Comparison of Full and Half-Sib Reciprocal Recurrent Selection

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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 ($\Delta q_A$) in a population using RRS is given by

$$\Delta q_A = \frac{k q_A (1 - q_A) (1 + (1 - 2 q_B) a) u}{2 \sigma_p^2}$$

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 $\sigma_p^2$ 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 $\sigma_{pF}^2$, $\sigma_{pH}^2$ the variances of full and half-sib family means (i.e. $\sigma_{p}^2$) respectively, the relative value of full to half-sib RRS will be

$$\frac{\Delta q_{AF}}{\Delta q_{AH}} = \frac{k_F \sigma_{pF}^2}{k_H \sigma_{pH}^2}$$

where $\Delta q_{AF}$, $\Delta q_{AH}$ 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, then

$$\sigma_{pF}^2 = \frac{\sigma_i^2 + \sigma_d^2}{d} + \frac{\sigma_r^2}{r} + \frac{\sigma_n^2}{nr}$$
where $\sigma_m^2$ is the variance among males,
$\sigma_f^2$ is the variance among females mated to the same male,
$\sigma_e^2$ is the environmental variance among plots,
$\sigma_a^2$ is the variance among individuals within plots.

With full-sib RRS $d = 1$, so
$\sigma_{FH}^2 = \sigma_m^2 + \sigma_f^2 + \sigma_e^2 + \frac{\sigma_a^2}{r} + \frac{\sigma_a^2}{n}.$

The expected values for $\sigma_m^2$ and $\sigma_f^2$ 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 $\sigma_{FH}^2$ relative to $\sigma_{FP}^2$, with several females, will depend on the relative magnitudes of additive and dominance variances, $\sigma_a^2$ and $\sigma_d^2$. If the additive and dominance variances are equal and $\sigma_a^2$ and $\sigma_d^2$ are negligible, $\sigma_d^2$ would equal $2 \sigma_m^2$ and $\sigma_{FH}^2$ could be reduced to $1/4$ of $\sigma_{FP}^2$ 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, $\sigma_a^2$ and $\sigma_d^2$ 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:

$\sigma_m^2 = .00044$
$\sigma_f^2 = .00027$
$\sigma_e^2 = .0010$

where $\sigma^2 = \sigma_m^2 + \sigma_f^2$ (Cerrate, 1967).

With four replicates and five females per male in the half-sib RRS:
$\sigma_{FH}^2 = .0047$
$\sigma_{FP}^2 = .0066.$

The ratio $\frac{\sigma_{FP}}{\sigma_{FH}} = 1.18$, 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 ($a = f$), multiplicative and complementary epistasis. In the epistatic models used, the additive and dominance models 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 $\sigma^2/r + \sigma^2/n$ was equal to 15 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