

Simulation of Cyclic Single Cross Selection*

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Summary. Computer simulation was used to compare Hallauer's cyclic single cross selection (*CSCS*) with reciprocal recurrent selection (*RRS*). Three epistatic and three non-epistatic models with 60 loci determining a single character provided the genetic base. The rate of advance over seven cycles was always greater for *CSCS* than for *RRS* on either a cycle or generation basis. No genetic conditions were found where *CSCS* failed to respond. The advantages of *CSCS* increases as the proportion of non-additive genetic variance increases. Genetic advance of the hybrid population was shown to result from the joint effects of an average change in gene frequency and complementary effects (nicking) of selection. Nicking effects accounted for most of the advance for some starting conditions. *RRS* generally had higher selection limits with no epistasis or low gene frequency of the dominant allele. *CSCS* generally had higher limits with epistasis or high frequency of the dominant allele. We suggested that *CSCS* begin with divergent genetic populations and strong selection intensity for three cycles. Final selection of superior single crosses was indicated when the lines were completely inbred.

There is growing experimental evidence that epistasis is of more than trivial importance in several economically important traits (e.g., Russell and Eberhart 1970, Sprague and Thomas 1967 and Stuber and Moll 1969). Russell and Eberhart (1970) found that 41% of the genetic variance was epistatic when averaged over nine traits in maize (*Zea mays* L.). If this situation is found to be more general, then a reassessment of selection systems is in order.

The choice of a selection system is among the most critical decisions a breeder must make. Once the system is chosen for a given genetic base, the limits of selection and the maximum rate of progress are determined. An objective method of choosing among the many mating-selection systems is a major problem. As stated by Cockerham (1961) "the nature and number of differences among the various methods of selection have so far defied the development of quantitative comparisons of all the alternatives." Although much is yet to be learned about genetic systems and the interaction of organisms with their environment, some processes are well known and may be mimicked by the computer. We have attempted to add one piece to the comparison picture with computer simulation of some simple genetic models.

Methods

The selection system described by Hallauer (1967 a, b) is the central method of this study. We will call this method cyclic single cross selection (*CSCS*). Briefly, *CSCS* uses the full-sib progeny test during each of the selfing cycles. Pairs of plants are selected and maintained

as pairs, with no recombination of the selected parents. Thus, the end product of this procedure after 5 to 7 cycles is a group of single-cross hybrids that have been tested and selected for high performance.

We searched for a selection method for comparison with *CSCS*. Desirable characteristics of this comparison method include 1. a well established method, 2. one with cyclic properties and 3. one with the immediate end product identical to *CSCS*. Reciprocal recurrent selection (*RRS*), as proposed by Comstock, Robinson and Harvey (1949), was chosen for the reference base. *RRS* is well established and cyclic but does not have the same immediate goals as *CSCS*. This restricts the comparisons to more general trends rather than absolute quantities.

The simulation routines used by Cress (1967) were modified and extended to permit epistasis between successive pairs of loci. The 60 bit words for the Control Data 6500 were used to simulate 30 pairs of loci. The organism simulated was bisexual, diploid, two alleles per locus, no linkage, with 30 pairs of loci determining a single quantitative character. The genetic composition of an individual was found by successively examining the 30 pairs of bits. Each pair of loci was given a value (Table 1) appropriate for the model and the genotypic value was found by simple addition. No distinction was made between coupling and repulsion phase linkage. The phenotypic value was obtained by adding a random, normally distributed variable with mean zero and variance 180. Heritability in the broad sense was always less than .25.

The populations *A* and *B*, with *CSCS*, each consisted of 960 individuals for three cycles of selection. We allowed selection to reduce the population size by half in each of the next four cycles. The remaining 60 paired individuals were selfed for three additional cycles with no selection. For the first seven cycles all parental selection was based on the mean of five full-sib progeny. The population size with *RRS* was kept at 90 individuals in *A* and *B* throughout the 20 cycles of selection. Based on the means of five half sibs, the highest performing members of *A* and *B* were random mated within a population before each cycle of testing and selection. Two selection intensities were used; mild, with 50% saved and strong, with 10% saved. For *CSCS* and 0.5 selection intensity, two selfed progeny were produced from each parent of the selected parental pairs. Two sub-pairs were randomly associated prior to

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Table 1. Genotypic values for one pair of unlinked loci for six models

Genetic Model*	Genotype								
	GGHH	GgHH	ggHH	GGHh	GgHh	ggHh	GGhh	Gghh	gghh
A	5	4	3	4	3	2	3	2	1
CD	5	5	3	5	5	3	3	3	1
OD	1	3	1	3	5	3	1	3	1
ON	1	4	5	4	5	4	5	4	1
AA	5	3	1	3	3	3	1	3	5
AD	5	2	3	2	3	4	3	4	1

* A — additive; CD — complete dominance; OD — overdominance; ON — optimum number; AA — additive by additive; AD — additive by dominance.

Table 2. Initial gene frequencies of the dominant allele

	Population B		
	.1	.3	.5
Population A	.1	Freq 1	
	.3	Freq 4	
	.5	Freq 2	Freq 5
	.7	Freq 3	Freq 6
			Freq 7

the next testing generation. Beginning with selection cycle 4, only one selfed progeny was produced from each parent and the population size was reduced by 50% through cycle 7. With 0.1 selection intensity, 10 selfed progeny were produced from each selected parent for three cycles and five selfed progeny for the next four

cycles. For both selection intensities three additional selfing generations were performed with no selection.

We examined six models, three non-epistatic and three epistatic (Table 1). Some of the models may rarely be found in natural populations, but were included to reflect differences that are not as obvious in less extreme models. The AA and AD models in Table 1 have only additive by additive and additive by dominance genetic variance respectively when gene frequency is exactly 0.5.

The probabilities used to generate the initial gene frequencies at each locus for populations A and B are shown in Table 2. These starting frequencies represent situations where populations A and B have identical genetic composition (Freq. 1, 4, and 7) and divergent composition (Freq. 2, 3, 5, and 6). Duplicate runs were made for some combinations to obtain an estimate of the variability of the results.

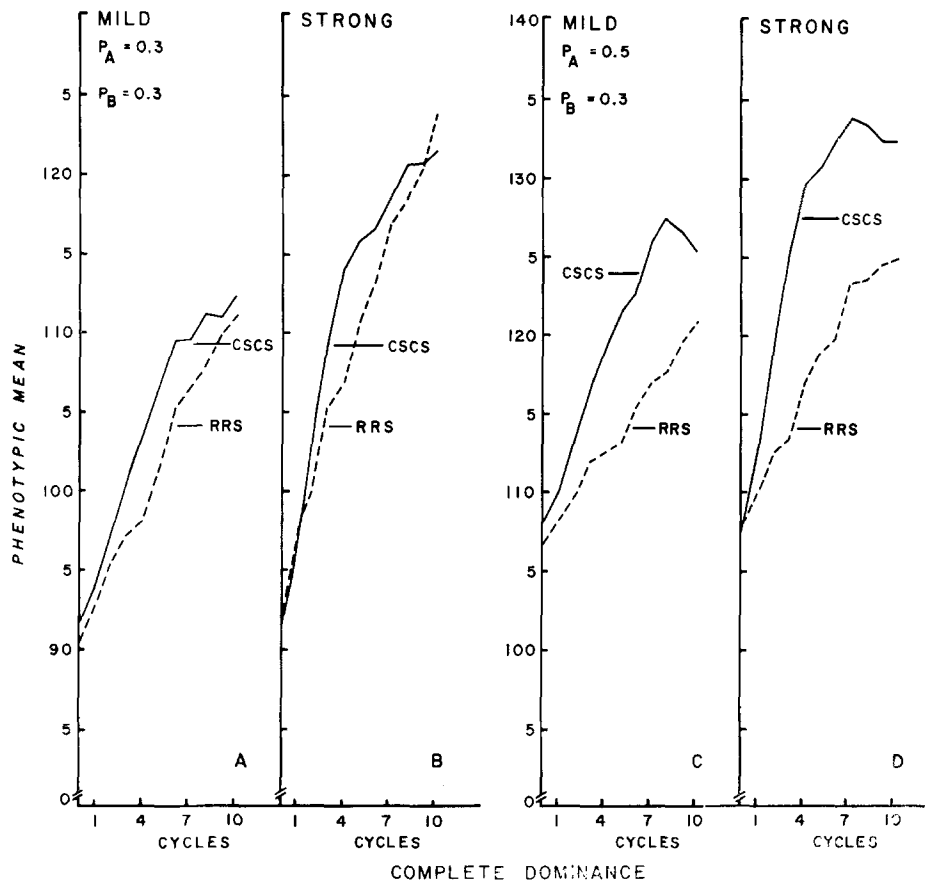


Fig. 1. Phenotypic mean of the hybrid population for 7 cycles of cyclic single cross selection (CSCS) and 10 cycles of reciprocal recurrent selection (RRS) — complete dominance

Results and Discussion

We recognize that *CSCS* and *RRS* are not competing systems in an absolute sense. The short range goals of *CSCS* and the long range goals of *RRS* dictate different conditions for their use. The two breeding methods have two obvious differences: 1. recombination of selected parents is an integral part of *RRS* and not allowed in *CSCS*, and 2. the rate of inbreeding is rapid with *CSCS* and much slower with *RRS*. The nature of simulation requires the establishment of a bench-mark. *RRS* is intended to be this standard. In our opinion, qualitative differences, such as the presence or absence of response to selection, or large quantitative differences are revealing characteristics of the two systems. Very slight differences were found between duplicate runs and were discontinued for computer efficiency.

The size of the starting populations for *RRS* and *CSCS* was considered at some length. There seemed to be no obvious choice of size that simultaneously keeps the total effort per cycle equal and uses the strengths of the two methods. In the absence of linkage, the effect of population size on the rate of progress by *RRS* is via inbreeding (Gill 1965). The inbreeding that does occur due to finiteness of the population should increase the rate of progress (Cress 1967). We could find no good reason to vary

the population size for *RRS* over the ten cycles of selection. In choosing the population size for *CSCS* we used the principle of equal effort averaged over the entire ten cycles. The strength of *CSCS* is in the early segregating generations, therefore, population size was larger during this period. If one considers the recombination generation required in *RRS* and the declining population in *CSCS* the total effort for the ten cycles is approximately the same.

Non-epistatic Models

Two starting gene frequencies that showed contrasting types of response were selected for graphical presentation for all models except the additive (Figs. 1 to 5). No figure presents results greatly different from other starting frequencies that are not shown. The values plotted were the mean response of the hybrid as measured by the test crosses. For *RRS*, 900 test-cross progeny were averaged at each cycle. For *CSCS* the test-cross progeny ranged from 4800 in cycle zero to 300 in cycles 7 through 10.

The trends of response for complete dominance and overdominance with *RRS* (Figs. 1 and 2) are the same as reported by Cress (1967). The ability of *CSCS* to respond to non-additive variance can be seen in the comparison to *RRS* in Fig. 2c and d. The equilibrium gene frequency of 0.5 was the least favorable for pro-

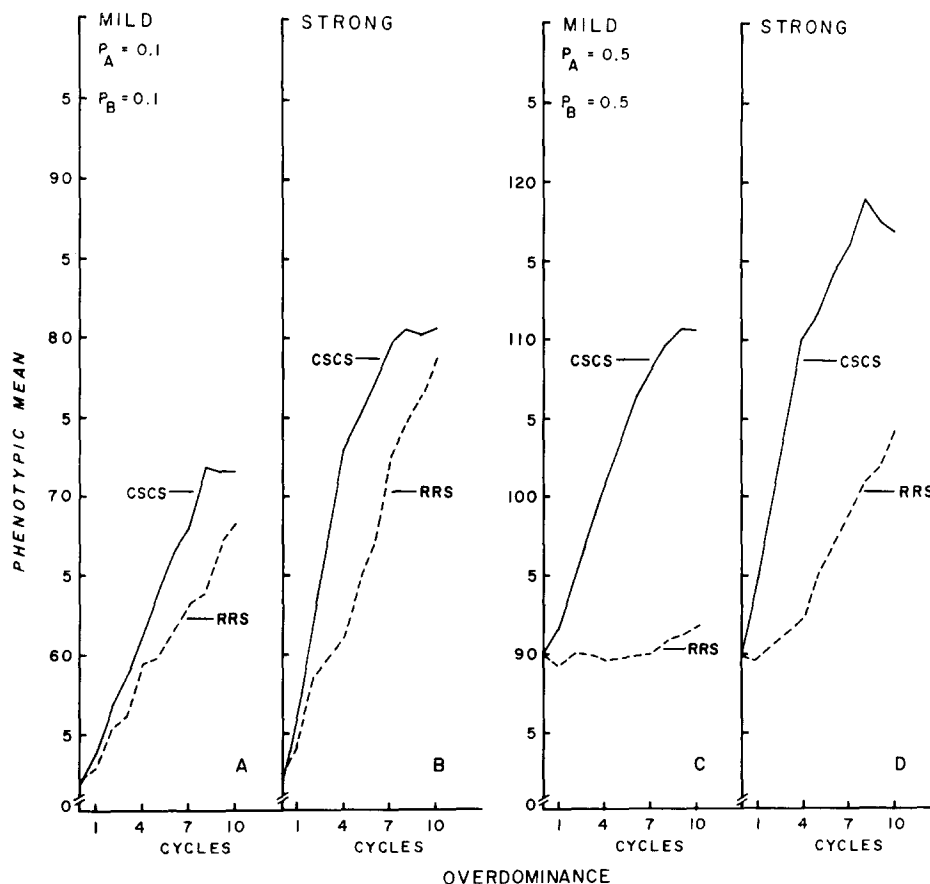


Fig. 2. Phenotypic mean of the hybrid population for 7 cycles of cyclic single cross selection (*CSCS*) and 10 cycles of reciprocal recurrent selection (*RRS*) — overdominance

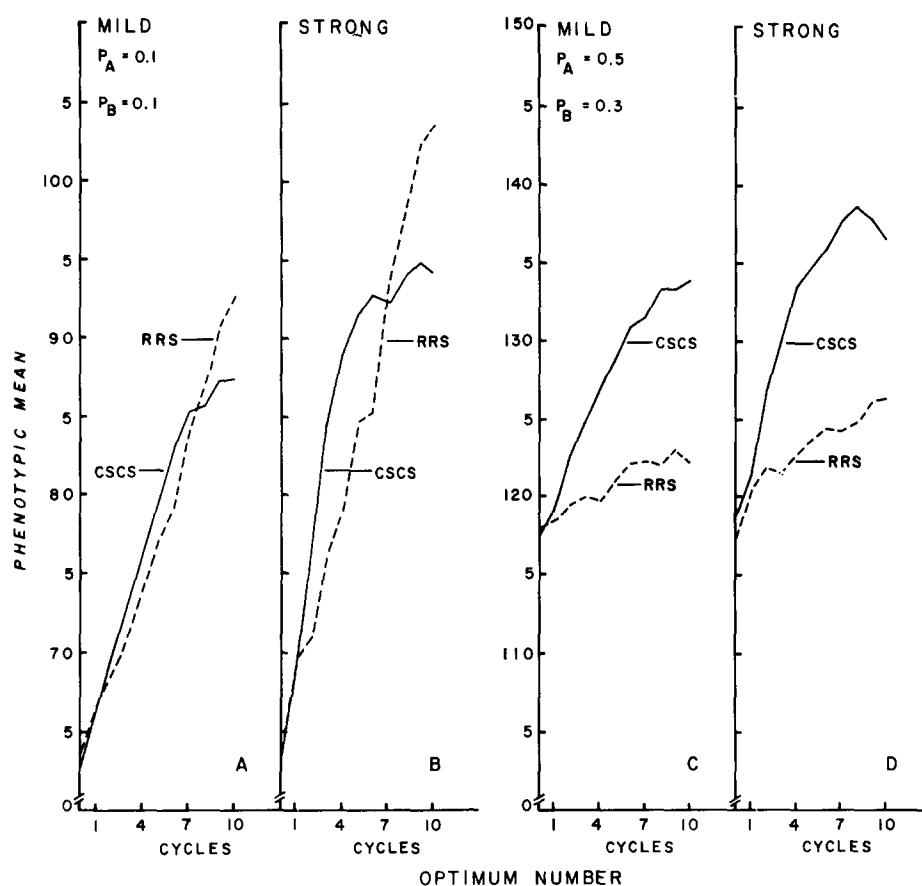


Fig. 3. Phenotypic mean of the hybrid population for 7 cycles of cyclic single cross selection (CSCS) and 10 cycles of reciprocal recurrent selection (RRS) — optimum number

gress by *RRS* with overdominance. The response to *CSCS* was always positive, regardless of the model, gene frequency or selection intensity. With the certain end to progress by *CSCS* after the lines are completely inbred, one can see the distinct advantage of strong selection in the early cycles.

Epistatic Models

All epistatic models gave sharply contrasting types of response when compared to *RRS* (Figs. 3, 4 and 5). It was not surprising to find certain equilibrium conditions for the additive by dominance model (e.g. Fig. 5, c and d) since the genetic variance was composed largely of dominance types for most starting gene frequencies. The optimum number and the additive by additive are qualitatively the same type of models. The former has a small amount of dominance variance but both have additive and additive by additive variance. For both of these models we found unstable selection equilibria (e.g. Fig. 3 c and d and Fig. 4 c and d).

Conditions of selection equilibrium are not likely with *CSCS* if the results for the three epistatic models examined are at all representative of the epistasis found in biological populations. This is in agreement with the advantages proposed for the method by Hallauer (1967a). An additional characteristic of *CSCS* seems to be a "built in" increment of increase.

The size of the increment is related to the model, the starting frequency and the selection intensity. In a biological population, selection intensity is the easiest to modify. There was no strong relationship between the increment of increase and the distance the initial population was from the maximum genotypic value of 150.

Rate of Progress per Generation

The cycle time for *CSCS* was two generations and for *RRS* was three generations. Fig. 6 and 7 show the rate of progress per generation averaged across the seven cycles of selection. The patterns are quite similar for mild selection, Fig. 6, and strong selection, Fig. 7. The size of the rate advantage for *CSCS* increases as the proportion of non-additive genetic variance increases. In the extreme case of additive by dominance, *RRS* did not significantly move the phenotypic mean in four of the seven gene frequencies after 20 cycles of mild selection.

Nicking of CSCS

Genetic progress by any selection system may be made by either a change in the average gene frequency at a locus or by complementary intra- and inter-locus changes or both. The complementary changes will be called the "nicking" effects of selection. When

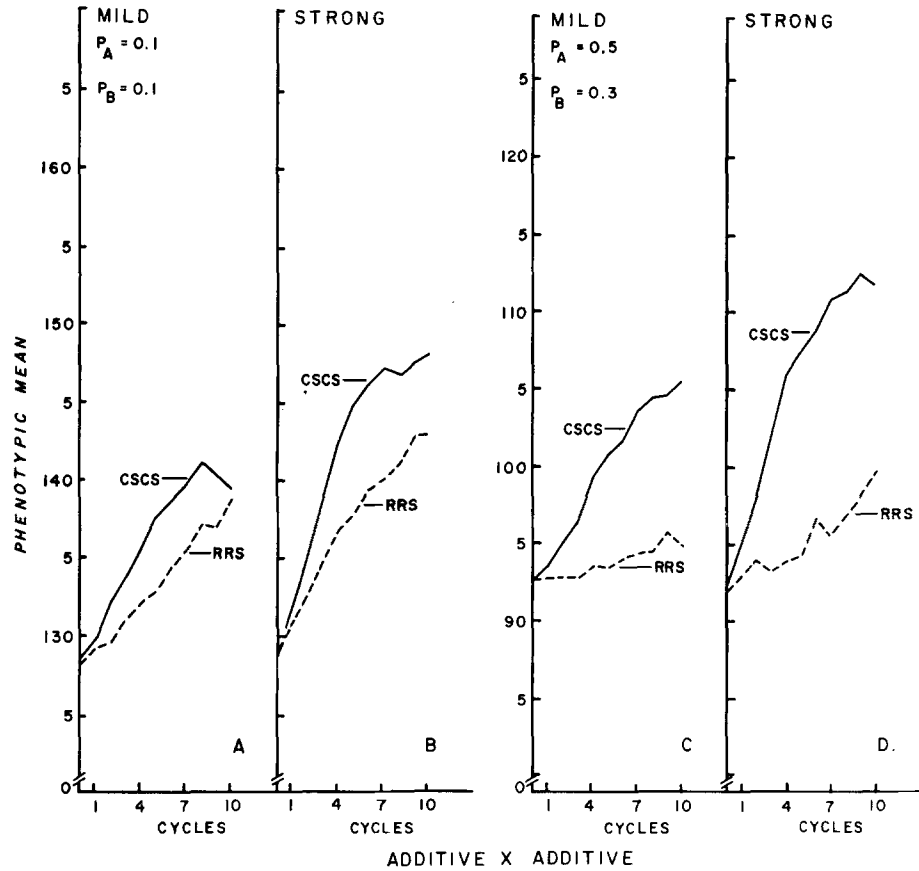


Fig. 4. Phenotypic mean of the hybrid population for 7 cycles of cyclic single cross selection (CSCS) and 10 cycles of reciprocal recurrent selection (RRS) -- additive by additive

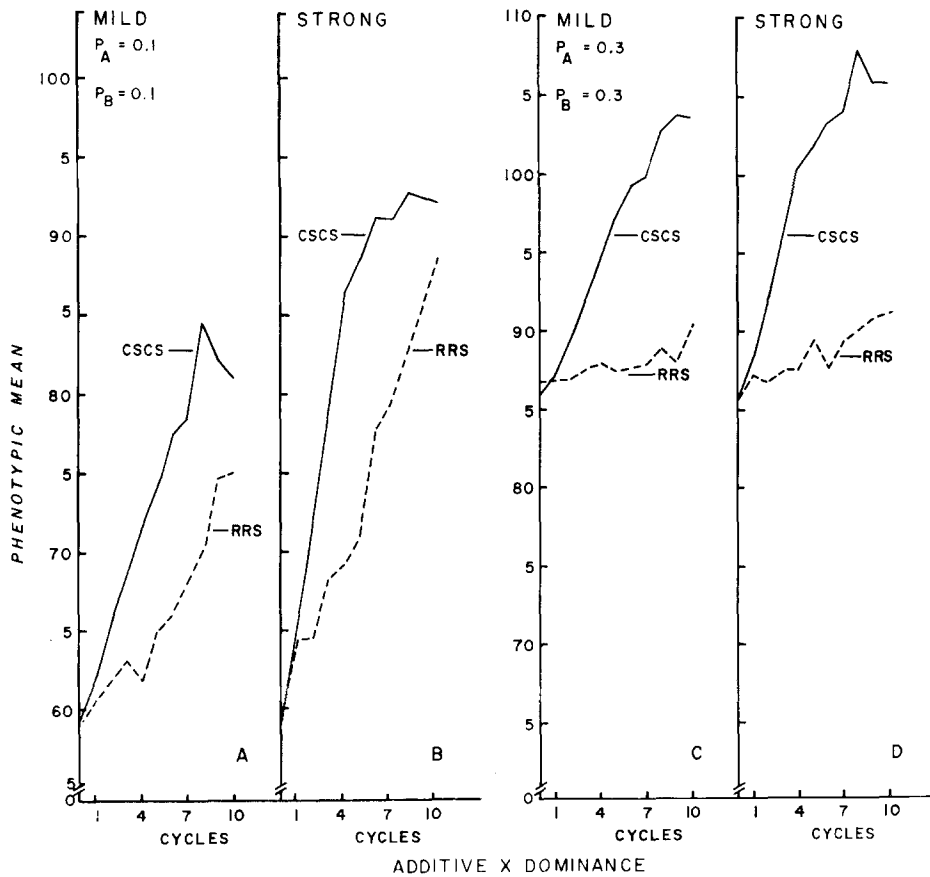


Fig. 5. Phenotypic mean of the hybrid population for 7 cycles of cyclic single cross selection (CSCS) and 10 cycles of reciprocal recurrent selection (RRS) -- additive by dominance

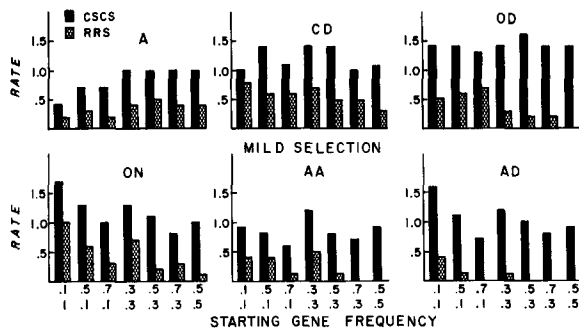


Fig. 6. Average rate of progress per generation for seven cycles of cyclic single cross selection (CSCS) and reciprocal recurrent selection (RRS) — mild selection

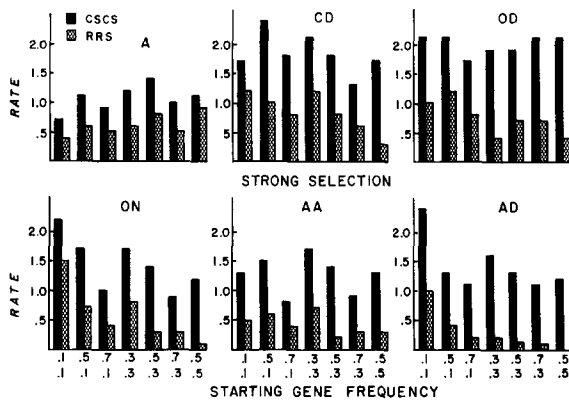


Fig. 7. Average rate of progress per generation for seven cycles of cyclic single cross selection (CSCS) and reciprocal recurrent selection (RRS) — strong selection

the final products of selection were inbred lines as in CSCS, the average gene frequency was easily determined. Thus, the expected genotypic value of the hybrid population was calculated by assuming a random distribution of alleles among individuals and equal gene frequency at all loci. The expected value and the observed value of the hybrid would be the same with an infinite population only if there were no nicking effects. Conversely, an estimate of the nicking effects may be obtained as the difference between observed and expected values. By definition, the nicking effects must be zero for the additive model. Nicking effects for the other models are given in Table 3. For the complete dominance and overdominance models all nicking is intra-locus. That is, selection for the dominant allele in one population tends to slow selection for the dominant allele at the corresponding locus in the alternate population. The nicking effects for the epistatic models were a combination of intra- and inter-locus changes. Large nicking effects were found for models that had large proportions of non-addi-

tive variance, particularly the overdominance and additive by dominance models.

Selection Intensity

A breeder is restricted by the number of pairs of individuals crossed at the beginning of the first cycle of CSCS. New recombinations within a line take place predominantly in the early generations. The within-line variation vanishes quickly with no gene exchange between the lines of a pair. This rapid dissipation of the within-pair genetic variance would seem to dictate strong selection for two or three cycles. We suggest that the initial populations be genetically diverse. The advantage seems to be a higher starting point for the hybrid and not from the rate of advance. It is suggested that the initial cycle begin with as many pairs as practical. Strong selection for three cycles associated with some reduction in the number of lines should select the better pairs and segregates. Subsequent selection is largely among pairs of crosses. Therefore, it would appear more efficient to defer further testing until the lines are essentially inbred.

Selection Limits

In Table 4 we have attempted to show the attained limits of CSCS and RRS. The hybrid population mean after 20 cycles of RRS was used as the limit. Only when the starting frequency in both populations was low (Freq. 1) would there be significant advance beyond 20 cycles. The phenotypic mean of the top three single crosses after 10 cycles (7 with selection) of CSCS was used as the attained limit. Using the raw figures in Table 4, we see that the limit attained by CSCS exceeds the limit of RRS most of the time. This is not a fair comparison since the phenotypic mean of 900 individuals shown for RRS is also very near the genotypic mean, while the three top single crosses are biased upward by the environmental variance. We can adjust these phenotypic values

Table 3. Nicking effects in the hybrid population with cyclic single cross selection

Genetic Model*	Selection Intensity	Initial Gene Frequency							
		.1	.5	.7	.3	.5	.7	.5	
CD	Mild	1.1	2.4	1.5	4.6	4.9	3.9	5.9	
	Strong	2.4	3.2	1.7	5.7	9.3	4.2	8.7	
OD	Mild	6.1	7.8	3.7	14.3	17.5	12.3	19.7	
	Strong	8.1	5.7	1.9	21.2	20.8	25.6	26.6	
ON	Mild	4.6	7.2	4.9	10.3	12.9	10.2	12.7	
	Strong	5.5	10.5	3.0	13.4	14.0	10.5	17.4	
AA	Mild	0.5	4.7	5.3	6.8	10.7	10.4	12.3	
	Strong	0.2	7.8	8.1	7.2	11.4	12.1	17.2	
AD	Mild	9.2	13.0	9.3	15.1	12.1	10.6	12.1	
	Strong	16.0	15.5	14.9	18.9	15.0	15.9	18.9	

* CD — complete dominance; OD — overdominance; ON — optimum number; AA — additive by additive; AD — additive dominance.

Table 4. Phenotypic means of the starting hybrid population (cycle 0), phenotypic means resulting from 20 cycles of reciprocal recurrent selection (RRS) and the means of the three highest single crosses resulting from 10 cycles (3 with no selection) of cyclic single cross selection (CSCS)

Genetic Model*	Selection Intensity	Selection Method	Initial Gene Frequency							
			.1 .1	.5 .1	.7 .1	.3 .3	.5 .3	.7 .3	.5 .5	
A Cycle 0	Mild	RRS	42†	66	78	66	78	90	90	
		CSCS	57	86	91	87	105	116	113	
	Strong	RRS	64	93	98	92	108	117	116	
		CSCS	56	91	97	96	109	118	122	
D Cycle 0	Mild	RRS	66	93	100	93	112	118	122	
		CSCS	53	96	116	91	107	122	119	
	Strong	RRS	100	127	141	119	130	137	130	
		CSCS	80	129	146	125	139	152	152	
OD Cycle 0	Mild	RRS	100	138	141	137	134	142	139	
		CSCS	87	142	153	132	152	157	157	
	Strong	RRS	52	90	109	80	90	100	90	
		CSCS	83	123	138	100	111	127	100	
ON Cycle 0	Mild	RRS	86	122	143	113	123	137	123	
		CSCS	93	136	141	114	122	130	121	
	Strong	RRS	94	130	147	122	133	140	129	
		CSCS	63	110	127	105	117	125	120	
AA Cycle 0	Mild	RRS	112	131	139	122	127	135	126	
		CSCS	104	144	150	141	144	149	145	
	Strong	RRS	125	139	140	133	133	137	135	
		CSCS	106	147	153	148	150	151	151	
AD Cycle 0	Mild	RRS	129	100	92	100	92	90	90	
		CSCS	145	125	102	128	104	97	96	
	Strong	RRS	153	120	114	128	119	114	119	
		CSCS	147	130	108	135	116	103	110	
AD Cycle 0	Mild	RRS	161	133	116	135	125	114	122	
		CSCS	59	90	94	86	90	90	90	
	Strong	RRS	89	100	100	92	93	93	91	
		CSCS	96	119	115	115	118	114	114	
Strong	RRS	101	107	103	101	95	102	103		
	CSCS	105	124	120	119	122	118	117		

* A — additive; CD — complete dominance; OD — overdominance; ON — optimum number; AA — additive by additive; AD — additive by dominance

† Cycle 0 values are the means of four runs.

closer to the genotypic by use of the normal order statistics of Harter (1961). The mean of the expected value of the three largest order statistics in a sample of size 60 is 1.99. The standard error of each single cross mean is six. Therefore, on the average, the values presented for CSCS in Table 4 are approximately 12 units larger than their genotypic value. With a 12 unit reduction for CSCS, the number of cases where the limit of RRS exceeds the limit of CSCS is approximately the same as the reverse. RRS generally has higher limits with no epistasis and low starting gene frequencies in both populations. The limits for CSCS tend to be higher with epistasis or when the starting gene frequencies were higher.

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