Theor Appl Genet (1986) 72:682–688

Comparison of selection methods for improvement of the population hybrid

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Received February 9, 1986; Accepted March 10, 1986
Communicated by A. R. Hallauer

Summary. The objective of this study was to compare several selection procedures with respect to expected genetic gain in the population hybrid across a range of initial allelic frequencies, degrees of dominance, and environmental variances. The methods compared were intrapopulation recurrent selection using full-sib or S_1 families, full-sib and two half-sib reciprocal recurrent selection procedures, and convergent improvement applied to populations. Comparisons were made by calculating expected allelic frequency changes for each method. The optimal selection method for a given set of allelic frequencies and degree of dominance depended little on the environmental variance. Partly because of its short cycle, full-sib intrapopulation selection was the most effective method for the majority of allelic frequency combinations when the degree of dominance was small and an off-season nursery could be used to make recombinations. With larger values for the degree of dominance, S_1 and reciprocal full-sib methods became optimal, the former method especially when favorable alleles had a high frequency and the latter when populations were highly divergent. When off-season nursery use was restricted to making self-pollinations or was absent, S_1 selection was optimal for the majority of allelic frequency combinations. Convergent improvement was superior only for extremely divergent allelic frequencies and then only when the degree of dominance was less than 0.10. Half-sib reciprocal methods were never optimal, although the gain for the standard half-sib reciprocal procedure differed little from that of full-sib reciprocal selection when the degree of dominance was 0.75.

Key words: Convergent improvement – Plant breeding – Predicted genetic gain – Recurrent selection

Introduction

The development of hybrid cultivars requires suitable source populations for the extraction of parental lines or clones. The importance of continual improvement of source populations is well understood (Comstock 1964; Sprague and Eberhart 1977). Many recurrent selection methods are available that have as their goal the improvement of the hybrid of two source populations, a goal which, if attained, would increase the mean performance of hybrid cultivars derived from the populations. The objective of this research is to compare several recurrent selection methods as to their effectiveness in improving the population cross, giving consideration to initial allelic frequencies, the degree of dominance, and the magnitude of environmental variation.

Comparison of recurrent selection methods by empirical experimentation is difficult. Such experiments require many years, and it is often impossible or impractical to maintain the controls necessary to prevent confounding the effects of breeding methods with other factors. Therefore, theoretical expectations of gain have frequently been used. Empig et al. (1981) and Hallauer and Miranda (1981) presented equations to predict the increase in the population hybrid mean resulting from a cycle of selection. Application of these equations to real populations requires estimates of the variance components of the population hybrid, which are seldom available. Moreover, the prediction equation for selfed progeny testing includes terms that are not expressible as functions of variance components.

Recommendations as to choice of breeding method for interpopulation improvement have been both few in number and limited in scope. Comstock (1964) recommended reciprocal recurrent selection where any amount of overdominance existed. S_1 progeny testing was suggested when overdominance was absent. Comstock, however, did not consider more than one type of reciprocal recurrent selection and did not directly compare reciprocal recurrent selection to intrapopulation methods.

Jones et al. (1971) used prediction equations and computer simulation to compare full-sib and half-sib methods of reciprocal recurrent selection. In their study, the advantage of the half-sib method in having a reduced phenotypic variance was more than offset by the higher selection intensity of the full-sib method, where the same set of testcross progenies can be used to identify lines of superior combining ability in both source populations. In simulations, full-sib reciprocal recurrent selection was generally superior to the half-sib method over a range of gene action models (additive, complete dominance, multiplicative epistasis, and complementary epistasis) and irrespective of the presence or absence of linkage.

Moll and Hanson (1984) reported on a long-term empirical comparison of half-sib reciprocal recurrent selection and intrapopulation full-sib selection in 'Jarvis' and 'Indian Chief' maize (*Zea mays* L.). After 10 cycles of selection with grain yield as the primary selection criterion, mean increases in yield in the population hybrid were 2.0% per cycle for full-sib selection and 2.7% for half-sib reciprocal recurrent selection. From a divergence analysis of a diallel series involving cycles 0, 8, and 10, the authors concluded that divergence for the full-sib populations resulted from additive-associated effects, whereas that for the reciprocal recurrent selection populations resulted primarily from additive effects in 'Jarvis' and dominance effects in 'Indian Chief'. The two selection methods, however, had similar effects on number of ears per plant.

Smith (1983) compared two populations of 'Iowa Stiff Stalk Synthetic' maize, BSSS(R) and BS13(HT), in crosses with synthetic BSCB1(R). BSSS(R) had been selected for 8 cycles in a half-sib reciprocal recurrent selection program with BSCB1(R) as tester. BS13(HT) had been subjected to 7 cycles of half-sib testcross selection with an unrelated, narrow-based tester. Selection intensity was approximately the same (10%) in each program. Gain per cycle, as measured by regression of yield on cycle number, was approximately 75% as large in BS13(HT) × BSCB1(R) as in BSSS(R) × BSCB1(R).

Recurrent selection methods for the improvement of the population hybrid may involve testing lines or families within each source population (intrapopulation methods) or may require testing hybrids made between source populations (reciprocal recurrent selection). In each of these methods, each source population is closed, and no exchange of genetic material occurs between them. Griffing (1963) compared theoretical, long-term limits to progress for several selection methods utilizing one or two populations of infinite size. He concluded that, in the case of partial dominance, ultimate improvement in the population hybrid would be maximized if the source populations were first intercrossed to produce a single, pooled population. Following intermating, this population would be split into two subpopulations that would then undergo reciprocal recurrent selection. Cress (1967) made a similar recommendation based on the results of a computer simulation.

While genetic recombination between source populations intended for interpopulation improvement may have some beneficial aspects, such recombination has been limited by most maize breeders in order to preserve heterotic relationships. The existence of distinct populations having known heterotic responses facilitates the development of commercial hybrids, because for each newly developed parental line there is an obvious choice of a tester from the opposite heterotic group.

As a method that combines limited introgression between heterotic populations with simultaneous selection to increase the frequency of favorable genotypes, convergent improvement might be considered as a population improvement method. Convergent improvement, proposed by Richey (1927) as a means to improve maize inbred lines without adversely affecting their combining ability, involves reciprocal backcrossing to transfer favorable, dominant alleles to each line of a single-cross hybrid. If the process is successful, the hybrid of backcross-derived lines is more homozygous than the original hybrid. This may have no deleterious effect on hybrid performance, and in fact may enhance it if additive or partial dominance is the primary type of gene action. Several investigators (Richey and Sprague 1931; Murphy 1942; Hayes et al. 1946; Sprague et al. 1959; Lonnquist 1960) have successfully used convergent improvement with specific inbred lines. An adaptation of convergent improvement for use with populations was devised and included in the comparisons reported here.

Breeding methods and selection response

Breeding methods were compared on the basis of expected genetic gain per year, subject to three different assumptions concerning the arrangement of growing seasons:

(I) one primary growing season each year with a second season available for making pollinations;
(II) same as (I) except that the second season can be used only for making self-pollinations;
(III) a single growing season per year.

The following breeding methods were considered:

(1) Full-sib family recurrent selection (FS), an intrapopulation method (Moll and Robinson 1966);
(2) S_1 recurrent selection (S1), also an intrapopulation method (Hull 1945);
(3) Half-sib reciprocal recurrent selection (RHS) (Comstock et al. 1949);
(4) A modification of half-sib reciprocal recurrent selection (RHS-1), proposed by Paterniani and described by Hallauer and Miranda (1981, p 181) as "HS-RRS1," in which intrapopulation half-sib families are used to produce the testcross progenies and also as the recombination units;
(5) Full-sib reciprocal recurrent selection (RFS) (Hallauer 1967; Lonnquist and Williams 1967);
(6) Convergent improvement (CI) (Table 1).

Table 2 shows the number of years required to complete a cycle of selection under each arrangement of growing seasons. The intrapopulation methods, FS and S1, were applied simultaneously to both source populations.

A second modification of half-sib reciprocal recurrent selection was proposed by Paterniani ("HS-RRS2" of Hallauer and Miranda 1981, p 182), in which one inflorescence of a prolific maize plant is used to produce testcross progenies while the second inflorence is used to make an intrapopulation half-sib family for recombination purposes. This method produces one-half the expected gain per cycle of RHS and, because it requires one year per cycle under arrangement I and two years per cycle under arrangement II or III, its gain per year is less than or equal to that of RHS. Therefore, this method was not considered.

Table 1. Procedure for convergent improvement of populations (A and B)

Season	Activity
1	Make population cross between A and B
2	Make backcross to A (producing A_2^B) and to B (producing B_2^A)
3	Make second backcross (producing A_3^B full-sib families) by randomly pairing plants from A and A_2^B and crossing them. Similarly, produce B_3^A full-sib families
4	Conduct replicated test of A_3^B and B_3^A full-sib families. Select superior families within each population
5 (= Season 1 of next cycle)	Randomly mate selected A_3^B families inter se to complete first cycle of selection. Similarly, intermate selected B_3^A families. Also bulk seed of selected families from A_3^A and cross to a similar bulk of selected B_3^A families to initiate a second cycle of backcrossing and selection

Table 2. Number of years required to complete a cycle of recurrent selection for six breeding methods with three arrangements of annual growing seasons

Recurrent selection method[a]	Arrangement		
	I	II	III
	Primary growing season + second season for pollination	Primary growing season + second season for self-pollinations only	Primary growing season only
	Year/cycle	Year/cycle	Year/cycle
FS	1	2	2
S1	2	2	3
RHS	2	3	3
RHS-1	2	3	3
RFS	2	3	3
CI	2	4	4

[a] FS = full-sib, S1 = S_1, RHS = half-sib reciprocal, RHS1 = half-sib reciprocal with intrapopulation half-sib families as testcross and recombination units, RFS = full-sib reciprocal, and CI = convergent improvement

Genetic gain in the population hybrid (A× B) depends on the changes in allelic frequency effected by selection on the source populations (A and B). Prediction equations derived by Comstock et al. (1949) and Empig et al. (1981) were used. Assumptions underlying these equations included the following: two alleles per locus, linkage equilibrium in source populations, normal distribution of phenotypes, lack of correlation between genotypic and environmental effects, and absence of epistasis and maternal and cytoplasmic effects.

Let H/h be a gene pair and let the mean genotypic values of the HH, Hh, and hh genotypes be a, d, and $-a$, respectively. Let p and q be, respectively, the frequencies of H and h in the initial population A, and let $r = p + y$ and $s = q - y$ be the frequencies of the same alleles in population B.

Expected allelic frequency changes (Δp) for population A are given in Table 3. Corresponding changes (Δr) for population B are obtained by substituting r, s, α_A, σ_B, and $-y$, respectively, for p, q, α_B, σ_A, and y in Table 3. For CI, the value of Δp includes a component (y/8), due to backcrossing alone, and an additional component, due to selection, which was determined from the frequency distribution of A_3^B backcross families in the manner of Empig et al. (1981).

Phenotypic variances (σ_{PA}^2, σ_{PB}^2, and $\sigma_{PA\times B}^2$) for each selection method were determined under the assumption of N independent loci with equal effects (a), allelic frequencies (p, r) and degrees of dominance (d). With these assumptions, phenotypic variances are given by $N\sigma_G^2 + \sigma_E^2$, where σ_G^2 = genotypic variance per locus $= \Sigma w\,(g^*)^2 - (\bar{g}^*)^2$, w = frequency of each genotypic class among families evaluated, g^* = genotypic value of each class, and σ_E^2 = environmental variance (including genotype × environment interaction). The value of σ_E^2 was assumed to be the same for all section methods.

Genetic gain per locus per cycle in the population hybrid is

$$\Delta G = \Delta p\,\alpha_B + \Delta r\,\alpha_A - 2d\,\Delta p\,\Delta r. \tag{1}$$

Total genetic gain per year was obtained by multiplying (1) by N and dividing by the cycle length in years.

The value $N = 100$ was used throughout this study. The arbitrary nature of this value does not endanger the generality of the conclusions, because expression (1) for genetic gain per locus is, apart from the negligible term in $\Delta p\,\Delta r$, linear in Δp and Δr. Therefore, when (1) is multiplied by N to obtain total selection response for different methods, the relative values of ΔG depend on N only through terms such as $\sigma_G^2 + \sigma_E^2/N$. Therefore, use of a range of values for σ_E^2 is an equivalent substitute for making the comparisons over a range of N.

Two values of σ_E^2 were used, 13.15 (higher heritability) and 54.82 (lower heritability). These were chosen so that the heritability among full-sib families [i.e., $\sigma_A^2[2(\sigma_A^2/2 + \sigma_D^2/4 + \sigma_E^2)]$, where σ_A^2 and σ_D^2 are, respectively, additive and dominance variance components] was 0.3 and 0.6 when $p = q = 0.5$ and $d = 0.75$ for each locus. These values represent the highest and lowest estimates of heritability for yield in full-sib families from the maize population BSSS, as reported by Hallauer and Miranda (1981, p 125). The value $d = 0.75$ is consistent with

Table 3. Expected change (Δp) in frequency of the favorable allele from the application of one cycle of different selection methods[a]

Method	Δp
FS	$(1/2)\,ipq\,\alpha_A/\sigma_{PA(FS)}$
S1	$ipq\,[\alpha_A + (p-1/2)d]/\sigma_{PA(S1)}$
RHS	$(1/2)\,ipq\,\alpha_B/\sigma_{PA\times B(RHS)}$
RHS-1	$(1/8)\,ipq\,\alpha_B/\sigma_{PA\times B(RHS\text{-}1)}$
RFS	$(1/2)\,ipq\,\alpha_B/\sigma_{PA\times B(RFS)}$
CI	$y/8 + \{(1/2)i\,(pq - y^2/16)\,\alpha_A + y\,[(q-p)a$ $+ (1-6pq)d]/8\}/\sigma_{PA(CI)}$

[a] i = standardized selection selection differential, p = initial frequency of favorable allele in population A, $q = 1-p$, $\alpha_A = a + d(q-p)$, $\alpha_B = a + (q-p-2y)d$; a, d, and $-a$ are respectively the mean genotypic values of homozygous dominant, heterozygous, and homozygous recessive genotypes, y = (frequency of favorable allele in population B) $-p$, and σ_{PA} and $\sigma_{PA\times B}$ are phenotypic standard deviations for families evaluated in each selection method

the summary of Hallauer and Miranda (1981, pp 115–123) for gene action in yield of maize.

Selection intensity was assumed to be 5% (i = 2.05) for RFS and 10% (i = 1.75) for the other methods. Jones et al. (1971) discussed the higher selection intensities possible with RFS.

Six levels of dominance were investigated by taking a = 1 and d = 0 (no dominance), 0.25, 0.50, 0.75 (three levels of partial dominance), 1.00 (complete dominance), and 1.25 (overdominance).

Results

For the smaller value of σ_E^2 (higher heritability), the selection method that produced the greatest expected gain in the population hybrid for each value of p, r, and d is shown in Figs. 1, 2, and 3, for season arrangements I, II, and III, respectively. Table 4 shows relative expected gains for all methods with d = 0.75.

Heritability had relatively little effect on the ranking of methods with respect to expected gain. With season arrangement III (Fig. 3), use of the lower heritability resulted in expansion of the regions where S1 was optimal at the expense of those where FS was optimal. With this exception, boundaries of the regions in Figs. 1, 2, and 3 generally shifted less than 0.1 allelic frequency units when heritability was changed. The rankings of the best three methods were influenced by heritability with only four of the 26 allelic frequency combinations shown in Table 4.

When complete off-season pollination facilities were available and degree of dominance was low, FS was the most effective method for the majority of allelic frequency combinations (Fig. 1). As d increased, RFS and S1 became optimal when the frequency of the favorable allele was high in one or both populations, respectively (Fig. 1).

When the off-season nursery was absent or available only for making self-pollinations, S1 was superior for the majority of allelic frequency combinations (Figs. 2 and 3). RFS was optimal when d was large and the populations highly divergent.

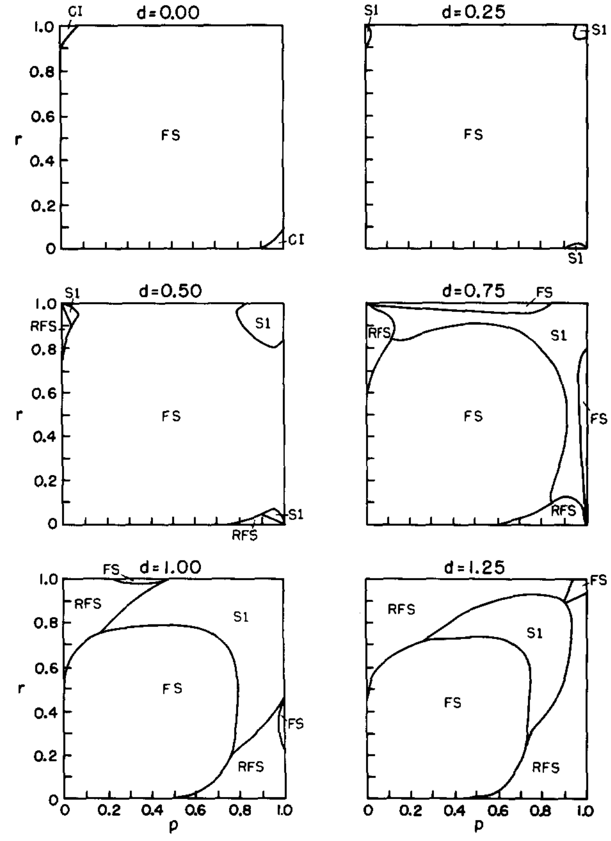

Fig. 1. Selection method producing greatest gain per year in population hybrid as a function of degree of dominance (d) and frequencies (p, r) of favorable allele in source populations, assuming full pollination capability in off-season nursery (CI = convergent improvement, FS = full-sib recurrent selection, RFS = full-sib reciprocal recurrent selection, S1 = S_1 recurrent selection)

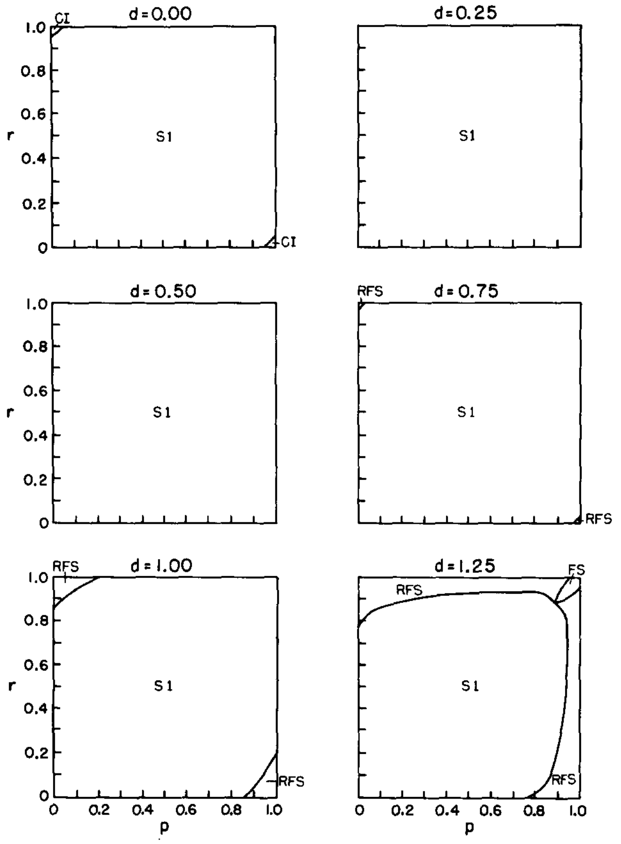

Fig. 2. Selection method producing greatest gain per year in population hybrid as a function of degree of dominance (d) and frequencies (p, r) of favorable allele in source populations, assuming self-pollination capability in off-season nursery (CI = convergent improvement, FS = full-sib recurrent selection, RFS = full-sib reciprocal recurrent selection, S1 = S_1 recurrent selection)

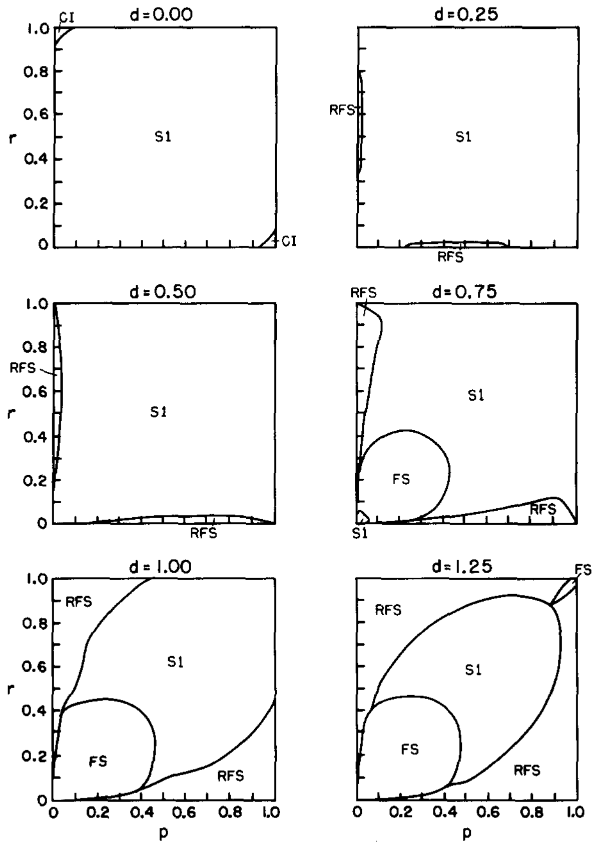

Fig. 3. Selection method producing greatest gain per year in population hybrid as a function of degree of dominance (d) and frequencies (p, r) of favorable allele in source populations, assuming no off-season nursery (CI = convergent improvement, FS = full-sib recurrent selection, RFS = full-sib reciprocal recurrent selection, S1 = S_1 recurrent selection)

CI was optimal only for extremely divergent allelic frequencies and then only when d was low. When $d > 0.10$, FS was superior to CI even in the most divergent situations. Absolute genetic gains for CI were negative for divergent allelic frequencies ($y > 0.5$ approximately) when $d = 0.75$ (Table 4). This was also true for d values as low as 0.25. Because when $d < 1$, the homozygous dominant (HH) is the most favorable genotype, a case could be made for CI on the basis of its tendency to increase the frequency of homozygotes (HH as well as hh) in the population hybrid. But even in this respect, other methods were generally superior. For example, with $d = 0.75$ and allelic frequencies such that $p/3 < r < 3p$, FS or S1 generally produced greater increases in the frequency of the HH genotype than CI and did so without concomitant increases in the frequency of hh.

For $d = 0.75$, gains for RHS showed a dependence on allelic frequency similar to that of RFS (Table 4). When populations were highly divergent, however, gains for RHS were slightly lower than those for RHS. Thus, RHS was never the optimal method (Figs. 1, 2, and 3). Gains for RHS1 were approximately one-third as large as those for RHS.

Conclusions

That the results showed only a weak dependence on the magnitude of environmental variance indicates that the observed relationships between selection methods have a general validity. For the heritability levels used here, the denominators of the expressions for Δp (Table 3) do not affect the ranking of selection methods as much as the numerators. Therefore the assumption of 100 loci with equal effects, allelic frequencies and degrees of dominance is not critical to the comparisons made in this study. Further, the presence of moderate amounts of epistasis, which would inflate phenotypic variance without affecting the numerator of the expressions for Δp, would not alter these results.

Because of its short cycle, FS was a very effective selection method when full off-season nursery services were available. Both FS and S1 have the advantage of simplicity and do not require self- and cross-pollination of the same plant.

Allelic frequencies in source populations are generally unknown, and the loci involved in conditioning a quantitative trait must be assumed to vary in allelic frequency, degree of dominance, and magnitude of effect. Nevertheless, the degree of adaptation or divergence of populations may be a consideration in choosing a selection method. Larger values of p would be expected in adapted populations or in those resulting from many cycles of selection in contrast to exotic or unselected populations. Thus it would be logical to apply S1 to a highly adapted population while adopting FS for exotic materials. Degree of divergence is important, since loci where y is large contribute to heterotic response. If two source populations exhibit substantial heterosis, it is likely that many loci with large y can be expected. As the degree of divergence increases, RFS becomes more advantageous. Without more information on the relative importance of loci with different allelic frequencies and dominance relationships, however, recommendations as to the optimal method for a specific population must remain tentative.

If it is desired to maintain closed source populations during the selection program, effective population size must be large enough to avoid serious genetic drift. This consideration favors FS over methods such as S1 and RFS that involve recombination of S1 lines, since the same effective population size can be maintained with half the number of full-sib families as S_1 lines (Ramalho 1977, as cited by Hallauer and Miranda

Table 4. Relative genetic gain per year in the population hybrid for six selection methods applied to two populations, as a function of allelic frequency, assuming degree of dominance = 0.75 and full pollination capability in an off-season nursery each year

		Relative genetic gain											
		High heritability[a]						Low heritability					
p[b]	r	CI[c]	RFS	FS	S1	RHS	RHS1	CI	RFS	FS	S1	RHS	RHS1
0	0.1	23[d]	32	43	32	27	9	14	20	29	23	17	5
0.1	0.1	39	45	77	57	47	15	31	39	64	50	36	10
0	0.3	31	58	69	51	49	18	19	41	51	41	35	10
0	0.5	17	64	70	55	55	21	5	48	49	43	41	12
0	0.7	- 13	58	52	47	49	18	- 25	41	32	34	35	10
0.1	0.3	44	59	93	69	60	20	31	43	68	53	40	11
0.1	0.5	30	61	87	67	59	21	17	45	61	52	41	12
0.1	0.7	1	53	64	55	49	17	- 10	38	41	40	33	10
0	0.9	- 60	32	17	24	27	9	- 67	20	9	14	17	5
0	1.0	- 89	0	0	0	0	0	- 92	0	0	0	0	0
0.1	0.9	- 42	29	25	29	26	8	- 49	18	14	18	15	4
0.1	1.0	- 69	1	6	5	1	0	- 72	0	4	3	0	0
0.3	0.3	50	58	100	74	64	22	37	44	75	59	42	12
0.3	0.5	41	54	89	68	58	19	29	40	65	54	38	10
0.3	0.7	19	43	65	54	44	14	8	30	44	41	28	8
0.5	0.5	39	45	78	60	49	16	28	32	55	48	31	8
0.5	0.7	25	34	56	47	35	11	15	23	37	36	21	6
0.7	0.7	20	24	40	36	24	7	13	15	25	26	13	4
0.3	0.9	- 16	23	28	29	21	6	- 23	14	18	19	12	3
0.3	1.0	- 38	2	10	7	2	0	- 41	1	7	6	1	0
0.5	0.9	0	17	25	25	16	4	- 6	10	16	17	9	2
0.5	1.0	- 16	2	10	8	2	1	- 19	1	7	6	1	0
0.7	0.9	6	11	18	19	10	3	2	6	11	13	5	1
0.7	1.0	- 4	2	7	7	2	0	- 6	1	5	5	1	0
0.9	0.9	4	4	7	10	4	1	2	2	4	6	2	0
0.9	1.0	0	1	2	3	1	0	0	0	1	2	0	0

[a] See text for description of heritability parameters

[b] p and r are respective frequencies of favorable alleles in the two source populations

[c] See text for description of selection methods

[d] Relative gain as percentage of the largest gain reported in the table

1981, p 189). This has the effect of permitting a higher selection intensity for FS if methods are compared on the basis of equal effective population size.

The poor performance of CI in this study does not necessarily conflict with the recommendation of Griffing (1963) and Cress (1967) that introgression between source populations be undertaken prior to selection. It indicates only that recurring cycles of backcrossing and selection are generally less effective than standard recurrent selection methodologies with respect to genetic gain per year.

The preference of Comstock (1964) for RFS whenever overdominance exists was not borne out by the results of this study. When the frequency of favorable alleles was intermediate or low in both source populations, FS was superior to RFS even when all loci displayed overdominance.

Superiority of RFS over RHS, as observed by Jones et al. (1971), was not marked (Table 4). If the relative gains (Table 4) are converted to gain per cycle, then expected gain from RHS exceeds that of FS, which is consistent with the empirical gains of Moll and Hanson (1984).

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