

The effects of major genes on quantitatively varying characters in barley

1. The GP *ert* locus

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Random inbred lines produced by doubled haploidy and single seed descent have been used to examine the effect of the GP *ert* locus on quantitatively varying characters in spring barley. In general the mean of the *erectoides* sub-population is lower than that of the corresponding *nutans* sub-population for characters such as thousand grain weight, main stem weight and single plant yield. Furthermore, allelic variation at the GP *ert* locus makes a large contribution to the additive genetic variation for a number of characters. A suitable strategy for the deployment of dwarfing genes in barley breeding programmes is discussed.

INTRODUCTION

During the past 30 years, barley breeders have endeavoured to produce short, stiff strawed varieties that respond to the use of nitrogenous fertilizers without lodging in adverse weather conditions. A large number of dwarfing genes have been identified and used in barley breeding programmes to produce lines resistant to lodging. One of the most commonly used types of short straw in European spring barleys is that associated with an erect juvenile growth habit and erect ear carriage. Sources of this gene include the semi-dwarf variety Golden Promise which is a gamma ray mutant of the variety Maythorpe. This variety has been widely grown in Scotland and the *erectoides* dwarfing gene has often been used in the SCRI spring barley breeding programme.

The dwarfing gene present in Golden Promise has been shown to be a recessive major gene (GP *ert*) and is located on the short arm of chromosome 7 (Thomas, Powell and Wood, 1984). Unfortunately the effects of this particular dwarfing gene on agronomic characters have usually been evaluated in varietal comparisons where the effects of the dwarfing gene are confounded with other genetic factors. Hence the effects of this gene on

quantitative characters and the consequences of its use in breeding programmes have not been fully explored. The best way to evaluate the effects of the dwarfing gene is to compare random inbred lines which can be classified for the alternative allele at the gene locus of interest. In this way the background genetic effect will be nullified. Random inbred lines have been produced by doubled haploidy from F₁ plants heterozygous for the *erectoides* gene in conjunction with single seed descent lines to investigate the relationship between the *erectoides* dwarfing gene and characters of agronomic importance.

MATERIALS AND METHODS

(a) *The material studied*

As part of a series of experiments conducted with the Genetics Department of the University of Birmingham, doubled haploids (DH), produced by the *Hordeum bulbosum* technique, and single seed descent (SSD) lines were generated from the following crosses:

Golden Promise × Mazurka (TT1)
Golden Promise × Ark Royal (TT3)
BH4/143/2 × Ark Royal (TT4)

Details of the experimental techniques used in deriving the material can be found in Huang, Dunwell, Powell, Hayter and Wood (1984) and Thomas and Tapsell (1983). Twenty DH lines were produced from the F_1 hybrids in the 3 crosses and 90 SSD lines were produced from F_2 seeds. In addition, 56 DH lines were produced from random F_2 plants in the TT4 cross.

(b) *The experiment*

(i) *The drilled experiment*

The 90 random SSD lines from each of the 3 crosses were advanced to the F_4 generation and then multiplied before assessment at the F_6 generation. This material was grown, together with 10 control varieties, in 1979 in a two replicate generalized lattice small plot yield trial at the Murrays Farm, East Lothian.

(ii) *The spaced plant experiment*

The F_1 and F_2 derived DH lines were grown together with 40 SSD lines in a replicated experiment in 1983, again at the Murrays Farm, East Lothian. The experimental design was a randomised complete block of two replicates. Single plants were spaced 5 cm apart within rows and 22.5 cm apart between rows. The experiment was netted to prevent bird damage.

(c) *The characters*

The material was scored for juvenile growth habit approximately 6 weeks after sowing. It was therefore possible to classify the inbred lines into two groups: an erect group which possessed the *erectoides* dwarfing allele and the tall (*nutans*) group which possessed the corresponding *nutans* allele. During the growing season the following characters were scored:

- (a) Awn emergence, scored as days from 1st June until awns emerged from the flag leaf sheath of the main stem (AE).
- (b) Ear emergence, scored as days from 1st June until ears fully emerged from the flag leaf sheath of the main stem (EE).
- (c) Maturity, scored on a 1 to 9 scale with 1-early, 9-late (Mat).
- (d) Lodging, scored on the drilled experiment on a 1 to 9 scale with 9 representing a completely lodged plot (Lod).

After harvest, sheaves were returned to the laboratory and 5 plants were chosen at random for experiment (ii). For experiment (i) five plants were taken at random from each plot before it was harvested with a small plot combine. The experiments were

scored for different sub-sets of the following characters:

- (e) Final height, measured from the base of the plant to the collar in cm. (Ht).
- (f) The number of fertile tillers per plant (TN).
- (g) The number of grains per ears on the main stem (GN).
- (h) The yield of grain on the main stem (MSW).
- (i) The length of the ear on the main stem (EL).
- (j) Thousand grain weight (TGW) calculated from (g) and (h).
- (k) Grain yield of the whole plant, single plant yield (SPY).
- (l) Neck length, measured in cm from the flag leaf auricles to the collar of the main stem (NL).
- (m) Bulk yield was measured on the drilled experiment in $g\ m^{-2}$ (BY).

RESULTS

(i) *Drilled plot experiment*

The results from the analyses of variance for the three populations (TT1, TT3 and TT4) observed under drilled plot conditions and segregating for alleles at the *GP ert* locus are given in table 1. There were significant differences between lines in the TT1 cross for: height, neck length, lodging, awn emergence, ear emergence, main stem weight, thousand grain weight, single plant yield and bulk yield. With the exception of main stem weight, tiller number and single plant yield in the TT3 cross, all the other variates scored in both the TT3 and TT4 crosses displayed significant variation. The fact that the mean square between lines was significant when tested against the error term indicated that there was significant additive genetic variation (D) for those characters. The magnitude of this variation can be calculated from the expected mean squares for the experiment since the between line component (σ_L^2) will give a measure of $\frac{7}{8}D$.

The main item of interest is the comparison between the *erectoides* and *nutans* populations. Although there were small differences between the three crosses, in general there were significant differences between the sub-populations for the majority of characters scored. By classifying the inbred lines into the two groups carrying the alternative allele, it is possible to assess the effects of the *GP ert* locus on mean performance in a random genetic background. The mean scores for the *nutans* and *erectoides* groups are given in table 2. It should be noted that for a number of characters such as thousand grain weight the mean of

Table 1 Analyses of variance for the 3 SSD populations derived from TT1, TT3 and TT4

Item	df	Ht M.S.	NL M.S.	Lod M.S.	AE M.F.	EE M.S.	GN M.S.	MSW M.S.	TGW M.S.	TN M.S.	SPY M.S.	BY M.S.
TT1												
1. Between lines	89	52.4‡	0.9‡	2.1‡	2.4‡	4.1*	4.4	188.5‡	14.8‡	0.0	669.7*	1,206.1†
a. GP locus	1	3428.4‡	9.9‡	68.8‡	12.7*	0.6	15.6	6137.6‡	883.3‡	0.1	12,947.1‡	18,763.4‡
b. Between lines within groups	88	14.1	0.8	1.3	2.3	4.1	4.2	120.9	5.0	0.0	530.2	1,006.6
2. Error	82	6.4	0.2	0.5	0.4	2.8	3.2	95.2	2.2	0.0	434.8	700.7
TT3												
1. Between lines	89	46.8‡	22.7†	4.2‡	2.4‡	16.1‡	4.1	131.2	14.8‡	0.1	600.8	813.7*
a. GP locus	1	2585.4‡	5.6	218.1‡	12.7*	40.6	0.1	2409.7‡	587.0‡	0.1	6,624.5	1.5
b. Between lines within groups	88	17.9	0.2	1.8	2.3	15.8	4.1	105.3	8.3	0.1	532.4	822.9
2. Error	82	9.0	0.1	0.4	0.4	3.3	2.4	96.4	4.2	0.1	710.8	560.9
TT4												
1. Between lines	89	46.4‡	0.2‡	2.4‡	14.2‡	23.7‡	3.9‡	147.9‡	15.6‡	0.0	280.8	1,681.0‡
a. G.P. locus	1	2293.3‡	2.4†	149.1‡	188.4‡	5.8	0.2	991.9‡	299.2‡	0.0	1,040.8	179.2
b. Between lines within groups	88	20.9	0.2	0.8	12.3	23.7	4.0	138.3	12.4	0.0	272.1	1,698.1
2. Error	82	5.6	0.1	0.4	1.2	3.8	1.9	46.6	2.9	0.0	130.4	628.7

* P = 0.05, † P = 0.01, ‡ P = 0.001.

Table 2 Means and ranges for the parents and sub-populations produced from TT1, TT3 and TT4 by SSD

		Ht	NL	Lod	AE	EE	GN	MSW	TGW	TN	SPY	BY
G. PROMISE × MAZURKA (TT1)												
Parental Means	GP	55.53	0.34	3.61	33.62	46.34	21.90	91.64	41.98	1.10	98.35	358.23
	Maz	69.88	2.95	1.95	31.98	42.69	23.73	105.18	44.19	1.10	110.70	404.44
<i>nutans</i>	Mean	67.54	1.44	4.17	33.55	44.88	22.35	103.50	46.33	1.29	126.38	393.41
	Min	58.27	0.06	0.93	30.60	40.50	15.90	70.66	42.29	1.00	77.13	326.17
	Max	77.27	4.06	7.49	36.83	51.02	25.80	123.79	53.35	1.70	166.40	451.88
<i>erect</i>	Mean	54.45	0.74	2.31	32.76	44.71	21.52	85.98	39.68	1.23	100.94	362.78
	Min	48.70	0.05	0.86	30.52	40.55	16.60	62.09	35.74	1.00	65.61	282.43
	Max	63.60	2.73	5.37	36.06	50.35	26.80	109.87	42.66	1.70	156.00	428.64
G. PROMISE × ARK ROYAL (TT3)												
Parental Means	GP	52.38	0.23	3.58	34.72	50.24	20.85	75.13	40.47	1.40	109.80	332.86
	AR	67.302	0.58	5.59	40.66	54.20	22.20	92.95	41.35	1.40	112.40	382.87
<i>nutans</i>	Mean	66.97	0.82	6.69	38.43	49.54	21.04	93.06	44.15	1.40	120.66	364.39
	Min	56.18	0.20	3.98	33.58	42.39	15.30	64.16	36.89	0.99	66.70	298.78
	Max	73.97	2.12	9.14	45.55	60.69	25.10	118.30	50.61	2.10	176.10	419.00
<i>erect</i>	Mean	55.01	0.26	3.21	35.88	51.04	21.22	81.51	38.45	1.31	101.50	364.06
	Min	46.36	0.40	0.82	33.24	45.09	17.00	59.00	32.18	0.99	58.90	309.13
	Max	61.00	0.60	6.62	39.90	59.92	24.20	94.39	42.89	1.69	136.80	424.31
BH4/143/2 × ARK ROYAL (TT4)												
Parental Means	BH4	53.84	0.02	3.00	34.39	59.17	20.50	79.70	38.71	1.12	82.46	369.68
	AR	71.09	0.78	5.25	39.28	52.14	23.20	94.73	40.79	1.21	103.29	456.71
<i>nutans</i>	Mean	65.73	0.46	5.21	38.40	52.76	19.83	83.09	42.07	1.11	89.42	381.49
	Min	49.23	0.08	2.00	31.62	43.34	15.70	39.29	35.31	0.94	39.37	290.43
	Max	75.35	2.57	7.50	46.52	61.15	24.73	105.00	49.39	1.76	141.75	475.80
<i>erect</i>	Mean	53.80	0.08	2.17	34.98	52.15	19.95	75.24	37.76	1.11	81.38	384.84
	Min	48.08	0.13	1.00	30.62	43.23	16.53	57.05	31.30	0.96	58.19	317.86
	Max	59.96	0.41	3.50	38.43	62.19	22.60	94.90	43.32	1.39	109.42	467.35

Table 3(a) Results from the analyses of variance conducted on the double haploid and SSD lines produced from the TT1 cross

Item	df	Ht M.S.	AE M.S.	GN M.S.	MSW M.S.	TGW M.S.	TN M.S.	SPY M.S.	Mat M.S.	EL M.S.
1. Reps.	1 (4)	22.2	0.0	15.8	75.0	4.7	27.0	5.8	0.0	1.6
2. Between DH lines	19 (4)	55.4	14.4*	13.5*	1,094.7*	54.4	9.3	19.1	6.0	2.1†
a. <i>ert v nutans</i>	1 (2b)	699.9‡	1.5	6.3	2,899.5*	185.3*	3.0	0.0	0.0	0.3
b. between lines										
within groups	18	19.6	15.1	13.9	994.5	47.1	9.7	25.6	7.0	2.2
3. Between SSD lines	39 (4)	114.1‡	15.5‡	15.0‡	1,399.0‡	93.1‡	10.4	22.0*	5.9†	3.0‡
a. <i>ert v nutans</i>	1 (3b)	2738.0‡	153.6‡	5.0	26,003.6‡	2293.5‡	0.0	135.3‡	0.0	6.6†
b. between lines										
within groups	38	45.0	11.8	16.3	751.5	35.2	3.4	19.0	6.1	2.9
4. Within lines	52 (8)§	30.7	6.2	6.1	526.8	34.8	12.7	14.8	3.3	0.6

* P < 0.05, † P < 0.01, ‡ P < 0.001.

§ Indicates the number of missing plots.

() Indicates the error mean square used in the V.R. test.

Table 3(b) Results from the analyses of variance conducted on the doubled haploid and SSD lines produced from the TT3 cross

Item	df	Ht M.S.	AE M.S.	GN M.S.	MSW M.S.	TGW M.S.	TN M.S.	SPY M.S.	Mat M.S.	EL M.S.
1. Reps	1 (4)	97.6	0.2	16.7	319.0	22.1	40.4	4.7	12.3	1.4
2. Between DH lines	19 (4)	246.1	30.5‡	18.1	1,578.0†	104.6	41.1†	61.1†	10.4†	4.0‡
a. <i>ert v nutans</i>	1 (2b)	2940.9‡	24.9*	53.8	14,344.0‡	1031.9‡	192.2†	281.8‡	24.9	10.2
b. between lines										
within groups	18	96.3	31.0	16.1	868.8	53.1	32.7	48.8	9.6	3.7
3. Between SSD lines	39 (4)	157.1‡	16.8‡	9.1	1,344.6*	87.1†	13.6	20.6	16.8‡	4.6‡
a. <i>ert v nutans</i>	1 (3b)	2718.0‡	229.9‡	11.7	18,416.6‡	1526.4‡	6.0	43.9	229.9‡	0.0
b. between lines										
within groups	38	89.7	11.2	9.0	895.3	49.3	13.8	20.0	11.2	5.1
4. Within lines	55 (5)§	60.7	5.8	11.6	727.2	42.1	19.2	22.1	4.7	1.3

* P < 0.05, † P < 0.01, ‡ P < 0.001.

§ Indicates the number of missing plots.

() Indicates the error mean square used in the V.R. test.

Table 3(c) Results from the analyses of variance conducted on F₁ and F₂ derived doubled haploids together with SSD lines from the TT4 cross

Item	df	Ht M.S.	AE M.S.	GN M.S.	MSW M.S.	TGW M.S.	TN M.S.	SPY M.S.	Mat M.S.	EL M.S.
1. Reps	1 (5)	175.7*	1.3	28.0	268.0	9.9	60.3	132.1*	6.3	0.2
2. Between F ₁ DH lines	19 (5)	213.4‡	15.7‡	20.6†	4,625.0‡	108.7‡	21.7	43.7*	10.1	3.5*
a. <i>ert v nutans</i>	1 (2b)	2830.9‡	14.4	94.1‡	59,881.1‡	566.6‡	0.0	119.4	24.4	28.5‡
b. between lines										
within groups	18	68.0	15.8	16.5	1,555.2	83.3	23.0	39.5	9.3	2.1
3. Between F ₂ DH lines	55 (5)	230.2‡	22.9‡	19.8	1,911.9‡	107.7‡	22.7*	38.7‡	7.9	4.7‡
a. <i>ert v nutans</i>	1 (3b)	8249.6‡	99.1‡	47.3*	39,589.5‡	2648.1‡	60.6*	248.6‡	17.5	72.1‡
b. between lines										
within groups	54	81.7	21.5	19.3	1,214.2	60.7	22.0	34.8	7.7	3.5
4. Between SSD lines	38 (1)§ (5)	125.1‡	23.5‡	24.8‡	3,662.0‡	61.8‡	17.2	30.7	5.3	7.6‡
a. <i>ert v nutans</i>	1 (4b)	1030.2‡	30.8*	297.5‡	102,724.3‡	201.6†	12.6	56.3	0.0	71.0‡
b. between lines										
within groups	37 (1)	100.7	23.3	17.4	984.6	58.0	17.3	30.0	5.5	5.9
5. Within lines	95 (20)§	38.7	6.6	8.0	991.1	23.9	15.3	24.1	6.6	2.2

* P < 0.05, † P < 0.01, ‡ P < 0.001.

§ Indicates the number of missing plots.

() Indicates the error mean square used in the V.R. test.

the *erectoides* group was significantly smaller than the *nutans* group. It is of considerable interest to note that the mean squares for the *erectoides* v. *nutans* item in the analyses of variance (table 1) were significant when tested against the between lines within groups item. This feature of the data is particularly important since it indicates that a significant portion of the additive variation is associated with allelic differences at the GP *ert* locus. This association between characters may be due to pleiotropy or linkage disequilibrium. Barley provides a unique opportunity to distinguish between these two mechanisms since populations derived by double haploidy from the F₁ generation and single seed descent will differ as a consequence of the number of rounds of gametogenesis.

(ii) *Spaced plant experiment*

The results of the analyses of variance conducted on the data from the spaced plant experiment grown in 1983 are given in tables 3(a), 3(b), and 3(c). The most important points to be noted from these tables are:

(a) There were significant differences between the means of the *erectoides* and *nutans* sub-populations and these differences were observed in both the DH and SSD generations.

(b) These data confirm the observation on drilled plots that a significant portion of the additive genetic variation was associated with allelic differences at the GP *ert* locus. The magnitude of this portion is the reduction in the additive genetic variation when it is re-estimated from the component of variance between lines within groups (Al-Banna, Jinks and Pooni, 1984).

Estimates (from the spaced plant experiment) of the total additive genetic variance (D) and that associated with allelic differences at the GP *ert* locus for the TT1, TT3 and TT4 cross are given in table 4. Since the SSD lines were at the F₇ generation but derived from F₄ single plants $\frac{7}{8}D$ was used in the estimates of D from the SSD population. Where there was no significant difference between lines, the additive genetic variance was not calculated. It can be seen from this table that alleles at the GP *ert* locus accounted for a large part of the additive genetic variation for characters such as thousand grain weight, main stem weight and single plant yield. The lines derived by SSD from F₂ individuals were bulked at the F₄ generation and have passed through 3 rounds of potential recombination and one would therefore expect a decreasing trend from F₁DH (1 round of recombination) to SSD lines in the contribution of the GP *ert* locus to estimates of D if the association is due to linkage disequilibrium. The significance of differences between estimates of D associated with the GP *ert* locus in the DH and SSD populations can be tested by maximum likelihood model fitting procedures (Pooni, Jinks and Pooni 1980). In effect, one fits a model to the between groups and between lines within groups mean squares assuming a single value of D but allowing the between lines within groups mean squares to take their own values. Since the number of lines within each subgroup was not equal, the harmonic mean was used to calculate the coefficient for the expected mean square. There is 1 degree of freedom left for testing the goodness of fit of the model in the TT1 and TT3 cross and two degrees of freedom in the case

Table 4 Estimates of the additive genetic variance (D) and that associated with allelic differences at the GP *ert* locus for the TT1, TT3 and TT4 crosses

		Ht	AE	GN	MSW	TGW	TN	SPY	Mat	EL	
TT1	F ₁ DH	Total D	0.0	4.1	3.7	284.0	0.0	0.0	0.0	0.0	0.7
		GP <i>ert</i>	0.0	0.0	0.0	50.1	0.0	0.0	0.0	0.0	0.0
	SSD	Total D	36.5	4.1	3.9	381.6	25.5	0.0	3.2	1.1	1.1
		GP <i>ert</i>	30.2	1.7	0.0	283.3	25.3	0.0	1.4	0.0	0.0
		$\chi^2_{(1)}$	—	0.8	0.0	0.5	—	—	—	—	0.8
TT3	F ₁ DH	Total D	92.7	12.4	0.0	425.4	31.3	11.0	19.4	2.9	1.4
		GP <i>ert</i>	74.9	0.0	0.0	359.0	25.8	4.2	6.1	0.0	0.0
	SSD	Total D	42.2	4.8	0.0	270.1	19.7	0.0	0.0	5.3	1.4
		GP <i>ert</i>	29.5	2.4	0.0	196.6	16.6	0.0	0.0	2.5	0.0
		$\chi^2_{(1)}$	0.1	0.5	—	0.0	0.0	—	—	0.5	1.5
TT4	F ₁ DH	Total D	87.3	4.6	6.3	1816.9	42.4	0.0	9.8	1.8	0.7
		GP <i>ert</i>	72.7	0.0	2.0	1534.9	12.7	0.0	0.0	0.0	0.7
	F ₂ DH	Total D	95.8	8.2	5.9	460.4	41.9	3.7	7.3	0.0	1.3
		GP <i>ert</i>	74.4	0.7	0.0	348.9	25.5	0.0	2.3	0.0	0.6
	SSD	Total D	37.8	7.4	7.4	1168.5	16.6	0.0	2.9	0.0	2.4
		GP <i>ert</i>	10.7	0.1	3.3	1168.5	1.7	0.0	0.3	0.0	0.8
		$\chi^2_{(2)}$	0.3	0.3	1.1	0.5	0.5	—	0.2	—	0.2

of the TT4 cross. Where there was no significant additive genetic variation a model was not fitted. The chi-squared (χ^2) values for these comparisons are also given in table 4 and apart from a border line significance in the case of ear length in the TT3 cross it can be seen that there were no significant differences between the estimates of D associated with the GP *ert* locus from the different populations. In other words the contribution of alleles at the GP *ert* locus did not appear to decrease following rounds of gametogenesis.

DISCUSSION

The results presented here have a number of implications for the use of dwarfing genes in breeding programmes. First, one can only adequately establish the effects of different dwarfing genes by the assessment of random inbred lines segregating for alleles at the gene locus of interest. In the three crosses examined, the mean scores of the *erectoides* sub-populations were lower than that of the *nutans* sub-populations for important agronomic characters such as: main stem weight, thousand grain weight and single plant yield. This result would suggest that the *nutans* group should not be *a priori* discarded in a breeding programme. However, the plant breeder often desires a low expression for some of the characters scored *e.g.*, height, awn emergence and ear emergence. For these characters, the plant breeder would be better to work with the *erectoides* sub-population. Considering all the characters, the breeder would try to achieve a suitable balance in their expression according to his objectives.

In variety production in an inbreeding species the most important genetic component is the additive genetic variance (D). This is the heritable portion of the phenotypic differences between homozygotes and is the fixable portion of the heritable variation (Mather and Jinks, 1971). Analyses of the data presented here have shown that the portion of D associated with the GP *ert* locus can be as high as 100 per cent. Allelic variation at this locus makes a large contribution to the variation for: thousand grain weight, main stem weight and single plant yield. This association could be due to pleiotropy or linkage disequilibrium. The F_1 DH, F_2 DH and SSD generations differ in respect to the number of rounds of gametogenesis that will have contributed to estimates of D . If the association is due to linkage disequilibrium a decreasing trend from F_1 DH to SSD would be anticipated. This trend is not apparent and thus the residual effects in the SSD population could

be due to pleiotropy and or residual tight linkages remaining after 3 rounds of gametogenesis. Al-Banna *et al.* (1984) working with *Nicotiana rustica* concluded that the pleiotropic effects of the major genes studied were not important. This would not appear to be the case with the present results and may reflect differences in the genetic architecture or the fact that the *erectoides* allele of Golden Promise was produced by mutagenesis and may therefore have associated with it a wider range of effects.

The major objective of most barley breeding programmes is to identify desirable recombinants. Considering table 2, it can be seen that although the mean score of the *erectoides* sub-population is generally lower than that of the *nutans* sub-population, the best line in the erect group exceeds the higher scoring parent. Hence by deriving random inbred lines by SSD, one is able to generate *erectoides* high scoring lines.

There is evidence that selection for quantitatively varying characters amongst homozygous families results in an increase in selection efficiency. Since the associations between the GP *ert* gene and quantitative characters remained after 3 rounds of recombination in the SSD generation it would suggest that F_1 derived DH lines would be equally effective in producing desirable *erectoides* lines.

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REFERENCES

- AL-BANNA, M. K. S., JINKS, J. L. AND POONI, H. S. 1984. The contribution of pleiotropy at the mop loci to continuous variation in *Nicotiana rustica*. *Heredity*, **52**, 95-102.
- HUANG, B., DUNWELL, J. M., POWELL, W., HAYTER, A. M. AND WOOD, W. 1984. The relative efficiency of microspore culture and chromosome elimination as methods of haploid production in *Hordeum vulgare* L. *Z. Pflanzenzucht*, **92**, 22-29.
- MATHER, K. AND JINKS, J. L. 1971. *Biometrical Genetics*, 2nd Edn. London: Chapman and Hall.
- POONI, H. S., JINKS, J. L. AND POONI, G. S. 1980. A general method for the detection and estimation of additive, dominance and epistatic variation for metrical traits IV. Triple test cross analysis for normal families and their selfs. *Heredity*, **44**, 172-192.
- THOMAS, W. T. B. AND TAPSELL, C. R. 1983. Cross prediction studies on spring barley. 1. Estimation of genetical and environmental control of morphological and maturity characters. *Theoret. Appl. Genet.*, **64**, 345-352.
- THOMAS, W. T. B., POWELL, W. AND WOOD, W. 1984. The chromosomal location of the dwarfing gene present in the spring barley variety Golden Promise. *Heredity*, **53** 177-183.