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Simulation of Response of Small Self-Fertilizing Populations to Selection for Quantitative Traits: I. Effect of Number of Loci, Selection Intensity and Initial Heritability under Conditions of no Dominance

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Summary. A genetic system was simulated in order to evaluate the effects of selection intensity and initial heritability on the genetic advance in a small population reproducing by selfing. A constant number of 40 individuals was measured in each generation. A quantitative trait was assumed to be controlled by 15, 30 or 60 independently segregating loci with equal additive effects, no dominance and no epistasis.

It was found that the genetic advance in each generation, and the maximum possible genetic advance, expressed in actual units of measurement, were larger when fewer loci were assumed to control the trait, or when the initial heritability was higher. When the results were expressed on the basis of the initial phenotypic standard deviation, the genetic advance was smaller when 15 loci were assumed to control the trait than when more loci were assumed. An intense selection of 0.05 was most effective when selection was practised for a few generations. When selection was continued for more generations, a selection of 0.10 to 0.25 was found to be more effective. This occurred earlier when fewer loci were assumed to control the trait, or when the initial heritability was lower. The maximum possible genetic advance was attained in most cases by a selection intensity of 0.20 to 0.25.

The additive genetic variance was decreased by selection at a faster rate, and its fixation occurred earlier, when fewer loci were assumed to control the trait, when selection was more intensive, or when the initial heritability was higher. The decrease of heterozygosity occurred at a faster rate when selection was more intensive or when the initial heritability was higher.

Introduction

Many important agricultural crop plants reproduce by self-pollination. Breeding procedures for improving these crops usually involve selection from the segregating progeny of a cross between two cultivars which are homozygous in almost all their loci. The selection is based on the phenotypic expression of a quantitatively inherited character, such as yield per unit area, and the mechanism of its inheritance is usually unknown. The plant breeder who plans the selection procedures has to decide what would be the size of the population to be tested in each generation and the intensity of selection. These decisions are made intuitively, because it is not possible to predict which selection procedure would bring the best results.

Griffing (1960) developed a theory for predicting the effect of truncation selection on quantitative traits in random-mating populations. He assumed infinitely large populations, relatively small effects of individual genes, and that the genetical parameters of the population, including its additive variance, were not affected by selection. The theoretical problems of predicting selection response in random-mating populations of finite size were examined by Kojima (1961), Robertson (1960 and 1970), and by Hill (1969).

Curnow and Baker (1968) developed formulae for predicting the effect of repeated cycles of selection in populations of finite size on the frequency of genotypes at a particular locus. They also investigated the case of selfing, assuming the genetic effects at each single locus to be very small relative to the total variation.

Pederson (1969) tried to evaluate the response to truncation selection of populations which reproduce by self-fertilization. He assumed infinitely large populations, selection based on individual performance, and small effects of individual loci relative to the total phenotypic standard deviation. Despite these simplifying assumptions, his formulas are approximate and rather complicated.

Most of these authors acknowledge the difficulties encountered in the theoretical treatment of response to selection in self-fertilizing populations of finite size. The simulation of such a system by an electronic computer may help in predicting the effects of selection under these conditions. Fraser (1957) introduced the use of computer simulation in genetics, and the technique was described in detail by Fraser and Burnell (1970).

Gill (1965) used computer simulation to evaluate the effect of selection in small random-mating populations and found that the actual advance was considerably smaller than that expected from the theory developed by Griffing (1960) for large populations. Bliss and Gates (1968) studied the effect of selection in simulated populations of self-pollinated plants, and found that realized genetic gain was reduced when a tight linkage was imposed. Selection in populations of 16 and 32 individuals resulted in reduced genetic gain compared with selection in populations of 64 or more individuals. A completely additive model was assumed for a metric character determined by 40 loci, with two alleles per locus and equal genetic effects at all loci. The selection intensity was 0.125 or 0.25.

The purpose of the work reported in this series is to determine which methods of selection for quantitative traits would be expected to cause the best genetic advance in populations of finite-size which reproduce by selfing. The first paper of this series evaluates the effects of the number of loci which control the expression of an additive quantitative trait, the intensity of selection, and the environmental variation relative to the genetical variance, on the advance under selection.

Materials and Methods

The computer program

A CDC-6400 computer was programmed to simulate reproduction by selfing and selection by truncation of individuals having the highest phenotypic values of a quantitative trait. The program was mostly written in 'Fortran', and some 'Assembler' subroutines were used to condense the gametic values of 60 loci into one computer word. The main program starts by reading the input for the initial parameters defining each simulation run. These parameters include the number of individuals in each generation, the number selected from them, the number of loci affecting the trait and the additive and dominance effects at each locus, the environmental variance, the number of generations, and a "starter" for the random-number generator which was different in each replicate. The following subroutines are called in the next stage:

(a) GENERT produces the initial population which resembles the F_2 generation of a cross between two homozygous lines differing in NL loci. The values of each gamete are determined as "1" or "0", with a uniform probability of 0.5, at each locus of NI individuals.

(b) ZYGOT calculates the genotypic and phenotypic values of each individual. Additive effects (a_i) for each "1" gamete, and dominance effects (d_i) for each heterozygous locus, are added for all the loci, resulting in the genotypic value (G) of the individual. The environmental effect (E) is simulated as a normally distributed random variable with a zero mean and a variance of s_E^2. The phenotypic value of the individual is the sum of G and E. The numbers of "11", "01" and "00" loci are counted for each individual.

(c) COMPT calculates the average genotypic and phenotypic values of the population, the total phenotypic variance, the components of this variance (additive, dominance and environmental) and the narrow-sense heritability. The percentages of the number of "11", "01" and "00" loci in the population are also calculated.

(d) For each generation of selection and selfing the subroutine SELECT is called. It arranges the NI individuals according to the rank of their phenotypic values and selects the NS highest ranking ones. Each of these selected individuals produces NP progeny by selfing. These NI (= NS × NP) individuals constitute the next generation.

The simulation of this generation is followed by calling subroutines ZYGOT and COMPT. The sequence of SELECT - ZYGOT - COMPT is called for each of the generations.

Experimental procedures

A quantitative character was assumed to be determined by 15, 30 or 60 independently segregating loci, with two alleles per locus and equal additive genetic effects at each locus. No dominance or epistatic effects and no linkage were assumed. The population consisted of a constant number of 40 individuals measured in each generation. The probability of each locus in the initial generation being "11", "01", or "00" was 0.25, 0.50 and 0.25, respectively.

The additive effect (a_i) of each gamete was 2, 1 or 0.5 units when 15, 30 or 60 loci were assumed, respectively. Thus, the expected genotypic value in the initial generation was 30 units in each case, and the expected additive variance was 30, 15 or 7.5, respectively, when 15, 30 or 60 loci were assumed. When 15 loci were assumed there were six levels of environmental variance, i.e., 0, 4, 16, 36, 64 or 100, the corresponding expected initial heritability being 1.00, 0.88, 0.65, 0.45, 0.32 or 0.23, respectively. In order to have the same values of initial heritability, the environmental variance was 0, 2, 8, 18, 32 or 50 for 30 loci, and 0, 1, 4, 9, 16 or 25 for 60 loci. It was thus possible to compare the effects of the number of loci at constant levels of initial performance and of initial heritability.

The effects of five different selection intensities (0.05, 0.10, 0.20, 0.25 and 0.50) were compared by selecting in each generation 2, 4, 8, 10 or 20 individuals with the highest phenotypic value, and each of these produced 20, 10, 5, 4, or 2 progenies, respectively, by selfing.

The simulations were designed as a 3 × 5 × 6 factorial experiment, with three levels of NL (number of loci), five levels of P (proportion selected) and six levels of H (initial heritability). Each combination of parameters was replicated six times, and in each replicate a different "starter" number was used to create the sequence of random numbers. Each run was continued for ten generations of selection. The mean genotypic values, the heritabilities and other data were recorded for each generation in each run. An analysis of variance of these results was calculated for each generation.

The genotypic values increased in a manner resembling an exponential function. Therefore, a function of the type

$$Y = A + B(1 - e^{-ct})$$

was fitted to the mean genotypic values for each set of parameters. In this function, t is the generation number, and A, B and c are constants. The value of B so obtained was used as a prediction of the selection limit.

Results

Genotypic means

The mean squares of the analyses of variance of the genotypic means in each generation are given in Table 1. The values of these means for several sets of parame-

Table 1. Mean squares of the analyses of variance for genotypic means in each generation

Source of variation	Degrees of freedom	Mean squares in generation 1	2	3	4	5	6	7	8	9	10
Replicates	5	18.60	41.25	54.62	39.98	29.71	35.23	34.60	34.31	34.20	33.57
NL	2	173.04^2	745.73^2	1144.51^2	1540.87^2	1838.47^2	1984.26^2	2055.41	2098,41^2	2170.81^2	2182.02^2
P	4	165.69^2	467.50^2	593.21^2	562.28^2	459.95^2	358.10^2	267.32^2	203.52^2	163.26^2	134.88^2
H	5	101.30^2	273.85^2	485.65^2	578.67^2	605.60^2	618.92^2	602.13^2	568.31^2	536.31^2	505.92^2
NL×P	8	1.77	4.86	6.09	7.04	7.99	8.89	11.07	11.54	12.85	13.48
NL×H	10	7.81^2	10.83^2	20.03^2	23.67^2	18.69^1	18.12^1	15.61	13.87	12.35	11.88
P×H	20	1.96	7.22^2	13.58^2	17.15^2	16.53^1	17.19^1	17.28^1	17.22^1	17.08^1	16.93
NL×P×H	40	0.61	1.31	1.79	4.23	4.74	4.80	4.58	4.40	4.17	4.16
Error	445	1.55	3.01	4.73	7.25	8.65	9.41	9.91	10.19	10.46	10.65

^{1},^{2} Significant, 0.05 and 0.01 levels, respectively.
NL = number of loci
P = intensity of selection
H = level of initial heritability.

ters are presented in Figs.1, 2 and 3. These results indicate that the effect of the number of loci was highly significant in all the generations. The effect of the number of loci, when compared on the basis of a constant level of initial performance, is given in Fig.1 (A, B). It was found that the advance under selection, expressed in this way, was always higher when a smaller number of loci was assumed. It may be desired to evaluate the effect of an assumed number of loci in cases when the initial phenotypic variance is actually measured. For this purpose, it would be desirable to express the advance under selection in units of the initial phenotypic standard deviation (s_{po}), as in Fig.1 (C, D). In this case it was found that the advance under selection was smaller when 15 loci were assumed, but the difference between 30 and 60 loci was very small.

A significant interaction between the number of loci and the initial heritability was detected in the first six generations. When the initial heritability was high, the effect of the number of loci on the genotypic mean was much larger than when the initial heritability was 0.65 or less.

The effect of selection intensity was highly significant in all the generations. It had no significant interaction with the number of loci, indicating that its effects are essentially similar for each number of loci. Average results for all values of initial heritability are presented in Fig.2 (A, B, C). It was found that a selection intensity of 0.05 brought about the highest advance in genotypic value during the early generations, but after four to six generations of such a selection a plateau was reached and any further advance was rather small. The interaction of selection intensity with the initial heritability was significant from the second to the ninth generations. The effects of selection intensity (P) should therefore be examined separately for each level of initial heritability (H). The effect of P for H = 1.00 (no environmental variance) is shown in Fig.2 (D, E, F). When the number of loci (NL) was assumed to be 15 or 30, P 0.05 gave the best results up to the fifth generation, but in later generations P 0.20 or P 0.10 gave better results. For NL 60, P 0.05 gave the best results in all the ten generations. Similar results were

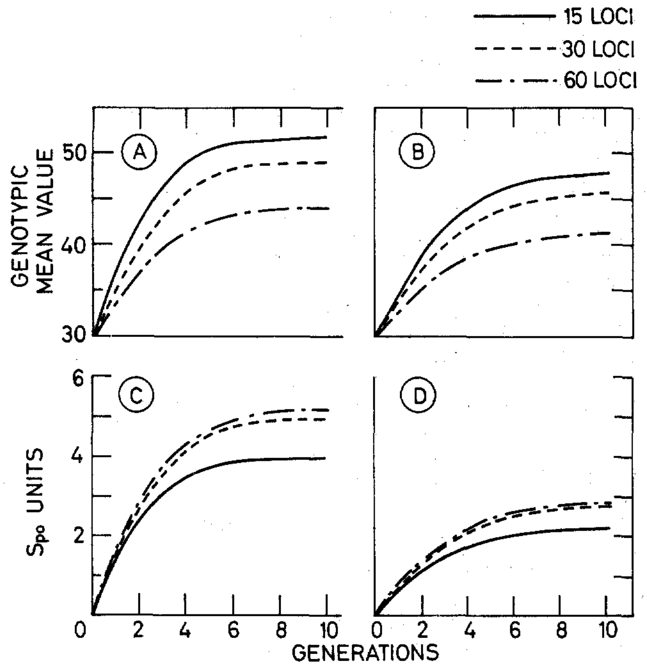

Fig.1. The effect of number of loci on the genotypic means when no dominance is assumed and there are 40 individuals in each generation, average values of all selection intensities. A,B, in actual units; C,D, in units of initial phenotypic standard deviation (s_{po}); A,C, initial heritability 1.00; B,D, initial heritability 0.45

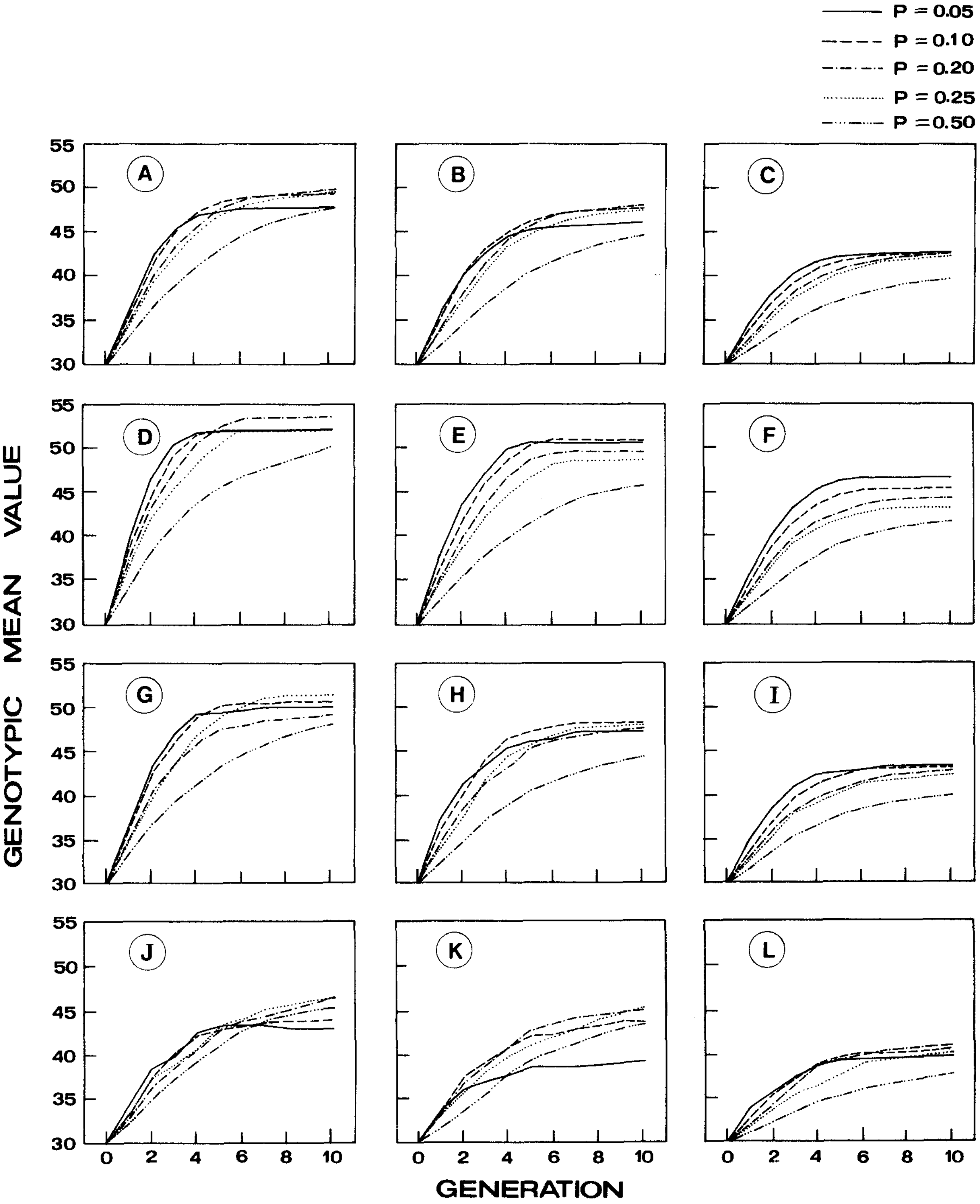

Fig.2. The effect of selection intensity (P) on the genotypic means, when no dominance is assummed and there are 40 individuals in each generation. A,D,G,J, 15 loci; B,E,H,K, 30 loci; C,F,I,L, 60 loci; A,B,C, average of all initial heritabilities; D,E,F, initial heritability 1.00; G,H,I, initial heritability 0.65; J,K,L, initial heritability 0.23

obtained for H = 0.65 (intermediate initial heritability), as illustrated in Fig.2 (G, H, I). The advantage of P 0.10 over P 0.05 was evident somewhat earlier in this case, and for NL 15 a selection intensity of P 0.25 gave the best results after the seventh generation. The results for H = 0.23 (low initial heritability) presented in Fig.2 (J, K, L), indicate that P 0.25 gave the best results after the seventh generation for NL 15. A se-

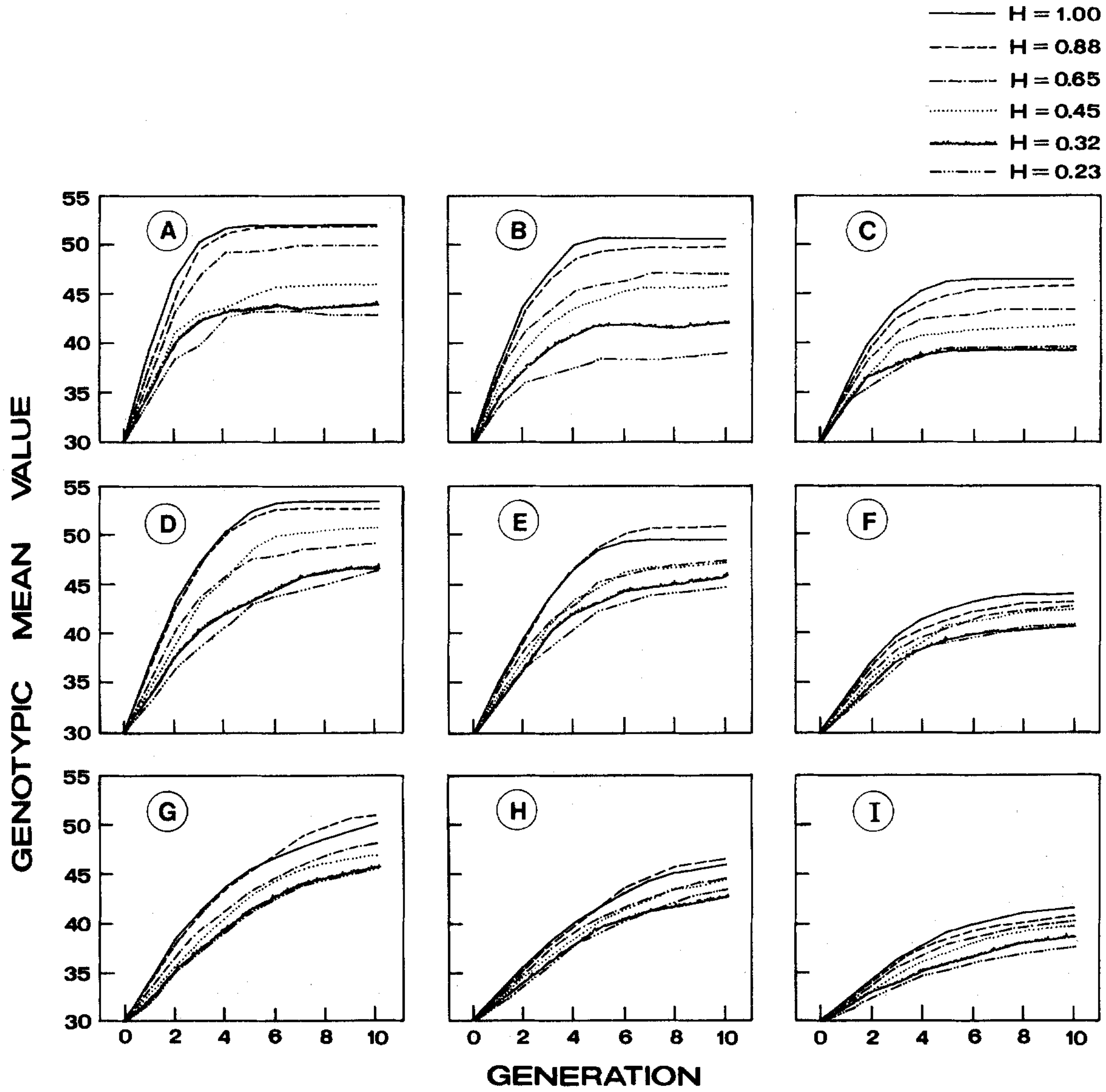

Fig.3. The effect of initial heritability (H) on the genotypic means, when no dominance is assumed and there are 40 individuals in each generation. A,D,G, 15 loci; B,E,H, 30 loci; C,F,I, 60 loci; A,B,C, selection intensity 0.05; D,E,F, selection intensity 0.20; G,H,I, selection intensity 0.50

lection intensity of P 0.20 gave the best results from the fifth to the eighth generation for NL 30, and after the seventh generation for NL 60.

The level of initial heritability had a significant effect on the advance in genotypic value in all the generations (Fig.3), but a significant interaction with the number of loci was found in the first six generations. The advance in genotypic value was larger when the initial heritability was higher, this effect being more prominent when a smaller number of loci was assumed. The interaction of initial heritability (H) and selection intensity (P) was significant in generations 2-9. The effect of H was more prominent in these generations when P was 0.05 than for higher values of P. There were no significant differences, in most cases, between heritability values of 1.00 and 0.88 or between 0.32 and 0.23.

Predicted limit of selection

The maximum possible advance in genotypic value, as calculated from a least-squares fit of an exponential function to the data, is given in Table 2. These results indicate that when the final results that may be achieved were given in actual units, or as percentage of the maximum theoretical limit (which is 30 units above the initial value, when all loci are homozygous for the better allele), selection appeared to be more effective for traits controlled by a smaller number of loci. However,

Table 2. Maximum possible progress in genotypic means, estimated by fitting an exponential function

Number of loci	Selection intensity	Percentage of maximum theoretical limit *							s_{po} units**
		Initial heritability							
		1.00	0.88	0.65	0.45	0.32	0.23	mean	mean
15	0.05	76	78	71	55	48	47	62	2.68
	0.10	77	82	73	68	65	50	69	2.92
	0.20	83	81	68	78	61	63	72	3.03
	0.25	79	78	79	65	61	62	71	2.96
	0.50	73	82	71	70	67	67	72	2.96
	mean	77	80	72	67	60	58	69	2.91
30	0.05	73	69	58	55	42	30	54	3.36
	0.10	75	73	65	55	54	47	62	3.70
	0.20	72	78	63	65	58	55	65	3.86
	0.25	69	67	67	60	70	58	65	3.79
	0.50	66	73	60	64	55	62	63	3.71
	mean	71	72	63	60	56	50	62	3.68
60	0.05	59	56	47	41	33	33	45	3.87
	0.10	55	51	48	38	41	37	45	3.80
	0.20	52	48	47	48	41	41	46	3.84
	0.25	48	51	47	51	43	39	46	3.86
	0.50	46	41	40	41	37	33	40	3.31
	mean	52	49	46	44	39	37	44	3.73
Mean of all loci		67	67	60	57	52	48	59	

* Thirty additional units when all loci are homozygous for the better allele

** s_{po} = phenotypic standard deviation in the initial generation.

Table 3. Mean squares ($X 10^2$) of the analyses of variance for heritabilities in each generation

Source of variation	Degress of freedom	Mean squares in generation									
		1	2	3	4	5	6	7	8	9	10
Replicates	5	10	4	3	4	3	2	2	1	0	1
NL	2	18**	12**	20**	46**	46**	47**	17**	3	3	0
P	4	8**	38**	86**	135**	231**	269**	216**	145**	89**	31**
H	5	783**	834**	828**	716**	460**	233**	69**	21**	12**	1
NL×P	8	2	2	2	4*	5*	8**	7**	0	0	0
NL×H	10	2	1	2	11**	16**	18**	5**	1	1	1
P×H	20	1	3**	3*	6**	27**	37**	38**	26**	15**	3**
NL×P×H	40	1	1	2	5**	5**	4**	3**	1	1	0
Error	445	1	1	2	2	2	2	1	1	1	1

*,** Significant, 0.05 and 0.01 levels, respectively
NL = number of loci
P = intensity of selection
H = level of initial heritability

when the results were expressed in units of the phenotypic standard deviation in the initial generation (s_{po}), 30 and 60 loci gave very similar results, but the maximum genotypic advance was smaller when 15 loci were assumed.

A selection intensity of 0.20 to 0.25 resulted in the highest predicted limit under the conditions assumed in this investigation. Selection intensities of 0.05 to 0.10 resulted in a lower predicted limit, especially with 15 or 30 loci, and of 0.50 resulted in a lower predicted limit with 60 loci. Lower initial heritabilities generally resulted in a lower predicted limit of selection, but initial heritabilities of 1.00 and 0.88 gave similar results.

Heritability

The mean squares of the analyses of variance of the heritability (i.e., the ratio of additive to total phenotypic variance) in each generation are given in Table 3. These indicate that the number of loci controlling the trait had a significant effect on its heritability in the first seven generations of selection: the decline of heritability was usually faster when a smaller number of loci was assumed.

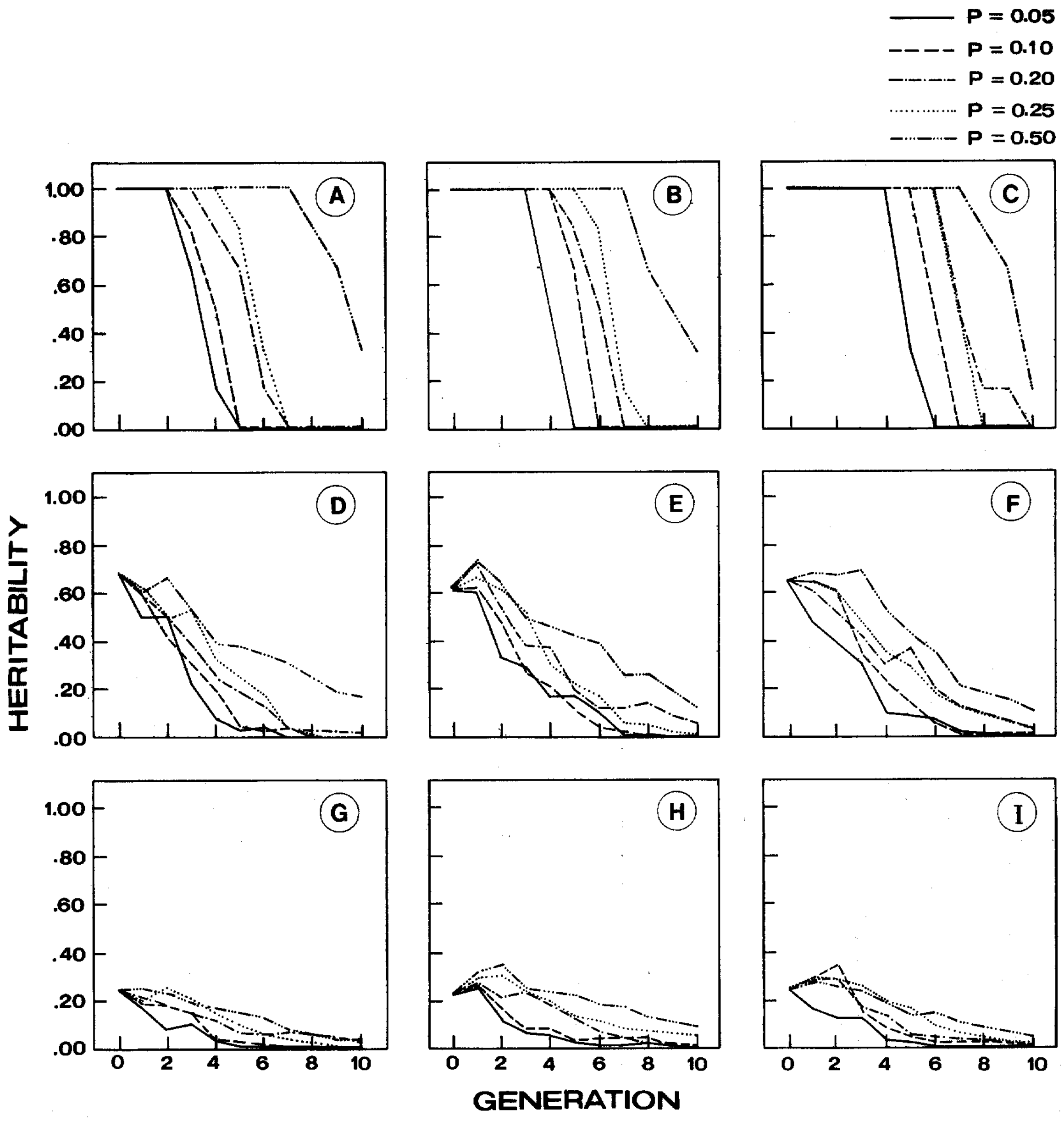

Fig.4. The effect of selection intensity (P) on the heritabilities, when no dominance is assumed, and there are 40 individuals in each generation. A,D,G, 15 loci; B,E,H, 30 loci; C,F,I, 60 loci. A,B,C, initial heritability 1.00; D,E,F, initial heritability 0.65; G,H,I, initial heritability 0.23

The effect of selection intensity (P) on the heritability after selection is presented in Fig.4. The decline of heritability was faster in most cases when a smaller percentage of the population was selected. For 30 or 60 loci, heritability actually increased in the first and second generations, when the selection intensity was 0.50 or 0.25. The effect of initial heritability (H) on the heritability after selection is presented in Fig.5. This effect was significant up to the ninth generation, but it was most prominent in the first four generations.

It is of some interest to learn the effect of the parameters studied on the time of occurrence of fixation, i.e., the complete loss of genetic variability as indicated by zero heritability. Fixation occurred in earlier generations when the number of loci (NL) was smaller, when the percentage of individuals selected (P) was smaller, and when the initial heritability (H) was higher. For 15 loci, the number of the generation (averaged over all H values and replications) in which fixation occurred was 5.6, 6.4, 7.8 and 8.4, for P values of 0.05, 0.10, 0.20 and 0.25, respectively, whereas for P 0.50 fixation occurred in most cases later than the tenth generation. For H values of 1.00, 0.88, 0.65, 0.45, 0.32 and 0.23 (averaged over all P values, except 0.50,

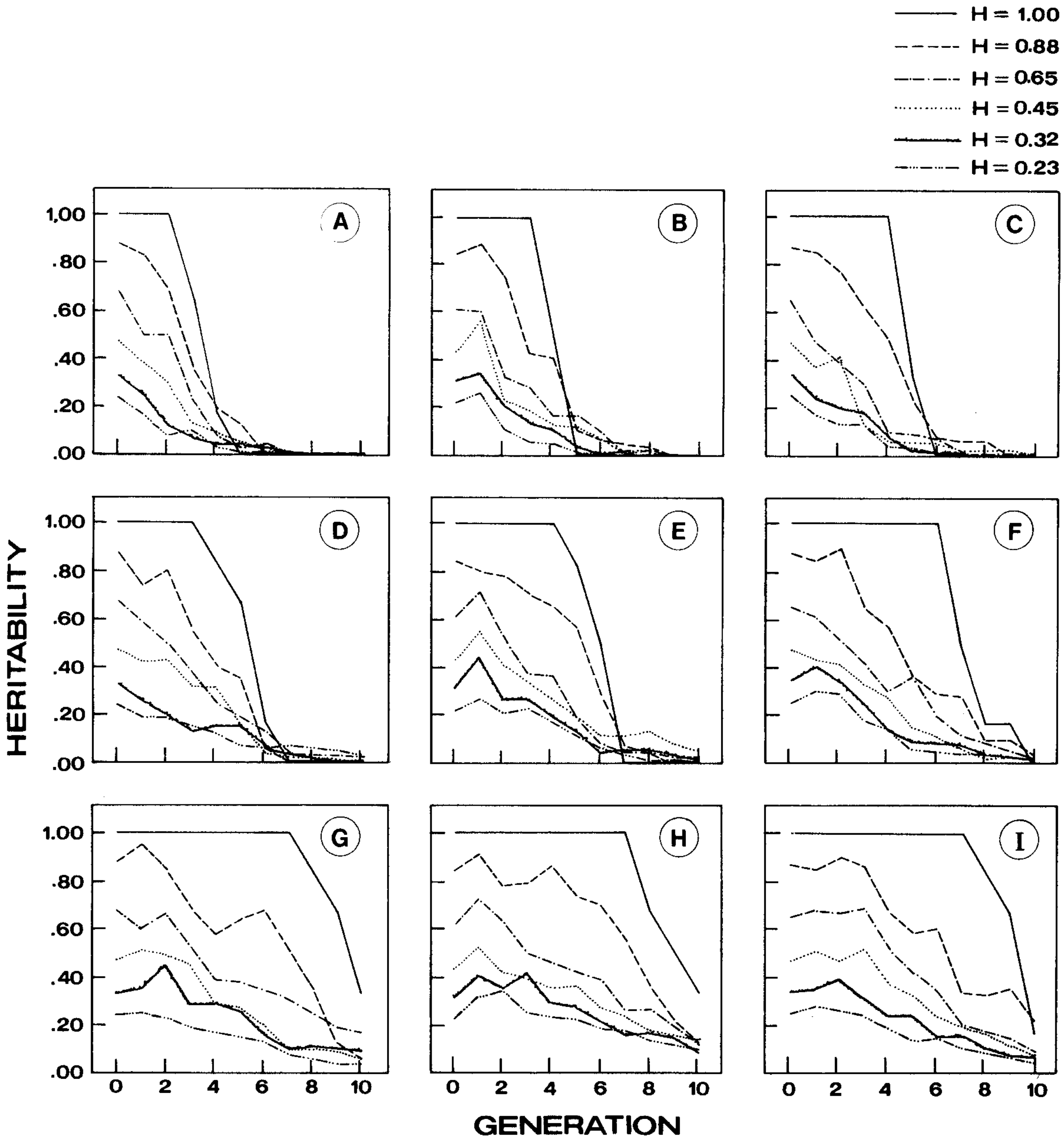

Fig.5. The effect of initial heritability (H) on the heritabilities, when no dominance is assumed and there are 40 individuals in each generation. A,D,G, 15 loci; B,E,H, 30 loci; C,F,I, 60 loci; A,B,C, selection intensity 0.05; D,E,F, selection intensity 0.20; G,H,I, selection intensity 0.50

and all replications) fixation occurred in generation 5.0, 5.9, 6.5, 7.3, 9.0 and 8.8, respectively, when 15 loci were assumed. When the number of loci was 30 or 60, fixation occurred in most cases after the tenth generation. In this case, the generation in which heritability reached 0.05 or less was 6.2, 6.3, 8.2 and 8.9, respectively, for P values of 0.05, 0.10, 0.20 and 0.25 (averaged over 30 and 60 loci, all H values and all replications). It was 7.4, 8.5, 8.3, 7.0, 7.0 and 6.3 for initial heritability values of 1.00, 0.88, 0.65, 0.45, 0.32 and 0.23, respectively (averaged over 30 and 60 loci, all P values except 0.50, and all replications). For P 0.50, heritability in the tenth generation was in most cases higher than 0.05.

Proportion of heterozygous loci

The proportion of heterozygous loci is expected to be 0.5 in the initial population, and 0.5^{n+1} in the n^{th} generation of selfing without selection. The results of our simulation indicated that selection caused some further reduction in the proportion of heterozygous loci in the population. Assuming the ratio of two successive generations to be q instead of 0.5, then the number of heterozygous loci in the n^{th} generation would be $0.5\,q^n$. The average values of this ratio were 0.459, 0.467, 0.483, 0.490 and 0.497 for selection intensities 0.05, 0.10, 0.20, 0.25 and 0.50, respectively. These values were on the average 0.458, 0.467, 0.468, 0.475, 0.497 and 0.497 for initial heritabilities of 1.00, 0.88, 0.65, 0.45, 0.32, and 0.23, respectively. Thus, a severe selection (low P) and a high initial heritability reduced the proportion of heterozygous loci under selection. There was no significant interaction between these two factors, and there was no appreciable effect of the number of loci.

Discussion

Effect of number of loci

When it was assumed that the trait, for which selection was practised, was controlled by a larger number of additive loci, the advance in the genotypic mean was found to be slower and the predicted limit of selection was lower when the results were expressed as percentage of the maximum theoretical limit. Similar results were reported by Bellmann and Ahrens (1966), who conducted simulation experiments on random-mating populations of 50 individuals under conditions of complete dominance and a selection intensity of 0.10. They found a slower advance under selection when 50 loci were assumed, than with 20 or 5 loci.

These results may be explained by the fact that when a larger number of loci contributes to a certain mean expression of a trait, the additive genetic variance is expected to be lower. When a quantitative trait is controlled by n loci having an equal additive effect a, the expected mean of the initial generation is

$$\overline{A} = na$$

and the expected additive standard deviation $s_a = \sqrt{\frac{na^2}{2}} = \overline{A}\sqrt{\frac{1}{2n}}$. Therefore, when the genotypic mean of the initial population ($\overline{A}$) is assumed to be constant, s_a would be expected to be smaller when n is larger. As the parameters were chosen in such a way that s_{po} (the initial phenotypic standard deviation) was proportional to s_a, the expected genetic advance under selection would be smaller when n is larger.

If the results are expressed in terms of the initial phenotypic standard deviation (s_{po}), it would be expected that similar responses to selection would be found regardless of the number of loci assumed to control the trait. The results for 30 and 60 loci were indeed found to be very similar on this basis, but when 15 loci were assumed there was a slower advance under selection and the predicted selection limit was lower. The lower response of 15 loci was evident from the first generation. The small number of loci brought about a faster decrease in additive variance and in heritability, thereby affecting the genetic advance in later generations more prominently.

Effect of selection intensity

A selection intensity of 0.05 gave the best results in all generations when 60 loci were assumed and the initial heritability was high. For lower initial heritabilities, a selection of 0.10 or 0.20 gave better or similar results after the fourth generation, and in some cases a selection of 0.25 resulted in a higher maximum possible advance. When a smaller number of loci was assumed to control the trait under selection, higher values of P were found to given better results in earlier generations. Therefore, when a larger number of loci is assumed, or when the initial heritability is high, a very intense selection (a smaller proportion, P, selected) would be expected to result in a better genetic advance for a larger number of generations. On the other hand, a high selection intensity was found to cause a strong decrease in genetical variance, heritability and heterozygosity and consequently an earlier occurrence of fixation.

Since a constant environmental variance was assumed, any change in heritability was associated with a change in the additive genetic variance. This variance would be expected to increase during the early generations, because of the decrease in heterozygosity brought about by selfing. On the other hand, finite population size and intensive selection tended to decrease this variance. It was found that in most cases the net effect was a decrease in heritability. However, an actual increase in heritability in the first and second generations was observed when the selection was less intense (P 0.50 or P 0.25) and 30 or 60 loci were assumed.

Bliss and Gates (1968) did not find a clear effect of selection intensity (o.25 as compared to 0.125) on the genetic gain under conditions of selfing in their simulation studies, but they found that the optimal selection intensity depended on the level of initial heritability. Robertson (1960) found that if individual selection for a quantitative trait is carried out from a constant number of random-mating individuals in each generation, the maximum advance at the limit is achieved when the best 0.50 are selected. Later, Robertson (1970) found that if selection is practised for t generations, the value of P (proportion selected) which gives the maximum response will be a function of t/T (where T is the number of individuals measured in each generation). He assumed that the change of genetic variance in time is determined only by inbreeding and is not affected by selection, and also that heritability is relatively low. The same trend, that the more generations selection is practised, the higher the optimum value of P, was found in our simulations, although those assumptions were not realized in our case and mating was not random.

Effect of initial heritability

When the initial heritability was 0.65 or less, the advance under selection was much slower and the maximum possible genetic advance was lower than when the initial heritability was high. This effect was less pronounced for traits controlled by many loci, or when a high proportion of individuals was selected. Bliss and Gates (1968) also found that when a more intense selection was practised (a lower proportion selected) the effect of heritability was more prominent.

The heritability after selfing and selection was affected significantly by the level of initial heritability up to the fourth generation, whereas in later generations this effect became much smaller. When the initial heritability was low, complete fixation occurred later. The decline in heterozygosity was faster when the initial heritability was higher.

Heritability (H) is often used to predict the advance under selection (ΔG) by the formula

$$\Delta G = iHs_p$$

where i is the standard selection differential and s_p the phenotypic standard deviation. This relationship is based on the assumptions of random mating and large populations. Although this formula is not applicable in our case, where selfing and small populations are assumed, the actual advance in the first generation was found to be very similar to the predicted ΔG when 30 or 60 loci were assumed. However, when 15 loci were assumed the actual advance in the first generation was considerably lower than the predicted ΔG. It was only 0.74, 0.77, 0.84, 088 and 0.99 of the predicted value when the selection intensity was 0.05, 0.10, 0.20, 0.25 and 0.50, respectively. It is impossible to predict the advance in later generations of selection because there was a considerable change in the magnitudes of H and s_p in each generation, caused by selfing, selection, and finite population size.

Implications for breeding methods

Selection under conditions of selfing causes a very fast decrease of heterozygosity and of genetic variance, especially when the heritability is high and the trait for which selection is practised is controlled by a relatively small number of loci. Consequently, the response to selection decreases earlier than under conditions of random mating.

Many practical breeding situations involve a trait controlled by many loci and, according to our findings, progress under selection is expected to be relatively slow in this case and only a small fraction of the possible potential genetic gain may be realized. For many economically important traits, relatively large environmental variances are encountered. We have found that under these conditions, the best advance during the first few generations would be obtained when a proportion of 0.05 is selected. However, under such an intense selection, genetic variance is lost very rapidly and therefore selection is effective for no more than three or four generations. On the other hand, when 0.10 to 0.25 of the population is selected, the initial progress is slower but better results are expected after more generations of selection. These conclusions are valid for a population size of 40 individuals, and it should be further investigated how different population sizes may modify them.

Under these conditions, two alternative procedures may be adopted by the plant breeder. He may practise intensive selection, say 0.05, for a few generations, and after that use another breeding method, such as intercrossing the best lines. Alternatively, he may practise less intensive selection, say 0.20, for a larger number of generations. It would be interesting to investigate the relative advantages of these alternative approaches under several genetic situations. Another problem that would be interesting to investigate is the effect of varying the selection intensity from one generation to another.

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Literature

Bellmann, K.; Ahrens, H.: Modellpopulationen in der Selektionstheorie und einige Ergebnisse aus Simulationsstudien. Züchter 36, 172-185 (1966)

Bliss, F.A.; Gates, C.E.: Directional selection in simulated populations of self-pollinated plants. Aust. J. Biol. Sci. 21, 705-719 (1968)

Curnow, R.N.; Baker, L.H.: The effect of repeated cycles of selection and regeneration in populations of finite size. Genet. Res. 11, 105-112 (1968)

Fraser, A.S.: Simulation of genetic systems by automatic digital computers. I. Introduction. Aust. J. Biol. Sci. 10, 484-491 (1957)

Fraser, A.; Burnell, D.: Computer models in genetics. New York: McGraw-Hill Book Co. 1970

Gill, J.L.: A Monte Carlo evaluation of predicted selection response. Aust. J. Biol. Sci. 18, 999-1007 (1965)

Griffing, B.: Theoretical consequences of truncation selection based on the individual phenotype. Aust. J. Biol. Sci. 13, 307-343 (1960)

Hill, W.G.: On the theory of artificial selection in finite populations. Genet. Res. 13, 143-163 (1969)

Kojima, K.: Effects of dominance and size of population on response to mass selection. Genet. Res. 2, 177-188 (1961)

Pederson, D.G.: The prediction of selection response in a self-fertilizing species. I. Individual selection. Aust. J. Biol. Sci. 22, 117-129 (1969)

Robertson, A.: A theory of limits in artificial selection. Proc. Roy. Soc. (London) B153, 234-249 (1960)

Robertson, A.: Some optimum problems in individual selection. Theoret. Pop. Biol. 1, 120-127 (1970)

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