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Effect of Various Parameter Combinations on Genetic Gain in Computer Simulated Two-Character Selection

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Summary. In a simulation study, the effect of various parameter combinations such as linkage, dominance, heritability, and economic weights on the individual trait means was investigated using additive genetic, genotypic and the phenotypic index of Elston (1963). The characters responded differently to these indices under various parameter combinations, indicating favourable and unfavourable effects of the mentioned parameters. Linkage was found to reduce the rate of progress through selection. Depression of genetic gain was greater where the genes governing a character showed dominance and/or heritability coefficients were low. It was, however, noticed that depression of genetic gain due to low heritability of a character could be avoided by assigning higher economic weight to that character. This suggests that desirable changes in the means of characters available for selection can be manipulated by choosing appropriate economic weights. The additive genetic index, where only the additive genetic variances and covariances go into its construction, does not seem to be affected by intra-allelic interactions since they add to variances and covariances due to dominance deviations and these have nothing to do with the additive genetic variances and covariances. It seems that from such studies, if conducted extensively incorporating still more parameters, conclusions may be drawn on the most suitable selection model for simultaneous selection under a given set of parameters available in real biological systems.

Introduction

In breeding, the simultaneous selection of several characters through selection indices is becoming important. The superiority of the selection index over other methods of selection has already been established through theoretical studies (Hazel and Lush, 1942; Cochran, 1951; Young and Weiller, 1961; and Singh, 1972). Studies have often been made of the expected genetic advance based on actual data, but reports are not available which advocate the genetic gains observed in practice through the use of selection indices. Recently, Singh (1972) discussed the problems associated with the construction and application of selection indices and made some suggestions to overcome such problems. For example, one objection to the application of selection indices is that individual traits are lost sight of during simultaneous selection. Furthermore, the effects of many genetic and non-genetic factors, such as linkage associations between the loci governing the traits, dominance, different economic weights assigned to the various traits and heritability, on the efficiency of different models of selection index remain unexplained. Therefore, an understanding of the performance of different types of indices, in terms of the changes that they bring about in individual trait means under various parameter combinations, needs immediate attention. Such knowledge may help in finding the best selection model under a given set of parameters for a population. Accordingly, the present investigation was undertaken to study the effect of linkage, dominance behaviour of alleles at different loci, different economic weights and different heritabilities on individual trait means during simultaneous selection.

2. Experimental Procedure

A model population was developed on computer, assuming $2n = 8$ chromosomes. For each chromosome, the presence of four loci was considered, two governing the character x and the other two governing character y. For all the loci held responsible for x, complete dominance was assumed. The loci governing y were assumed to have no dominance. Different degrees of linkage and heritability were considered. This assumed biological system was simulated following the technique of Bellmann and Ahrens (1966) and Singh *et al.* (1967). Three different selection indices were constructed and used for selection in this population:

$I^{(A)}$ – additive genetic index (only the additive genetic variances and covariances were used for construction)

$I^{(G)}$ – genotypic index (total genotypic variances and covariances were used for index construction)

$I_E^{(P)}$ – phenotypic index (an index given by Elston 1963, having the following form:
$I_E^{(P)} = \Pi\,(P_i - K_i)$ where P_i is the i^{th} measurement on an individual and K_i the lowest measurement in the series of i^{th} measurements).

The first two indices were constructed according to the method described by Henderson (1963).

The various treatment combinations studied in this investigation are given in Table 1. In this table, r stands for the recombination frequency: h_x^2 and h_y^2 were the heritabilities; $\underline{a}(\frac{1}{1})$ means that both the traits, x and y, had equal economic weights, whereas in $\underline{a}(\frac{1}{4})$ character x was weighted four times to y. In variant 1, $h_x^2 = h_y^2 = 0.8$, whereas in variants 2 and 3, $h_x^2 = 0.2$ and $h_y^2 = 0.8$.

Table 1. *Details of parameter combinations (variants*) examined in the present investigation*

Indices	Variant 1 $(h_y^2 = h_x^2;\ \underline{a}(\frac{1}{1}))$			Variant 2 $(h_y^2 > h_x^2;\ \underline{a}(\frac{1}{1}))$			Variant 3 $(h_y^2 > h_x^2;\ \underline{a}(\frac{1}{4}))$
	$r = 0.005$	0.05	0.5	0.005	0.05	0.5	0.05
$I^{(A)}$	×	×	—	×	×	—	×
$I^{(G)}$	×	×	×	×	×	×	×
$I_E^{(P)}$	×	×	—	×	×	—	—

* Only the variants with the multiplication signs (×) have been studied.

Table 2. *Maximum genetic gain (ΔG) obtained in x and y during simultaneous selection through selection indices*

Indices	Variant 1				Variant 2				Variant 3	
	$r = 0.005$		0.05		0.005		0.05		0.05	
	ΔG_x	ΔG_y	ΔG_x	ΔG_y	ΔG_x	ΔG_y	ΔG_x	ΔG_y	ΔG_x	ΔG_y
$I^{(A)}$	3.639	7.860	7.481	7.729	−1.20	8.00	3.51	8.00	7.55	5.84
$I^{(G)}$	3.987	7.359	7.120	7.740	−1.55	8.00	2.75	8.00	7.01	6.57
$I_E^{(P)}$	3.303	6.536	5.300	7.700	−1.91	7.88	3.94	8.00	—	—

3. Results

a. The Maximum Genetic Gain in x and y

Maximum genetic gain (ΔG) obtained during the selection in x and y are given in Table 2. From the data it is clear that:

1) In variant 1 when the case of loose linkage ($r = 0.05$) was considered, the gains achieved in characters x and y were similar for both the indices $I^{(A)}$ and $I^{(G)}$. The improvement in the mean of y was, however, higher than for x for the index $I_E^{(P)}$.

2) For both the cases of linkage in variant 2 and for tight linkage ($r = 0.005$) in variant 1, the improvement in character y was significantly greater than in character x.

3) In variant 3, where only the two indices, $I^{(A)}$ and $I^{(G)}$ were considered for loose linkage ($r = 0.05$), the genetic gain in x was higher than in y.

It is apparent from these results that the two characters, x and y, responded differently during index selection. The reason for this differential response could be assigned to individual or combined effects of the following factors:

i) varying degrees of linkage.
ii) presence or absence of dominance.
iii) differences in heritability of the characters.
iv) different economic weights assigned to the characters.

b. Effect of Linkage

First-hand information on the effect of linkage can be obtained from Table 2 by comparing genetic gains observed in x and y for loose linkage ($r = 0.05$) with the gains observed for tight linkage ($r = 0.005$). This comparison could, however, be made for variants 1 and 2 only, because in variant 3 only the loose linkage was considered. It was quite obvious from the data that genetic gain in x was invariably less in tight linkage than in loose linkage. This was true for both variant 1 and variant 2, irrespective of the type of selection index used. For genetic gain in y, all indices behaved in a similar manner and linkage seemed to have no effect. Genetic gains in both loose and tight linkages were almost the same.

The data presented in Table 2 provided information about total genetic gain observed in individual characters for those generations in which at least one of the traits had reached its maximum or near maximum. These values are not directly comparable as they have not been recorded for the same generation. The following ratios were, therefore, calculated for each generation and used as a measure of linkage effect on genetic gain:

$$R_x = \frac{\overline{Ph}_x(0.005)}{\overline{Ph}_x(0.05)} \times 100 \quad \text{and}$$

$$R_y = \frac{\overline{Ph}_y(0.005)}{\overline{Ph}_y(0.05)} \times 100\,.$$

Here $\overline{Ph}_x$ and $\overline{Ph}_y$ were the phenotypic means in x and y, respectively, and 0.005 and 0.05 the recombination frequencies.

The above expressions denote the relative means of traits in tight linkage compared with loose linkage. R_x and R_y-values have been plotted against each generation in Fig. 1. From these figures the following points were obvious::

1) R_y-values were higher than R_x-values in indices $I^{(G)}$ and $I_E^{(A)}$. This means that, although both the characters x and y were affected by tight linkage, the depression of genetic gain in x was strikingly greater than in y.

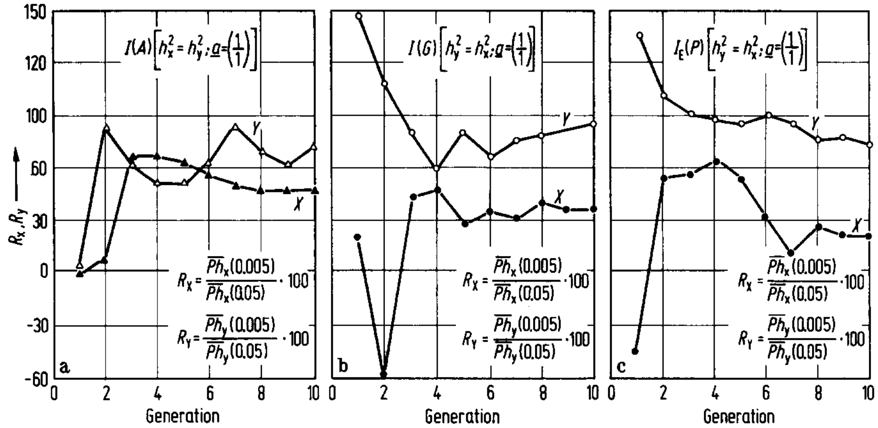

Fig. 1. Effect of linkage on genetic gain in absence (I^A) and presence of dominance [$I^{(G)}$ and $I_E^{(P)}$]

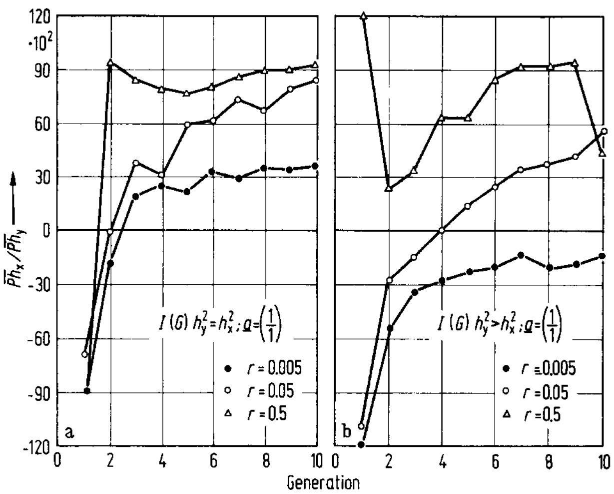

Fig. 2. Combined effect of linkage and dominance on genetic gains during selection

2) The range of R_x-values in $I^{(A)}$ was 50 to 70 per cent compared with the range of 30 to 40 per cent in $I^{(G)}$ and 0 to 62 percent in $I_E^{(P)}$. Furthermore, in the case of $I_E^{(P)}$, the values were mostly below 30 per cent except in generations 2 to 5. This clearly indicated that depression in genetic gain of x due to tight linkage was greater in $I^{(G)}$ and $I_E^{(P)}$ than in $I^{(A)}$.

3) In the case of index $I^{(A)}$, R_x and R_y-values were almost in the same range indicating that the two characters were almost equally affected by linkage depression.

c. Combined Effect of Dominance and Linkage

To evaluate the combined effect of linkage and dominance, the relative improvement in x against the gain in y, i.e. $\frac{\overline{Ph}_x}{\overline{Ph}_y} \times 100$, was plotted for each generation in Fig. 2. These ratios were calculated only up to the tenth generation because, in many of the cases in this investigation, one of the characters reached its maximum in this very generation. It was, therefore, thought proper to select the 10th generation for all cases of comparison.

The gain in x compared with y was less in the case of tight linkage than in loose linkage of variant 1 (Fig. 2a). Furthermore, there was a successive increase in the relative improvement of x with each generation, though the rate of improvement in loose linkage was faster than in tight linkage. The relative change in the mean of x to y for free recombination ($r = 0.5$) was the highest of all the cases examined here (Fig. 2a). From the second generation onward to the 10th generation, the $\overline{Ph}_x/\overline{Ph}_y$. 100-values fell in the range of 80 to 95 per cent. In general, it appeared that with a successive increase in the degree of linkage, there was a corresponding decrease in the relative improvement of x to y. In other words, the change in mean of the character x, being governed by genes showing dominance, becomes less with an increase in the degree of linkage.

A similar trend could be observed in variant 2 (Fig. 2b) also. Here the change in mean of x was more adversely affected than in variant 1. Throughout the selection period, i.e. up to the 10th generation, the mean of x remained in the range of negative values for

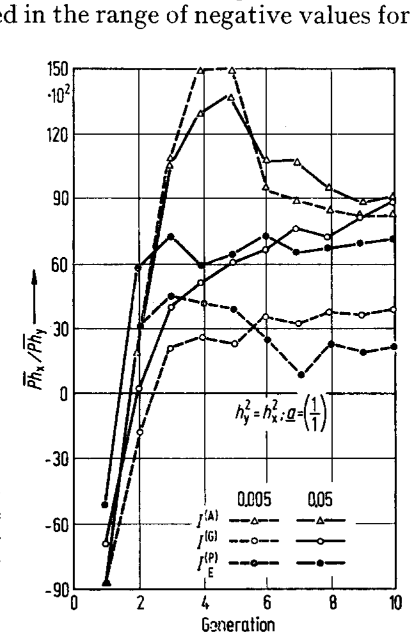

Fig. 3. Effect of linkage and dominance on comparative performances of selection indices

tight linkage ($r = 0.005$). Even with loose linkage ($r = 0.05$), positive values could be achieved only after the 5th generation and a level of about 60 per cent could be attained in the tenth generation. So far as free recombination was concerned, the relative gain in x fell mostly in the range of 30 to 90 per cent.

Fig. 3 provides a direct comparison of three indices in variant 1 for two degrees of linkage (i.e. $r = 0.005$ and $r = 0.05$) with respect to relative changes in x and y. As the characters had equal heritabilities and, at the same time, were assigned equal economic weights, the differential improvement in x and y (i.e. deviation of $\overline{Ph}_x/\overline{Ph}_y$-values from 100) may be due either to intralocus interactions or to the combined effect of linkage and dominance. For index $I^{(A)}$, where only the additive genetic variances and covariances were required to construct the index, the dominance behaviour of alleles at the loci governing character x had nothing to contribute to the variances and covariances. Consequently, the behaviour of the ratio, $\overline{Ph}_x/\overline{Ph}_y \times 100$, was similar in both loose and tight linkages. From generations 3 to 5 the ratios were higher for tight linkage, whereas from generations 6 to 10, they were higher for loose linkage. This randomness may be attributed to the random nature of the selection process. Further more, the ratios for $I^{(A)}$ were greater than those for $I^{(G)}$ and $I_E^{(P)}$ for loose as well as for tight linkage. The indices $I^{(G)}$ and $I_E^{(P)}$ were, however, able to bring about more genetic advance in x compared with y in the presence of loose linkage. For none of these indices was the ratio greater than 40 per cent in tight linkage, whereas in loose linkage the values were mostly in the range of 60 per cent (after the 4th generation).

The conclusion, drawn from these results are: (i) the genetic gain is adversely affected both by linkage and dominance; (ii) the depression effect of dominance on genetic gain becomes greater where linkage also becomes tighter; and (iii) the additive genetic index remains free from such depression, provided that other factors are not operative.

d. Combined Effect of Linkage, Dominance and Heritability

Comparing Fig. 2a with Fig. 2b, it is obvious that in variant 2, compared with variant 1, the change in mean of x is even less. This further depression in genetic gain of x may be interpreted as due to an additional factor of low heritability. The heritability of x in variant 2 was only 0.2, compared with 0.8 for that of y. It is clear that tight linkage, intra-locus interaction and low heritability reduce the selection gain and, consequently, affect the efficiency of the selection index.

e. Effect of Different Economic Weights

To find out the effect of unequal economic weights on the individual trait means during selection, variant 3 was studied together with variant 2 (Fig. 4a and b).

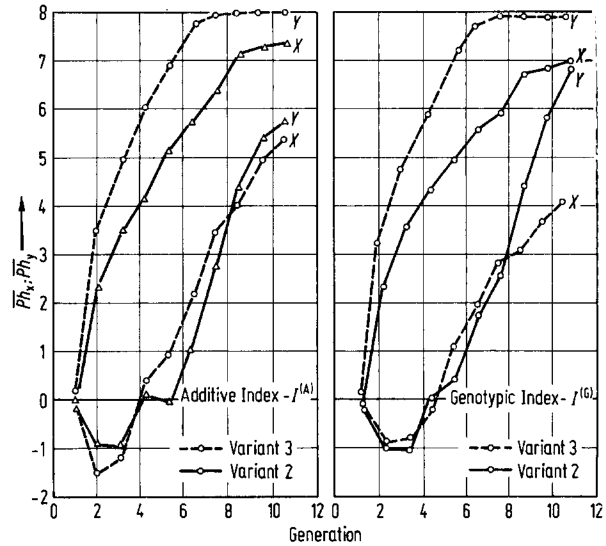

Fig. 4. Change in means of x and y during simultaneous selection using different economic weights

In both cases, heritability coefficients of y were higher than those of x. However, in variant 3 the character x was weighted four times with respect to y, whereas in variant 2, x and y were equally evaluated i.e. $\underline{a}\binom{1}{1}$.

It is evident from Fig. 4 a and b that the rate of change in the mean x for variant 2 was slower than in y, both for $I^{(A)}$ and $I^{(G)}$. The genetic gain achieved in x in the tenth generation could reach up to 56 per cent and 69 per cent of the maximum by $I^{(G)}$ and $I^{(A)}$, respectively. On the other hand, the maximum genetic gain in y (i.e. 100%) was achieved as early as the 7th generation by both indices. In contrast, for variant 3, where the character x was weighted four times with respect to y, the gain in the mean of x was much faster than in y. This was true both for $I^{(A)}$ and $I^{(G)}$. It thus appears that the genetic gain in a character having low heritability can be enhanced by assigning higher economic weight to that character.

4. Discussion

Effectiveness of selection in a population depends on the amount of genetic variability present. This genetic variability is generally reflected in terms of the heritability coefficients of the characters under study. Genetic variability, in turn, depends on the relative proportions of heterozygotes and homozygotes, and the release of variability is associated with the strength of linkage between the loci governing different characters. The aim of simultaneous selection in bringing about harmonious development of all the characters may, therefore, be affected by a number of factors, such as heritability, dominance, linkage, and economic weighting. It is evident from the results discussed here and also from the results of other investigations (Fraser, 1960; Martin and Cockerham, 1960; Gill, 1965; Qureshi and Kempthorne, 1968; and others) that an increase in the degree of linkage is associated with a decrease in genetic gain. It may be that the release of variability available for selection becomes less with higher degrees of linkage. Depression in genetic gain is still more where the character concerned is governed by loci showing dominance. Similar observations have also been made by Bellmann and Ahrens (1966), Singh *et al.* (1967) and Hill (1970).

Reduction in genetic gain due to low heritability is easy to explain. Genetic gain is known to be a function of heritability and selection differential. As heritability describes the relative proportion of genetic variance to phenotypic variance, low heritability would mean less genetic variability available for selection. It seems, however, plausible to avert the depression on genetic gain due to low heritability by assigning higher economic weight to the character concerned. There is no genetic explanation for this phenomenon. It is simply a mathematical manipulation which provides a higher b-value for a character which otherwise would have been rated low. This is done by taking a-times the variances and covariances associated with that character, while estimating the b-values from a formul $a\sum b_i P_{ij} = \sum a_i G_{ij}$ which provides the estimates of b-values in such a manner that the correlation between index and the "Merit" (breeding value) of an individual becomes maximum (Henderson, 1963).

Although no reports are available in the literature indicating the effect of different parameter combinations on the individual trait means during simultaneous selection, the effect of some of the parameters, such as linkage, size of the populations, number of loci governing a character, dominance etc., have been worked out through simple simulation selection experiments (Bellmann and Ahrens, 1966, Singh *et al.* 1967; Jain and Allard, 1966; Lewontin, 1965; and Hill and Robertson, 1966 etc.). These results have also indicated the favourable and unfavourable effects of these parameters, separately and in combinations, on the genetic gain. This means that the gain expected under a particular set of parameters could be predetermined and, accordingly, a suitable selection model could be formulated. Further studies are, therefore, strongly recommended as the information thus collected might be used as a guideline for choosing the most efficient selection model for a given population.

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