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COMPARISON OF SOME SELECTION PROCEDURES AND OBJECTIVES IN FABA BEANS (*VICIA FABA* L.). I. DIRECT AND INDEX SELECTION FOR SEED YIELD

D. L. C. BRINKHORST-VAN DER SWAN and A. PH. DE VRIES

Department of Plant Breeding (IvP), Agricultural University, Wageningen, the Netherlands

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Vicia faba, faba bean, seed yield, direct selection, index selection, independent culling levels selection.

SUMMARY

Starting with two heterogeneous F_2 populations, each based on 20 cross combinations, different selection procedures were applied for four consecutive selection cycles. Three of the selection procedures involved seed yield per plant (SYP): (i) direct selection for SYP (DSY); (ii) indexselection for SYP (ISY) with plant length, the ratio of the vegetative top to plant length, end of grain filling and duration of the generative stage as auxiliary characters and finally; (iii) independent culling levels selection (ICL) for the index described above and crude protein content. For ICL-selection the attention is focussed on SYP in this paper.

For all three selection procedures, predicted and realized responses were calculated and expressed as percentage of a corresponding non-selected population. The intensities of selection differed over selection methods and generations, mostly due to practical constraints.

As far as predicted responses are concerned, ISY-selection seemed to be slightly superior to DSY-selection and DSY-selection to ICL-selection. This order may partly be due to differences in selection intensity. However, none of the predictions was very accurate, but the predictions of ICL-selection seemed to be the most accurate. This has been ascribed also to the relative mild selection intensity applied in ICL-selection. It is concluded that a decision in favour of a complicated selection procedure like index selection based on predicted responses only cannot be defended. As far as realized responses are concerned, DSY-selection seems to be slightly superior to the other two selection procedures, as it is the only procedure that resulted in a more or less stable positive response to selection.

The auxiliary characters, especially plant length, showed a marked correlated response to all three selection procedures. In case of direct selection for SYP this seemed paradoxical with the inefficiency of index selection, but, it may reflect the differences in the genuine genotypic correlations and the estimated genotypic correlations.

INTRODUCTION

Faba bean (*Vicia faba* L.) is considered to be a potential protein crop for the temperate regions because of its high protein content. However, the high protein content has to go together with a sufficiently high and stable seed yield resulting in high protein yield.

Progress in protein yield is often small, probably because of a low heritability of seed yield, a most important component of protein yield. In a trial with 33 Faba bean varieties, 90% (R^2, the coefficient of determination) of the genetic variation in protein yield was explained by variation in seed yield (DE VRIES, 1978a). Improvement of seed yield might improve protein yield, provided seed yield and protein content are not negatively correlated. In the same trial the genetic correlation coefficient between crude protein content and seed yield was not significant. So selection for seed yield should have no effect on protein content and vice versa.

These preliminary results led to a research project in which selection for the components of protein yield was investigated instead of selection for protein yield itself. In this paper the results of the selection for seed yield are presented. The results of the selection for protein content will be reported in a second paper (DE VRIES & BRINKHORST, 1986).

With respect to seed yield three selection procedures were compared. The first procedure, direct selection for seed yield, may be considered as standard procedure. Index selection might improve on this standard approach. Therefore, the second procedure comprised index selection for seed yield. The third procedure consisted of independent culling levels selection for yield index and high protein content. For seed yield the last procedure may give an indication of the possible implications of selection for another character simultaneous with selection for seed yield.

The rather optimistic prospects for index selection are mainly based on predicted responses, i.e. theoretical comparisons (e.g. BRIM et al., 1959; BYTH et al., 1969; EAGLES & FREY, 1974). When not only predicted responses but also realized responses are compared, index selection is not always superior to direct selection (e.g. BYTH et al., 1969).

In the experiment described in this paper, an attempt has been made to compare the selection methods employed not only on their theoretical merits but especially on their practical merits.

MATERIALS AND METHODS

Two highly heterogeneous mutually independent populations, A en B, were created in 1976. Both populations comprised in 1978 equal numbers of F_2-plants of 20 crosses, i.e. per population four mother varieties each crossed with each of five father varieties. More detailed information has been given by DE VRIES et al., (1980). The populations were kept apart throughout the entire project and were split into subpopulations by applying different selection procedures and/or selecting for different objectives. Within each subpopulation the type of selection from which the subpopulation originated was applied every generation until the F_6 in 1982.

Five types of selection were applied, i.e. direct selection for SYP (seed yield per plant), index selection for SYP, direct selection for high and for low CP (crude protein content of the seeds) and independent culling levels selection for SYP index and high CP. The thus derived subpopulations will be referred to as DSY (direct selection for yield), ISY (index selection for yield), HP (selection for high protein), LP (idem for low protein) and ICL (independent culling levels selection for SYP index and high CP) respectively. To allow an overall evaluation of the different types of selection a random subpopulation (RP-F_2) representing the unselected F_2-population was taken and maintained until the F_6. To estimate the realized response per cycle of selection, a corresponding random subpopulation was selected out of each relevant subpopulation e.g. RP-DSY. These subpopulations were only grown and tested in the next generation and not maintained afterwards.

As Faba beans do show a considerable extent of natural outcrossing (BOND & POULSEN, 1983), the concept 'line' is replaced by 'plant progeny' in the case of the offspring of an individual plant and by 'family' in the case of the offspring of a plant progeny. Up to and including the F_4 generation one or more plots per plant progeny were grown, but selection was on individual plant basis and not on plot basis. Within the F_5 generation, again one or more plots per plant progeny were grown, but instead of individual plants, as before, entire plant progenies were selected. So in the F_6 generation, F_4-derived families were grown. The general design, which was the same for populations A and B, is presented in Figure 1. The indicated numbers of plants, plant progenies (PP) and families (Fam.) are the intended numbers. Generally, the plots were sown in a slightly higher density and thinned to the intended density afterwards. Deviations from the general design owing to loss of material or lack of seed never resulted in adjustment of the design for the next generation, but could have a rather important impact on the intensity of selection i (Figure 2). This applied especially to the intensity of selection exerted on the F_3, as in this generation a substantial loss of material occurred from heavy infestation with *Fusarium solani*.

The plant progenies, i.e. F_2 till F_5, were grown in one-row plots. With individual plant selection each plot comprised seven plants of which two were border plants. In the F_5 no use was made of border plants and observations were conducted on entire

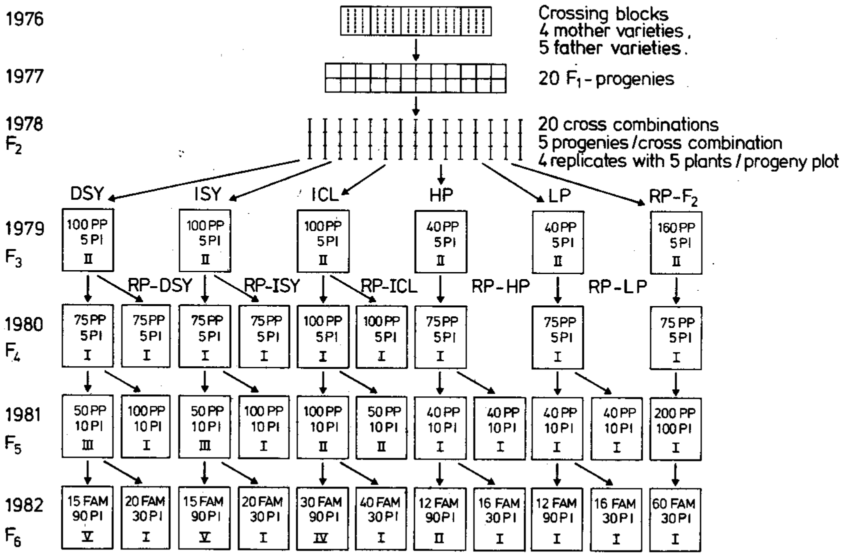

Fig. 1. Selection scheme per Faba bean population (A and B). Both the generation and the year in which it was grown are indicated. The number of plant progenies (PP) equals the number of plants selected in the previous generation; the number of F_4-derived families (Fam.) equals the number of plants progenies selected in F_5. Pl is the net plot size expressed as number of plants. The roman numerals refer to the number of replicates.

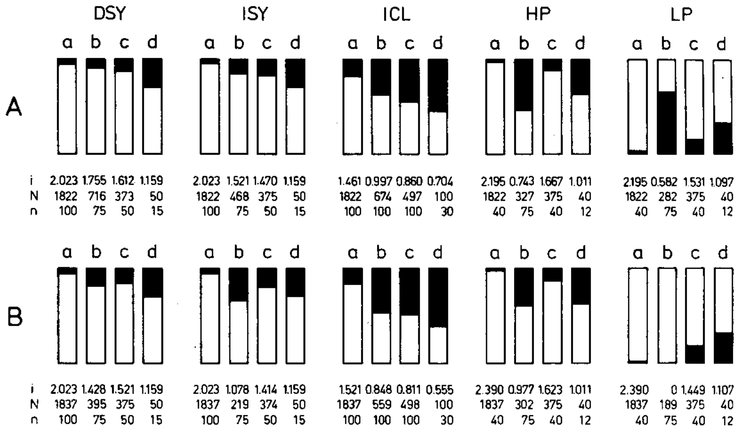

Fig. 2. Selection intensities applied in Faba bean populations A and B. a, b, c, and d denote selection from F_2 to F_3, from F_3 to F_4, from F_4 to F_5 and from F_5 to F_6 respecitvely.
i = selection intensity
N = number of plants or plant progenies (F_5) submitted to selection
n = number of plants or plant progenies (F_6) selected.
The shaded area corresponds to the percentage best plants (plants progenies) actually providing the progeny for the next cycle. The selection intensity i is calculated according to this percentage. The selection intensity for ICL-populations applies for both characters culled for.

plots. To avoid border effects, five one-row plots were sown in a single row without interspace. This may have enhanced competition effects, which are inevitable with one-row plots.

In the F_6 each row contained 30 plants, the random subpopulations were grown in three-row plots and the other subpopulations in five-row plots. The first and the last row of each plot were border rows. Depending on the character, observations and measurements were made on a per plot basis or the mean of a random sample of 10 plants per plot was used as plot measurement. In all generations plant density was 25 plants per m^2 with 40 cm between rows and 10 cm between plants within rows. Crop management was normal and implied a modest use of fertilizers, seed treatment and application of herbicides and pesticides as far as necessary.

The F_2 was grown in complete randomized block design. A detailed description of the analysis is given by DE VRIES et al., (1980). Starting with the F_3, each subpopulation was analyzed separately. For estimation of population parameters, the F_3 and F_4 were analyzed as though the individual plants of a plant progeny were independent replicates in a randomized design. The F_5 and F_6 were tested and analyzed on a per plot basis, so these were truly complete randomized designs.

Statistical analysis involved estimation of population parameters such as mean, genetic and environmental components of variance and coefficients of correlation. Genotypic values or parameters are designated by g, environmental values by e and phenotypic values by p.

The genetic and the environmental variances of a character were estimated from an analysis of variance. To estimate the genetic covariance between two characters a and b, an analysis of variance was made for the sum of these characters. The estimates of the genetic variances of the sumcharacter a + b and of the single characters a and b allowed estimation of the genetic covariance between a and b. This genetic covariance was used to calculate the genetic correlation between a and b as

$$r_g(a, b) = \frac{\text{cov}\,(g_a, g_b)}{\text{var}\,g_a \,.\, \text{var}\,g_b}$$

The phenotypic correlation between a and b was estimated on an individual plant basis.

The characters measured varied with the subpopulations involved and with the generations. Initially only SYP and characters necessary for selection or evaluation of the realized response were measured. Gradually more characters were measured in some of the subpopulations, allowing a more elaborate comparison of the selection methods. The characters involved in this study were:

SYP:	Seed yield per plant, in g.
CP:	Crude protein content of the seed as fraction of dry matter (colorimetrically determined after destruction as Ni × 6.25, with Ni the nitrogen content).
PL:	Plant length after ripening, in cm.
RTP:	Ratio of podless top to total plant length.
EGF:	End of grain filling (last pod entirely black) in days after May 31.
DGS:	Duration of generative stage: days between onset of flowering (the standard petal of the first flower unfolded) and EGF.

Selection theory and prediction of responses. For each of the three types of selection it is possible to give a theoretically justified prediction of the response to selection. In each case the realized response can be estimated as the difference between the subpopulation in the next generation and its corresponding random population. Predicted and realized responses can be compared by expressing them on a relative scale, thus eliminating differences between years.

DSY. The response to selection is predicted by $R = h^2S$, with h^2 the heritability and S the selection differential. The heritability is estimated as

$$h^2 = \frac{\sigma_g^2}{\sigma_p^2} = \frac{\sigma_g^2}{\sigma_g^2 + \sigma_e^2} \quad \text{(broad sense heritability)}$$

The selection differential is calculated as the difference between the (sub)population mean and the mean of the plants or families selected. This response is truly a prediction in sofar the response in the next generation is involved.

ISY. SMITH (1936) developed the index selection theory for selecting simultaneously two or more (economically important) characters in a breeding program. The index selection method of Smith maximizes the expected genetic gain of the total economic value. The index is defined as $I = \sum_{i=1}^{m} b_i p_i$, a linear combination of m observed phenotypic values p_i multiplied by their respective relative weights b_i. The total economic value or aggregate genotype is defined as $H = \sum_{j=1}^{n} a_j g_j$, a linear combination of n unknown genotypic values g_j multiplied by their respective relative economic values a_j. Several authors, among whom BRIM et al., (1959) and LIN (1978) have pointed out that the set of auxiliary characters involved in I and the set of economic characters involved in H do not need to be identical or may even be completely different.

In this study index selection for one character, i.e. SYP was applied so $H = g_{SYP}$. The auxiliary characters included in the index were PL, RTP, EGF and DGS. This set gave the highest mean expected selection response to index selection of the A and B F_2 populations whenever a maximum of four characters was to be included in the index (DE VRIES et al., 1980). To maximize the expected genetic gain per selection cycle, the relative weights of the auxiliary characters need to be recalculated every year in spite of the fact that the same set is used. The relative weights are solved from $bP = G$, in which b is the vector of relative weights, P the phenotypic covariance matrix of the auxiliary characters and G the vector (or matrix with one column) of genetic covariances between the auxiliary characters and SYP. The expected genetic gain in SYP is expressed as $R(SYP) = i\sqrt{b'G}$. The selection intensity i can be determined from the normal distribution tables, provided the distribution of the index values is normal (FALCONER, 1981, p. 174–177).

ICL. ICL selection is a widely used method to select simultaneously for two or more characters. The prediction of response to selection is not too complicated as long as the characters under selection are not correlated.

YOUNG & WEILER (1960) gave exact formulas to predict the response to ICL selection in the case of two correlated characters x and y with a normal, bivariate distribution:

$$R(x) = \sigma_x R(x') = \sigma_x\{\alpha_1 S(x') + \alpha_2 S(y')\} \text{ and}$$

$$R(y) = \sigma_y R(y') = \sigma_y\{\beta_1 S(x') + \beta_2 S(y')\}, \qquad (1)$$

in which x′ and y′ are the characters x and y after standardization, R and S are the predicted response and the selection differential of the indicated variable, σ_x and σ_y are the phenotypic standard deviations of x and y.

α_1, α_2, β_1 and β_2 are constants to be calculated as follows:

$$\alpha_1 = \frac{h^2_{x'} - \rho h_{x'y'}}{1 - \rho^2} \qquad \alpha_2 = \frac{h_{x'y'} - \rho h^2_{y'}}{1 - \rho^2}$$

$$\beta_1 = \frac{h_{x'y'} - \rho h^2_{y'}}{1 - \rho^2} \qquad \beta_2 = \frac{h^2_{y'} - \rho h_{x'y'}}{1 - \rho^2} \qquad (2)$$

in which $h^2_{x'}$, $h^2_{y'}$ are the heritabilities of x′ and y′, $h_{x'y'}$ the ratio of the genetic covariance between x′ and y′ and the product of the phenotypic standard deviations of x′ and y′, and ρ the phenotypic correlation coefficient.

If x and y are uncorrelated, x′ and y′ are also uncorrelated. Statistically, $\rho = 0$ and $\text{cov}(x', y') = 0$ are equivalent, so in the case of uncorrelated characters $h_{x'y'} = 0$. When x and y are uncorrelated, the constants α_1, α_2, β_1 and β_2 reduce to $\alpha_1 = h^2_{x'}$, $\alpha_2 = 0$, $\beta_1 = 0$, $\beta_2 = h^2_{y'}$, and the predicted response can be calculated directly as

$$R(x) = \sigma_x R(x') = \sigma_x h^2_{x'} S(x') = h^2_x S(x)$$

$$R(y) = \sigma_y R(y') = \sigma_y h^2_{y'} S(y') = h^2_y S(y) \qquad (3)$$

Exact prediction of the response to ICL-selection when one of two correlated characters involved is an index, is an unsolved problem as far as we know. Estimation of the statistics of the index, a linear combination of characters, seems feasible. However, this would result in a prediction of the response of the selection criterion (i.e. the index), instead of a prediction of the response of the selection goal. Estimation of the statistics of the total economic value, an aggregate characteristic, does not seem feasible.

In our experiment index selection was applied for only one character, namely seed yield per plant. With ICL-selection for SYP itself instead of an index and CP the simplified prediction formulas (3) would have been permissible as in preliminary experiments no correlation could be established between SYP and CP. It was assumed that a comparable result would have been obtained if the correct estimates of the statistics were available. Consequently, the responses to ICL-selection have to be calculated as though the index and CP are completely independent. This means that each response has to be estimated by its usual prediction method without interference of the other character under selection. In the case of index selection, the method is described above.

RESULTS

For several reasons the actual selection intensity varied considerably over generations (Figure 2). Generally, a relatively low selection intensity indicates that selection was not free from constraints. A heavy infestation with *Fusarium solani* resulted in a substantial loss of plants in the F_3 generation. The number of plants submitted to selection (N) as indicated in Figure 2 for each subpopulation deviates considerably from the intended number of plants (1000) (Figure 1). This reduction of material prior to selection inevitably resulted in a low selection intensity. In the last cycle the percentage plant progenies to be selected was relatively high (30%) and consequently the intensity relatively low. However, in all generations submitted to selection, including F_3 and F_5, the actual intensity was lower than the intensity in accordance to the percentage of plants (plant progenies) selected. The entries were ranked according to a specific selection criterion within each subpopulation and the n best entries were selected. When one or more of those n entries had an insufficient number of seeds to grow the next generation as intended, the next best entry with a sufficient number of seeds was selected. In this way, the proportion of entries actually providing the progeny for the next cycle, could become substantially larger than the proportion n/N.

Mean values for seed yield per plant from F_2 to F_6 of the RP-F_2 subpopulations did show a rather good agreement between the populations A and B with exception of the F_3 generation (Table 1). Within each population the differences between subpopulations were relatively small as compared to the differences between generations.

Table 1. Seed yield per plant (g) from F_2 to F_6 of the A and B Faba bean RP-F_2 subpopulations.

	F_2	F_3	F_4	F_5	F_6
Population A	36.2	18.2	17.6	25.7	28.2
Population B	36.1	30.6	19.8	26.2	29.6

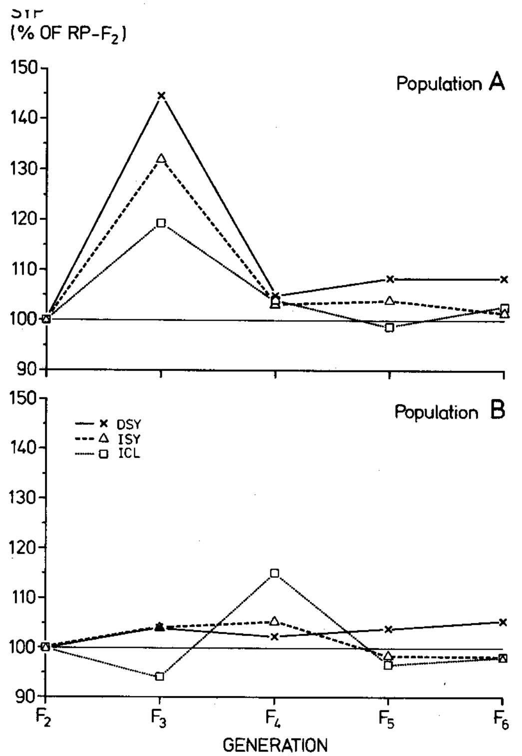

Fig. 3. SYP expressed as percentage of the corresponding RP-F_2 from F_2 to F_6 of the DSY, ISY and ICL subpopulations of the Faba been populations A and B.

To facilitate comparison between selection procedures, seed yield per plant has been expressed as percentage of the corresponding RP-F_2 subpopulation in Figure 3. Considering the differences between generations as shown in Table 1, there was again a rather good agreement between A and B, except for the F_3. Almost certainly the aberrant F_3 results were due to differences in infestation with *Fusarium solani.* The peaks in Figure 3 most likely reflect a depressed yield level of the RP-F_2 in population A and not an important increase in the yield level of the other subpopulations.

In population A the ranking of the subpopulations is more or less the same in all generations. In population B there are some changes in rank of the subpopulations, but the F_5 and F_6 show the same ranking. In both populations the DSY-subpopulation outyielded the corresponding RP-F_2 in all generations, although the differences are small. In general, the yield level of the ISY-subpopulations is somewhat lower than that of the corresponding DSY-populations, so index selection did certainly not improve the selection efficiency. The relative yield level of the ICL-subpopulations, especially in population B, was initially more variable than that of the corresponding DSY- and ISY-subpopulations, but in F_5 and F_6 there was hardly any difference with the ISY-subpopulations. In this experiment the efficiency of index selection for yield did not decrease because of simultaneous selection for protein content (CP). This result seems to be rather unexpected, as the selection intensity for index was considerably

Table 2. Predicted and observed responses to selection for SYP, expressed as percentage of the appropriate Faba bean population.

Subpopulation		Generation							
		population A				population B			
		F_3	F_4	F_5	F_6	F_3	F_4	F_5	F_6
DSY	Predicted	16	20	15	5	17	19	16	7
	Observed	45	12	1	−5	4	−0	−7	−0
ISY	Predicted	22	21	15	9	25	3	18	9
	Observed	33	7	4	−8	4	−5	−3	5
ICL	Predicted	16	9	5	2	19	11	5	1
	Observed	19	2	−5	4	−6	−0	1	−3

lower in the case of ICL-selection (Figure 2).

The differences between the subpopulations have not been tested, as no satisfactory test is available.

Predicted and observed responses to selection for SYP are presented in Table 2 for the subpopulations DSY, ISY and ICL. The predictions are made as indicated in 'Materials and Methods' for each of the selection methods. To eliminate year effects, the predicted responses are transformed from g/plant into per cent of the mean yield (SYP) of the subpopulation under selection and the observed responses are transformed from g/plant into per cent of the mean yield (SYP) of the random subpopulation which represents the unselected subpopulation of the previous generation. In Table 2 the generations mentioned are those for which the responses are expected (predicted) or in which the responses are measured (observed). So, selection in one generation gives responses (predicted and observed) in the next one.

Generally, the responses were overestimated by the prediction methods, although there were a few exceptions: the F_3 of population A and the F_6 of ICL-A.

The observed responses in the F_3 of population A are probably unrealistic. They most likely reflect the depressed yield level of RP-F_2 in this generation as a result of the *Fusarium solani* infestation. The response of the F_6 of ICL-A was underestimated, but the difference is marginal. In all other instances the response was more or less seriously overestimated. The predictions for ICL-subpopulations seem to be somewhat more accurate than those for DSY and ISY-subpopulations.

In Table 3 the phenotypic correlations between SYP and CP of RP-F_2 and ICL subpopulations of populations A and B are presented. These correlations were generally low, even when statistically significant. If the same trend holds in case of phenotypic correlations between index and CP, the bias due to predicting the responses for ICL-selection as though the characters involved were uncorrelated, should be of minor importance. An exception may have to be made for selection in the F_2-generation. In this case the predicted response may have been biased due to ignoring the phenotypic correlation between index and CP.

The evolution from F_2 to F_6 of the auxiliary characters included in the index is presented in Table 4. The data sets for both DSY-subpopulations are incomplete and

Table 3. Phenotypic correlations between SYP and CP from F_2 to F_5 for RP-F_2 and ICL subpopulations of Faba bean populations A and B.
$*0.01 < P \leqslant 0.05$; $** P \leqslant 0.01$

	Population A				Population B			
	F_2	F_3	F_4	F_5	F_2	F_3	F_4	F_5
RP-F_2	0.25**	0.13**	0.21**	-0.15*	0.43**	-0.12*	0.23**	-0.11
ICL		0.08*	0.03	-0.08		0.02	0.04	-0.11

Table 4. Development from F_2 to F_6 of the auxiliary characters included in the index in the subpopulations RP-F_2, DSY, ISY and ICL of the Faba bean populations A and B. Open places indicate non-existing subpopulations. Whenever in an (existing) subpopulation a character has not been observed, this is indicated by –.

	Population A					Population B				
	F_2	F_3	F_4	F_5	F_6	F_2	F_3	F_4	F_5	F_6
PL (cm)										
RP-F_2	92	62	83	113	105	81	73	77	110	108
DSY		–	87	133	121		–	85	131	128
ISY		78	100	146	133		87	94	134	133
ICL		74	99	136	123		80	95	136	119
RTP										
RP-F_2	0.44	0.45	0.50	0.46	0.44	0.47	0.45	0.54	0.51	0.46
DSY		–	–	0.40	0.37		–	–	0.42	0.38
ISY		0.37	0.46	0.35	0.33		0.38	0.50	0.40	0.35
ICL		0.40	0.47	0.36	0.35		0.39	0.49	0.37	0.39
EGF (days)										
RP-F_2	95	89	78	82	67	94	91	79	83	68
DSY		–	–	86	70		–	–	87	70
ISY		97	86	88	69		100	88	86	69
ICL		93	83	88	70		98	83	88	68
DGS (days)										
RP-F_2	89	75	76	78	66	90	79	78	80	68
DSY		–	–	–	67		–	–	–	68
ISY		78	79	79	64		83	85	79	68
ICL		73	77	79	65		79	80	79	66

are used only for comparison with other subpopulations. In the case of ISY selection, the selection criterion consisted of a linear combination of the auxiliary characters; in the case of ICL selection this applied to one of the two selection criteria. Index selection has induced a considerable change in the level of the auxiliary characters except DGS, although this is less obvious for EGF in the F_6, owing to a hot, dry summer. The level of the auxiliary characters of the DSY-subpopulations resembles more that of ISY and ICL than that of RP-F_2, an apparent result from the correlation

Table 5. Ranges over generations and subpopulations and generation means of the heritabilities of SYP, PL, RTP, EGF, DGS and CP of the Faba bean populations A and B.

	Population A						Population B					
	range	mean					range	mean				
		F_2	F_3	F_4	F_5	F_6		F_2	F_3	F_4	F_5	F_6
SYP (g)	0.06–0.41	0.12	0.25	0.15	0.24	0.08	0.11–0.56	0.11	0.29	0.21	0.23	0.33
PL (cm)	0.22–0.61	0.48	0.40	0.50	0.37	0.33	0.17–0.78	0.52	0.51	0.59	0.41	0.25
RTP	0.06–0.76	0.35	0.24	0.16	0.60	0.31	0.09–0.75	0.33	0.40	0.26	0.62	0.25
EGF (days)	0.10–0.72	0.33	0.52	0.26	0.50	0.41	0.19–0.72	0.39	0.38	0.33	0.49	0.45
DGS (days)	0.08–0.63	0.19	0.36	0.17	0.41	0.54	0.18–0.69	0.31	0.38	0.23	0.45	0.54
CP (% of dm)	0.26–0.57	0.45	0.45	0.39	0.43	0.27	0.12–0.59	0.53	0.53	0.43	0.51	0.12

between SYP and the auxiliary characters.

In Table 5 ranges over generations and subpopulations and generation means of the heritabilies of SYP, the auxiliary traits and CP are given. In general, the heritability of SYP was low (mostly < 0.3). The heritabilities of the auxiliary characters, as expected mostly higher than those of SYP, did vary, but no general tendency can be detected. There was no general decrease of heritabilities, i.e. a decline of genetic variation nor systematically higher or lower heritabilities in one of the subpopulations.

In Table 6 ranges over generations and subpopulations and generation means of the genetic correlations between SYP and the auxiliary characters are given. In general, these correlations decreased, especially from F_2 to F_3 and from F_5 to F_6. In a few instances, the correlation even changed sign.

The values of b-coefficients for index selection are presented in Table 7. The magnitude and sign of the b-coefficients show considerable variation over populations, generations and subpopulations. This may reflect important changes in the estimates of genetic correlations of auxiliary characters with SYP (Table 6) and/or in phenotypic correlations between auxiliary characters (not presented).

Table 6. Ranges over generations and subpopulations and generation means of genetic correlations with SYP from F_2 to F_6 of the characters PL, RTP, EGF and DGS of the Faba bean populations A and B.

	Population A						Population B					
	range	mean					range	mean				
		F_2	F_3	F_4	F_5	F_6		F_2	F_3	F_4	F_5	F_6
PL	–0.19–0.96	0.80	0.67	0.47	0.73	0.02	0.02–0.82	0.82	0.52	0.56	0.53	0.25
RTP	–0.98–0.33	–0.64	–0.43	–0.61	–0.47	0.12	–0.58–0.22	–.58	–0.14	–0.29	–0.15	0.03
EGF	–0.04–0.82	0.82	0.41	0.37	0.52	0.14	0.03–0.89	0.89	0.20	0.42	0.47	0.43
DGS	–0.24–0.74	0.74	0.54	0.31	0.26	0.16	0.09–0.90	0.90	0.41	0.28	0.37	0.44

Table 7. Values of b-coefficients used to calculate the selection indices in the F_2 and the F_3 to F_5 of the subpopulations ISY and ICL of the Faba bean populations A and B.

Character	Sub-population	Generation							
		Population A				Population B			
		F_2	F_3	F_4	F_5	F_2	F_3	F_4	F_5
PL	RP-F_2	1.292				1.448			
	ISY		0.101	0.173	0.126		0.003	0.159	0.243
	ICL		0.100	0.040	0.042		0.216	0.046	0.035
RTP	RP-F_2	7.172				82.738			
	ISY		-3.955	-20.185	2.764		-2.616	0.912	-34.326
	ICL		–4.130	0.459	–0.288		12.371	4.372	8.397
EGF	RP-F_2	4.693				2.805			
	ISY		0.147	–0.631	0.166		–0.047	–0.107	–0.609
	ICL		–0.003	–0.018	0.099		–0.230	0.200	–0.142
DGS	RP-F_2	–4.677				-1.209			
	ISY		0.153	0.234	0.053		0.123	0.058	0.480
	ICL		0.048	0.112	0.064		0.297	–0.170	0.009

DISCUSSION

Previous to a discussion of the selection procedures in comparison with each other, some remarks have to be made on the generally disappointing responses to selection. Figure 3 reveals two rather remarkable features of the responses to selection. Firstly, the maximum relative yield level of all selection methods was reached after only one or two cycles of selection. Secondly, the final relative yield level of all subpopulations was remarkably low. For both effects a plausible explanation can be given.

The stagnation of the response to selection may have been due to selection of heterozygotes in later generations. If seed yield shows a certain extent of heterosis, the most heterozygous plants will have the highest yield level. In the F_2 all plants are highly heterozygous and there will be hardly any differences in level of heterozygosity between the plants. In an ordinary autogamous crop, selection of heterozygotes will more or less seriously slow down the rate of progress, but it will not prohibit all success, as all plants will eventually be more or less homozygous. However, Faba beans do show a considerable extent of natural outcrossing. Bond & Poulsen (1983) reported in a review estimates ranging from 4 to 84% with an average of about 35% outcrossing. With such an extent of outcrossing, selection of heterozygotes may prohibit any progress from selection, as the most heterozygous plants will be found in the offspring of cross-fertilized plants. Therefore, selection of heterozygotes may render the selection rather ineffective. There are some indications that the hypothesis described above is correct.

The broad sense heritability remained more or less stable (Table 5), which indicates that either there was no heterosis at all or a certain extent of heterozygosity is maintained. The representation of the maternal varieties (data not presented) showed some remarkable irregularities. In all yield selections the same maternal varieties became overrepresented. This applies for population A as well as population B. These varieties happen to be the same that showed the highest percentage outcrossing in the crossing blocks designed to generate the populations A and B, as reported by DE VRIES (1978b). The percentages reported ranged from 3 to 26%, which is low compared to literature data for Faba beans. However, outcrossing up to 26% will result in a relative large proportion of newly formed heterozygotes in every generation.

The ineffectiveness of the selection procedures applied seems to have been emphasized by some unintended selection for seed yield in the RP-F_2 subpopulations. The representation of the maternal varieties in the RP-F_2's showed the same tendency as in the yield selections, although less pronounced. Nevertheless, it indicates a tendency towards selecting the offspring of maternal varieties with the highest percentage outcrossing. This will probably have resulted in a slightly enhanced yield level due to maintenance of a modest level of heterozygosity in the RP-F_2 subpopulations. However, it is rather unlikely that these effects have been very pronounced as all maternal varieties remained represented in the RP-F_2.

Direct comparison of the selection procedures by means of the results obtained is complicated by differences in selection intensity. Initially the same number of plants was selected per procedure concerning selection for yield (Figure 1). However, the selection intensities were not the same (Fig. 2), due to the minimum number of seeds required to grow the next generation, a finally lower number of plants than intended, and, in case of ICL selection, the simultaneous selection for protein content. As mentioned before, the infestation with *Fusarium* did have a serious impact on the selection intensities. Later on the number of plants or progenies selected in ICL-subpopulations was even larger than in DSY- and ISY-subpopulations. This enlarged the differences in selection intensities. In spite of these complications some conclusions can be drawn.

According to predicted responses, index selection was slightly superior to direct selection for yield (Table 2), sometimes in spite of a lower selection intensity. Because of *Fusarium* the F_3 of the ISY-B subpopulation was decimated before selection, which resulted in a very low selection intensity (Fig. 2). Consequently the F_4 was the only generation with a higher predicted response for direct selection for yield. Generally, selection procedures are compared at equal selection intensities, e.g. PESEK & BAKER (1970), EAGLES & FREY (1974) and MOLL et al., (1975). In this experiment a practical restriction (a sufficient number of seeds to grow the next generation) prohibited equal selection intensities. Without such a restriction or any unintended losses of material, the theoretical superiority of index selection probably would have been more pronounced.

GALLAIS (1984) distinguishes two types of index selection for only one character, which usually is yield. The first type does not include yield itself and should have the advantage of being cheaper or easier to perform. The efficiency of selection is about the same or sometimes even somewhat lower than the efficiency of direct selection. The second type includes yield itself and should enhance the efficiency of selection. In our experiment the set of auxiliary characters used gave the highest predicted response to selection of the F_2-populations even when compared to any set of at most four characters including yield itself (DE VRIES et al., 1980). It has never been checked whether the set used gave the highest predicted response in subsequent generations. However, theoretically, index selection based on this set remained superior to direct selection. As this index is probably not cheaper nor easier to perform than direct selection, it must have a higher efficiency to be of practical importance.

As far as predictions are concerned, ICL-selection appears somewhat inferior to both DSY- and ISY-selection except for the first selection cycle (Table 2). In this first selection cycle the predictions for ICL- and DSY-selection were equal. This may reflect the differences in selection intensity (Fig. 2). The relative low selection intensity for ICL resulted inevitably in a lower predicted response compared to ISY, but this effect was completely compensated by the theoretical superiority of index selection when compared to DSY. In subsequent generations the superiority of index selection decreased and the differences in selection intensities seemed to become more important. These two effects may explain the predicted inferiority of ICL-selection to both DSY- and ISY-selection.

The predictions do not seem to be very precise for any of the three selection procedures applied. Highly inaccurate predicted responses to index selection were also found by PESEK & BAKER (1970). In our experiments there was a general tendency to overestimate the response which seemed to be the least for ICL-selection. The same tendency can be found in the paper of EAGLES & FREY (1974). These authors compared five selection procedures with oats, among which direct selection for seed yield, index selection with seed and straw yield as main characters and ICL-selection for seed and straw yield, at a selection percentage of 25 and 10%. At both selection intensities ICL-selection tended to give the lowest overestimation as far as yield is concerned, while differences in overestimation between direct and index selection seemed to be negligible. For all selection methods a more serious overestimation was found at the highest selection intensity, i.e. 10% selected. The amount of overestimation expressed in g/plot was partly related to the response, expressed also in g/plot, but even with the amount of overestimation expressed as percentage of the response, the accuracy of the prediction seemed slightly better at 25% selected. So, both ICL-selection in itself and a lower selection intensity tended to give a slightly more accurate prediction of the response. This tendency was confirmed by our results.

The sources of overestimation may be partly the same for all three selection methods. The predictions are made in another environment than the environment in which the realized response is measured. This may introduce a bias from genotype × environment interaction (BRIM et al., 1959; MOLL et al., 1975). Deviations from the assumptions on which the selection theories are based, may have a relative large impact on the predictions. This applies for example to nonnormality (BYTH et al., 1969). The reliability of the predictions depends heavily on the error in the estimates of variances and covariances (BRIM et al., 1959). According to LIN (1978) the efficiency of index selection is more effected by errors in the estimation of the genetic correlations than in those of the heritabilities. MOLL et al. (1975) and BOS (1981, p. 93–94) found large differences in the estimates of genetic correlations obtained via different estimation methods. Probably such estimates are subject to relatively large errors.

In our experience a decision in favour of a more complicated and time-consuming selection method such as index selection cannot be defended. In spite of its theoretical superiority to direct selection, viz. a higher predicted response to selection, no practical advantage whatsoever has been found. The realized response of index selection was slightly inferior to that of direct selection, index selection was more complicated to perform and undesired changes in auxiliary characters were more pronounced.

In both populations (A and B) the best results were obtained with direct selection for seed yield per plant. This selection method was not only the best method, but also the only method that resulted in a more or less stable, positive response to selection as compared to the corresponding RP-F_2 subpopulation (Fig. 3). So, the index used did not enhance the efficiency of selection nor did it provide any other advantage such as being easier or cheaper to perform. MANNING (1956) obtained a high response to index selection in four consecutive selection cycles in cotton. The response was measured by comparison with an open pollinated variety. Manning's experiment indicated that index selection can be efficient, but as no comparison with direct selection was made, nothing can be said about the relative efficiency. GALLAIS (1984) reports index selection being more efficient than direct selection for dry matter yield in forage maize. Here, direct selection can be seriously hampered by damage such as lodging, interfering with accurate yield measurements. However, indirect selection can be hampered by an undesired correlated response of a character not directly involved in the selection procedures (GALLAIS, 1984). In our experiment an undesired response was found in all subpopulations.The mean plant length increased and all selections were very susceptible to lodging (unpublished results). As plant length was one of the auxiliary characters in index selection, this was to be expected in the case of ISY or ICL subpopulations. However, a comparable, undesired, correlated response was found in the DSY subpopulations. This seems paradoxical with the disappointing results of index selection.

Index selection did not result in a marked increase of SYP, whereas direct selection for SYP did result in a rather pronounced response of the auxiliary characters used in the yield index. This paradox may have the same origin as the relative large inaccuracy of the predictions of index selection, i.e. insufficient precision of the estimates of the genotypic correlations. As mentioned above, different estimation methods may bring forth large differences in the estimates of the genotypic correlation, and the efficiency of index selection seems quite vulnerable to errors in the estimates of the genotypic correlations. Now it can be assumed that a character which yields fairly high estimates of genotypic correlation with SYP in two independent populations, is really correlated with SYP. The realized correlated response of such a character when selecting for SYP itself, does not depend on the estimates of the genotypic correlation and may reflect the genuine genotypic correlation.

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