube growth. Both methods require cloning of the investigated plants, such that part of them is available for incompatibility tests while the other parts are left to freely pollinate in an isolated field once the selfcompatible plants have been eliminated. The problem arising from the introduction of the self-fertility gene could be avoided if it were possible to outwit the incompatibility mechanism temporarily, i.e. if self-fertility and production of I_1 lines could be achieved by other means than the use of a genetic self-fertility mechanism.

This may indeed be possible by growing the rye plants under high temperature conditions. Preliminary tests, in which clonal plants of the same genotype were grown under normal field conditions and in a growth chamber in as high a temperature as 30°C (day and night) during anthesis, showed that the self-fertility could be raised from about 1.4% to 9.1% (Wricke 1974). Unpublished data show, that the mean seed number after selfing could be raised to an average of about 15 seeds per ear which mean an average fertility of about 20-25%. The variability of seed set under high temperatures was very high. It is believed that this value can still be increased if the environmental conditions under which the incompatibility mechanism is most effective are investigated more intensively. The advantage of I_1 lines derived by such a method would be their self-incompatibility under normal field conditions and the problem of the removal of a genetically determined self-fertility would not arise.

The investigations show that, in spite of the disadvantages mentioned, selection on the performance of I_1 lines is promising. It should be especially successful with crops like rye where previous intensive breeding achieved, most probably, an average or even higher frequency of the favourable genes.

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