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Comparison of Full and Half-Sib Reciprocal Recurrent Selection[1]

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Summary. Full and half-sib reciprocal recurrent selection (RRS) were compared algebraically and with computer simulation. The relative performance of the two schemes depended on the selection intensity and the environmental variance. Full-sib RRS was favoured at less intense selection and when the environmental variance was large relative to the total genetic variation. As selection intensity increased its advantage declined. Full-sib RRS enables a breeder to combine the efficient development of new hybrids with population improvement and should be a valuable technique in plant breeding.

I. Introduction

Comstock, Robinson and Harvey (1949) proposed a selection procedure to make maximum use of both general and specific combining ability. The method (reciprocal recurrent selection — RRS) consists of selecting males in each of two populations based on the performance of their progeny derived from matings to several females of the opposite population. When a large number of females are used, a progeny group is a half-sib family, and so this method will be referred to as half-sib RRS.

A modification of this technique is being used in selecting corn populations to produce superior hybrids at this station. This technique is referred to as full-sib RRS. As with half-sib RRS, individuals in two populations, A and B, are selected based on their crossbred progeny performance. An individual from A is mated to an individual from B, and as well both individuals are selfed. This requires seed set on two ears of at least one of these individuals. Selection is based on performance of full-sib families rather than a mixture of full and half-sib families with half sib RRS. Both parents of the best families are selected and the selected parents are then random-mated within populations.

The chief advantage of full-sib RRS is that superior families can be reproduced if they are found, since seed from both parents is available. These will differ only in so far as recombination has occurred in selfing the parents. Thus, the cross between two populations can be improved while, at the same time, superior hybrids can be released when they are obtained. With half-sib RRS we have seed only from the plants used as males, and superior families cannot be reconstituted.

Since both parents of superior families are selected, more individuals can be evaluated with full-sib RRS than with half-sib RRS. Thus, for a similar amount of labour, higher selection intensities and/or larger population sizes can be maintained.

Full-sib RRS is inferior to half-sib in that the estimate of the breeding value of an individual depends upon the breeding value of its mate, and a full-sib family will be a less accurate estimate of a parent's breeding value than a half-sib family.

The value of full-sib RRS relative to half-sib RRS will depend on the balance between the higher selection intensity possible under the former scheme and the increased accuracy of breeding value estimation of the latter. The relationships were investigated algebraically and with computer simulation.

II. Theoretical evaluation

For a single locus with two alleles the change in gene frequency (Δq_A) in a population using RRS is given by

$$\Delta q_A = \frac{k\, q_A\, (1 - q_A)\, \{1 + (1 - 2\, q_B)\, a\}\, u}{2\, \sigma_{\bar{P}}}$$

where, q_A, q_B are the frequencies of the desired allele in populations A and B, $2\,u$ is the mean difference between genotypic values of homozygotes in the trait being selected, a is the level of dominance, k is the standardized selection differential, and $\sigma^2_{\bar{P}}$ the variance among family means (Comstock *et al.*, 1949).

If k_F and k_H are the selection differentials with full and half-sib RRS, and $\sigma^2_{\overline{PF}}$, $\sigma^2_{\overline{PH}}$ the variances of full and half-sib family means (i. e. $\sigma^2_{\bar{P}}$) respectively, the relative value of full to half-sib RRS will be

$$\frac{\Delta q_{A\,F}}{\Delta q_{A\,H}} = \frac{k_F\, \sigma_{\overline{PH}}}{k_H\, \sigma_{\overline{PF}}}$$

where $\Delta q_{A\,F}$, $\Delta q_{A\,H}$ are the expected gene frequency changes in population A with full and half-sib RRS respectively.

If each male is mated to d females and the family tested r in replicates with n plants per replicate,

$$\sigma^2_{\overline{PH}} = \sigma^2_m + \frac{\sigma^2_f}{d} + \frac{\sigma^2_r}{r} + \frac{\sigma^2_e}{n\,r}$$

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where σ^2_m is the variance among males,

σ^2_f is the variance among females mated to the same male,

σ^2_r is the environmental variance among plots,

σ^2_e is the variance among individuals within plots.

With full-sib RRS $\underline{d} = 1$, so

$$\sigma^2_{\overline{PH}} = \sigma^2_m + \sigma^2_f + \frac{\sigma^2_r}{r} + \frac{\sigma^2_e}{n\,r}\,.$$

The expected values for σ^2_m and σ^2_f for intra- and inter-varietal progenies are given in terms of gene frequency, level of dominance and gene effects by Compton, Gardner and Lonnquist (1965). If populations are in linkage equilibrium and epistasis is not important, the intra-varietal male component contains $^1/_4$ of the additive genetic variance while the female component contains $^1/_4$ of the additive genetic variance plus $^1/_4$ of the dominance variance. Thus, for intra-varietal families the expected value of the female component will not be less than that of the male component. For particular gene frequencies in the two populations, the female component may be less than the male component with inter-varietal crosses but when contributions of many loci are combined it will normally be at least as large as the male component.

The reduction in $\sigma^2_{\overline{PH}}$ relative to $\sigma^2_{\overline{PF}}$, with several females, will depend on the relative magnitudes of additive and dominance variances, $\frac{\sigma^2_r}{r}$ and $\frac{\sigma^2_e}{n\,r}$. If the additive and dominance variances are equal and $\frac{\sigma^2_r}{r}$ and $\frac{\sigma^2_e}{n\,r}$ are negligible, σ^2_f would equal $2\,\sigma^2_m$ and $\sigma^2_{\overline{PH}}$ could be reduced to $^1/_3$ of $\sigma^2_{\overline{PF}}$ if sufficient females were used. To compensate for this reduction the selection differential would need to be about 1.7 times greater with full-sib RRS than with the half-sib RRS to give similar response. Normally, $\frac{\sigma^2_r}{r}$ and $\frac{\sigma^2_e}{n\,r}$ are not negligible and the reduction in variance by using several females would be less than in the above example.

Typical values for the variance components in Nebraska tests for yields in kg. per plant are:

$$\sigma^2_m = .00014$$
$$\sigma^2_f = .00027$$
$$\sigma^2 = .0010$$

where $\sigma^2 = \sigma^2_r + \frac{\sigma^2_e}{n}$ (Cerrate, 1967).

With four replicates and five females per male in the half-sib RRS:

$$\sigma^2_{\overline{PH}} = .0047$$
$$\sigma^2_{\overline{PF}} = .0066.$$

The ratio $\frac{\sigma_{\overline{PF}}}{\sigma_{\overline{PH}}} = 1.18$, so that the selection differential would need to be about 1.2 times greater for full than half-sib RRS to give similar response.

III. Computer Simulation

(*i*) *Models and Methods*

The above comparison of full and half-sib RRS was based on considerations of a single locus. If epistasis or linkage are present, prediction is difficult. With full-sib RRS both parents of favourable combinations would be selected. Although these combinations will be broken down with random mating, they may be more likely to reoccur than with half-sib RRS where only one parent is selected. The two schemes were compared with different types of gene action.

The models used contained 28 loci with two alleles per locus. Effects of genes and levels of dominance were the same for all loci. Loci were either completely independent or all loci were on one chromosome with recombination value of 1% between adjacent loci.

Models used included additive, complete dominance ($a = 1$), multiplicative and complementary epistasis. In both epistatic models there was complete dominance at individual loci and loci were considered in blocks of four, with effects among blocks additive. In the multiplicative model effects within a block were multiplicative, while in the complementary model the favourable gene was necessary at all four loci to produce an improvement over the least favoured genotype. The genotypic values for the dominance and epistatic models for individuals with favourable genes at one to four loci are given in Table 1. In the additive model the difference between homozygotes was the same as for the dominance model.

Table 1. *Contributions to genotypic value by groups of four loci with 0 to 4 loci having favorable alleles*

Model	Number of loci with one or two favorable alleles				
	0	1	2	3	4
Dominance	0	2	4	6	8
Multiplicative epistasis	1	1.5	2.25	3.375	5.0625
Complementary epistasis	0	0	0	0	8

In both full and half-sib RRS, individuals were evaluated by the performance of ten crossbred progeny, with five females per male being used in the half-sib RRS. A random normal deviate was added to the genotypic mean to allow for variation among plots and individuals within plots and the parents of the highest families were selected and random-mated within populations to produce the next generation. The random normal deviate was chosen such that $\sigma^2_r/r + \sigma^2_e/n\,r$ was equal to 16 in terms of the units in Table 1. This ensured that the contribution of any locus to the phenotypic variance among families was small ($< 10\%$).

In most cases, the proportion selected was 10/20 with half-sib RRS and 10/40 with full-sib RRS. Five replicates of each selection study were run for 20 cycles. The genetic models used are summarized in Table 2, and the expected initial values of additive, dominance and epistatic variance are also given.

(*ii*) *Results*

The mean responses to selection for the complete dominance model with gene frequencies of 0.5, with no linkage and proportions selected of 10/20 and 10/40 with half and full-sib respectively, are shown in Fig. 1. Full-sib selection gave greater response throughout the selection period. Since the linear regression coefficients of response on generations

Table 2. *Initial components of genetic variation for the models used and ratios of the standard deviations of full and half-sib RRS*

Model	Genetic Component					$\frac{\sigma_{\overline{PF}}}{\sigma_{\overline{PH}}}$
	q_A*	q_B	V_A+	V_D	V_I	
Additive	.5	.5	14.000	0	0	1.07
Dominance	.5	.5	14.000	7.000	0	1.10
	.25	.75	13.125	3.938	0	1.08
Multiplicative epistasis	.5	.5	5.913	2.957	0.335	1.05
	.25	.25	4.839	0.806	0.361	1.05
Complementary epiastasis	.5	.5	39.867	19.936	37.099	1.22

* q_A; q_B are the initial gene frequencies of the favorable allele in populations A and B.

\+ V_A is the additive variance, V_D is the dominance variance, and V_I is the epistatic variance. $\sigma_{\overline{PF}}$, $\sigma_{\overline{PH}}$ are standard deviations of full and half-sib families.

accounted for 90% or more of the variation in the mean of the cross during the first ten cycles, these are given in Table 3, together with the ratio of the two regression coefficients.

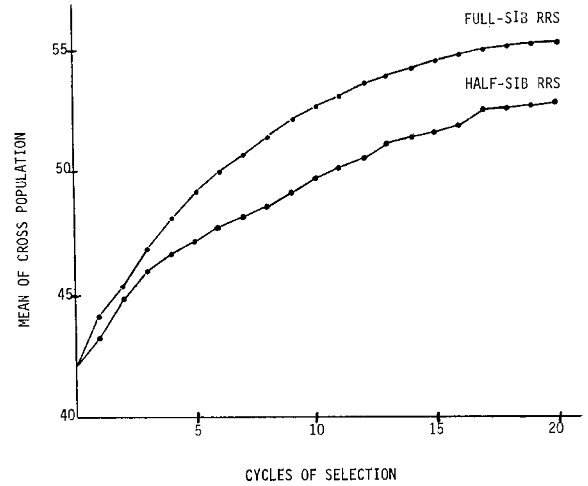

Fig. 1. Response to selection for the complete dominance model with no linkage (units as in Table 1)

In most cases, full-sib selection gave greater response than half-sib selection. The selection intensities used were less than those often used in plant breeding. The ratio of the selection differentials of full-sib RRS to that of half-sib RRS will be less with more intense selection, if schemes of the same size were compared. The selection differential is 1.62 times greater for 10/40 than 10/20 selection, but that for 10/80 is only 1.29 times greater than for 10/40. The dominance model was run at the higher intensities and there was little difference between the methods.

The value used for the environmental variance was larger relative to the genetic variances than might be the case in practice. The ratio of the standard deviations of family means (i. e. $\sigma_{\overline{PF}}/\sigma_{\overline{PH}}$) decreases as the environmental variance increases. In the example mentioned with corn earlier, the ratio $\sigma_{\overline{PF}}/\sigma_{\overline{PH}}$ was 1.18. For all except the complementary epistatic model this ratio was smaller (Table 2). The advantage of full-sib RRS over half-sib RRS would have been smaller if smaller values had been used for the environmental variance.

Table 3. *Regressions of mean genotypic value of cross population on cycle of selection with full-sib RRS (b_F) and half-sib RRS (b_H) for the conditions used. The values are the average of five replicates*

Proportion selected with full-sib RRS	Genetic model	q_A	q_B	c*	b_F**	b_H**	b_F/b_H
10/40	Additive	.5	.5	.5	1.31	0.78	1.68
	Dominance	.5	.5	.5	1.03	0.73	1.41
				.01	0.88	0.58	1.52
		.25	.75	.5	0.83	0.63	1.31
				.01	0.89	0.64	1.39
	Multiplicative epistasis	.5	.5	.5	0.70	0.43	1.62
				.01	0.52	0.38	1.36
		.25	.25	.5	0.56	0.52	1.06
				.01	0.52	0.32	1.62
	Complementary epistasis	.5	.5	.5	3.46	2.55	1.36
				.01	3.43	3.08	1.12
10/80	Dominance	.5	.5	.5	1.07	1.07	1.00
20/80	Dominance	.5	.5	.5	1.00	0.73	1.36

* c = recombination value between adjacent loci.

** Standard errors of regression coefficients, computed from variance among replicates were approximately 0.06.

IV. Discussion

The results from simulation followed the results from theory for the ten cycles considered. There are many models which could have been considered but the theoretical formula given should give a reasonable prediction of the relative performance of the two schemes.

The long-term response of the two methods will depend largely on the effective population size which can be maintained. The response over cycles 11 to 20 of the simulation was generally less than during the first ten cycles. This was not surprising with the small population sizes used. For any long-term selection program, large populations are needed to avoid loss of genetic variation due to random drift and to give greater response to selection (Robertson, 1960). Full-sib RRS will enable the breeder to maintain a larger effective population size than half-sib RRS but this would reduce the higher selection differential possible. The breeder would need to decide whether to sacrifice short-term gain to make greater long-term gain.

In corn breeding there will be selection for two-earedness in the nursery in the full-sib RRS in order to produce the progenies required. To the extent that multiple-earedness is correlated with yield (Lonnquist, 1967) this would add to the selection response. Selection for two-earedness could also be incorporated into a half-sib RRS program, but this generally has not been done.

A major advantage of using full-sib RRS is the ability to reproduce high-performing families to produce commercial hybrids, using the extraction procedure suggested by Hallauer (1967) and Lonnquist and Williams (1967). This enables a breeder to combine the efficient development of these new hybrids with population improvement and it should prove a valuable technique in plant breeding. Experimental evaluation of it is needed, and such work is now underway at this station.

Literature

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Brief Notic / Kurze Mitteilung

The Gesellschaft für Genetik e. V. München is holding its Third Annual Meeting in Göttingen (Germany) from May 20th—May 22nd, 1971

The scientific meeting will begin on May 21st at 9 AM. Main themes of this day are to be:

a) Production of haploids and their uses in breeding

b) New approaches to investigation and use of heterosis.

During the evening, a round table discussion will take place concerning the theme
"Plant breeding and its importance in nutrition of the world".

On May 22nd, proffered papers will be read in the fields of:

a) Molecular and Classical Genetics

b) Breeding of grains.

Forms for registration can be obtained by writing the Institut für Pflanzenzüchtung der Universität Göttingen, D-34 Göttingen (Germany BRD), Von-Siebold-Straße 8.