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The choice of selection index in kale (*Brassica oleracea* L.) population improvement

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Summary. The use of selection indices was explored in a kale (*Brassica oleracea* L. var. *acephala*) breeding programme aimed at increasing digestible organic-matter (DOM) yield, and lowering S-methyl cysteine sulphoxide (SMCO) and thiocyanate ion (SCN^-) contents by half-sib family selection. The predicted overall response with the optimum index (1.59) was slightly better than with the base index (1.56) which in turn was superior to the desired gains index (1.41). All three indices were expected to increase height and reduce amino acid content, mainly because of genetical correlations between DOM yield and height ($r=0.76$) and between SMCO and amino acid contents ($r=0.81$). Elimination of these correlated responses with the desired gains index would result in virtually no progress, and with the restricted index an undesirable increase in SMCO content would occur.

Key words: Kale breeding – Half-sib family selection – Efficiency of selection

Introduction

Marrow-stem kale (*Brassica oleracea* L. var. *acephala*) is an outbreeding crop species grown for feeding cattle (*Bos taurus*) and sheep (*Ovis aries*). At the Scottish Crop Research Institute (SCRI), population improvement by half-sib family selection is being used to increase digestible organic-matter (DOM) yield, and to lower the contents of the haemolytic factor, S-methyl cysteine sulphoxide (SMCO), and the indole glucosinolates which release the goitrogenic thiocyanate ion (SCN^-) on hydrolysis.

Index selection is a highly efficient method of multitrait selection (Lawrence 1981; Pesek 1981). The optimum index of Smith (1936), the restricted index of Kempthorne and Nordskog (1959), the base index of Williams (1962) and the desired gains index of Pesek and Baker (1969) were explored for their use in kale. The basic theory and use of these indices were reviewed by Lin (1978) and simple examples were given by Wricke and Weber (1986).

The relative efficiencies of these indices were compared for the selection of 14 out of 84 half-sib families. Ways of eliminating predicted correlated increases in height and reductions in amino acid content were investigated. The optimal number of replications for maximising the response to selection was estimated for a total trial size of 168 plots. The reliability of the optimum index was determined.

Materials and methods

The breeding method

Using blowflies as pollinators 84 half-sib families were produced in a polythene tunnel in 1984. They were assessed in 1985 at Mylnefield, Invergowrie, near Dundee in a randomised complete block trial with two replicates. Each plot comprised 5 rows 6 m long with 50 cm between rows.

The trial was sown on 6 May, 1985 with a Webb precision drill set to achieve 5 cm seed spacing. A bulk sample of 16 young leaves between 15 and 20 cm long was taken from each plot on 2 October, 1985, freeze dried and analysed for SCN^- and SMCO contents. Gosden's methods (1978, 1979) were used, although for SMCO the chromatographic column was removed from the analytical system so that a unit of 10 columns could be used and the amino-acids fraction was also collected, estimated and expressed in glycine equivalents (Griffiths 1984). Plant height was recorded for all plots on 24 October, 1985, after the period of rapid stem growth. The trial was harvested on 5 and 6 November, 1985, one replicate each day, with a modified Mais Prinz forage harvester set to cut the plants at ground level. The fresh-weight yield of the centre three rows of each plot was recorded and a chopped sample oven dried at 80 °C for 20 h to determine dry-matter (DM) content. DOM content was determined by the method of Allison and Borzucki (1978), and the DOM yield of each plot calculated.

Single-row selection plots of all the half-sib families were sown on 21 June, 1985. On 24 March, 1986 14 plants from each of the best 14 families were selected for seed production, thus completing the breeding cycle. The families were chosen by index selection. The choice of numbers was discussed by Bradshaw (1986).

Selection indices

With each selection index an index score (I) was calculated for each half-sib family from the formula:

$$I = b_1 x_1 + b_2 x_2 + b_3 x_3 \quad (= b' x \text{ in matrix notation})$$

where traits 1 to 3 were DOM yield, SMCO content and SCN^- content, respectively; x was the phenotypic deviation of the half-sib family mean (mean of 2 replicates) from the population mean and the weights (b) were calculated as follows. Using matrix notation:

$b = P^{-1} G a$, optimum index (Smith 1936);
$b = a$, base index (Williams 1962);
$b = G^{-1} k$, desired gains index (Pesek and Baker 1969).

The phenotypic (P) and additive genetic (G) variance-covariance matrices were estimated from analyses of variance and covariance for single traits and pairs of traits, respectively. The relative economic values (a) and desired genetic gains (k) chosen were equal in phenotypic standard deviation ($\sqrt{V_P}$) units:

$$a = \frac{1}{\sqrt{V_P}} \quad \text{and} \quad k = \sqrt{V_P}.$$

For each index the predicted responses (R) to selection of the best 14 families were estimated:

$$R = G\, b \cdot \frac{\Delta I}{\sigma_I^2} \quad \text{optimum and base indices, and}$$

$$R = k \cdot \frac{\Delta I}{\sigma_I^2} \quad \text{desired gains index,}$$

where ΔI is mean of families selected minus mean of all families and σ_I^2 is the variance of I.
The overall response (R) was also estimated:

$$R = a_1 R_1 + a_2 R_2 + a_3 R_3.$$

The predicted correlated responses (R_c) in height and amino acid content were estimated from their additive genetic covariances (g's) with the traits in the indices:

$$R_c = (b_1 g_{1c} + b_2 g_{2c} + b_3 g_{3c}) \cdot \frac{\Delta I}{\sigma_I^2}.$$

The predicted responses to selection were estimated when these correlated responses in height and amino acid content were eliminated by including them in the desired gains index with their k's set equal to zero and also by constraining their responses to zero in the restricted index.

Maximising the response to selection

The optimum index was used in the breeding programme and the optimal number of replications (r) for maximising the response to selection was estimated for a total trial size of 168 plots. Phenotypic variance-covariance matrices for r = 1, 2, 3 and 4 were constructed from the estimated additive genetic and 'error' variance-covariance matrices. The responses to selection for 14 families selected out of 168, 84, 56 and 42, respectively, assessed were then estimated:

$$R = G\, b \cdot \frac{i}{\sqrt{b' P\, b}}$$

where the intensity of selection (i) was obtained from the tables in Becker (1975).

In each case four sets of economic values were examined, namely the reciprocals of the phenotypic standard deviations for r = 1, 2, 3 and 4. This was necessary because the same set was required for all cases to obtain a fair comparison, but there was no a priori reason to prefer one set to another.

Reliability of the optimum index

As a guide to the reliability of the estimated index the latent roots (λ) of the determinantal equation

$$|G - \lambda P| = 0$$

were calculated and examined as suggested by Hayes and Hill (1980). These latent roots are the heritabilities of the transformed and uncorrelated variables $Q' x$, where Q is the matrix of latent (column) vectors. Their associated economic values (α) were also calculated:

$$\alpha = Q^{-1} a.$$

As a further guide to the reliability of the estimated index a 90% confidence interval was constructed for the predicted response by the method of Tai (1986).

Results

After a slow but even establishment, the plants made rapid growth during the wet summer, and by harvest were tall with high DOM yields. The population mean, heritability and the predicted responses to selection for each trait are shown in Table 1. The predicted responses for DOM yield and SCN^- content were greatest with the optimum index and least with the desired gains index. The reverse was true for SMCO content. The overall responses were 1.59, 1.56 and 1.41 for the optimum, base and desired gains indices, respectively.

All three indices were expected to increase height and reduce amino acid content. There was a relatively large genetical correlation (Table 2) between DOM yield and height (r = 0.76) and between SMCO content and amino acid content (r = 0.81). Elimination of these correlated responses (Table 3) with the desired gains index would result in virtually no progress, and the restricted index would lead to more progress with

Table 1. Population means, heritabilities and predicted responses to index selection in kale

Parameter	Traits in index			Correlated responses	
	DOM yield tonnes/ha	SMCO g/kg DM	SCN$^-$ mg/100 g DM	Height cm	Amino acids g glycine/kg DM
Optimum index	0.34	−0.40	−5.7	3.5	−0.36
Base index	0.31	−0.50	−5.3	2.7	−0.44
Desired gains index	0.25	−0.59	−4.3	1.3	−0.50
Population mean	9.59	6.65	50.9	115.3	8.75
Heritability	0.51	0.40	0.63	0.75	0.29

Table 2. Additive genetic (and phenotypic) correlations between five traits of kale

Traits	Traits			
	Height	DOM yield tonnes/ha	SMCO	Amino acids
DOM yield tonnes/ha	0.76 (0.50)	–	–	–
SMCO	0.11 (0.18)	−0.37 (−0.04)	–	–
Amino acids	0.43 (0.25)	−0.11 (−0.09)	0.81 (0.49)	–
SCN$^-$	−0.10 (0.03)	−0.35 (−0.15)	0.06 (0.34)	0.44 (0.35)

Table 3. Predicted responses to index selection with kale when correlated height and amino acid content responses are eliminated

Index	Trait			Overall response
	DOM yield tonnes/ha	SMCO g/kg DM	SCN$^-$ mg/100 g DM	
Desired gains index	0.01	−0.03	−0.2	0.06
Restricted index	0.02	+0.47	−7.4	0.47

Table 4. The effect of the number of replicates(r) on the predicted responses to optimum index selection in kale

r	Families assessed	Intensity of selection[a]	Traits			Overall response
			DOM yield tonnes/ha	SMCO g/kg DM	SCN$^-$ mg/100 g DM	
1	168	1.821	0.39	−0.42	−7.0	1.85
2	84	1.480	0.38	−0.45	−6.3	1.76
3	56	1.250	0.34	−0.42	−5.6	1.59
4	42	1.069	0.30	−0.39	−4.9	1.41

[a] 14 families were selected

SCN$^-$ content, no progress with DOM yield and an undesirable increase in SMCO content.

The effect of varying the number of replicates of each family on the response to optimum index selection is shown in Table 4 when the economic values were the reciprocals of the phenotypic standard deviations for $r = 2$. Using those for $r = 1$, 3 and 4 gave very similar responses for each of the three traits and the same ranking for the overall responses. The overall response and the responses for DOM yield and SCN$^-$ content were greatest with one replicate whereas the response for SMCO content was greatest with two replicates. The responses for two replicates (Tables 1, 4) are slightly different because the former were calculated using the actual index scores, whereas the latter were calculated using the theoretical intensity of selection (i) and the theoretical variance of index scores ($b'Pb$).

The latent roots of P^{-1} G were 0.78, 0.60 and 0.24, and their corresponding economic values were 0.606, 1.779 and −0.728, respectively. There were no faulty roots outside the range 0 to 1, the roots were dissimilar, and the highest economic value was associated with the second root which had a relatively high value. Therefore, there was no reason to treat the estimated optimum index with caution. The lower and upper confidence limits (90% interval) for the predicted response R were 0.85 R and 1.21 R, respectively.

Discussion

The overall predicted response to selection was greatest with the optimum index. This was expected as the index is optimal because the weights (*b*) were calculated to maximise the overall response by considering the relative economic values and heritabilities of traits and genetical correlations between traits. The SCRI kale breeding programme is particularly suited to selection with this index. The phenotypic and additive genetic variance-covariance matrices can be estimated from the assessment trial of the half-sib families themselves, and hence new weights estimated each generation without the need to produce and assess additional families solely for the purpose. For a fixed number of plots in the assessment trial, the number of replicates can only be increased at the expense of the number of families assessed. It was found that increasing the number of replicates beyond the minimum of two required to estimate the additive genetic variance-covariance matrix would reduce the overall and the individual responses to selection and hence be undesirable. Two replicates were indeed used, and neither an examination of the latent roots of P^{-1} G, as suggested by Hayes and Hill (1980), nor the confidence limits for the expected response calculated by Tai's (1986) method, provided reasons for treating the estimated optimum index with caution.

The base index was proposed by Brim et al. (1959) and investigated by Williams (1962) because of concern over the reliability of weights estimated from variance-covariance matrices subject to sampling errors. The weights in the base index are simply the relative economic values and hence require no estimation, but the relative economic values cannot take account of differences in heritabilities and differences between corresponding genotypic and phenotypic correlations. Although such differences occurred, the overall predicted response to the base index was similar to the optimum index, and the predicted changes in the individual traits also were similar. Eagles and Frey (1974) reported the base and optimum indices were about equally efficient with oats (*Avena sativa*), whether judged by the predicted or actual responses. Elgin et al. (1970) with alfalfa (*Medicago sativa*) also reported the optimum index was no better than the base index and attributed this to poor estimation of the weights: a North Carolina Design 1 with only 20 males and 2 females per male was used to estimate the additive genetic variance-covariance matrix.

The desired gains index was proposed by Pesek and Baker (1969) because assigning relative economic values was a problem and deterred practical breeders from using the optimum index. However, their desired gains are subjective economic values which can be used in the optimum index in the absence of objective values. It was not possible to assign objective values to DOM yield, SMCO content and SCN^- content because the effects of changes in these traits on the economics of milk and meat production have not been quantified. Therefore, equal values in phenotypic standard deviation units were used in the optimum index and the phenotypic standard deviations were chosen as the desired gains. In both cases the same value judgement was made, namely that increasing DOM yield by 0.53 tonnes/ha, and decreasing SMCO and SCN^- contents by 1.3 g/kg DM and 9.1 mg/100 g DM, respectively, would be equally valuable. The difference between the two indices is that the desired gains index constrains the responses in this ratio by giving more weight to a trait with a low heritability, and vice versa, and hence has a lower overall response than the optimum index. The predicted overall response was lower with the desired gains index, and the predicted response for SMCO content was greater at the expense of DOM yield and SCN^- content.

All three indices were expected to increase height and lower amino acid content, mainly as a result of the large genetical correlations between DOM yield and height and between SMCO and amino acid contents. Elimination of these correlated responses was explored as tall kales are prone to lodging, and lowering amino acid content is also undesirable.

The restricted index maximises the overall response subject to the constraint of no correlated responses. The overall response was reduced and achieved by an increased response for SCN^- content more than compensating for a negative response for SMCO content, and virtually no response for DOM yield. Pesek (1981) used the restricted index to prevent protein content in spring wheat (*Triticum aestivum*) decreasing because of a high negative correlation with yield and found that the overall response was greatly reduced. Rosielle and Frey (1975) found that severe restrictions on heading date and height in oats reduced the expected advance for grain yield, and very severe restrictions gave a negative expected advance. The desired gains index was also tried by setting the desired gains of height and amino acid content to zero, as suggested by Pesek (1981). Virtually no overall response was obtained because of the nature and magnitude of the genetical correlations.

It was concluded that to make good progress towards the objectives of increased DOM yield and reduced SMCO and SCN^- contents some increase in height and decrease in amino acid content would have to be accepted. It was decided to use the optimum index as there was no good reason for rejecting this theoretically superior index, although it is recognised that objective economic values and a more detailed assessment of the accuracy of the index should be sought.

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