

## Performance of recombinant inbred lines in Brussels sprouts (*Brassica oleracea* var. *gemmifera*)

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**Summary.** Performance of a random array of recombinant inbred lines derived by single seed descent from five different source populations of Brussels sprouts (*Brassica oleracea* var. *gemmifera*) is presented. A total of 2,356 lines were tested in trials during 1985 and 1986. Three of the source populations were derived from double crosses between  $F_1$  hybrids. These hybrids show a considerable heterotic advantage over their inbred parents for the most important agronomic traits. The recombinant inbred lines performed, on average, less well than the parental inbred material, indicating that additive  $\times$  additive genic interactions may make a significant contribution to the performance of current inbred material. Nevertheless, the very large variation among the recombinant inbred lines permitted many lines to be identified which outperformed the best parental inbred for all traits. Two lines outperformed the reference  $F_1$  hybrid, Gower, for an index that included marketable yield and quality. Consideration was also given to the dangers of misinterpreting phenotypically based proportions. Accordingly, response equations were used to ascertain the real genetic progress that was made. Advance seemed small when compared with the large heterotic effect, which is consistent with the segregation of a large number of loci. The distribution of the recombinant inbred lines was compared to predictions made from early generation trials. There was broad agreement but significant discrepancies existed which, it is suggested, may arise from the effects of genotype-environment interactions.

**Key words:** Brussels sprouts – Inbred lines – Predictions – Heterosis

### Introduction

During recent years  $F_1$  hybrids of Brussels sprouts (*Brassica oleracea* var. *gemmifera*) have completely replaced open-pollinated cultivars. This development may be attributed both to their superior uniformity and to their generally improved vigour and performance. Most commercial hybrids exhibit considerable heterosis with respect to their inbred parents which, for yield, can increase the performance of a hybrid to about 150% of that of the best parent (Smith et al. 1985). The genetic basis of this heterosis has been shown from triple test cross studies (Kearsey 1984) to be consistent with the dispersion of partly dominant increasing alleles between the two parents. From these findings it was concluded that it should be possible to extract superior recombinant inbred lines from existing  $F_1$  hybrids. Such performance may only be obtained, however, in a recombinant inbred line with close to the best possible homozygous combination of genes. In practice, the ease with which this optimum may be attained will depend upon several factors, particularly the number of segregating loci and the dominance ratio. Published work quantifying the likely potential of inbred lines per se in the Brussels sprouts crop is limited to early generation prediction trials from which Rogers et al. (1987), using an  $F_3$  trial design, found that 0.7% of a random array of recombinant inbred lines could be expected to be superior to their source  $F_1$  hybrid for yield. A similar study by Kearsey (1984), using a triple test cross design, arrived at the rather higher estimate of 4.0%.

These findings challenge the status of  $F_1$  hybrids as the natural choice for commercial Brussels sprouts culti-

vars. The concept that inbred lines could replace  $F_1$  hybrids gains extra credibility because of the high seed production costs for  $F_1$  hybrids (Johnson 1984). Inbred cultivars, provided that they are sufficiently self-compatible, could reduce these costs. Whilst this may represent a reasonable objective, Johnson (1984) raised an important note of caution by emphasizing the need to obtain a satisfactory performance not only for yield but also for quality, lodging, disease resistance and sprout number, which contribute to the value of the crop and possibly also to the yield stability.

While the predictive trials (Rogers et al. 1987; Kearsey 1984) were being conducted, a programme involving single seed descent (SSD) and anther culture (AC) was in progress to produce inbred lines which could act as a test of these predictions. The present paper reports the results from two trials of SSD and AC lines.

These trials had two objectives. First, to examine the distribution of a random sample of the SSD lines with respect to production characters and to compare them with the earlier predictions. Second, to select a number of potentially superior lines for inclusion in larger plot trials in following years.

## Materials and methods

The project was initiated in 1980 when a trial was grown to identify the best starting material for a large-scale inbreeding programme conducted by SSD. This trial included 23  $F_1$  hybrids with 22  $F_2$  and 22 double cross (DC) populations derived from them, together with two open-pollinated (OP) cultivars, one experimental synthetic population and five representative parental inbred lines (Smith et al. 1985). Following this trial, five source populations were selected to initiate the SSD programme. The origins of these five groups of material are as follows: A. Roem van Kloosterburen (OP), B. Experimental synthetic, C. Pinnacle  $\times$  Nym (DC), D. Lunet  $\times$  Gower (DC), E. NVRS (1)  $\times$  Warwick (DC). Each of these populations initiated 1,000 SSD lines.

### 1985 trial

The bulk of the material available for inclusion in the 1985 trial was 1,000 of the most advanced SSD lines (groups A–D); these had been inbred for three generations (to the equivalent of  $F_3$ ). Also available in 1985 were 131 spontaneously diploid lines produced by anther culture (group F) from three sources, Gower  $F_1$  (53 lines), Nym  $F_1$  (35 lines) and the Pinnacle  $\times$  Nym DC (43 lines) (Ockendon 1984). The controls included the  $F_1$  hybrids, Gower and Lunet, and the parental inbred lines were represented by the four parents used to produce the Pinnacle  $\times$  Nym DC.

The trial was set out in two sections: (a) A random sample of 30 lines from each of the groups A–D and the 131 AC lines. Five lines from each of the SSD groups were replicated in each of two plots and each control entry was replicated in at least three plots. All other entries were represented by a single plot. Plots were completely randomized within a single block and all the plots were harvested and recorded from this section of the trial. (b) Included 880 SSD lines not utilized in Sect. (a). Thirty of these lines were chosen at random and were replicated in two

plots which were randomized throughout the section. Further control material was also included and replicated in two or more plots. All replicated plots were harvested. The remaining 850 SSD lines were represented by a single plot and set out in four blocks corresponding to the groups A–D. These single-plot entries were inspected and only harvested if they surpassed the breeder's subjective standard.

Seed was sown in 40 mm peat blocks at the end of March. The seedlings were raised in Dutch light frames and transplanted to the field at the end of May. In both sections, each plot consisted of a single row of 12 plants spaced 60 cm between plants and between rows; the central 10 plants of each row were harvested. All  $F_1$  hybrid controls were guarded on either side by a row of randomly chosen SSD material, which was not assessed. The two sections of the trial occupied a large rectangular area made up of 14 beds of 130 single row plots. In order to correct for variability over this area, the inbred line GA<sub>1</sub> (one of the parents in each of the hybrids, Gower, Nym and Warwick) was chosen to be planted in every 40th plot throughout the trial to act as a systematic control.

From the beginning of September onwards, each plot was inspected once a week to determine whether or not it was ready for harvesting. The criteria used for this decision were subjective, but the intention was to harvest the plot when it had achieved the maximum marketable yield. Plots designated as ready were cut during the following week and the sprout buttons were graded into marketable and non-marketable categories. The marketable buttons were graded by size into large (diameter > 3.5 cm), medium (2.5 cm–3.5 cm) and small (< 2.5 cm). Each grade was weighed and scored for overall quality of the buttons on a scale of 1–5 (1 represents poor quality). Five characters based on whole plot records are presented. Marketable weight (MWt) is the mean weight, in grammes, of marketable sprout buttons per plant. Average quality (AQ) is the average quality taken over the three size grades weighted by the yield of sprouts in each grade. These two characters were combined to give an index, the details of which are shown in the results section. The harvest date (HD) is presented in days from September 1st. Sprout number (SN) is the mean total number of sprout buttons per plant.

### 1986 trial

In 1986 the design followed that of Sect. (b) used in 1985. Available for the 1986 trial were a total of 1,355 new SSD lines (three generations inbred) from each of the groups A–E plus 383 AC-derived lines from the  $F_1$  hybrids, Gower, Nym and Dorema. A random sample of 16 SSD lines that had been raised in the 1985 trial was included in the 1986 trial using residual seed; each of these lines was replicated in two plots and all were harvested. Hybrid, parental inbred and systematic controls were included and the same trial techniques and records were taken as for 1985. The sowing date was 1 week earlier than in 1985.

## Results

For each trait the data from the systematic control (GA<sub>1</sub>) were used to determine linear or nonlinear regressions onto the position of each plot of the field. In 1985 significant ( $P < 5\%$ ) reductions in the residual variation were obtained using linear regressions of the following characters onto the row position: sprout number, accounting for 12% of the residual variation and marketable weight of medium size buttons, which accounted for

22% of the residual variation. Also in 1985 significant linear regressions onto the bed position were found for harvest date and marketable weight of small size bottoms, both of which accounted for 9% of the residual variation. No further significant reduction in residual variation was possible by using either multiple linear or non-linear models. Many of the SSD lines were only represented by a single-row plot and, therefore, to enhance the accuracy of selections, it was desirable to remove as much of the macro-environmental variation as possible. It was assumed that the detection of a significant regression slope indicated an underlying gradient in the field and that all genotypes were affected equally. Accordingly, the data for each of the above characters and, hence, characters derived from them (e.g. MWt and AQ), were adjusted using the linear regression equations. The same approach was used for the 1986 data but no significant regressions were revealed. Unfortunately in 1986 the GA<sub>1</sub> material established poorly, and consequently many plots had gaps and less than ten plants available for harvest. A regression of total marketable weight against the final number of plants per plot was significant ( $P=0.024$ ) and was used to adjust the marketable weight scores for GA<sub>1</sub> to the score expected from a complete plot of ten plants. Only GA<sub>1</sub> was seriously affected by the loss of plants and, hence, by these effects of reduced field density.

One of the objectives of these two trials was to make selections of the best SSD lines. Such selections can be based upon the subjective decisions of a breeder but may also involve the use of objective quantitative data. In the case of Brussels sprouts, marketable yield and button quality may be identified as the two major components of merit. Accordingly it was decided to formulate an index of breeding merit based upon the characters, MWt and AQ, giving each of these equal weighting in standard deviation units.

The procedure used to develop an index of breeding merit was as described by Falconer (1981). Estimates of between-line ( $\sigma_b^2$ ) and within-line ( $\sigma_w^2$ ) components of variation were obtained from analyses of variance of the random samples of replicated SSD lines raised in 1985 (46 lines) and 1986 (29 lines; this included 13 lines not previously grown in 1985). For SSD lines at the equivalent of the F<sub>5</sub> generation  $\sigma_b^2$  includes only a small proportion of non-additive genetic variation and  $\sigma_w^2$  provides an estimate of the environmental variation applicable to plots. The narrow-sense heritability of line means ( $h_n^2$ ) based on ten plants has, therefore, been estimated as  $\sigma_b^2 / \sigma_p^2$  (Table 1), where the phenotypic variance  $\sigma_p^2$  is equal to  $\sigma_b^2 + \sigma_w^2$ . The index equations were set up using the data in Table 1 and economic weights were equal to  $1/\sigma_p^2$ . The solution obtained for 1985 was:

$$I = 0.0048 \text{ MWt} + 1.2 \text{ AQ}$$

**Table 1.** Phenotypic variances and narrow heritabilities of SSD line means for marketable weight (MWt) and average quality (AQ) and the phenotypic and between line covariances in 1985 and 1986

Trait	1985		1986	
	$\sigma_p^2$	$h_n^2$	$\sigma_p^2$	$h_n^2$
MWt	25,799	0.758	40,926	0.739
AQ	0.469	0.759	0.349	0.578
	$w_p^2$	$w_b^2$	$w_p^2$	$w_b^2$
Cov <sub>MWt, AQ</sub>	56.53	48.56	22.64	8.173

and for 1986 was:

$$I = 0.0034 \text{ MWt} + 0.87 \text{ AQ.}$$

These equations were used in 1985 and 1986, respectively, to construct an index score for each plot.

Analyses of variance showed that only for harvest date and sprout number were there significant differences between the four SSD groups, but that for all characters there was a highly significant ( $P < 1\%$ ) difference between lines, reflecting the considerable genetical variation released by recombination. Bartlett's tests showed that the estimates of the between-line mean squares from the four groups were homogeneous for all characters. Mean performance for each SSD group together with the standard errors and degrees of freedom, which are based upon the between-line mean square, are listed in Table 2. Also in Table 2 is the mean performance of these four groups in 1985 and the mean performance of the random sample of lines raised in 1986. These two samples were not equally represented by the four groups and, therefore, may not be equivalent to each other. To check if this presented a problem, the 1985 sample was partitioned into a subset of lines corresponding to those repeated in 1986 and a subset including all remaining lines. These two sets were compared, but no significant differences were found for any of the characters. Table 3 presents the mean scores of the hybrid and parental inbred controls. The parental mean represents the average of the four parent lines which contributed to the Pinnacle  $\times$  Nym DC. Bartlett's tests for homogeneity of the between-replicate plot variance were not significant in 1986 and, therefore, permitted the pooling of the estimates of error variation from all the non-segregating sources (F<sub>1</sub> hybrids, inbred parents and the replicated sample of SSD lines). In 1985 the estimates of error variation from the inbred parents and those from the replicated sample of SSD lines were homogeneous. The estimates from the F<sub>1</sub> hybrids were, however, significantly different to the pooled estimates from the inbred material for three of the characters (MWt, Index and SN). This observation is consistent with the presence of a mean-variance correla-

**Table 2.** Mean scores for the random sample of SSD lines in 1985 and 1986. The standard errors (S.E.) are based on between family mean squares and the degrees of freedom (D.F.) are equal to the number of lines - 1

Material	Year	No. plots	D.F.	MWt <sup>a</sup>		AQ		Index		HD		SN	
				mean	S.E.	mean	S.E.	mean	S.E.	mean	S.E.	mean	S.E.
Group A	1985	38	30	379	28.7	2.70	0.117	4.92	0.219	63.5	4.89	53.3	2.57
Group B	1985	37	31	318	29.1	2.67	0.113	4.60	0.222	81.0	4.95	48.5	2.61
Group C	1985	44	32	312	26.7	2.47	0.122	4.34	0.203	81.1	4.54	37.2	2.39
Group D	1985	54	40	311	24.1	2.70	0.094	4.60	0.183	80.6	4.10	40.7	2.16
Means	1985	173	133	328	13.5	2.63	0.052	4.60	0.103	74.9	2.29	44.3	1.21
	1986	31	15	539	45.3	2.46	0.152	4.02	0.230	58.0	3.94	52.6	3.75

<sup>a</sup> MWt, AQ, HD and SN are marketable weight, average quality, harvest date and sprout number, respectively

**Table 3.** Mean scores for the hybrid and parental inbred controls in 1985 and 1986. Standard errors (S.E.) and degrees of freedom (D.F.) are based on replicate plots

Material	Year	No. plots	D.F.	MWt <sup>c</sup>		AQ		Index		HD		SN	
				mean	S.E.	mean	S.E.	mean	S.E.	mean	S.E.	mean	S.E.
Gower (F <sub>1</sub> )	1985	10	18	997	47.5	3.73	0.103	9.05	0.267	71.8	3.03	53.8	3.31
	1986	12	147	1,061	36.2	3.63	0.109	6.86	0.158	69.3	2.94	58.0	1.54
Lunet (F <sub>1</sub> )	1985	5	18	1,088	67.2	3.89	0.145	9.67	0.377	76.1	4.28	73.6	4.68
	1986	10	147	1,196	39.7	3.95	0.120	7.61	0.173	70.6	3.22	71.9	1.69
GA <sub>1</sub>	1985	45	78	518	12.2	3.28	0.057	6.25	0.090	58.2	1.69	41.8	0.82
	1986	60	147	786 <sup>a</sup>	16.2	3.37	0.049	5.67 <sup>a</sup>	0.071	62.8	1.31	56.9	0.69
Parental mean	1985 <sup>b</sup>	23.8	78	409	16.8	2.96	0.078	5.36	0.124	80.8	2.33	38.4	1.13
	1986	22.1	147	606	26.7	2.65	0.080	4.42	0.117	72.3	2.16	46.1	1.14

<sup>a</sup> Adjusted to compensate for poor plant establishment: unadjusted, MWt = 827, Index = 5.82

<sup>b</sup> The number of replicate plots per parental line differed; the figure given here is based on the harmonic mean which in 1985 = 5.95 and in 1986 = 5.52

<sup>c</sup> MWt, AQ, HD and SN are marketable weight, average quality, harvest date and sprout number, respectively

**Table 4.** The difference (P - SSD; 1985) between the average of the four parents and the mean single seed descent (SSD) performance for the Pinnacle × Nym DC. The probability level given is for the t test against H<sub>0</sub>: P - SSD = 0

Trait <sup>c</sup>	P - SSD	S.E.
MWt	96.7	31.52 **
AQ	0.49	0.145 ***
Index	1.02	0.238 ***
HD	-0.29	5.103 N.S.
SN	1.16	2.645 N.S.

\*\*, \*\*\* and N.S. indicate probabilities of <1%, <0.1% and >5% respectively

<sup>c</sup> MWt, AQ, HD and SN are marketable weight, average quality, harvest date and sprout number, respectively

tion which has been previously identified in this material for marketable yield and sprout number by Smith et al. (1985). For the analyses presented in the present paper, the removal of this correlation by the use of a scale transformation is not necessary but, because of the lack of homogeneity, the error sources used for the F<sub>1</sub> hybrids have not been pooled with those for the inbred material.

In 1985 the four parents of the Pinnacle × Nym DC were grown together with a random array of recombinant inbred lines derived from this cross (group C). This enabled a test for the presence of additive × additive epistasis. For any DC, in the absence of epistatic interactions, the mean of the four parents contributing to the DC would be expected to equal the mean of a random array of recombinant inbred lines derived from it. Epistasis, on the other hand, could either inflate or deflate the average of the parental lines and, therefore, this equality would no longer hold true. For the available Pinnacle × Nym material, the SSD lines were not fully inbred but were at the equivalent of F<sub>5</sub> and, therefore, the mean of the SSD sample may be inflated by dominance effects. However, the level of inbreeding is such that the influence of dominance is likely to be small (1/8 the dominance in the DC). The results of these tests for additive × additive interactions are shown in Table 4, which gives the differences (P - SSD) between the four parental means (P) and the mean of the Pinnacle × Nym SSD lines (SSD), together with the standard error of the differences and the significance of the deviations from

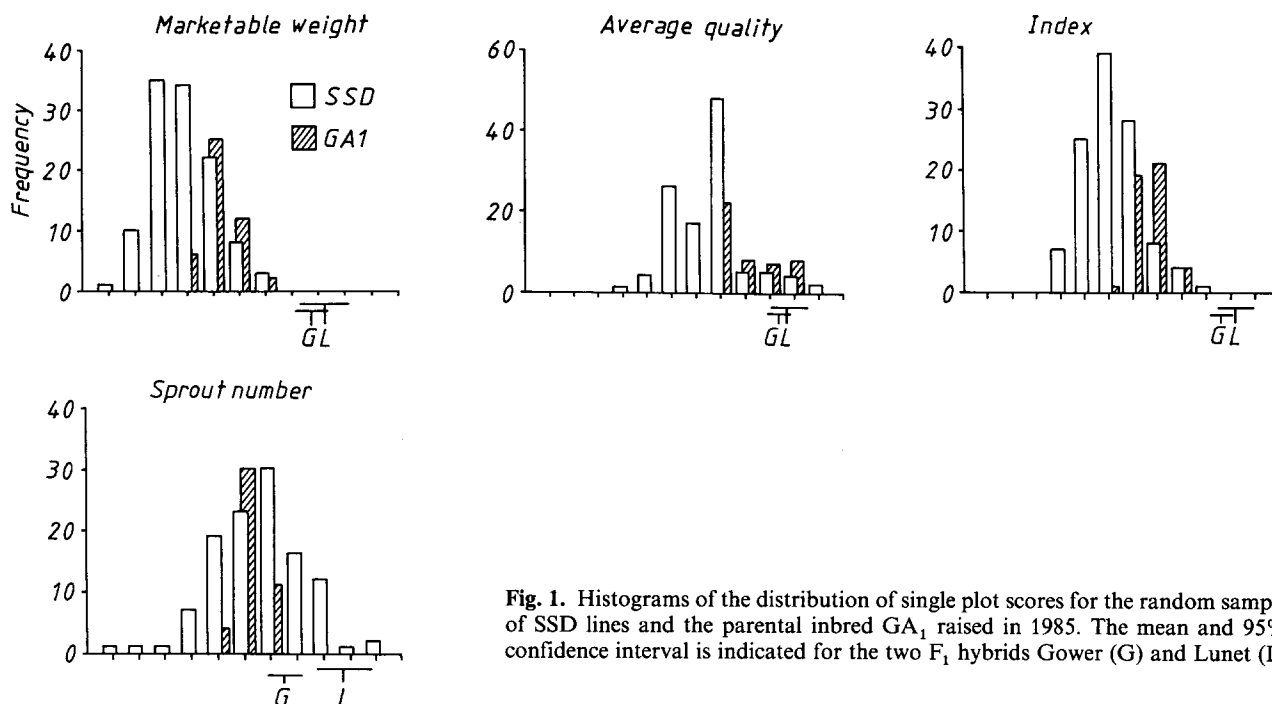


Fig. 1. Histograms of the distribution of single plot scores for the random sample of SSD lines and the parental inbred  $GA_1$  raised in 1985. The mean and 95% confidence interval is indicated for the two  $F_1$  hybrids Gower (G) and Lunet (L)

Table 5. Percentages of SSD lines scoring greater than or equal to the mean performance of  $GA_1$  and Gower. Data for groups A–D have been accumulated over both seasons; group E was only raised in 1986

Group	No. lines	Percent lines > $GA_1$				Percent lines > Gower			
		MWt <sup>b</sup>	AQ	Index	SN <sup>a</sup>	MWt	AQ	Index	SN <sup>a</sup>
A	428	8.3	1.2	4.9	81.5	0.5	0.7	0.0	3.7
B	241	5.4	2.9	2.9	80.6	0.4	2.1	0.0	19.4
C	647	4.8	1.1	1.6	45.8	0.0	0.1	0.0	0.0
D	559	10.2	8.0	9.6	37.9	0.0	4.8	0.2	6.9
E	480	3.5	2.1	2.7	—	0.6	1.5	0.4	—
All 1985	1,001	10.5	5.8	8.5	62.1	0.0	3.4	0.1	16.2
All 1986	1,355	3.4	1.1	1.5	—	0.4	0.7	0.1	—

<sup>a</sup> Percentages based on the fully harvested sample from 1985, which included 28, 31, 24 and 29 lines for groups A–D, respectively

<sup>b</sup> MWt, AQ, HD and SN are marketable weight, average quality, harvest date and sprout number, respectively

zero. For marketable weight, average quality and the index, the parental means were significantly greater than the SSD means, indicating the presence of positive additive  $\times$  additive epistasis in the parental lines for these characters. This is consistent with the early generation predictions made for this material from triple test cross (Kearsey 1984) and  $F_3$  trials (Rogers et al. 1987; Werner et al. 1986).

The distribution of the 1985 random sample of SSD lines was compared with that for the replicate plots of the best parental inbred,  $GA_1$  (Fig. 1). Also shown is the mean performance of the two reference  $F_1$  hybrids, Gower and Lunet. The distribution shows that many SSD lines have more sprout buttons than either the pa-

rental control (62%) or Gower (16%) and that lines may also be produced which outperform Lunet, which is itself noted for high sprout number. For the remaining characters, however, relatively few lines outperformed the best plots of  $GA_1$  and for marketable weight and the index, not one outperformed either of the hybrids controls. Data from the complete trial describing the relative performance of the best SSD lines are presented in Table 5. It was assumed that all SSD lines raised during both 1985 and 1986 which outperformed  $GA_1$  for either marketable weight or average quality were harvested. Although this was the objective of the preliminary field assessment of the lines, any errors would lead us to underestimate the proportion of lines superior to  $GA_1$ . For groups A–D,

the proportion of lines exceeding the  $GA_1$  mean and the Gower mean have been accumulated over the two seasons. Overall figures are also presented for the two seasons separately. The percentage superior to  $GA_1$  differed substantially between the two years. Reference to Tables 3 and 4 will show that for marketable weight, the 1986 season produced greater yields and that the inbred material made larger yield gains than the hybrid material. Furthermore, the improved of  $GA_1$  was substantially greater than for the remaining inbred material. Such genotype-environment interactions may explain both the reduced proportion of lines outperforming  $GA_1$  in 1986 and the increase (for marketable weight) in the proportion better than the hybrid Gower. One line from each season did show overall performance (based on the index) superior to Gower, indicating that high performance inbred material is possible in this crop; however, neither of these lines surpassed the better hybrid, Lunet, in overall performance.

The proportions described above are based upon the phenotypic performance of single-row plots of each SSD line and, hence, the distribution of these lines includes both genetical and environmental variation. The true breeding merit of these lines must, therefore, be rather less promising than suggested by the above proportions. An additional problem presented by the low replication factor is that superior inbred lines cannot be identified with precision. Nevertheless, it is possible to select the best lines and estimate their mean performance in the next generation, thereby giving an indication of the breeding progress which can be realized. This has been done for the 1985 lines using the index to select jointly for marketable weight and average quality using equal weighting. Thirty lines were selected from a total of 1,132 (131 doubled haploid lines produced by anther culture were included), representing a selection intensity of 2.65%. Following the procedure of Falconer (1981), it may be estimated that the correlated mean response of marketable weight in the next generation will be 252 g/plant and for average quality will be 1.10 units. This would represent a gain of 171 g/plant over the average marketable weight of the four parents, together with a 0.77 unit gain for average quality. With respect to the best parental inbred ( $GA_1$ ), the gains expected are 62 g/plant and 0.45 units, respectively. Since these figures are based upon an average of 30 lines, it is clear that the best will improve upon the overall  $GA_1$  performance, but it is unlikely that any will achieve the standard of the hybrid Gower (Table 3).

## Discussion

Recombinant inbred lines capable of outperforming  $F_1$  hybrids were observed for each of the major traits of

agronomic value. Although the frequency with which this was achieved was low for marketable weight, this provides further evidence to support the view of Jinks (1983) that heterosis is caused by the dispersion of partly dominant increasing alleles. However, the doubts raised by Johnson (1984) are also vindicated, since only two lines superior to Gower for the index were observed and even these, when assessed for a range of minor traits such as lodging, waste weight and powdery mildew, proved in overall performance to be inferior to Gower. The main conclusion to be drawn is that whilst superior inbred lines may be possible in principle, in practice the breeding gain from a single cycle of inbreeding is at present insufficient to enable inbred lines to challenge  $F_1$  hybrids as commercial cultivars.

It seems likely that the limited genetic advance made during this project is mainly a consequence of a large number of gene loci segregating in the source populations. This hypothesis is supported by crude estimates of the number of effective factors. If complete dominance and equal gene effects are assumed, the number of effective factors ( $k$ ) is given by  $k = [h]^2/D$ , where  $[h]$  = Gower - mean SSD,  $D = 8/7 \sigma_b^2$  and  $\sigma_b^2$  is the component of variation between SSD lines. This solution will underestimate  $k$  if the dominance is incomplete and then the expanded expression  $k = [h]^2/(fD)$  may provide an improvement; in this case estimates of the dominance ratio ( $f$ ) obtained from a TTC experiment by Setter (1988) were used. For marketable weight, with  $[h] = 663$ ,  $D = 22,349$  and  $f = 0.60$ , the former method estimates  $k$  as 19.7 and the latter as 32.8. In situations where large numbers of loci are segregating in the source population, it follows that only modest progress can be made towards the optimum genotype in a single cycle of inbreeding but that such progress may be sustained over a further one or two cycles. Using *Drosophila melanogaster* as a model organism, Eggleston (1985) demonstrated improvement in inbred line performance, for the heterotic egg production trait, which was maintained for three cycles of inbreeding. At the end of this programme the best inbred lines substantially outperformed the initial hybrid and were of comparable performance to the best new hybrids. The sustained improvement of inbred material in an outcrossing species has also been witnessed during the recent history of maize (*Zea mays* L.) breeding. Schnell (1974) and Duvick (1984) reported that, for the period between 1910 and 1970, the relative contribution of dominance to the performance of  $F_1$  hybrids has steadily declined. However, this study also showed that inbred lines had, by 1970, failed to achieve the yield performance of their  $F_1$  hybrids, which suggests that many genes are involved and that further gains in inbred performance may be expected (Wricke and Weber 1986). Observations such as these suggest that intercrossing of the best SSD lines from the current programme should release sufficient

genetical variation for a second cycle of inbreeding to produce progress comparable to that made in the first cycle. In the long-term, inbred lines may approach the performance of the best  $F_1$  hybrids, however the short- and medium-term prospects indicate the continuation of  $F_1$  hybrids. The best products of the current array of SSD lines may have an important role as improved parental material for such hybrid cultivars.

The verification of the presence of additive  $\times$  additive interactions has important consequences for the breeding of inbred material in this crop. For the two main characters, marketable weight and average quality, the additive  $\times$  additive interaction is positive, which indicates that the parental material is good, in part, because of favourable gene combinations. Whilst this is very desirable in terms of the performance of specific inbred material, it has the disadvantage that beneficial gene combinations are lost during the recombination phase of the breeding programme. Whilst genetical advance is still possible owing to the segregation of the additive component, the disruption of pre-existing favourable epistatic interactions does inevitably reduce the improvement in performance that may be achieved from one cycle of inbreeding.

Jinks and Pooni (1976) proposed that early generation predictions may assist plant breeders to discriminate between source populations at the outset of a breeding programme and, thereby, to limit their efforts to the most productive material. Predictive  $F_3$  (Rogers et al. 1987) and TTC trials (Kearsey 1984) were conducted in early generations of the material presented in this paper. The  $F_3$  studies concluded that for marketable weight, 0.7% of lines would outyield Gower, 0.3% of lines would be superior for quality and 35% would have more sprouts. From the TTC trials, the comparable figures were 4.0%, 0.1% and 18.0%. The observed proportions of lines exceeding Gower for these three traits taken over both 1985 and 1986 was 0.2%, 1.8% and 16.2%. Chi-square tests show that for these three characters, there is a significant difference between the predictions from the  $F_3$  or TTC trials and the observations. Furthermore, the proportions observed for 1985 differ appreciably from those for 1986 for both marketable weight and average quality. Such discrepancies may be a consequence of genotype-environment interactions; hence, the  $F_3$  predictions, which are in good agreement with the 1986 observations but not those from 1985, may indicate that the environmental conditions of 1982 (when the  $F_3$  trial was conducted) were more similar to those of 1986 than 1985. In both prediction trials, each family was raised in a plot of 6  $\times$  6 plants from which the central, fully guarded, 16 plants were harvested.

In the current trial, single-row plots were used with each plant surrounded by members of its own family within the row but by different inbred lines in the two

adjacent rows. This difference probably has greatest effect with respect to the  $F_1$  controls, which may benefit from the relaxed competition more than inbred material. This would lead to the assessment trials tending to underestimate the proportion of lines which exceed Gower for vigour-related traits such as marketable weight and sprout number. Nevertheless, the estimates from both predictive trials have demonstrated some value as broad indicators of the ease or difficulty with which superior recombinant lines may be achieved for each character. It would seem that for crops such as Brussels sprouts and barley (*Hordeum vulgare* L.) (Caligari et al. 1985), where seasonal genotype-environment interactions can be substantial, it will not be possible to use early generation predictions to obtain a reliable estimate of the absolute potential within single crosses. It is more likely that prediction techniques will prove most valuable if used to compare and rank a range of crosses. Thomas et al. (1986) used barley to demonstrate that when early generations of several crosses are grown within the same season, the effects of genotype-environment interactions do not seriously affect the ability to rank the crosses correctly. This evidence suggests that early generation predictive trials may provide genetical information that permits the selection of whole crosses at an early stage, but it remains unclear as to whether the costs and effort required for these special trials can be justified in commercial plant breeding programmes when compared to a more conventional and empirical approach.

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