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Index versus tandem selection after repeated generations of selection

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Summary. A theoretical comparison between two multiple-trait selection methods, index and tandem selection, after several generations of selection was carried out. An infinite number of loci determining the traits, directional and truncation selection, discrete generations and infinite population size were assumed. Under these assumptions, changes in genetic parameters over generations are due to linkage disequilibrium generated by selection. Changes continue for several generations until equilibrium is approached. Algebraic expressions for asymptotic responses from index selection can be derived if index weights are maintained constant across generations. Expressions at equilibrium for genetic parameters and responses are given for the index and its component traits. The loss in response by using initial index weights throughout all generations, instead of updating them to account for changes in genetic parameters, was analyzed. The benefit of using optimum weights was very small ranging from 0% to about 1.5% for all cases studied. Recurrence formulae to predict genetic parameters and responses at each generation of selection are given for both index and tandem selection. A comparison between expected response in the aggregate genotype at equilibrium from index and tandem selection is made considering two traits of economic importance. The results indicate that although index selection is more efficient for improving the aggregate breeding value, its relative efficiency with respect to tandem selection decreases after repeated cycles of selection. The reduction in relative efficiency is highest with the highest selection intensity and heritabilities and with negative correlations between the two traits. The advantage of index over tandem selection might be further reduced if changes in genetic parameters due to gene frequency changes produced by selection, random fluctuations due to the finite size of the population, and errors in estimation of parameters, were also considered.

Key words: Selection index – Tandem selection – Multiple selection – Linkage disequilibrium

Introduction

In multiple-trait selection, use of a selection index is expected to be more efficient than tandem selection (Hazel and Lush 1942; Young 1961; Finney 1962). Theoretical comparisons among multiple-trait selection methods have been carried out by considering expected responses in the first generation of selection. However, if selection is continued for more than one generation, expected responses change because of changes in genetic parameters induced by selection. Consequently the relative efficiencies of different methods can be altered.

Changes in genetic parameters by selection are due to linkage disequilibrium and gene-frequency changes. Bennett and Swiger (1980) examined the effects of both causes on changes in genetic variance and correlation under three different two-trait selection methods (index, independent culling levels, and extreme selection). Results from their simulations showed that index selection gave the highest rates of response through 14 generations of selection.

In the early generations of selection most change in genetic parameters is due to the linkage disequilibrium generated by selection, which is the only cause if

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the number of loci and population size are infinite (Bulmer 1971, 1980). Under these assumptions genetic parameters approach equilibrium values after few generations. Several studies (Wray and Hill 1989; Dekkers 1990; Villanueva and Kennedy 1991) have compared theoretically different methods of selection for improvement of a single trait at the equilibrium. The relative efficiency of these methods at the equilibrium, and in some cases their ranking, changed with respect to that expected in the first generation of selection.

In the present study, the relative efficiency of two multiple-trait selection methods (tandem and index selection) was compared at equilibrium where expected rates of response to selection have reached their limiting values. This is illustrated for the situation of joint selection for improvement of two traits. An infinitesimal genetic model and a population of infinite size with discrete generations was assumed. Theoretically, index weights should be recalculated for each generation of selection in order to account for changes in genetic parameters. However, in practice, first generation index weights are often used across generations. The theoretical gain in efficiency by using an optimum index for each generation was investigated for a range of parameters.

Index selection

Consider that economic value depends linearly on n traits. Then the aggregate breeding value (H) of an individual is given by $H=\mathbf{a}'\mathbf{g}$, where $\mathbf{a}'$ is a $1\times n$ row vector of relative economic values and $\mathbf{g}$ is a $n\times 1$ column vector of additive genetic values. Improvement in H is achieved by selecting individuals on the basis of the index $I=\mathbf{b}'\mathbf{p}$, where $\mathbf{b}'$ is a $1\times n$ row vector of weighting factors and $\mathbf{p}$ is a $n\times 1$ column vector of phenotypic values. For simplicity, the traits included in the aggregate genotype are assumed to be the same as those included in the index, with only one observation recorded on each trait. Index weights are obtained from the usual selection index equations, $\mathbf{b}=\mathbf{P}^{-1}\mathbf{G}\mathbf{a}$ where $\mathbf{P}$ is a $n\times n$ variance–covariance matrix of phenotypic measures of traits and $\mathbf{G}$ is a $n\times n$ genetic variance–covariance matrix among traits. Directional and truncation selection on the index is practised and selected individuals are randomly mated.

Genetic parameters and responses at generation t

Because genetic parameters change with selection, recalculation of the weighting factors in the index at each generation of selection has been proposed by several authors (e.g., Lin 1978; Caballero 1989; Wray and Hill 1989). The optimum weights at any generation t are obtained from $\mathbf{b}_t=\mathbf{P}_t^{-1}\mathbf{G}_t\mathbf{a}$ where $\mathbf{P}_t$ and $\mathbf{G}_t$ are respectively the phenotypic and genetic variance–covariance matrices at generation t.

Genetic variances and covariances needed to construct the G_t and P_t matrices can be obtained using expressions given by Villanueva and Kennedy (1990), which are based on results obtained by Pearson (1903) and Bulmer (1971). Selection based on the index can be considered as a case of selection on a single trait and the traits included in the index can be considered as correlated traits indirectly selected. The genetic variance of any trait included in the index ($\sigma^2_{G_i}$, $i=1,2,\ldots,n$) at generation t is given by

$$\sigma^2_{G_i(t)}=\sigma^2_{G_i(t-1)}[1-(1/2)r^2_{G_iI(t-1)}k] \\ +(1/2)[\sigma^2_{G_i(0)}-\sigma^2_{G_i(t-1)}] \tag{1}$$

where the subscripts in brackets represent generation number, r_{G_iI} is the coefficient of correlation between the genetic value of trait i and the index and k is $i(i-x)$ where i is the standardized intensity of selection and x the standardized deviation of the truncation point from the population mean for the index. The first part of the right-hand side in Eq. (1), $\sigma^2_{G_i(t-1)}[1-(1/2)r^2_{G_iI(t-1)}k]$, refers to the new disequilibrium induced by selection in generation $t-1$ whereas the second part, $(1/2)[\sigma^2_{G_i(0)}-\sigma^2_{G_i(t-1)}]$, corresponds to the recovery of the variance due to free recombination. If selection intensity differs in both sexes, then $k=0.5(k_m+k_f)$, where subscripts m and f refer to males and females, respectively. Equation (1) is equivalent to

$$\sigma^2_{G_i(t)}=(1/2)\sigma^2_{G_i(t-1)}[1-r^2_{G_iI(t-1)}k]+(1/2)\sigma^2_{G_i(0)}$$

which relates to the decomposition of the variance into between- and within-family components. The between-family component is reduced each generation of selection by a factor $r^2_{G_iI(t-1)}k$ whereas the within-family component is unaffected by selection.

The genetic covariance between two traits i and j included in the index (genetic covariance between two traits indirectly selected) at any generation t can be obtained from

$$\sigma_{G_iG_j(t)}=\sigma_{G_iG_j(t-1)}-(1/2)r_{G_iI(t-1)}r_{G_jI(t-1)}\sigma_{G_i(t-1)} \\ \times\sigma_{G_j(t-1)}k+(1/2)[\sigma_{G_iG_j(0)}-\sigma_{G_iG_j(t-1)}] \tag{2}$$

Phenotypic (co)variances can be obtained simply by adding to the genetic (co)variances the corresponding environmental (co)variances. The latter are assumed constant across generations.

The value of r_{G_iI} at any generation t is

$$r_{G_iI(t)}=\frac{\sigma_{G_iI(t)}}{\sigma_{G_i(t)}\sigma_{I(t)}}$$

where σ_{G_iI} is the covariance between the genotypic value of trait i and the index and σ_I is the standard deviation of the index. If genotype-environment covariances are null then σ_{G_iI} at each generation is equal to the covariance between the genotypic value of trait i and the genetic index ($\sigma_{G_iG_I}$) as defined by Lin and Allaire (1977). Then, $\sigma_{G_iI(t)}$ can be obtained using the expression for the genetic covariance between the given trait under direct and another trait under indirect selection:

$$\begin{aligned}\sigma_{G_iI(t)} &= \sigma_{G_iG_I(t)}\\ &= \sigma_{G_iG_I(t-1)}[1-(1/2)h^2_{I(t-1)}k]\\ &\quad +(1/2)[\sigma_{G_iG_I(0)}-\sigma_{G_iG_I(t-1)}] \qquad (3)\end{aligned}$$

where h^2_I is the heritability of the index.

The variance of the index (σ^2_I) in generation t is

$$\sigma^2_{I(t)} = \mathbf{b}'_t\mathbf{P}_t\mathbf{b}_t. \qquad (4)$$

The genetic variance and heritability of the index are defined following Lin and Allaire (1977) and Nordskog (1978):

$$\begin{aligned}&\sigma^2_{G_I(t)} = \mathbf{b}'_t\mathbf{G}_t\mathbf{b}_t\\ &h^2_{I(t)} = \sigma^2_{G_I(t)}/\sigma^2_{I(t)} = \mathbf{b}'_t\mathbf{G}_t\mathbf{b}_t/\mathbf{b}'_t\mathbf{P}_t\mathbf{b}_t. \qquad (5)\end{aligned}$$

These two parameters relate to the concept of genetic index introduced by Lin and Allaire (1977).

Expected response to selection in aggregate breeding value per generation is

$$R_{H(t)} = i\sigma_{HI(t-1)}/\sigma_{I(t-1)}$$

where σ_{HI} is the covariance between the aggregate breeding value and the index which is given by

$$\sigma_{HI(t)} = \mathbf{b}'_t\mathbf{G}_t\mathbf{a}$$

if there are no genotype-environment covariances. The expected genetic response per generation of the ith trait is

$$R_{i(t)} = i\sigma_{G_iI(t-1)}/\sigma_{I(t-1)}.$$

Although the optimum weights of the index are those obtained by accounting for the effects of selection, in practice initial weights are used through successive generations of selection. In this case the total (σ^2_I) and genetic ($\sigma^2_{G_I}$) variances of the index at any generation t can be obtained recurrently from the expressions derived by Bulmer (1971) for the phenotypic and genetic variances of a trait under direct selection:

$$\begin{aligned}\sigma^2_{I(t)} &= \sigma^2_{I(t-1)}[1-(1/2)h^4_{I(t-1)}k]\\ &\quad +(1/2)[\sigma^2_{I(0)}-\sigma^2_{I(t-1)}] \qquad (6)\end{aligned}$$

and

$$\begin{aligned}\sigma^2_{G_I(t)} &= \sigma^2_{G_I(t-1)}[1-(1/2)h^2_{I(t-1)}k]\\ &\quad +(1/2)[\sigma^2_{G_I(0)}-\sigma^2_{G_I(t-1)}]. \qquad (7)\end{aligned}$$

These expressions are based on the assumption that the difference between total and genetic variance of the index is constant across generations; i.e., $\sigma^2_{I(t)}-\sigma^2_{G_I(t)} = \sigma^2_{I(t-1)}-\sigma^2_{G_I(t-1)}$, which does not occur if index weights are optimized each generation. Therefore, (6) and (7) are equivalent to (4) and (5) respectively only if index weights are constant across generations.

Table 1 shows the expected response per generation in the aggregate genotype at equilibrium from using optimum weights each generation ($R^*_{H(L)}$) as a proportion of the expected response from using initial index weights across generations ($R_{H(L)}$). Only two traits were considered of economic importance. Several initial heritabilities for the two traits and several initial phenotypic ($r_{P_1P_2(0)}$) and genetic correlations ($r_{g_1g_2(0)}$) between the traits were considered. Phenotypic and

Table 1. Ratio of expected response per generation in H at equilibrium from index selection using optimum weights to response in H using initial weights, $R^*_{H(L)}/R_{H(L)}$, for several combinations of initial phenotypic and genetic correlations, $r_{P_1P_2(0)} = r_{G_1G_2(0)}$, heritabilities, $h^2_{1(0)}$ and $h^2_{2(0)}$, relative economic weights, **a**′, and selected proportion of individuals, p

$r_{G_1G_2(0)}$	$h^2_{1(0)}$	$h^2_{2(0)}$	p = 1%			p = 50%		
			a′ = (1 1)	**a**′ = (1 2)	**a**′ = (1 3)	**a**′ = (1 1)	**a**′ = (1 2)	**a**′ = (1 3)
0.8	0.2	0.5	1.0025	1.0015	1.0011	1.0014	1.0009	1.0007
	0.5	0.2	1.0025	1.0039	1.0048	1.0014	1.0023	1.0028
0.5	0.2	0.5	1.0034	1.0017	1.0011	1.0020	1.0010	1.0007
	0.5	0.2	1.0034	1.0056	1.0066	1.0020	1.0034	1.0040
0.2	0.2	0.5	1.0034	1.0014	1.0008	1.0020	1.0008	1.0005
	0.5	0.2	1.0034	1.0056	1.0056	1.0020	1.0034	1.0034
0.0	0.2	0.5	1.0035	1.0012	1.0005	1.0021	1.0007	1.0003
	0.5	0.2	1.0035	1.0055	1.0045	1.0021	1.0033	1.0027
−0.2	0.2	0.5	1.0038	1.0010	1.0004	1.0023	1.0006	1.0002
	0.5	0.2	1.0038	1.0053	1.0028	1.0023	1.0032	1.0017
−0.5	0.2	0.5	1.0049	1.0006	1.0001	1.0029	1.0004	1.0001
	0.5	0.2	1.0049	1.0036	1.0000	1.0029	1.0022	1.0000
−0.8	0.2	0.5	1.0077	1.0001	1.0000	1.0046	1.0001	1.0000
	0.5	0.2	1.0077	1.0073	1.0153	1.0046	1.0045	1.0092

genetic correlations were assumed to be equal. Also different relative economic weights were investigated. Initial genetic variance was the same for each trait, and environmental variance was varied to give heritabilities of 0.2 or 0.5. The intensities of selection practised corresponded to selected proportions of 1% and 50%.

The advantage of updating the index each generation over maintaining it constant increases with selection intensity. When genetic correlations are equal to phenotypic correlations there is no benefit if heritabilities of both traits are equal. In this case, $\mathbf{b}_t = h_t^2 \mathbf{a}$ where $h_t^2 = h_{1(t)}^2 = h_{2(t)}^2$ and $R_{H(L)}^* = R_{H(L)}$ even when genetic parameters are changing. If heritabilities are unequal and both traits have equal economic weights, the advantage of updating the index is greater with negative correlations (Table 1). If the two traits have different economic importance, the benefit of using optimum weights each generation is, in general, greatest when the most important trait has the lowest heritability. The percentage increase in the response in the aggregate genotype by accounting for the effects of selection is in general very small and ranges from 0% to 1.53% for the parameters considered. This result agrees with Gomez-Raya and Burnside (1990a) who developed a procedure to obtain optimum index weights which maximize response at the equilibrium.

Genetic parameters and responses at equilibrium

If weighting factors of the index are maintained constant throughout all generations of selection, expressions for the limiting values of the genetic parameters and responses can be obtained easily. Updating index weights to account for changes in genetic parameters is probably not worthwhile because, in most cases, the increase in response is insignificant.

The genetic variance ($\sigma_{G_I(L)}^2$) and heritability ($h_{I(L)}^2$) of the index at equilibrium can be obtained from:

$$\sigma_{G_I(L)}^2 = \frac{\sigma_{G_I(0)}^2}{1 + h_{I(L)}^2 k}$$

and

$$h_{I(L)}^2 = \frac{-1 + \sqrt{1 + 4h_{I(0)}^2 k[1 - h_{I(0)}^2]}}{2k[1 - h_{I(0)}^2]}$$

(Gomez-Raya and Burnside 1990b). The limiting value of the genetic variance of trait i ($\sigma_{G_i(L)}^2$) can be obtained from (1) by putting $\sigma_{G_i(t-1)}^2 = \sigma_{G_i(t)}^2 = \sigma_{G_i(L)}^2$ and is given by

$$\sigma_{G_i(L)}^2 = \frac{\sigma_{G_i(0)}^2}{1 + r_{G_iI(L)}^2 k}.$$

The value of r_{G_iI} at equilibrium is

$$r_{G_iI(L)} = \frac{\sigma_{G_iI(L)}}{\sigma_{G_i(L)} \sigma_{I(L)}}.$$

Expressions for $\sigma_{G_iI(L)}$ and $\sigma_{I(L)}^2$ are:

$$\sigma_{G_iI(L)} = \frac{\sigma_{G_iI(0)}}{1 + h_{I(L)}^2 k}$$

and

$$\sigma_{I(L)}^2 = \frac{\sigma_{I(0)}^2}{1 + h_{I(L)}^4 k}$$

which can be derived from (3) and (6) respectively.

If environmental variances are constant in successive generations, the heritability of trait i at equilibrium ($h_{i(L)}^2$) is

$$h_{i(L)}^2 = \frac{h_{i(0)}^2}{1 + r_{G_iI(L)}^2 k[1 - h_{i(0)}^2]}.$$

From (2) the limiting value of the covariance between two traits included in the index is

$$\sigma_{G_iG_j(L)} = \sigma_{G_iG_j(0)} - r_{G_iI(L)} r_{G_jI(L)} \sigma_{G_i(L)} \sigma_{G_j(L)} k$$

and the limiting value of the genetic correlation between them is

$$r_{G_iG_j(L)} = r_{G_iG_j(0)}[1 + r_{G_iI(L)}^2 k][r_{G_jI(L)}^2 k] - r_{G_iI(L)} r_{G_jI(L)} k$$

Finally, expected responses per generation at equilibrium will be given by

$$R_{H(L)} = i\sigma_{HI(L)}/\sigma_{I(L)}$$

and

$$R_{i(L)} = i\sigma_{G_iI(L)}/\sigma_{I(L)}$$

if intensity of selection is kept constant.

Tandem Selection

With tandem selection only one of the n traits is selected at a time. Assume that the trait selected for is alternated in successive generations; i.e., for two traits, selection is based on trait 1 at generation t, trait 2 at generation t+1, trait 1 at generation t+2 and so on.

Assume the same selection intensity is applied on all traits and is constant across generations. Suppose trait m is selected at generation t−1. Then the genetic variance of any trait i at generation t is

$$\sigma_{G_i(t)}^2 = \sigma_{G_i(t-1)}^2[1 - (1/2) r_{G_iG_m(t-1)}^2 h_{m(t-1)}^2 k] + (1/2)[\sigma_{G_i(0)}^2 - \sigma_{G_i(t-1)}^2]$$

and the genetic covariance between traits i and j is

$$\sigma_{G_iG_j(t)} = \sigma_{G_iG_j(t-1)} - (1/2)h^2_{m(t-1)} r_{G_iG_m(t-1)} r_{G_jG_m(t-1)} \times \sigma_{G_i(t-1)} \sigma_{G_j(t-1)} k + (1/2)[\sigma_{G_iG_j(0)} - \sigma_{G_iG_j(t-1)}].$$

The expected genetic response of trait i is

$$R_{i(t)} = i h_{m(t-1)} r_{G_iG_m(t-1)} \sigma_{G_i(t-1)}.$$

To predict response in aggregate breeding value, the response expected in each individual trait is multiplied by its relative economic value:

$$R_{H(t)} = a_1 R_{1(t)} + a_2 R_{2(t)} + \cdots + a_n R_{n(t)}$$

Expressions for the limiting values of genetic parameters when tandem selection is applied could be used to compare this selection method with other alternatives (e.g., selection index) in a general manner. Unfortunately, it was not possible to obtain these equilibrium formulae. With two traits involved, genetic parameters asymptote to two different equilibrium values and it does not seem possible to simplify these equations.

Comparison between methods

Comparison between index and tandem selection is based on the expected responses per generation in the aggregate breeding value at selection equilibrium. Because limiting values of genetic parameters under tandem selection were not obtained, generalization has not been possible. Several combinations of parameters, however, were considered and recurrence formulae were used to obtain limiting values.

Table 2 shows the relative efficiency of index selection with respect to tandem selection (ratio of expected R_H from index selection to expected R_H from tandem selection) in the initial generations [$RE_{(1)}$] and at equilibrium [$RE_{(L)}$]. Two traits were considered economically important. Different and equal initial heritabilities for both traits were considered. Phenotypic and genetic correlations were equal and different initial values were investigated. Two different relative economic weights were examined. Assumed selection intensities corresponded to selected proportions of 1% and

Table 2. Relative efficiency of index selection with respect to tandem selection in the initial generation, $RE_{(1)}$, and at equilibrium, $RE_{(L)}$, for several combinations of initial phenotypic and genetic correlations, $r_{P_1P_2(0)} = r_{G_1G_2(0)}$, heritabilities, $h^2_{1(0)}$ and $h^2_{2(0)}$, relative economic weights, **a**′, and selected proportion of individuals, p

$r_{G_1G_2(0)}$	$h^2_{1(0)}$	$h^2_{2(0)}$	a′ = (1 1)			a′ = (1 2)		
			$RE_{(1)}$	$RE_{(L)}$		$RE_{(1)}$	$RE_{(L)}$	
				p = 1%	p = 50%		p = 1%	p = 50%
0.8	0.2	0.2	1.05	1.04	1.04	1.06	1.04	1.05
	0.2	0.5	1.27	1.15	1.18	1.34	1.21	1.23
	0.5	0.2	1.27	1.15	1.18	1.21	1.11	1.13
	0.5	0.5	1.05	1.03	1.04	1.06	1.04	1.04
0.5	0.2	0.2	1.15	1.11	1.12	1.18	1.13	1.14
	0.2	0.5	1.24	1.13	1.15	1.33	1.20	1.23
	0.5	0.2	1.24	1.13	1.15	1.18	1.09	1.11
	0.5	0.5	1.15	1.08	1.10	1.18	1.10	1.12
0.2	0.2	0.2	1.29	1.21	1.23	1.34	1.25	1.27
	0.2	0.5	1.34	1.19	1.22	1.46	1.28	1.32
	0.5	0.2	1.34	1.19	1.22	1.29	1.18	1.20
	0.5	0.5	1.29	1.16	1.18	1.34	1.20	1.23
0.0	0.2	0.2	1.41	1.30	1.33	1.49	1.37	1.40
	0.2	0.5	1.45	1.26	1.30	1.59	1.37	1.42
	0.5	0.2	1.45	1.26	1.30	1.42	1.28	1.31
	0.5	0.5	1.41	1.22	1.26	1.49	1.29	1.33
−0.2	0.2	0.2	1.58	1.42	1.46	1.71	1.54	1.58
	0.2	0.5	1.61	1.36	1.41	1.79	1.49	1.56
	0.5	0.2	1.61	1.36	1.41	1.63	1.43	1.48
	0.5	0.5	1.58	1.31	1.36	1.71	1.41	1.47
−0.5	0.2	0.2	2.00	1.74	1.80	2.31	2.01	2.08
	0.2	0.5	2.02	1.62	1.70	2.31	1.82	1.92
	0.5	0.2	2.02	1.62	1.70	2.31	1.96	2.03
	0.5	0.5	2.00	1.53	1.63	2.31	1.77	1.88
−0.8	0.2	0.2	3.16	2.65	2.78	4.47	3.75	3.93
	0.2	0.5	3.17	2.34	2.51	3.76	2.75	2.96
	0.5	0.2	3.17	2.34	2.51	9.55	6.82	7.35
	0.5	0.5	3.16	2.19	2.38	4.47	3.10	3.37

50%. If both traits have different heritabilities, and/or if their relative economic weights are different, response in the aggregate breeding value under tandem selection asymptotes to two different limits in successive generations. It seems appropriate to compare index and tandem selection at equilibrium by considering the average response in two consecutive generations. Limiting values were reached at about generation 6 and then average response in aggregate genotype of generations 6 and 7 from tandem selection was compared with response in generation 6 from index selection (with index selection only one limit is approached). However, response of the aggregate genotype in the first generation of selection from tandem selection depends upon which trait is directly selected in generation 0. For this reason, and because average response in two consecutive generations is considered at equilibrium, the initial expected response in the aggregate genotype considered in tandem selection was the average of the response when trait 1 is selected in generation 0 and the response when trait 2 is the trait selected. In index selection, index weights were optimized each generation.

Although index selection is more efficient than selection at equilibrium, its superiority decreases relative to the first generation. The loss in efficiency is greatest with the highest selection intensity. The difference between $RE_{(1)}$ and $RE_{(L)}$ is greatest with negative correlations and with the highest heritabilities. When correlations are negative, the reduction in the relative efficiency of the index increases with the absolute value of the correlations. The reverse occurs in general when correlations are positive; the loss is smallest with the highest correlations.

Discussion

Expected responses at selection equilibrium have been used in this study to compare the efficiency of index selection versus tandem selection. In the first generation of selection, genetic progress in the aggregate breeding value is expected to be greater with index than with tandem selection (Hazel and Lush 1942; Young 1961). At equilibrium, index selection was also more efficient than tandem in all the cases. However, accounting for reductions in phenotypic and genetic variances and covariances by selection led to a reduction in the relative efficiency of index selection. Young (1961) showed that in the first generation, the relative efficiency of the index is highest when the phenotypic correlation between the traits is low or negative. However, this is also the situation where the loss in relative efficiency of the index after repeated generations of selection is greatest. Contrary to the first generation (Young 1961), the relative efficiency of the index at equilibrium depends on selection intensity, with the highest relative efficiency occurring with the lowest intensity of selection. Thus, the loss in relative efficiency of the index, from the first generation to the equilibrium, increases with increasing selection intensity. Also, the long-term efficiency of tandem selection can be improved in some situations by alternating selection on traits every several generations rather than every generation.

An experimental comparison between index and tandem selection was carried out by Sen and Robertson (1964). Although the response in the aggregate breeding value after eight generations in index-selected lines was superior to the response in tandem-selected lines, the relative efficiency of the index was smaller than expected from base population parameters. This result is in agreement with theoretical expectations described in the present study. However as the authors pointed out, experimental results were difficult to interpret due to the considerable variation between replicates in selection response. Also, assumptions of the model considered in this theoretical study may not hold in the experimental study.

Changes in genetic parameters due to gene frequency changes produced by selection have been ignored because an infinitesimal genetic model was assumed. With a finite number of loci controlling the traits, genetic variances and covariances can initially increase or decrease according to gene frequency changes. However, in the long term genetic variances and covariances will decrease (Lin 1978). These reductions probably will affect the expected response from index selection more than the response from tandem selection leading to a further reduction in the relative efficiency of the index. Also, prediction of rates of responses from index and tandem selection assumes infinite population size. In finite populations, inbreeding leads to a further reduction in genetic variances and covariances. Genetic response from index selection can be proportionally reduced more (relative to response from tandem selection) because of its greater accuracy of prediction which can lead to greater rates of inbreeding.

Variances and covariances needed for the construction of the index and for predicting responses have been assumed to be known without error. Studies on the effects of errors in parameter estimates on the efficiency of multitrait-selection indices (Tallis 1960; Williams 1962a,b; Harris 1964; Sales and Hill 1976; Hill and Thompson 1978; Hayes and Hill 1980; Hill and Meyer 1984) show that inaccurate estimation of population parameters can lead to high overprediction of expected gains and loss in the efficiency of the index. Also, errors in the relative economic weights used result in loss of efficiency with the selection index, although predicted responses are not highly sensitive to this type of error (Lin 1978; James 1982).

Wray and Hill (1989) compared different selection indices with different information of relatives for a single trait and concluded that their relative efficiencies changes from first generation to equilibrium. Dekkers (1990) arrived to the same conclusion when comparing selection on best linear unbiased prediction (BLUP) of breeding value with selection on phenotype. In all these cases relative differences among different methods decreased at equilibrium with respect to the first generation. The efficiency of methods that predict breeding values more accurately decreased proportionally more than the efficiency of less accurate methods due to the fact that the decline in genetic (co)variances by linkage disequilibrium increases with the accuracy of selection. The same result is observed in this work, where two multiple-trait selection methods are compared. Consideration of all factors affecting long-term response (gene frequency changes by selection and inbreeding and errors in estimation of parameters) may yield even more similarity in the efficiency of the different selection methods. However, the ranking of the different selection procedures is not generally affected by selection. Thus, the selection method chosen in a particular breeding program will likely be the same regardless of whether the effect of selection on genetic parameters is considered or not.

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