The effects of major genes on quantitatively varying characters in barley

2. The *denso* and daylength response loci

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The effects of the *denso* dwarfing gene and a locus determining daylength response on quantitative characters have been examined in random inbred lines. Since random inbred lines were produced from F₁ hybrids by doubled haploidy and single seed descent it was possible to quantify the contribution of each individual locus to the additive genetic variation (*D*) for any given character. It was observed that the contribution of these loci to estimates of *D* decreased following rounds of recombination which therefore demonstrated that in these cases the association between major genes and quantitative characters was due to linkage disequilibrium. The implications of these findings to barley breeding programmes are discussed.

INTRODUCTION

The isolation of single genetic factors affecting quantitatively varying characters is of great interest to plant breeders. Such associations may be due to pleiotropic effects and/or linkage disequilibrium. For the plant breeder the distinction between pleiotropy and tight linkage may not always be important, but since major genes are frequently manipulated in breeding programmes it is essential to examine the effects of such genes on agronomic characters. By producing random inbred lines it has been shown that the GP *ert* locus can influence the expression of quantitative characters in spring barley (Powell, Thomas, Caligari and Jinks, 1985). Investigations using lines developed in this way allow the advantages and disadvantages of a particular genetic locus to be assessed in terms of other agronomic characters. The GP *ert* locus appeared to be associated with reduced grain weight, height and caused a reduction in single plant yield. An alternative simply inherited source of short straw is the recessive

denso dwarfing gene (Haahr and von Wettstein, 1975). This gene confers a prostrate growth habit and is present in the variety Universe. In this paper the analysis of random inbred lines is extended to include the *denso* dwarfing gene and a locus determining daylength response which is present in the variety Clipper (Thomson and Matthews, 1981). Furthermore by comparing the contribution of alleles at these loci to estimates of the additive genetic variance (*D*) in F₁ derived doubled haploids and single seed descent lines it is possible to assess the relative contribution of pleiotropy and linkage disequilibrium to any associations that may be detected. This information will enable the barley breeder to adopt the most efficient strategy for the deployment of these major genes in breeding programmes.

MATERIALS AND METHODS

Twenty doubled haploids (produced by the *Hordeum bulbosum* technique) were produced from

F₁ hybrids of the following spring barley crosses:
Universe × Mazurka (TT2)
Clipper × Ymer (TT5)

In addition single seed descent (SSD) lines were derived from F₂ individuals and 40 such lines from each cross were used in the present experiment. Parents, doubled haploids (DH) and SSD lines were grown in a replicated, randomised spaced plant experiment in 1983 at the Murrays Farm, East Lothian. Universe possesses the *denso* allele giving a prostrate growth habit while Mazurka has the *nutans* allele. This cross will therefore segregate for alleles at the *denso* locus. Clipper, an Australian variety, is responsive to long days ("early") when compared to European varieties and is adapted for growth in a restricted season such as a South Australian winter. Data from the F₂ generation and F₁ derived doubled haploids indicated that this daylength response is controlled by a single major gene. The TT5 cross will therefore segregate for alleles at this locus. It was thus possible to classify the inbreds from the TT2 cross into two sub-groups (the *denso* and *nutans* groups) and similarly the TT5 cross could be classified into "early" and "late" groups. The method of sowing and details of scoring procedures may be found in Powell, Thomas, Caligari and Jinks (1985). The characters scored were: height (Ht), thousand grain weight (TGW), yield of grain on the main stem (MSW), ear length (EL), number of fertile tillers (TN), number of grains per ear (GN), maturity (Mat), awn emergence (AE) and single plant yield (SPY).

RESULTS

The analysis of variance for the 9 variates scored on the Universe × Mazurka cross are presented in table 1. There were significant differences between

DH lines for height, ear length and tiller number. The SSD lines displayed significant between line variation for height and maturity. In the case of the DH population there were significant differences between the two sub-populations (*denso* and *nutans* groups) for height, ear length and single plant yield indicating an association between this locus and these quantitatively varying characters. The means of the *denso* and *nutans* populations differed in the SSD population not only for height (as did the DH) but also for grain number and awn emergence.

Estimates of the total additive genetic variation (*D*) and that associated with the *denso* dwarfing gene (calculated using the method of Al-Banna, Jinks and Pooni, 1984) for the DH and SSD lines are given in table 2. In the case of height, estimates

Table 2 Estimates of the total additive genetic variance (*D*) and that associated with the *denso* locus for the DH lines and SSD lines

TT2 (Universe × Mazurka)	Ht	EL	Mat
D. Haploids (Total <i>D</i>)	44.9	1.5	0.0
<i>denso/nutans</i> allele	25.8	1.5	0.0
%	57.5	100.0	—
SSD Lines (Total <i>D</i>)	24.8	0.0	1.7
<i>denso/nutans</i> allele	8.6	0.0	0.0
%	34.7	0.0	0.0

of *D* associated with the *denso* locus decreased from 57.5 per cent in the DH lines to 34 per cent in the SSD lines. This corresponds to one round of gametogenesis in the DH generation and 3 rounds of gametogenesis in the SSD lines. A more

Table 1 Analyses of variance on the nine variates scored on the TT2 cross

	df	Ht M.S.	TGW M.S.	MSW M.S.	EL M.S.	TN M.S.	GN M.S.	Mat M.S.	AE M.S.	SPY M.S.
1. Bet. Reps	1	225.90*	39.47	668.00	8.05	3.09	4.48	16.06*	20.51	48.19
2. Det. DH	19	139.06*	31.06	1040.00	5.55*	18.45	29.69*	5.86	14.03	22.50
a. <i>denso</i> v <i>nutans</i>	1	1067.87‡	5.46	397.00	65.62‡	39.53	0.80	4.09	0.00	122.04*
b. Bet. lines										
within groups	18	87.46	32.48	1075.72	2.21	17.28	31.30	5.96	24.81	16.97
3. Bet. SSD	37 (2)§	106.00‡	39.70	648.88	1.94	17.01	12.11	8.30*	18.95	22.98
a. <i>denso</i> v <i>nutans</i>	1	1025.95‡	113.70	1689.70	3.56	35.06	66.34*	9.37	253.43‡	44.25
b. Bet. lines										
within groups	36 (2)§	86.34	37.64	619.96	2.00	17.45	11.27	8.73	13.49	22.18
4. Within lines	48 (12)§	49.25	41.33	859.03	2.61	13.05	15.41	4.43	12.87	15.65

* $P < 0.05$, † $P < 0.01$, ‡ $P < 0.001$.

§ Indicates number of missing plots.

striking example is provided in the case of ear length. In the DH population all the additive genetic variation was associated with the *denso* gene, but following rounds of gametogenesis the contribution of alleles at this locus to *D* totally disappeared. Snape and Simpson (1981) using DH lines developed by the *H. bulbosum* system also noted undesirable effects on agronomic characters associated with the *denso* gene. These authors, however, concluded that these effects were due to pleiotropy. By including the SSD lines it has been clearly shown that the associations, observed in this experiment, with the *denso* gene were due to linkage disequilibrium.

The analyses of variance for the Clipper × Ymer cross are given in table 3. There was significant additive genetic variation for all nine variates scored. The means of the DH sub-populations (7 *early*: 13 *late*) differed for height, main stem weight, ear length, grain number and awn emergence. The means of the SSD sub-populations (12 *early*: 27 *late*) differed for awn emergence and maturity. Estimates of the portion of (*D*) associated with the daylength response locus are presented in table 4. The contribution of the daylength response locus to quantitative variation in the DH population ranges from 100 per cent (awn emergence) to 0.0 per cent for thousand grain weight.

The most striking feature of these data however, was the reduction in the contribution of the daylength response locus to quantitative variation following rounds of recombination. With the exception of maturity and awn emergence, as noted above, the daylength response locus did not contribute to quantitative variation in the SSD population. These data demonstrate very clearly that the association between the daylength response locus and quantitative variation was due to linkage disequilibrium rather than pleiotropy.

DISCUSSION

The objectives of this investigation were to show the need for examining the effects of major gene loci on characters of agronomic importance. Clearly the *denso* and daylength response loci are associated with quantitative, agronomic characters. By comparing the contributions of individual loci to the additive genetic variance in the DH and SSD populations it has been demonstrated that in these cases the associations are due to linkage disequilibria. The means and ranges for the parents, DH and SSD lines for the TT5 cross are given in table 5 where awn emergence is omitted as it was used to classify the sub-populations. By

Table 3 Analyses of variance of the nine variates scored on the TT5 cross

TT5 (Clipper × Ymer)		Ht	TGW	MSW	EL	TN	GN	Mat	AE	SPY
	df	M.S.	M.S.	M.S.	M.S.	M.S.	M.S.	M.S.	M.S.	M.S.
1. Bet. reps.	1	100.45	6.28	637.30	14.12†	1.72	2.36	6.79	80.34*	51.17
2. Bet. DH	18 (1)§	132.80†	69.25*	1,962.30‡	7.83‡	11.41	49.37†	4.64	65.27‡	25.11
a. "early" v "late"	1	572.12†	0.00	14,781.6‡	76.84‡	30.12	505.92‡	0.40	1015.28‡	13.79
b. Bet. lines										
within groups	17 (1)§	106.96	79.92	1,208.22	3.77	10.31	22.51	4.89	9.39	100.33
3. Bet. SSD	38 (1)§	145.13‡	127.58‡	2,900.00‡	6.95‡	24.81‡	59.83‡	10.07‡	77.96‡	43.05‡
a. "early" v "late"	1	19.56	91.04	234.30	0.15	40.85	2.06	51.61‡	1723.48‡	3.21
b. Bet. lines	37 (1)§	148.52	128.57	2,972.05	7.13	24.37	61.39	8.95	33.49	44.13
within groups										
4. Within lines	44 (16)§	46.94	39.46	621.18	1.44	11.08	15.68	3.16	17.88	15.48

§ Indicates number of missing plots.

Table 4 Estimates of the portion of the additive genetic variation associated with the daylength response locus

	Ht	TGW	MSW	EL	TN	GN	Mat	AE	SPY
D. Haploids (Total <i>D</i>)	42.9	14.9	670.6	3.2	0.0	16.8	0.0	25.7	0.0
"early"/"late" locus	12.9	0.0	377.0	2.0	0.0	13.4	0.0	23.7	0.0
%	30.1	0.0	56.2	63.7	0.0	79.8	—	100.0	—
SSD Lines (Total <i>D</i>)	43.0	38.6	997.0	2.4	6.0	19.3	3.0	26.3	12.1
"early"/"late" locus	0.0	0.0	0.0	0.0	0.0	0.0	0.5	20.8	0.0
%	0.0	0.0	0.0	0.0	0.0	0.0	16.4	74.0	0.0

Table 5 The means and ranges for the parents, F_1 doubled haploids and single seed descent lines from the TT5 cross

			Ht	TGW	MSW	EL	TN	GN	Mat	SPY
Parental Means	Clipper		48.36	56.71	86.50	6.38	9.85	16.15	2.88	6.98
	Ymer		59.19	53.76	168.28	12.12	9.31	31.22	4.30	11.24
Doubled Haploids	"early"	Mean	51.12	55.10	106.10	7.31	11.20	19.62	3.21	8.92
		Min	47.50	39.30	81.90	6.70	6.60	17.75	1.50	4.95
		Max	59.40	62.40	140.40	8.65	14.00	25.00	6.50	13.25
	"late"	Mean	59.40	53.10	146.50	9.93	9.26	27.15	3.83	10.25
		Min	41.00	41.15	95.00	7.15	6.40	22.70	2.00	5.90
		Max	67.20	60.55	175.80	11.65	11.00	30.90	5.00	15.75
	"early"	Mean	55.30	53.66	122.90	8.51	10.47	22.85	2.78	9.21
		Min	48.20	44.16	98.40	7.50	6.70	18.39	0.95	4.55
		Max	62.20	56.56	149.00	10.40	14.65	28.50	5.00	13.55
	SSD	Mean	55.20	51.22	125.00	9.04	9.00	23.47	4.42	8.80
		Min	37.40	27.74	62.90	4.22	5.70	14.25	1.15	4.90
		Max	73.10	67.34	181.20	13.25	10.28	31.50	7.00	13.49

generating random inbred lines and classifying the lines for alleles at any one locus it is possible to produce inbreds which exceed the higher or lower scoring parent. In the early stages of a breeding programme selection is largely visual and it has been considered both effective and efficient to fix simply inherited characters in the F_2 generation. The evidence presented here for the two genes studied clearly indicates that this approach is inadvisable. In this paper and that dealing with the *GPert* locus (Powell, Thomas, Caligari and Jinks, 1985) two of the possible situations explaining the association between major genes and quantitatively varying characters have been demonstrated, *i.e.* tight linkage/pleiotropy and linkage which is broken down following three rounds of gametogenesis. Both these mechanisms are relatively easily dealt with in a breeding programme. In the case of very tight linkage or pleiotropy, random inbred lines produced by SSD or DH from F_1 hybrids will be equally effective. Where linkage disequilibrium is implicated, rounds of gametogenesis should be encouraged to allow undesirable linkages to be broken down and hence SSD would be a suitable strategy. Alternatively DH could be produced from F_3 or later generations. Other relationships could theoretically exist *e.g.* a desirable allele at a major gene locus linked to desirable quantitative character expression, in this case DH produced from F_1 hybrids would clearly prove to be advantageous. Many other relationships could be envisaged but the methods

described in this paper, which are not confounded with background effects, allows the breeder to examine the relationships between major genes and agronomic characters and then adopt the most suitable strategy for the deployment of major genes.

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