DIRECTIONAL SELECTION IN SIMULATED POPULATIONS OF SELF-POLLINATED PLANTS*

By F. A. Bliss† and C. E. Gates‡

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Summary

Selection for a metric trait was practised in populations of self-pollinated plants simulated on a high-speed electronic computer.

Realized genetic gain from two methods of selection was reduced when tight linkage was imposed. The effects of linkage were not diminished by either reducing selection intensity or increasing population size. Linkage caused estimates of additive genetic variance to be biased negatively more frequently than positively, on a per trial basis. However, the magnitude of positive bias was greater.

Selection in populations of 16 and 32 individuals resulted in reduced genetic gain compared to selection in populations of 64, 128, and 256 individuals. Predictions of genetic gain based on statistics estimated from F_2 generations of the larger populations showed good agreement with realized genetic gain.

Mass selection until additive variance was exhausted produced greater gain than did selection only among pure lines. However, the latter method may show equal or greater efficiency when other biological and environmental factors are considered.

It is shown that the portion of total possible genetic gain expected from one cycle of selection (defined as from F_2 to F_5–F_8) decreases as the number of genes conditioning a trait becomes large. For such traits, recurrent cycles of crossing followed by selection are necessary to fully utilize the variability arising from an initial hybridization.

I. Introduction

The essential features common to most plant-improvement programmes are selection within an initial population of genetically variable individuals and use of the selected material as either commercial varieties or as a base for another cycle of selection (Comstock and Robinson 1952). The breeder must first identify the populations that afford the greatest potential for genetic gain. He must then determine the breeding method and the basis for selection which make maximum use of this potential efficiently. Finally, the breeder of self-pollinated plants must decide upon the genetic structure of the final product. Varieties may consist of non-segregating populations resulting from single pure lines or composite mixtures of pure lines, or hybridization techniques which utilize inbred lines in either specific hybrid combinations or bulk populations may be developed.

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† Department of Genetics, University of Minnesota, St. Paul, Minnesota; present address: Department of Horticulture, University of Wisconsin, Madison, Wisconsin.

‡ Agricultural Experiment Station, University of Minnesota, St. Paul, Minnesota; present address: Institute of Statistics, Texas A & M University, College Station, Texas 77843.

Studies of natural, experimental, and hypothetical plant populations suggest that predominant self-pollination does not always result in genetically uniform populations (Allard 1965). The recombinational systems of these plants may be less restrictive than commonly thought, and the populations quite complex. Allard and Hansche (1964) suggest that individual or populational buffering may be useful in designing mixtures of pure lines or composite crosses. Such populations may be better buffered and have much to offer in improving and stabilizing performance, while meeting the demands for uniformity and utilizing the advantages of diversity.

It seems unlikely that dominance variance will play an important role in determining breeding methods for self-pollinated crops. Matzinger (1963) points out that in almost every case where F_1's have been suggested for use homozygous lines have been isolated that are equal or superior to the F_1. Hanson, Probst, and Caldwell (1967) state that since evolutionary forces have been operating on gene combinations primarily in a homozygous state, the evolution of interacting systems involving dominance should be of secondary importance. Matzinger suggests that the main criterion for use of F_1 hybrids should be the magnitude of superiority of the crossbred families, since hybridization difficulties can usually be overcome. In the most extensive studies reported, he found the predominant type of genetic variance to be additive. When dominance and epistasis were estimated, there was some evidence for each in certain cases but the significant estimates were often negative. He suggests that even where additive $\times$ additive epistasis makes up a large portion of the genetic variance, homozygous genotypes will still be desired. However, it may be advantageous to reduce selection intensity in the early stages of a breeding programme to allow opportunity for desirable gene combinations to come together.

The results reported herein arise from a study designed to evaluate and quantify the effects on genetic gain of linked loci, intensity of selection, heritability of the trait under selection, and population size, and factors affecting genetic gain for two methods of selection.

II. Experimental

(*a*) *Parameters*

Populations of self-pollinated plants were simulated. A metric character was determined by 40 loci, 10 being equally distributed to each of four linkage groups, with two alleles per locus and equal genetic effects at all loci. A completely additive model was assumed and no dominance or epistasis was allowed.

The probabilities of recombination were 0·5 (no linkage), 0·05, and 0·005, and were equal between each pair of adjacent loci in each linkage group. The quantitative character for which selection was practised was modified by a random, non-genetic factor having zero mean and variance σ_e^2. The non-genetic variance was either zero or made equal to three times the additive genetic variance in the F_2 generation, to correspond to expected heritabilities of 1·00 and 0·25 respectively.

The sizes of populations studied were arbitrarily placed at 16, 32, 64, 128, and 256 individuals per generation. Each F_2 population resulted from crossing two homozygous parents which were generated by the procedure described in the following section. An equal number of progeny was produced from each parent and the size of the unselected population was held constant.

Two methods of selection were practised. Method 1 (mass selection) consisted of selecting, on the basis of individual phenotype, either the best eighth or the best quarter of the population for parents of the following generation. Selection was begun in the F_2 generation and continued without regard to family structure until additive genetic variance was exhausted or for a maximum of 20 generations. Method 2 consisted of generating an F_2 population of the specified size, then advancing each F_2 by single seed descent until the population consisted of homozygous individuals or for a maximum of 20 generations. Selection was then practised among homozygous individuals or pure lines in the final populations. Method 2 is similar to the modified pedigree system proposed by Brim (1966).

(*b*) *Computer Programme*

The C.D.C. 1604 electronic computer was programmed to simulate the events pertinent to reproduction and inheritance in a plant population reproducing solely by self-fertilization, and to give information concerning the genetic state of the population. Each computer run was begun by specifying the genetic conditions for a particular selection experiment as determined by the values of the parameters. The factors that were varied with each set of conditions were probability of recombination between linked loci, intensity of selection, heritability of the trait under selection, and population size.

Two homozygous parents were generated at the beginning of each replicate run, the first by a random process whereby the probability of either a favourable or an unfavourable allele at each locus was 0·5. The second parent was generated as the complement of the first to insure heterozygosity of the F_1 at all loci. In the succeeding generations, the required number of pairs of gametes was generated from each parent to bring the population to the specified constant size. One member of each linkage group was chosen at random and a random walk carried out along the chosen chromosome to determine the crossover sites. The genes on the initially chosen chromosome were taken as genes for the gamete until crossing-over occurred, after which genes were taken from the homologous chromosome until all loci on each chromosome were filled. The probability of crossing-over was specified at the beginning of each run and was unchanged throughout. Each pair of gametes was combined to form an offspring and the process repeated until the prescribed number was produced.

The genotypic value of an individual was obtained by detecting the number of favourable alleles at each locus, multiplying by the genetic value (0·5), and summing over all loci. The genotypic mean and additive genetic variance of each generation were calculated and stored.

The individual phenotype was determined as $P = G + \sigma_e d$, where G is the genotypic value, σ_e is the expected value of the standard deviation due to non-genetic factors, and d is an $N(0,1)$ random deviate. Phenotypic means and variances of each generation were calculated and stored. Individual phenotypic values were ranked in descending order and the appropriate proportion having the highest phenotypic values was selected as parents of the following generation (method 1), or as the best homozygous individuals (method 2).

III. Results

(*a*) *Heritability, Method of Selection, and Selection Intensity*

The total genetic gain realized from mass selection (method 1) was greater than that realized from selecting the best individuals from a population of pure lines (method 2). When tight linkage (0·005) was imposed and small populations used, both selection methods produced nearly equal results (Tables 1 and 2).

It is of interest to know whether reduced selection intensity would allow increased opportunity for gene recombination and afford greater potential for genetic gain without the need for recurrent cycles of hybridization and selection. Lower selection intensity (0·25) resulted in no greater genetic gain than when more

TABLE 1

REALIZED GENETIC GAIN FROM MASS SELECTION OF INDIVIDUAL PHENOTYPES (METHOD 1)

Portion of Population Selected	Expected Heritability, F_2 Generation	Population Size	Recombination 0·5		Recombination 0·05		Recombination 0·005	
			Realized Genetic Gain	% of Total Possible Gain	Realized Genetic Gain	% of Total Possible Gain	Realized Genetic Gain	% of Total Possible Gain
0·25	0·25	16	7·00±1·47	35·0	3·69±0·24	18·5	4·00±1·00	20·0
		32	8·19±1·35	40·9	5·72±0·62	28·6	4·09±1·34	20·5
		64, 128, 256*	10·50±0·46	52·5	9·62±0·86	48·1	5·94±1·04	29·7
0·25	1·00	16	9·75±1·11	48·8	6·50±0·87	32·5	8·50±0·87	42·5
		32	11·00±0·70	55·0	8·25±1·11	41·3	5·25±0·95	26·3
		64, 128, 256*	11·58±0·62	57·9	10·50±0·69	52·5	7·00±0·83	35·0
0·125	0·25	16	3·75±1·79	18·8	5·50±0·87	27·5	3·00±0·91	15·0
		32	6·50±1·04	32·5	7·25±0·75	36·3	6·75±0·86	33·8
		64, 128, 256*	9·75±1·16	48·7	7·58±0·81	37·9	5·98±1·09	29·9
0·125	1·00	16	10·75±0·85	53·8	8·50±1·19	42·5	5·50±0·87	27·5
		32	10·75±0·86	53·8	9·50±0·87	47·5	6·00±0·58	30·0
		64, 128, 256*	12·92±0·89	64·4	10·50±1·10	52·5	7·83±1·12	39·2

* Data for population sizes 64, 128, and 256 were pooled. Mean values were not significantly different, and Bartlett's χ^2 tests for homogeneity of variances were not significant.

TABLE 2

PREDICTED AND REALIZED GENETIC GAIN FROM SELECTION IN POPULATIONS ADVANCED TO FIXATION (METHOD 2)

Portion of Population Selected	Expected Heritability, F_2 Generation	Population Size	Theoretical Expected Gain	Recombination 0·5			Recombination 0·05			Recombination 0·005		
				Predicted Genetic Gain	Realized Genetic Gain	% of Total Possible Gain	Predicted Genetic Gain	Realized Genetic Gain	% of Total Possible Gain	Predicted Genetic Gain	Realized Genetic Gain	% of Total Possible Gain
0·25	0·25	16	2·56	2·64±0·20	2·33±0·52	11·7	2·10±0·27	1·95±0·50	9·8	2·59±0·40	2·68±0·66	13·4
		32		2·67±0·22	2·38±0·29	11·9	2·32±0·45	2·26±0·35	11·3	3·33±0·51	3·30±0·51	16·5
		64		2·57±0·13	2·86±0·25	14·3	2·99±0·28	2·83±0·36	14·2	2·52±0·44	2·76±0·46	13·8
		128		2·58±0·08	2·57±0·10	12·9	2·47±0·19	3·00±0·28	15·0	2·15±0·15	2·25±0·11	11·5
		256		2·56±0·07	2·26±0·18	11·3	2·23±0·25	2·06±0·26	10·3	2·26±0·68	1·76±0·40	8·8
0·25	1·00	16	4·04	4·25±0·16	3·90±0·33	19·5	3·42±0·22	3·13±0·43	15·7	3·88±0·49	3·73±0·63	18·7
		32		3·98±0·18	3·86±0·31	19·3	3·62±0·36	3·69±0·38	14·9	4·48±0·48	4·48±0·47	22·4
		64		4·09±0·13	4·04±0·19	20·2	4·33±0·25	4·11±0·23	20·6	3·94±0·43	4·06±0·47	20·3
		128		4·08±0·08	4·00±0·04	20·0	3·93±0·23	4·26±0·23	21·3	3·60±0·15	3·60±0·13	18·0
		256		4·03±0·08	3·85±0·09	19·2	3·69±0·23	3·52±0·25	17·6	3·67±0·69	3·23±0·42	16·2
0·125	0·25	16	3·32	3·55±0·28	2·60±0·62	13·0	2·72±0·35	2·60±0·59	13·0	3·36±0·52	3·40±0·85	17·0
		32		3·46±0·29	2·90±0·38	14·5	3·01±0·58	2·78±0·54	13·9	4·32±0·66	3·93±0·34	19·7
		64		3·33±0·17	3·46±0·28	17·3	3·87±0·37	3·55±0·45	17·8	3·27±0·57	3·50±0·58	17·5
		128		3·35±0·10	3·23±0·16	16·2	3·20±0·24	3·87±0·26	19·3	2·79±0·20	2·71±0·15	13·6
		256		3·31±0·08	3·16±0·09	15·8	2·89±0·32	2·44±0·18	12·2	2·92±0·88	2·15±0·42	10·8
0·125	1·00	16	5·24	5·52±0·21	4·85±0·41	24·3	4·43±0·29	3·85±0·44	19·3	5·05±0·63	4·45±0·66	22·3
		32		5·17±0·23	4·95±0·37	24·8	4·69±0·46	4·50±0·38	22·5	5·81±0·62	5·58±0·51	27·9
		64		5·31±0·17	5·26±0·19	26·3	5·61±0·32	5·36±0·29	26·8	5·11±0·56	5·04±0·58	25·2
		128		5·29±0·11	5·17±0·08	25·9	5·10±0·30	5·35±0·32	26·8	4·70±0·21	4·37±0·13	21·9
		256		5·22±0·10	4·97±0·16	24·9	4·79±0·30	4·57±0·28	22·9	4·75±0·89	3·89±0·57	19·5

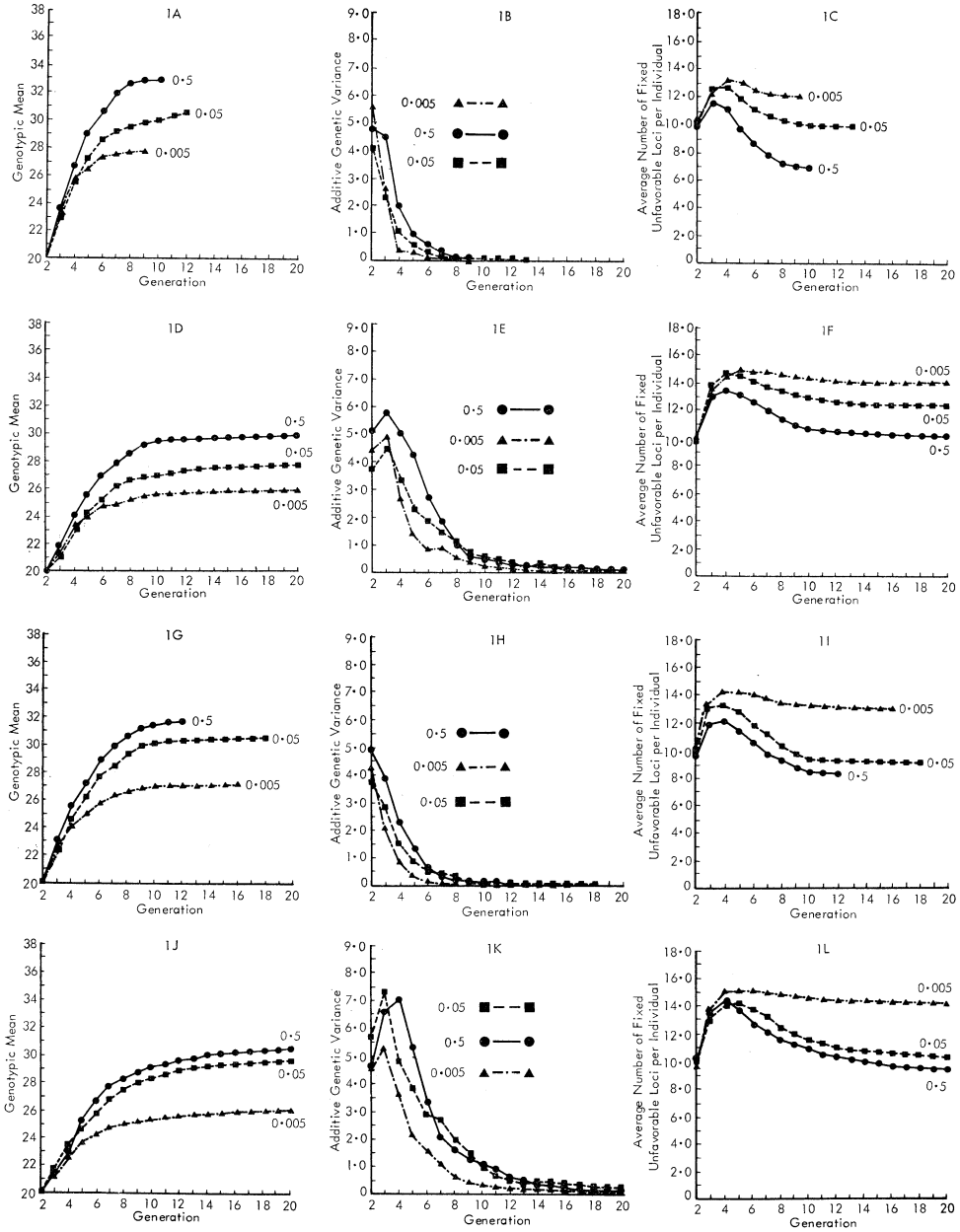

Fig. 1.—Effect of linked genes (probabilities of recombination 0·5, 0·05, and 0·005) on genetic gain, additive genetic variance, and fixation of unfavourable loci during mass selection (method 1) of the best eighth (*A–F*) and the best quarter (*G–L*) of the population, the heritabilities being 1·0 (*A–C*, *G–I*) or 0·25 (*D–F*, *J–L*).

intense mass selection (0·125) was practised in segregating generations, regardless of either the tightness of linkage or the magnitude of heritability (Table 1). Additive genetic variance increased in the early generations when heritability was low and it was exhausted more slowly under less intense selection (Figs. 1*B*, 1*E*, 1*H*, and 1*K*). Since selection is practised only after the genotypes are fixed in method 2, reducing the selection intensity would be of no value. However, the genetic gain at both selection intensities are presented for comparison (Table 2).

(*b*) *Population Size*

Selection within populations of 16 and 32 individuals per generation (small populations), as opposed to populations of 64, 128, and 256 individuals (large populations) generally resulted in reduced genetic gain and larger standard errors. When mass selection was practised, the small populations were quite restrictive, especially when heritability was low. Since no differences in genetic gain or variance of the means were detected between populations of 64, 128, and 256 individuals, the results were pooled for presentation (Table 1).

The expected genetic gain from selection by method 2 was estimated using the variance components determined for the F_2 generation. Mean values of predicted genetic gain and realized genetic gain showed good agreement when predictions were based on the variance components estimated from the larger populations (Table 2). However, even in the larger populations, realized gain fell short of predicted values when there was tight linkage between loci.

(*c*) *Linked Loci*

The effect of linked loci on additive genetic variance was measured in the F_2 generation and when the population was fixed as homozygous individuals. Using a completely additive model, the expected values of additive variance were 5·0 and 10·0, respectively. Estimates of additive variance and the genotypic mean were computed from 10 replicate computer runs for each set of parameters and a 95% confidence interval was constructed from each variance estimate using the χ^2 criterion (Steel and Torrie 1960).

Most confidence intervals constructed for those runs in which probability of recombination was 0·5 included the expected additive variance. When linkage was imposed, a large number of confidence intervals failed to include the expected variance, with poorer fits associated with tighter linkages. Additive variance was biased downward more frequently than upward based on the number of times the upper limit of the confidence interval was less than the expected variance (Table 3). However, the average magnitude of positive bias was greater than that of negative bias. Mean values of additive genetic variances associated with probabilities of recombination of 0·05 and 0·005 were not significantly different from values based on no linkage.

Increasing the population size did not alter the effects of linkage, since both the magnitude and direction of bias to additive variance appeared to be the same for all sizes of populations. Correlations between $\log_e$ of additive variances of the F_2 and fixed generations and correlations between $\log_e$ of heritabilities of the F_2 and

TABLE 3

EFFECT OF LINKAGE ON ADDITIVE GENETIC VARIANCE IN THE F_2 GENERATION AND AT FIXATION

Means based on 10 replicate runs

Recombination Frequency	Population Size	F_2 Generation				Fixed Generation				Mean Number of Generations to Fixation
		Genotypic Mean	Additive Genetic Variance	N_1*	N_2†	Genotypic Mean	Additive Genetic Variance	N_1*	N_2†	
0·5	16	20·07±0·15	5·597±0·434	0	0	19·48±0·19	10·362±1·257	1	1	11·6±0·60
	32	20·06±0·12	4·934±0·434	0	1	19·89±0·23	10·732±0·631	0	0	12·8±0·79
	64	20·00±0·06	5·156±0·300	0	1	20·01±0·12	10·469±0·444	0	0	15·4±0·70
	128	19·92±0·16	5·101±0·204	0	0	20·05±0·12	10·248±0·428	0	0	16·1±1·71
	256	19·96±0·05	4·993±0·148	0	1	19·97±0·05	9·932±0·210	0	0	26·4±2·50
0·05	16	20·13±0·17	3·698±0·508	0	1	20·10±0·30	6·937±1·320	0	3	10·3±0·44
	32	19·93±0·12	4·347±0·958	1	4	20·14±0·16	9·305±1·859	1	3	11·9±0·47
	64	19·84±0·13	5·888±0·650	3	2	19·65±0·20	12·325±0·973	3	1	14·3±0·82
	128	19·88±0·09	4·951±0·559	2	3	20·01±0·15	9·615±0·974	2	3	14·0±0·60
	256	19·89±0·03	4·241±0·384	1	5	19·91±0·04	8·538±0·614	0	5	15·4±0·60
0·005	16	20·15±0·17	5·242±1·430	2	0	20·27±0·22	9·583±2·979	2	2	10·2±0·79
	32	20·11±0·18	6·762±1·234	4	3	20·27±0·25	13·006±2·197	5	3	9·6±0·57
	64	20·09±0·10	5·251±1·138	2	3	20·06±0·06	11·636±2·483	3	3	12·4±0·66
	128	19·95±0·11	4·018±0·320	0	6	19·89±0·09	8·215±0·574	0	6	11·6±0·41
	256	20·03±0·05	4·739±1·359	2	5	20·00±0·06	9·432±2·393	2	5	12·6±0·51

* Number of replications in which 95% confidence interval does not include expected variance, the lower limit being too high.

† Number of replications in which 95% confidence interval does not include expected variance, the upper limit being too low.

fixed generations suggested that the fixed populations were usually biased in the same direction and to the same degree as the F_2 from which they were derived. This positive correlation was greater when tight linkage was imposed and heritability was high (Table 4).

TABLE 4

REALIZED HERITABILITIES AND CORRELATIONS

Correlations between logarithms of realized heritabilities of the F_2 and final generations when expected heritabilities are 0·25 and 0·40 respectively, and between logarithms of additive variance of F_2 and final generations when expected heritability is 1·0 are recorded

Population Size		Realized Heritability		Correlations between Heritabilities	Correlations between Additive Variances
		F_2	Final		
16	0·5*	0·272±0·04	0·536±0·08	0·43 (−0·28, 0·83)†	0·56 (−0·11, 0·88)
32		0·296±0·04	0·433±0·03	0·66 (0·05, 0·91)	0·70 (0·13, 0·92)
64		0·249±0·01	0·478±0·03	0·22 (−0·48, 0·74)	0·65 (0·04, 0·91)
128		0·251±0·01	0·419±0·02	−0·02 (−0·64, 0·62)	0·55 (−0·12, 0·88)
256		0·250±0·01	0·413±0·01	0·04 (−0·61, 0·65)	−0·03 (−0·65, 0·61)
16	0·05*	0·235±0·04	0·276±0·03	0·43 (−0·28, 0·83)	0·84 (0·46, 0·96)
32		0·259±0·06	0·365±0·04	0·77 (0·29, 0·94)	0·97 (0·88, 0·99)
64		0·310±0·03	0·425±0·02	0·16 (−0·52, 0·72)	0·87 (0·53, 0·97)
128		0·255±0·03	0·428±0·04	0·84 (0·44, 0·96)	0·95 (0·79, 0·99)
256		0·221±0·02	0·376±0·02	0·51 (−0·17, 0·86)	0·91 (0·64, 0·98)
16	0·005*	0·324±0·04	0·372±0·08	−0·16 (−0·72, 0·52)	0·92 (0·62, 0·98)
32		0·371±0·06	0·419±0·07	0·65 (0·03, 0·91)	0·94 (0·77, 0·99)
64		0·245±0·04	0·389±0·05	0·84 (0·44, 0·96)	0·98 (0·91, 0·99)
128		0·215±0·02	0·350±0·02	0·94 (0·76, 0·99)	0·94 (0·75, 0·99)
256		0·213±0·04	0·346±0·05	0·75 (0·23, 0·94)	0·99 (0·97, 0·99)

* Recombination frequency. † 95% confidence interval.

Reduced genetic gain resulted when loci were tightly linked regardless of the method of selection, the intensity of selection, or the size of populations. The greatest reduction was in small populations when heritability of the trait was low. Gain from mass selection appeared to be reduced more than that from selection among pure lines (Tables 1 and 2).

IV. DISCUSSION

(a) *Evaluation of Results*

Anderson (1939) suggested that closely linked loci may greatly reduce the chances of recombination and impose severe restrictions on both the frequencies of gametes and the kinds of gametes that appear with any frequency. Gates (1954) showed that linkage contribution to additive genetic variance was a function of the balance between coupling and repulsion linkages, number of loci, closeness of linkages, and relative values of favourable alleles; and that this contribution could be either positive or negative. When he considered all possible F_1 genotypes

resulting from six heterozygous loci, the repulsion phases were more numerous due to spatial configuration in 50 of the 64 genotypes. This predominance was offset by greater contributions when bias was positive than when it was negative. The results of replicate computer runs presented herein agree with the previous work of Gates. When the F_1 parent contained a random association of coupling and repulsion phases, negative bias to additive variance occurred more frequently than positive bias. However, the average magnitude of positive bias was greater. In families where additive variance was biased downward, genetic gain was reduced compared to families in which the genes assorted at random. Since additive variance is independent of population size, increasing the population beyond the point where sampling errors cease to be a factor is unlikely to reduce linkage bias or greatly increase realized genetic gain. A system of intermating prior to selection, which allows the additive variance to approach values obtained for random gene assortment, would be advantageous in these families.

Hanson (1959) suggested on the basis of theoretical calculations that up to four intermating cycles should precede selfing generations to allow break-up of linkage groups. Miller and Rawlings (1967) found that when a cotton population resulting from a wide cross was allowed to reproduce by mixed intermating and selfing for six successive generations, it provided a better source of selection material than did the F_2. At least part of this superiority was attributed to the break-up of initial linkage groups in the original material. Their data suggest that coupling-phase linkages were important for six traits and repulsion-phase linkages for one trait studied.

Considerable efficiency can be gained in a breeding programme if selection is practised in populations of an optimum size. When populations are extremely small genetic gain may be restricted by random loss of favorable alleles, while very large populations within families may preclude the use of more families. Allard (1960) states that no rules can be drawn as to the number of F_2 individuals and F_3 families that should be grown, but that few breeders use less than 50 F_3 families and usually grow many more. The ratio of F_2 individuals to F_3 families ordinarily varies from about 10 : 1 to 100 : 1.

Selection in populations of 16 and 32 individuals resulted in reduced genetic gain and large standard errors for both methods of selection studied. No differences in genetic gain were detected when mass selection or selection among homozygous individuals was practised in populations of 64, 128, and 256 individuals. Based on these results, populations of at least 64 individuals per generation should be sufficiently large to allow steady improvement from selection provided other factors are not limiting. Populations of this size should also be sufficient for early generation predictions, assuming that satisfactory procedures are also available for obtaining unbiased estimates of the necessary parameters.

Selection based on individual phenotype in early generations has often been ineffective, particularly when heritability is low. Johnson, Robinson, and Comstock (1955) found that estimates of genotypic variance based on single trials were likely to be inflated if genotype–environment interactions were large, and that predictions would not be realized in other years or at other locations. Attempts to overcome such difficulties and to aid selection have been made by testing more advanced lines

such as F_3 and F_4 families in replicated trials. In a study of two soybean populations, Brim and Cockerham (1961) found additive variance to be the main component of genetic variance for nine characters studied. Progress from selection among progenies increased as the parents of the progenies became more inbred. However, little was gained by inbreeding the parents beyond the F_4.

Mass selection in early generations has been reported to be effective in some cases, particularly for trials possessing high single plant heritability. Romero and Frey (1966) reported that mass selection in the F_3–F_6 generations reduced plant height as well as shifted the means of two correlated traits in oats. Sufficient genetic variance remained to allow improvement from further selection. They cite additional examples of the effectiveness of mass selection in both cross- and self-pollinated crops.

Further evaluation of the two methods of selection must be made in terms of the time and facilities required as well as the total genetic gain per selection cycle. Mass selection (method 1) requires each generation to be grown under conditions similar to those where the crop will be grown commercially. Thus with many crops it will be possible to grow only one generation per year. Since selection is required for 6 or 7 generations to obtain maximum genetic gain (Figs. 1*A*, 1*D*, 1*G*, and 1*J*), one cycle of mass selection may be of considerable duration.

Use of a modified pedigree system similar to method 2 allows the families to be advanced as rapidly as the length of the plant's life cycle permits. Since selection is practised only in the final population, only this generation must be grown under commercial conditions. Sufficient quantities of seed may then be produced to allow replication of families as an aid to selection. It should be possible in some crops to proceed through two or three recurrent cycles (i.e. from the F_2 to the F_5–F_8 for each) of crossing the best individuals followed by selection among pure lines in the same length of time required for one complete cycle of mass selection.

(*b*) *Proportion of Possible Gain from Selection*

The realized genetic gain from selection following the hybridization of two homozygous parents was considerably less than the total possible genetic gain, using either method of selection. Mass selection of the best one-eighth of the population in each generation under the conditions of no linkage and heritability of 1·0 produced only about 60% of the possible gain. When the best individuals were selected from a population of homozygous individuals, only 25% of the possible gain was realized under the most favourable combinations studied (Table 2).

The expected genetic gain ($\Delta\bar{Y}$) from selecting individuals based on their phenotypic values from a population of pure lines is:

$$E(\Delta\bar{Y}) = k\sigma_P[4\sum_{i=1}^{n}\bar{q}_i(1-\bar{q}_i)u_i^2]/\sigma_P^2,$$

where

$E(\Delta\bar{Y})$ = the expected change in the genotypic mean,
k = the standardized selection differential,
σ_P^2 = the phenotypic variance among individuals,
u_i = the genotypic effect of the ith locus, and
$\bar{q}_i$ = the frequency of the favourable allele at the ith locus.

If the genotypic value of a population of pure lines developed without selection is

$$\sum_{i=1}^{n} (2\bar{q}_i - 1)u_i,$$

and the genotypic value of the "best possible" pure line is

$$\sum_{i=1}^{n} u_i\bar{q}_i \text{ or } \sum_{i=1}^{n} u_i \text{ when } \bar{q}_i = 1{\cdot}0,$$

then the total genetic gain possible is:

$$\sum_{i=1}^{n} u_i - \sum_{i=1}^{n} u_i(2\bar{q}_i - 1) = 2\sum_{i=1}^{n} u_i(1-\bar{q}_i),$$

where u_i = the genotypic effect of the ith locus, and $\bar{q}_i = 0{\cdot}5$ = the frequency of the favourable allele at the ith locus in the unselected population.

Assuming that genotypic effects of n loci are equal, it can be shown (R. E. Comstock, personal communication) that the proportion of the total possible genetic gain expected from selection depends on the number of loci controlling the character for which selection is practised, as well as heritability and selection intensity. The proportion of the total possible gain expected from selection is:

$$k[4\sum_{i=1}^{n} \bar{q}_i(1-\bar{q}_i)u_i^2]/\sigma_P^2 \sum_{i=1}^{n} (1-\bar{q}_i)u_i.$$

When heritability $= 1{\cdot}0$ ($\sigma_P^2 = \sigma_g^2$), the proportion of total possible gain is:

$$k\{[\sum_{i=1}^{n} \bar{q}_i(1-\bar{q}_i)u_i^2]/[\sum_{i=1}^{n} (1-\bar{q}_i)u_i]^2\}^{\frac{1}{2}} = kn^{-\frac{1}{2}},$$

where n = the number of loci, all having equal genetic effects, and $\bar{q}_i = 0{\cdot}5$ = the frequency of the favourable allele at the ith locus in the unselected population. Likewise it can be shown that when heritability is less than $1{\cdot}0$, the proportion of total possible genetic gain is $k(H/n)^{\frac{1}{2}}$, where heritability $H = \sigma_g^2/\sigma_P^2$, and σ_g^2 is the additive genetic variance.

The need for recurrent cycles of crossing the best individuals followed by selection becomes even more apparent when the effects of various combinations of parameters on genetic gain are considered (Table 5). Even though selection may be quite intense the expected proportion of genetic gain from one cycle of selection remains small when the number of loci affecting a trait is large and heritability is low. A large amount of the potential arising from an initial hybridization is likely to remain unused if only a single cycle of selection follows.

(c) *Implications of Non-additive Genetic Variances*

Dominance and epistasis have been found for some traits in nearly all studies reported. However, the magnitude of these variance components is often low relative to additive variance and their importance in determining optimum breeding procedures for self-pollinated crops is questionable. Clearly, genetic gain based on the selection of homozygous individuals or pure lines will not be affected even though dominance variance may be expressed in segregating generations. Few generalizations can be drawn about the likelihood of epistasis being an important

source of variation. Where adequate estimates exist the importance of epistasis varies widely. If epistatic variances make up a considerable portion of the total genetic variance, opportunity should be provided for desirable gene combinations to come together before selection is too intense; and progress is likely to be slower than if genetic variance were completely additive.

TABLE 5

PROPORTION OF THE TOTAL POSSIBLE GENETIC GAIN EXPECTED FROM ONE CYCLE OF SELECTION IN A POPULATION OF HOMOZYGOUS INDIVIDUALS

Portion of Population Selected	No. of Loci Affecting Trait	Herit-ability	Expected Genetic Gain	Portion of Population Selected	No. of Loci Affecting Trait	Herit-ability	Expected Genetic Gain
0·01	10	1·0	0·84	0·125	10	1·0	0·53
		0·25	0·53			0·25	0·33
	40	1·0	0·42		40	1·0	0·26
		0·25	0·27			0·25	0·17
	100	1·0	0·27		100	1·0	0·17
		0·25	0·17			0·25	0·11
0·05	10	1·0	0·65	0·25	10	1·0	0·41
		0·25	0·41			0·25	0·26
	40	1·0	0·33		40	1·0	0·19
		0·25	0·21			0·25	0·13
	100	1·0	0·21		100	1·0	0·13
		0·25	0·13			0·25	0·09

Ramey and Miller (1966) obtained significant estimates of dominance variance for only two traits in a cotton population resulting from a wide cross. Miller and Rawlings (1967) found that when this population was maintained by mixed intermating and selfing, a simple additive model was sufficient to explain the changes in generation means, variances, and genotypic correlations that were observed. The results of a diallel analysis of eight inbred cotton lines by Miller and Marani (1963) suggested that the major portion of the genetic variance was due to additive effects. Heterosis estimates were significant for all characters indicating the presence of non-additive gene effects. This, however, was not useful heterosis since the best F_1's were not significantly better than the best parents. White (1966) concluded from a diallel analysis of five cotton parents that additive variance was present for four of the six characters analysed. Dominance components were significant for two traits, but their magnitudes were small compared to the additive components. Epistasis did not appear to be operating to control any of the characters measured. However, the data of Hanson, Probst, and Caldwell (1967) suggest that epistasis may be an important source of variability for some characters of soybeans. They propose the use of a recurrent selection scheme that allows intermating of improved genotypes, and that overcomes a possible initial decrease in the population mean that may be associated with a break-up of desirable gene combinations when intermating occurs. In addition to maximizing the potential of epistasis, this scheme should also be effective if variability is largely additive, since the use of an intermated population would minimize some of the restrictions often found in breeding programmes of self-pollinated crops.

Mass selection in early generations may be effective when single plant heritability of a trait is high or when it may be increased by using refined experimental techniques such as those used by Gardner (1961). Large dominance and epistatic variances may influence such things as predictions based on early generation estimates, rate of gain, and the selection limits attained before the population becomes nearly homozygous. The effects of other factors such as linkage, population size, and selection intensity appear to be variable and often depend on the levels of the other parameters. In studies of large, simulated populations of random-mating individuals, Young (1966) found that, assuming a simple additive model, genetic gain could be accurately predicted using observed heritabilities, provided that the heritabilities were re-estimated at intervals. Linkage had no apparent affect on prediction. Assuming a dominance model, predictions were less accurate, particularly when selection intensity was high. With both models, a trait with high initial heritability lost most of its additive variance in less than 10 generations of intense selection. Traits having low heritability, subjected to less intense selection, often retained more than one-half the additive variance even after 30 generations of selection. Martin and Cockerham (1960) found that tight linkages, particularly when the population was either in linkage equilibrium or repulsion phase, slowed genetic advance. When tight linkage was combined with intense selection in small populations the population mean was fixed at a lower value than the maximum value obtainable. Similar patterns of selection response were observed whether the genetic model included only additive gene effects or both additivity and dominance. Latter (1965) found that the selection limit of a character controlled by genes having large effects was proportionately reduced as linkage intensified, with appreciable effects from recombination values less than 0·10. This was true provided the effects of parameters such as population size were not of overriding importance. Jain and Allard (1964) studied the joint effects of linkage, degree of dominance, epistasis, and inbreeding on the genotypic constitution of populations reproducing by self-fertilization and random outcrossing. The results varied according to conditions involved; however, inbreeding greatly affected the interrelationships among the other factors.

The assumption that additive gene effects account for the total genetic variance of a quantitatively inherited trait is undoubtedly an over-simplification of the actual situation even in completely self-pollinated species. Since alleles of qualitatively inherited genes express various degrees of dominance, and since epistasis is commonly observed between some loci, it seems likely that the same would be true for genes controlling quantitative characters. However, the experimental data available indicate that although dominance and epistasis are sometimes detected, the magnitude of each compared to that of additive variance is often small. Thus complex situations that may arise from interactions between non-additive genetic components and various population parameters would also be expected to be of minor importance in determining the effectiveness of a breeding programme. Improvement programmes for self-pollinated crops that allow all the additive variance to be used efficiently will probably account for much of the improvement realized. However, adjustments should be made to utilize additional sources of variability where substantial amounts exist.

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