Original article

Experimental study of the efficiency of a reduced index in *Tribolium*

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Abstract – The relative efficiency of a reduced index (IR) relative to a full index (IF) was compared in an experiment with *Tribolium*. The selection objective included pupal length, adult weight, and egg mass. The reduced index was based on pupal length and adult weight, whereas the full index was based on these traits and also on egg mass. There were five generations of selection with four replicates, and a selected proportion of 20%. For each replicate, an unselected control was produced. Responses were significant in the IF and IR lines. Responses for the selection objective differed significantly between lines ($p < 0.01$). The efficiency of the IR line relative to the IF line was 0.52, similar to the expected efficiency of 0.51. The IF and IR lines did not differ significantly for pupal length nor adult weight, whereas the response for egg mass in the IF line was significantly different from the response in the IR line. Realized heritability was greater in the IF line (0.63 ± 0.05) than in the IR line (0.37 ± 0.16). The deleted trait (egg mass) has high heritability and genetic and phenotypic correlations nearly equal to zero with the other two traits included in the selection criterion. The results show the importance of including index traits with high genetic value that are independent of other traits, and they could be useful in breeding programs simultaneously considering production and reproduction traits with nearly zero correlations between them.

reduced index / full index / relative efficiency / *Tribolium*

Résumé – **Étude expérimentale avec *Tribolium* de l'efficacité d'un index de sélection réduit.** L'efficacité de l'index de sélection réduit (IR) a été comparée à celle de l'index complet (IF) dans une expérience avec *Tribolium*. L'index réduit était fondé sur la longueur de la pupe et le poids de l'adulte alors que l'index complet reposait sur ces deux traits et sur la masse d'œufs. On a conduit 4 réplications de 5 générations de sélection sur la longueur de la pupe, le poids de l'adulte et la masse d'œufs, avec un taux de sélection de 20 % et une lignée contrôle non sélectionnée par réplication. Les réponses à la sélection étaient significatives pour les deux types d'index mais elles étaient différentes entre lignées ($p < 0.01$). Relativement aux lignées IF, l'efficacité des lignées IR était de 0,52, une valeur semblable à l'efficacité attendue (0,51). Les lignées IF et IR n'étaient pas significativement différentes en ce qui concerne la longueur de la pupe et le poids de l'adulte, mais la réponse sur la masse d'œufs était

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différente pour les deux types d'index L'héritabilité réalisée était supérieure dans les lignées IF (0,63 ± 0,05 contre 0,37 ± 0,16) La masse d'œufs, caractère supprimé dans IR, a une forte héritabilité et une corrélation génétique presque nulle avec les deux autres caractères de l'objectif de sélection Les résultats illustrent expérimentalement combien il est nécessaire d'inclure dans l'index tout trait qui est important mais qui est indépendant génétiquement des autres caractères en sélection. Ceci pourrait s'appliquer en particulier dans les programmes d'amélioration qui s'intéressent simultanément aux caractères de production et de reproduction faiblement corrélés génétiquement

index réduit / index complet / efficacité relative / _Tribolium_

1. INTRODUCTION

The number of traits included in a Smith-Hazel selection index is generally equal to that included in the aggregate genotype, but there are cases in which the index is based on fewer traits than the aggregate genotype (reduced index) or the index may contain more traits than the aggregate genotype (augmented index). Examples of the first type are those programs which simultaneously consider production and quality or reproduction criteria, and where the breeder wants to evaluate the effect on selection efficiency of dropping a trait in the selection index Examples of the augmented index are those that include traits without direct economic values but which have great effect on other traits which have economic value (sexual maturity and egg production in laying hens). The relative efficiency of these indices relative to the original index can be measured as the ratio of the selection responses in the aggregate genotype which they produce. Cunningham [3] proposed a faster and more convenient way of calculating the relative efficiency of a reduced index and hence the contribution made by each trait The relative importance of one trait in the index can be evaluated by the reduction in the correlation between the index and aggregate genotype caused by deleting that trait from the index. If the trait contributes little to efficiency, the trait may be deleted from the index even though the trait is economically important.

In a pig breeding program, Hovenier *et al.* [7] used production and meat quality traits in both breeding goal and index, and alternatively dropped meat quality traits from the index and only used production traits. Correlations between index and breeding goal were 0.34 and 0.31, respectively, whereas total selection responses were 5.94 and 5.36. Inclusion of meat quality traits in the breeding goal, but not in the index, is an interesting option because there are no costs for quality measurements and the relative loss of response for production traits is small Parratt and Simm [12] used selection indices for terminal sires in sheep. The aggregate breeding value comprised growth rate, killing-out proportion and carcass lean proportion, whereas the selection criteria included growth rate and ultrasonic or X-ray tomography estimates of carcass composition. Correlations between the index and the aggregate breeding value were about 0 38 and 0 39 and the rates of response to selection in economic value were 0.87 and 0.90, respectively. Dropping ultrasonic or tomography measurements from the index reduced the correlation to 0.37 and

the rate of response in economic value to 0.86, indicating that selection on growth rate alone is highly efficient. The aggregate value used by Simm *et al.* [14] in sheep comprised carcass lean weight and carcass total fat weight, index measurements were live weight, ultrasonic fat depth and ultrasonic muscle depth. The correlation between the index and the aggregate value was 0.23, this correlation fell to 0.18, 0.15 and 0.07 when muscle depth or fat depth or both were omitted from the index. Expected rates of response from selection on the total index or live weight alone were 407.51 and 117.33, respectively

Amer *et al.* [1] developed a selection index for terminal sires of beef cattle The breeding objective was made up of production traits (carcass weight, carcass conformation score, and carcass fat score) and calving traits (gestation length, and calving difficulty). Failure to record all calving traits (birth weight, gestation length, and calving difficulty) in the selection index resulted in an expected reduction of 8% in the expected response to selection from the index where both calving traits and production traits (400-day weight, ultrasonic measurements of fat and muscle depths, and muscling score) were recorded. Weight at 400 days appeared to be the most critical recorded trait since the proportional expected reduction in selection response when it was dropped from the total index was 0 21 Cunningham [3] gave an example in pigs concerning the use of the three traits 180-day weight, market score, and litter productivity, both in the aggregate genotype and the index If the pig weight was dropped from the index, the expected rate of response for the aggregate value would be reduced by 45 59%. The corresponding reductions when the other two traits were dropped from the index were 2 33% for market score and 7.93% for litter productivity.

The objective of this study was to compare reality to theory, by checking whether the predicted efficiency of a reduced index was actually achieved. A reduced index based on pupal length and adult weight in *Tribolium* was used, relative to a full index considering both of these traits and egg mass; phenotypic and genetic correlations between the deleted trait and the others were nearly zero The selection objective comprised pupal length, adult weight, and egg mass

2. MATERIALS AND METHODS

The base population of *Tribolium castaneum* used for this study was the Consejo which has been maintained in this laboratory since 1964, as a large population with random selection. All lines were kept at 33 °C and 70% relative humidity on a medium of 95% whole-wheat flour and 5% dried brewer's yeast. The traits measured and selected for were pupal length, adult weight, and egg mass Pupal length was scored to the closest 0.1 mm at 21 days; both adult weight and egg mass were scored to the closest 0.1 mg, at 31 days and between 28 and 30 days, respectively.

There were four replicates and five generations of selection per line. To start each replicate, 20 males and 20 females were sampled as pupae from the population cage and randomly paired. Five male and five female offspring

Table I. Variances and covariances used to construct the selection indices

Trait	Pupal length	Adult weight	Egg mass
Pupal length	3 77 [a]	1.08 [a]	0 [a]
	6.95 [b]		
Adult weight	2.54 [b]	2 50 [a]	0 [a]
		5.42 [b]	
Egg mass	0 [b]	0 [b]	27.04 [a]
			48 95 [b]

[a] Genetic values.   [b] Phenotypic values.

from each mating pair were assessed as candidates for selection (200 individuals in each generation, line and replicate). The 20 males and 20 females with the highest ranks based on the selection criterion from a given line were selected and randomly mated in pairs, avoiding sibmatings; the selected proportion was therefore 20%. For each replicate, an unselected control was produced.

Selection was intended to improve the objective $H = a_1g_1 + a_2g_2 + a_3g_3 = a'g$, where g_1, g_2 and g_3 are the breeding values for pupal length, adult weight and egg mass, respectively. The economic weights a_1, a_2 and a_3 were all equal to 1. Two selection criteria were used: full selection index (line IF) and reduced selection index dropping the egg mass information (line IR). In both lines, selection for pupal length and adult weight was based on individual performance. The full index (line IF) for females was: $I = b_1x_1 + b_2x_2 + b_3x_3 = b'x$, where x_1, x_2 and x_3 are the phenotypic values for pupal length, adult weight and egg mass, respectively. The full index for males was: $I = b_1x_1 + b_2x_2 + b_3m_3 = b'x$, where m_3 is the mean of the male's full sisters for egg mass. The reduced index (line IR) was: $I = b_1x_1 + b_2x_2 = b'x$. Index coefficients were calculated as: $b = P^{-1}Ga$, where P is the covariance matrix between traits in the index, and G is the covariance matrix between traits in the index and the objective function.

The elements of the covariance matrices (P_{ij} and G_{ij}) are given in Table I and are based on the parameters of the base population, estimated by regression analysis from the offspring-parent relationship, except that phenotypic and genetic covariances with trait 3 were nearly zero and then set to zero. With these estimates, the full index was: $0.55x_1 + 0.40x_2 + 0.56x_3$ for females, and $0.55x_1 + 0.40x_2 + 0.66m_3$ for males, whereas the reduced index was $0.55x_1 + 0.40x_2$.

Mean response per generation was calculated as the regression coefficient of the difference by generation between selected and control lines on generation number. Standard errors of observed responses were calculated from the square root of the variance among regression coefficients divided by the number of replicates. A two-way analysis of variance [16] of the mean responses by line and replicate was also done, following the model: $y_{ij} = m + L_i + R_j + e_{ij}$, where y_{ij} is the mean response for line i and replicate j, m is a constant, L_i is the effect of the selection criterion ($i = 1, \ldots, 2$), R_j is the effect of the replicate ($j = 1, \ldots, 4$), and e_{ij} is the residual.

Expected responses to selection for each trait in generation $n+1$ are:

$$\Delta_{n+1} = \frac{G_n b \imath}{\sqrt{b'P_n b}}$$

where $\Delta' = (\Delta g_1 \; \Delta g_2 \; \Delta g_3)$, and $\imath$ is the standardized selection differential for the selection criterion. The recurrent relationship of the G matrix taking into account the effect of selection [2], is [17]:

$$G_{n+1} = \left(0.5G_n + 0.5K(b'P_n b)^{-1}G_n bb'G_n\right) + 0.5G_0 = G_{n+1}^{\text{between}} + G_{n+1}^{\text{within}}$$

where $K = -\imath(\imath - c)$, is the change in variance as a result of selection, c being the point of truncation corresponding to the fraction selected. The change in the P matrix is the same as that shown for the G matrix ($P_n - P_0 = G_n - G_0$) To take into account the effects of drift (sampling effects and inbreeding), the between and within genetic variance matrices were corrected according to formulas reported by Keightly and Hill [8] and Langlois [9], respectively.

Expected response in H is:

$$\Delta H = a_1 \Delta g_1 + a_2 \Delta g_2 + a_3 \Delta g_3 = \imath \sigma_I$$

where σ_I is the standard deviation of the index. The efficiency of the reduced index relative to the full index was calculated as the ratio of the rates of response in H that they produce, which is simply the ratio of the standard deviations of the two indices. Alternatively, the relative efficiency can be measured as [3]

$$\sqrt{1 - \frac{b_3^2/W_{33}}{\sigma_I^2}}$$

where W_{33} is the diagonal element of P^{-1} corresponding to b_3 which was dropped from the full index in forming the reduced index.

3. RESULTS

Generation means for H and each component trait (pupal length, adult weight and egg mass) are shown for each line in Figures 1, 2, 3 and 4, respectively (replicates pooled). Mean observed responses and standard errors are included in Table II. The difference between lines was significant ($p < 0.01$) for H with the mean response in the IF line being about twice that in the IR line Selection response was significantly different from zero in both lines ($p < 0.01$). Efficiency of the reduced index (line IR) relative to the full index (line IF) was 0.52. Mean observed response for pupal length was similar in both lines and significantly different from zero ($p < 0.01$). Similarly, the rate of response per generation for adult weight was significantly different from zero for both IF ($p < 0.05$) and IR ($p < 0.01$) lines, but responses in the two lines did not differ significantly. The mean observed response for egg mass in the IF line was important and significant ($p < 0.01$). Although this trait was not measured

Table II. Mean observed responses by line and generation [1] and expected responses in the first (G_1) and fifth (G_5) [2] generations (IF = full index, IR = reduced index).

Trait	Line	Observed response	G_1	G_5
H value	IF	2.24 ± 0.12 [a]	5.55	3 87 (4.38)
	IR	1.16 ± 0.08 [b]	2.83	1.96 (2.27)
Pupal length	IF	0.66 ± 0.04 [a]	0 88	0 61 (0 69)
	IR	0.72 ± 0.07 [a]	1.73	1.20 (1.39)
Adult weight	IF	0.37 ± 0.05 [a]	0.56	0.39 (0 44)
	IR	0.44 ± 0.04 [a]	1.1	0.76 (0 88)
Egg mass	IF	1.21 ± 0.10	4.11	2.87 (3.25)

[1] Expressed as a deviation from the mean value of the control at each generation.
[2] Expected response taking into account only the effect of selection in brackets.
[a,b] Means within a trait with no common superscript differ significantly between lines $(p < 0.01)$.
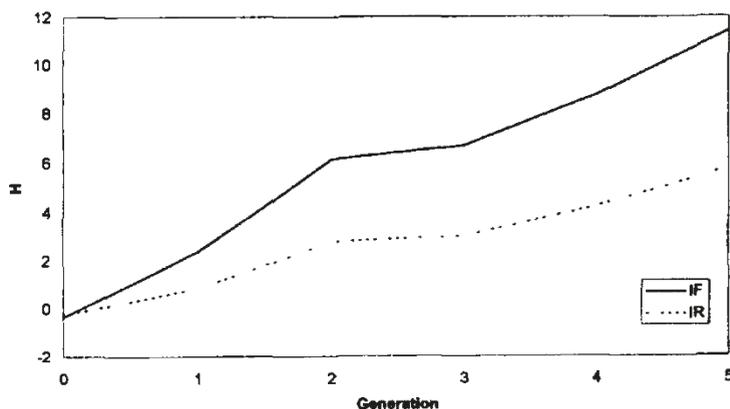

Figure 1. Means of aggregate genotype (H) by line and generation expressed as deviations from the control line at each generation (IF = full index, IR = reduced index)
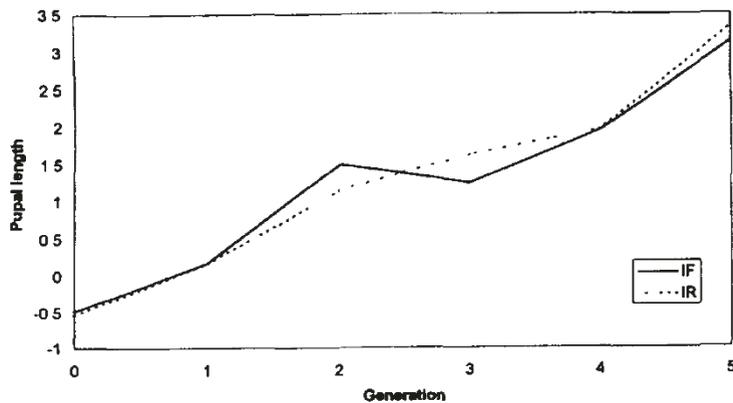

Figure 2. Means of pupal length by line and generation expressed as deviations from the control line at each generation (IF = full index, IR = reduced index).
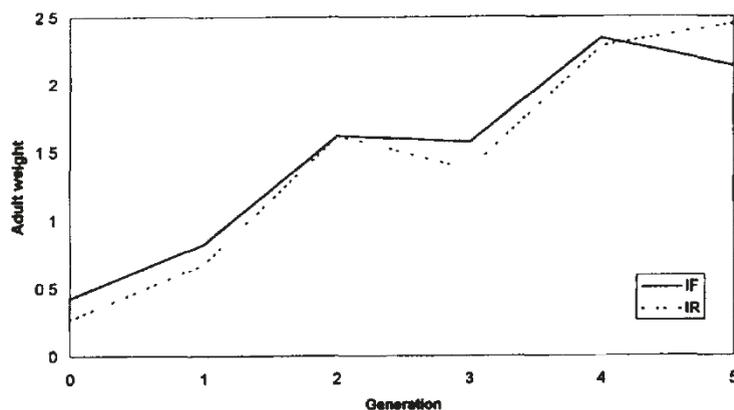
Figure 3. Means of adult weight by line and generation expressed as deviations from the control line at each generation (IF = full index, IR = reduced index).
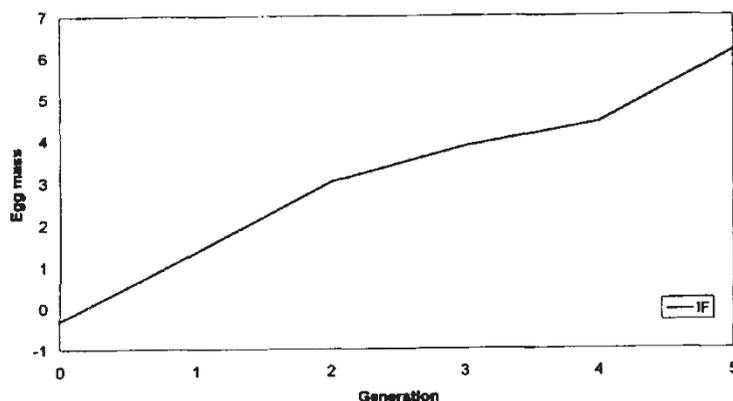

Figure 4. Means of egg mass in line IF (full index) by generation expressed as deviations from the control line at each generation.

in the IR line until the fifth generation, the initial mean egg mass in the base population did not differ significantly from that at the end of the experiment; expressed as deviations from the control line, the means were -0.30 and 1.16, respectively.

Expected responses to selection for the selection objective in the IF and IR lines given in Table II show that selection should lead to greater response in line IF. The efficiency of the reduced index with respect to the full index is expected to be 0.51, either at the fifth or at the first generation; the same relative efficiency was expected when the effects of drift were not taken into account. The observed response was less than the expected response, with the proportion of observed to predicted responses ranging from about 58% (at the fifth generation taking into account the effects of selection and drift) to 51% (at the fifth generation taking into account only the effect of selection) to 40% (at the first generation). Observed and expected responses were in good agreement for pupal length and adult weight in line IF, although the expected response

considerably overestimated the observed response for egg mass in this line, and for pupal length and adult weight in line IR.

Selection response as a proportion of the applied selection differential (realized heritability) was calculated as the regression of generation means on the cumulative realized selection differentials. Realized heritability was greater in the IF line (0.63 ± 0.05) than in the IR line (0.37 ± 0.16); the realized heritability was significant in line IF ($p < 0.01$). The heritability of the index estimated in the base population as the regression of the genetic index on the selection index [10,11] was 0.57 for the full index and 0.49 for the reduced index. Standardized selection differentials averaged over generations were similar in the IF and IR lines (1.26 and 1.21, respectively), and not very different from that intended, based on the normality assumption (1.39). Selected proportions were slightly greater than the intended proportion (20%) in both lines, ranging from 20 to 21%. Secondary selection differentials for pupal length and adult weight in the IR line (2.15 and 0.68) were similar to the secondary selection differentials for these traits in the IF line (2.13 and 0.79); the secondary selection differential for egg mass in line IF (1.62) was intermediate between those for the other traits.

4. DISCUSSION

The goal of this experiment was to compare the efficiency of a reduced index (line IR) relative to the full index (line IF), given a condition of evident inferiority for the former with respect to the latter (phenotypic and genetic correlations between the deleted trait and the other traits, equal to zero). The relative efficiency of the reduced index measured as the ratio of the observed responses in the H value was 52%. This result is in agreement with the theoretical efficiency of 51% based on the ratio of the rates of expected responses. The theoretical relative efficiency was the same if the theoretical expected responses were calculated at generation 1 or at generation 5 of selection. This finding shows that the errors in the expected responses will affect the absolute rate of response in each line although similar results will be achieved for the relative rate of response. In this way, the results apply either to the first or to the final generations of selection when the genetic parameters may have changed due to selection and drift. The full index and the reduced index were equally effective in changing pupal weight and adult weight, both lines having significant responses for these traits. Although the observed response for egg mass in the IF line was less than expected, the rate of response per generation was important and significant. Selection for IR resulted in no change for egg mass, showing that significant improvement cannot be made in egg mass when selection is based solely on the reduced index because of the zero correlations between traits in the reduced index and egg mass. A value of zero for the genetic correlation between pupal length or adult weight and egg mass is consistent with the behavior of this line for the observed response in egg mass.

The alternative way of calculating the theoretical efficiency of the reduced index relative to the full index [3] gave the same result as indicated before, the diagonal element of P^{-1} being 0.0204 in females and 0.0485 in males. The value

of the egg mass information in the full index can be stated as the percentage change in response which would be expected to result if that trait were omitted from the index. This reduction as a percentage is $100 - 51 \approx 49\%$, so if egg mass were dropped from the index, the rate of response for H would be expected to be reduced by 49%, which shows that the trait is important for the aggregate H. The correlation between the full index and the selection objective was 0.74 in females and 0.61 in males. Dropping egg mass from the index reduced the correlation to 0.34, indicating that selection on the reduced index alone would be highly inefficient. In contrast, if pupal length or adult weight were dropped from the full index, the rate of genetic progress for H would be expected to be reduced by only $100 - 95 = 5\%$ and $100 - 98 = 2\%$, respectively, so a selection experiment comparing the relative efficiency of both of these reduced indices to the full index would be expected to be of lesser value.

The results obtained in the reduced and full index lines are in agreement with theoretical expectations shown by Gjedrem [4–6] and Sivanadian and Smith [15] for an augmented index with three traits relative to an original index with two traits. The extra response obtained in the IF line was very large (about twice as great as that in the IR line). The added trait (egg mass) had high heritability (0.55) and genetic and phenotypic correlations equal to zero with the other traits included in the selection index (pupal length and adult weight). Sivanadian and Smith [15] reported large extra response for the case most similar to that in this experiment (Case 24), with similar relative product of heritability (h^2) and economic weight (a) for all the traits and all correlations equal to zero. In general, the change in response will be larger when the correlation among the traits is negative and the value of (ah^2) for the added trait is high, showing the importance of including traits with high genetic-economic value that are independent or negatively correlated to other traits. Sivanadian and Smith [15] indicated that reliable results can be obtained with samples of 800 individuals for indices with two and three traits, which is the number of animals recorded in each line and generation of this experiment.

As expected, given the conditions of the experiment (number of traits, economic values and heritabilities for the traits, and phenotypic and genetic correlations between them), the results obtained for reduced indices in breeding programs simultaneously considering production and quality or reproduction traits have been very variable. Hovenier et al. [7] reported that the efficiency of an index which used only production traits was about 90% with respect to an index which used both production and meat quality traits. Heritability of the quality traits was intermediate (0.3) but high (0.6) for intramuscular fat content. Phenotypic correlations between production and quality traits did not differ significantly from zero, except for intramuscular fat content (values ranging from -0.3 to 0.3). Genetic correlations between daily gain and quality traits were favorable (maximum was 0.45) but unfavorable between lean content and quality traits (minimum was -0.45). Parratt and Simm [12] found similar rates of selection response for an index using only growth rate and an index using both growth rate and carcass quality. Heritability of carcass quality was low (about 0.2), whereas phenotypic and genetic correlations were favorable (about 0 5) Simm et al. [14] showed that dropping one or two quality traits from the full index led to proportional losses in expected response ranging from

0.2 to 0.7, in disagreement with the low estimate reported for the heritability of both quality traits (about 0.2) and the favorable phenotypic and genetic correlations (about 0.4). In contrast, dropping the measurement of carcass quality from the index reduced selection response by only 0.02 to 0.05, as it should have been expected, in the study of Parratt and Simm [12] and for several indices suggested to improve lean meat production in beef cattle [13]. The moderate reduction in response reported by Amer et al. [1] for an index with no measurements for reproduction traits, with respect to the full index for both production and reproduction traits, was in agreement with the low to medium estimates of heritability (0.1–0.3) and phenotypic (0–0.3) and genetic (0–0.6) correlations found in this study.

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