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Genetical analysis of chromosome 5A of wheat and its influence on important agronomic characters

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Summary. Chromosome 5A of bread wheat, *Triticum aestivum* carries the major gene, *Vrn1*, which is one of the main determinants of the winter/spring growth habit polymorphism in this species. Genetical analysis of this chromosome has been carried out using single-chromosome recombinant lines to establish the pleiotropic effects of this locus and two other major genes, *q* determining ear morphology and *b1* determining the presence of awns, on important agronomic characters. The three major genes were located on the long arm of chromosome 5A with a gene order of: centromere–*b1*–*q*–*Vrn1*. Analysis of quantitative characters from a winter sowing revealed pleiotropic effects of *Vrn1* or the effects of closely linked loci on the characters plant height, tiller number and spikelet number. However effects on ear emergence time were not associated with *Vrn1* but with *q* as were effects on spikelet number and ear length. In addition a locus determining yield/plant was located between *Vrn1* and *q*. Independant loci determining height and ear length were apparent on the short arm of chromosome 5A. From a spring sowing, however, there was a large pleiotropic effect of *Vrn1* on ear emergence time, as well as the effects previously detected. In addition, associated with *q* were effects on plant height and grain size which were not expressed from the winter sowing.

Key words: Wheat – Vernalisation genes – Agronomic characters

Introduction

The ability of bread wheat, *Triticum aestivum* to tolerate aneuploidy has led to the development of cytogenetical techniques which enable single chromosomes to be manipulated in a directed manner. By combining these techniques with phenotypic assessments of genotypes differing by specific chromosomes it has been possible to dissect the genetical variation for important agronomic characters chromosome by chromosome (Law and Worland 1973; Snape et al. 1977; Snape and Law 1980; Law et al. 1981).

A character that has received detailed attention is the time to flowering under different environments and its relationship to geographic and seasonal adaptation. Generally, wheat varieties are classified as spring or winter wheats corresponding to their time of sowing. The major physiological determinant of this difference is the requirement of winter sown varieties for a period of growth under low temperature, vernalisation, before floral initiation proceeds.

The genetical control of the winter/spring polymorphism has been established using aneuploid lines and chromosome substitution lines. Although many chromosomes have been implicated, major effects are associated with just two, 5A and 5D (Morrison 1960; Tsunewaki 1966; Halloran 1966; Halloran and Boydell 1967; Law et al. 1976). The detailed analysis of Law et al. (1976) also showed that these effects are due to single major genes, *Vrn1* and *Vrn3*, located distally on the long arms of these chromosomes.

In northern european wheat varieties *Vrn1* appears to be the predominant locus responsible for the polymorphism (Snape et al. 1976; Snape and Parker, unpublished). Also examination of the variation at this locus in a range of varieties has shown that there appears to be a multiple allelic series conferring different degrees of "earliness" and "lateness" within both winter and spring categories. The importance of this simple genetical control is that by exploiting the variation it is possible to transform winter varieties into spring varieties by substituting a spring allele for a winter allele at the *Vrn1* locus. Law et al. (1981) were able to demonstrate this using the high yielding British winter wheat 'Hobbit' as the recipient variety and by producing the substitution line of chromosome 5A from an accession of *T. spelta* which carries a potent spring allele.

The substitution line behaved as a conventional spring wheat and lines derived from it showed yielding ability as good as commercial spring varieties. These results indicated that the genetical differences between a high yielding spring wheat and a high yielding winter wheat may only be a function of vernalisation genes and not of other genes for adaptation and yielding ability. To examine this hypothesis further and to establish the pleiotropic effects of the *Vrn1* locus on other characters, detailed genetical analysis of the differences between 'Hobbit' and the 'Hobbit' (*T. spelta* 5A) substitution line was carried out using single-chromosome recombinant lines (Law 1967). The results of these analyses are presented here.

Materials and methods

Experimental genotypes

The Hobbit (*T. spelta* 5A) substitution line was developed by the methods described by Law and Worland (1973) using the 'Hobbit' monosomic 5A line as the recurrent parent. This latter line had previously been developed by six generations of backcrossing to 'Hobbit'. Five backcrosses of the monosomic substitution to this monosomic were performed prior to the extraction of the disomic substitution.

Following its development the disomic substitution line was crossed to the recipient variety 'Hobbit' to form a single-chromosome heterozygote. Random, homozygous single-chromosome recombinant lines were then produced using the method described by Law (1966). Initially, the hybrid was crossed as male parent to the Hobbit monosomic 5A line. In the resulting progeny monosomic plants were identified by cytological examination of mitotic chromosomes in root-tip preparations. Each of these plants contained a 5A chromosome which was the product of recombination between the Hobbit and *T. spelta* 5A chromosomes in the single-chromosome heterozygote. The monosomic recombinant plants were selfed, and disomic recombinants recognised by cytological examination of their progeny. In total, 95 different, homozygous disomic recombinant plants were extracted, grown to maturity and allowed to self-pollinate. The seed from these disomic plants was then used to assess the genotype of each recombinant line for major gene markers and to assess the effects of the homologous chromosome variation on quantitative characters of agronomic importance.

In addition to the recombinant lines, non-recombinant 'parental' lines were developed by crossing the original substitution line and 'Hobbit' to the 'Hobbit' monosomic 5A line. Monosomics and then, subsequently, disomic plants were extracted and these selfed to produce a group of lines homozygous for the non-recombined Hobbit 5A chromosome and a group homozygous for the non-recombined *T. spelta* 5A chromosome. These parental lines provide a test of genetic segregation in the backgrounds of the 'Hobbit' monosomic line and the substitution lines caused by possible residual heterozygosity remaining after recurrent backcrossing. These lines also provide an estimate of the whole-chromosome difference between the homologous parental chromosomes for quantitative characters.

The experiments

1) Classification of recombinant lines at major gene loci. The *T. spelta* 5A chromosome carries a potent allele promoting spring habit at the *Vrn1* locus and the 'Hobbit' 5A an allele for winter habit (Law et al. 1981). To classify the individual recombinant lines for these alleles three plants of each line were grown to maturity without prior vernalisation in a growth room maintained at 20 °C under 16 h days. The parental lines were grown as controls.

In addition to *Vrn1,* the *T. spelta* 5A differs from the 'Hobbit' 5A at two major gene loci which affect ear morphology. Firstly, the locus *q* confering a speltoid ear type (McKay 1954) and secondly *b1,* which affects the production of awns (Watkins and Ellerton 1940). The alleles on *T. spelta* 5A confer a speltoid, awned phenotype and the alleles on the 'Hobbit' 5A a square, unawned phenotype. The disomic recombinant plants were each classified by eye for their genotypes at these two loci.

2) Assessment of the agronomic performance of the parental and recombinant lines. To assess the pleiotropic effects of the major gene loci and particularly *Vrn1* on major agronomic characters two field experiments were carried out.

In the first experiment 73 recombinant lines together with 19 of each of the parental groups were grown from a sowing in mid-October. The timing of the sowing provided an environment in which the vernalisation requirement of all 'winter' lines would be fully satisfied whilst being, late enough in the autumn not to allow precocious development of 'spring' lines.

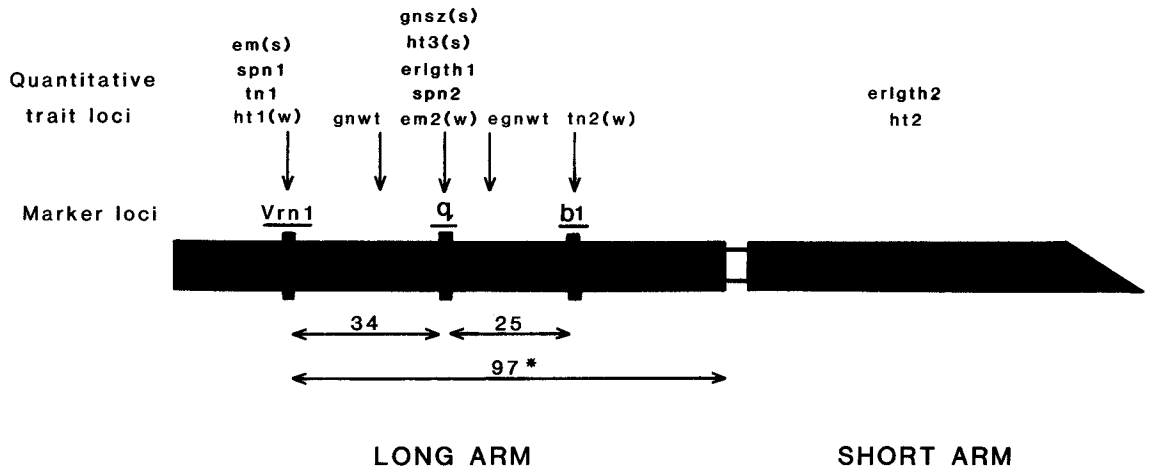
A second experiment was sown in the spring, in the first week of March. This contained the same genotypes as the first and was designed to be early enough to provide 'winter' genotypes with a short period of vernalisation to enable them to flower but still late enough to produce a large difference in flowering time between *Vrn1* and *vrn1* genotypes.

These two experiments were sown adjacently with five replicate blocks. Within each replication each genotype was represented by a single row plot of 11 plants, spaced 10 cm apart within rows and rows spaced 30 cm apart. During growth and at maturity a range of agronomic characters was measured on each plot including flowering time, scored as days to ear emergence from the 1st June. In the spring sown experiment, growth habit, either erect or prostrate was scored by eye immediately following the period of tiller formation to provide an ancillary measurement of the winter or spring habit of each individual line. At maturity four random leading tillers were taken from each plot and used for the evaluation of single tiller yield components. The remainder of each plot was harvested and plot yields measured. The data was transformed to values per plant or per tiller for analysis.

Results

1) Genotypic classifications at major gene loci and linkage estimation

The measurements of flowering time in the growth-room experiment showed a bimodal distribution with a division of the recombinant lines into the two parental classes. All 95 lines were unambiguously classified as 'spring' types possessing *Vrn1* or 'winter' types possessing *vrn1.* These latter lines, like the 'Hobbit' 5A



* Data of Law, Worland, & Giorgi (1976)

Fig. 1. Recombination map for chromosome 5A. Distances between major gene loci are given in cM. Probable positions of quantitative trait loci are given relative to the marker loci. Abbreviations for qtl: em = ear emergence time; ht = plant height; spn = spikelet number/ear; tn = tiller number; gnwt = grain weight/plant; egnwt = grain weight/ear; gnsz = grain size; erlth = ear length. s = effects expressed from a spring sowing, w = effects expressed from a Winter sowing

Table 1. Genotypic frequencies for major gene loci on chromosome 5A in the population of single chromosome recombinant lines

Phenotype			Genotype	No. lines
Spring (S)	speltoid (SP)	awned (A)	*Vrn1 q b1*	28
S	SP	U	*Vrn1 q B1*	9
S	SQ	A	*Vrn1 Q b1*	3
S	SQ	U	*Vrn1 Q B1*	9
W	SP	A	*vrn1 q b1*	14
W	SP	U	*vrn1 q B1*	2
W	SQ	A	*vrn1 Q b1*	8
Winter (W)	square (SQ)	unawned (U)	*vrn1 Q B1*	22

parental lines, had greatly delayed flowering times, produced excessive vegetative growth and on flowering produced small sterile ears. These classifications were consistent with scores from the spring sown field experiment of growth habit following tiller formation. All lines classified as possessing *Vrn1* showed an erect habit and all lines with *vrn1* a prostrate habit. Consistent classifications of phenotypes at the *q* and *b1* loci were obtained from observations of the original disomic plants and their field grown progenies.

The complete genotypic classification for the three marker loci is shown in Table 1. From these data the recombination distances between the three loci can be calculated and the gene order established. Clearly the three loci are linked confirming that they are all located on the long arm of chromosome 5A (McIntosh 1973). *Vrn1* is located distally on the long arm and segregates independently of the centromere (Law et al. 1976). Consequently the gene order on 5AL must be: centromere–*b1*–*q*–*Vrn1*, since the least frequent classes *Vrn1 Q b1* and *vrn1 q B1* will be the double recombinants. These data give per cent recombination frequencies of 29.5 ± 4.68 and 23.2 ± 4.33 between *Vrn1* and *q*, and *q* and *b1*, respectively. This latter value agrees with estimates from previous studies (McIntosh 1973) and the combined distances confirm that *Vrn1* segregates independently of the centromere. The recombination map of chromosome 5A from these data, expressed in cM is shown in Fig. 1.

2) Analysis of quantitative characters: winter sown experiment

a) Non-recombinant lines. The analysis of variance of difference within and between the non-recombinant parental groups for a range of characters is shown in Table 2. For four characters, plant height, grain weight/plant, spikelet number and 50 grain weight, significant differences were obtained between replicate lines within the 'Hobbit' 5A group. This indicates that the background of the 'Hobbit' monosomic 5A line contained some residual heterozygosity following six backcrosses to Hobbit. Similarly the *T. spelta* 5A lines exhibited variation which results from both heterozygosity in the

Table 2. Analysis of variance of differences within and between non-recombinant parental groups and mean performance for a range of agronomic characters from the winter sowing

Item	df	Mean squares							
		Ear emergence time (days)	Height (cm)	Tiller no./ plant	Grain weight/ plant (g)	Spikelet no.	Ear length (cm)	Grain weight/ ear (g)	50 grain weight (g)
Between parental groups	1	1,061.0***	4,368***	17.96	2.35	29.64***	481.00***	3.491*	0.0008
Between 'Hobbit' 5A lines	18	1.1	30***	3.43	33.19***	1.75**	0.38	0.223	0.0075*
Between *'T spelta'* 5A lines	18	10.5***	41***	9.96***	105.50***	2.04***	2.13***	1.256***	0.2936***
Error	144	0.8	8	2.65	1.88	0.47	0.28	0.224	0.0024
		Means							
'Hobbit' 5A		12.05	78.2	10.55	19.99	20.79	9.95	3.27	2.047
T. Spelta 5A		7.33	87.8	9.94	20.21	20.00	13.13	3.54	2.060

Significance levels: * = 0.05–0.02; ** = 0.01–0.001; *** < 0.001

Table 3. Analysis of variance of differences between recombinant lines from the winter sowing

Item	df	Mean squares							
		Ear emergence time	Height	Tiller no./plant	Grain weight/ plant (g)	Spikelet no./ear	Ear length	Grain weight/ ear	50 grain weight (g)
Between lines	72	13.62***	195.2***	8.147***	73.78***	1.696***	7.99***	0.963***	0.1830***
Between genotypic classes	7	75.34***	531.1***	18.615*	108.71	4.019*	48.67***	3.148***	0.0744
Between replicate lines within genotypic classes	65	6.97***	159.0***	7.020***	70.02***	1.446***	3.62***	0.782***	0.1947***
Error	288	0.80	7.3	2.911	21.91	0.263	0.24	0.126	0.0246

Significance levels: * = 0.05–0.01; ** = 0.01–0.001; *** < 0.001

'Hobbit' monosomic lines and in the substitution line. As would be expected from the parallel development of the monosomic and substitution line the amount of residual variation, represented by the relative values of the between line mean squares, is much greater for the *T. spelta* 5A group.

Over and above the residual genetic variation there are significant differences between the means of the parental groups, Table 2, indicating differences between the 5A chromosome of *T. spelta* and its homologue from 'Hobbit'. *T. spelta* 5A appears to confer an earlier flowering time, a taller final plant height, a higher grain weight/ear and a longer ear; but a lower spikelet number/ear. Whether these differences are pleiotropic effects of the marker genes or of separate loci can be evaluated by examining the variation between the recombinant lines.

b) Recombinant lines. The analysis of variance of differences between the recombinant lines, where the variation has been partitioned into comparisons between and within the eight genotypic classes for the three marker loci, is shown in Table 3. The total between lines variation is significant for all characters. When this variation is partitioned the significance of the between genotypic classes item shows that genetical differences for all characters except grain weight/plant and 50 grain weight are associated with segregation of the three markers and therefore with chromosome 5A. Thus allelic differences for ear emergence time, plant

Table 4. Mean performance of major gene phenotypic classes from the winter sowing

Phenotype			No. lines	Ear emergence time (days)	Height (cm)	Tiller no./plant	Grain weight/ plant (g)	Spikelet no./ear	Ear length (cm)	Grain weight/ ear (g)	50 grain weight (g)
S	SP	A	25	6.19	89.3	10.64	25.22	20.08	12.94	3.78	2.168
S	SP	U	6	6.07	94.8	12.04	26.63	20.16	13.22	3.63	2.167
S	SQ	A	1	7.80	92.4	12.40	26.98	20.65	11.95	3.56	2.280
S	SQ	U	8	8.82	89.8	11.93	24.23	20.79	11.78	3.35	2.260
W	SP	A	12	7.08	87.1	10.53	24.78	19.86	12.38	3.81	2.237
W	SP	U	1	8.00	80.6	12.93	25.75	20.01	11.70	3.56	2.120
W	SQ	A	5	8.92	85.2	10.56	22.00	20.62	11.00	3.31	2.172
W	SQ	U	15	8.79	83.7	11.07	22.31	20.20	10.58	3.22	2.167

Table 5. Mean performance of individual allele classes and residual within class variation: Winter sowing

Allele		No. lines	Ear emergence time (days)	Height (cm)	Tiller no./plant	Grain weight/ plant (g)	Spikelet no./ear	Ear length (cm)	Grain weight/ ear (g)	50 grain weight (g)
Vrn1		40	6.74***	90.3***	11.16	25.28***	20.25	12.73*	3.668*	2.189
vrn1		33	8.16	85.1	10.85	23.26	20.14	11.33	3.455	2.192
q		44	6.46***	89.3*	10.85***	25.30**	20.03***	12.80***	3.763***	2.185
Q		29	8.79	87.0	11.27	22.94	20.45	11.03	3.282	2.197
b1		43	6.80***	88.3	10.64***	24.76	20.09*	12.54***	3.729***	2.190
B1		30	8.23	87.5	11.56	23.80	20.34	11.46	3.346	2.190
Residual, within groups MS	*Vrn1/vrn1*		11.2	163***	8.14	69.6	1.70	5.63*	0.920	0.1855
	q/Q		7.1	184***	8.05	67.9	1.51	4.25*	0.692	0.1854
	b1/B1		11.2	197***	7.22	73.7	1.64	6.68**	0.795	0.1855
Between parental *T. spelta* 5A lines MS			10.5	41	9.96	105.5	2.04	2.13	1.256	0.2936

Significance levels for differences between alleles: * 0.05–0.01; ** 0.01–0.001; *** < 0.001

height, spikelet number, ear length and grain weight/ear are present between the Hobbit 5A and *T. spelta* 5A chromosomes. The significance of variation within the genotypic classes indicates that there is also genetical variation which is independent of the marker loci. Some of this variation may be due to segregation of these background genes responsible for the variation observed between the *T. spelta* and 'Hobbit' parental lines. For height, however, the magnitude of the variation is significantly greater within the marker classes than that shown by the *T. spelta* parental lines (see Table 2). This implies that there is a height gene(s) on chromosome 5A which is segregating independently of markers on the long arm of this chromosome and the background. This could suggest a locus controlling plant height located on the short arm of 5A in addition to the long arm effects.

The mean performance of each of the eight genotypic classes is shown in Table 4. These confirm that alleles producing an earlier flowering time, a taller plant, a larger ear with less spikelets but a greater grain weight are carried by the *T. spelta* 5A chromosome, effects suggested previously from examination of the means of the parental groups.

To examine if these effects are a pleiotropic expression of the individual marker loci or of closely linked genes the data may be partitioned further to give comparisons between and within classes for the alternative alleles. Table 5 presents the means for each marker allele together with its residual between line within groups variation. A significant difference between the alleles implies a pleiotropic effect of the locus or the effect of a closely linked gene whilst the significance of the residual variation implies that there are gene(s) present segregating over and above the effect of the marker locus.

From this sowing, differences between the homologous chromosomes in ear emergence time appear to be

associated not with *Vrn1* but with *q*. Evidently the winter sowing provides sufficient vernalisation to remove the effect of *Vrn1* allelic variation and the earlier emergence time of the *T. spelta* 5A genotype is associated with a separate gene. This may be a pleiotropic effect of *q* on stem elongation or a gene for 'earliness' per se. However an effect on height is undoubtedly associated with *Vrn1*, or a closely linked locus, because the *Vrn1* versus *vrn1* comparison is highly significant. This is in addition to a gene(s) already shown to be segregating independently of the markers and probably located on the short-arm and responsible for the significant residual variation. Also associated with both *Vrn1* and *q* is an effect on grain weight/plant. This was not detected in the analysis of variance, presumably because of a less sensitive test. However it is apparent from Table 4 that all genotypic classes with *Vrn1* from *T. spelta* are higher yielding than their *vrn1* counterparts. Thus 5A of *T. spelta* carries a 'yield increasing' gene, probably located between *Vrn1* and *q*.

Associated with *q* and *b1* are effects on tiller number/plant, spikelet number/ear, grain weight/ear and ear length. These are obviously also 'yield' genes but must be independent of the grain weight/plant locus since the *T. spelta* allele reduce tiller number and spikelet number relative to 'Hobbit' 5A alleles. In contrast, however, for the gene(s) affecting grain number/ear, it is the *T. spelta* 5A allele which increases expression. This latter effect is presumably obtained from an increased grain number since no effect on grain size was detected. These results indicate independent loci affecting yield components on 5A with increasing alleles dispersed between the two homologues. Presumably these could be recombined to produce a higher yielding derivative – an adapted gene complex for increased yield. However, the effect on spikelet number is probably a pleiotropic effect of the *q* locus resulting from the change in ear morphology. The difference in ear length is also likely to be an effect of *q*, again an obvious result of the change in ear morphology. In addition, however, the significance of the residual mean square for ear length indicates a further gene on 5A segregating independently of the marker loci. Thus a gene possibly located on the short arm affecting ear length appears to be present.

3) Analysis of quantitative characters: spring sown experiment

The genetical differences between the parental and recombinant lines for all characters detected in the winter sown experiment were also expressed in the spring sown experiment. In addition variation for 50 grain weight was present which was not expressed from the winter sowing. Table 6 presents the mean performance for the marker gene classes together with the between lines within classes mean squares. These data confirm loci affecting grain weight/plant, spikelet number, ear length and grain weight/ear as being closely linked to or pleiotropic effects of the *q* locus. Although the mean performance of these characters changed over sowings no interaction with environments was present. These results also confirm the presence of loci for plant height and ear length presumed to be on the short arm.

For the characters ear emergence time, height and tiller number, however, there is an interaction with time of sowing. Clearly the large difference between homo-

Table 6. Mean performance of individual allele classes and residual within class variation: Spring sowing

Allele	No. lines	Ear emergence time (days)	Height (cm)	Tiller no./plant	Grain weight/ plant (g)	Spikelet no./ear	Ear length (cm)	Grain weight/ ear (g)	50 grain weight (g)
Vrn1	40	21.74***	82.8	7.65***	16.26*	19.11	11.66***	3.044***	2.151***
vrn1	33	32.16	81.3	8.54	15.28	18.91	10.32	2.784	2.007
q	44	23.49***	84.4***	8.04	17.14***	18.78***	12.00***	3.125***	2.162***
Q	29	30.94	78.8	8.08	13.81	19.38	9.62	2.626	1.970
bl	43	24.94***	83.1	8.06	16.85***	18.82***	11.64***	3.076***	2.134***
bl	30	28.61	80.7	8.05	14.34	19.30	10.20	2.712	2.017
Residual, within groups MS	*Vrn1/vrn1*	32.7	191***	4.57	38.7	3.22*	7.53***	0.560	0.1597
	q/Q	102.7***	156***	5.59	26.3	2.83	2.80*	0.341	0.1411
	bl/Bl	154.4***	187***	5.59	32.1	2.99	7.24***	0.482	0.1692
Between parental *T. spelta* 5A lines MS		27.1	33	3.92	33.9	1.45	1.08	0.512	0.1228

Significance levels: * 0.05–0.01; ** 0.01–0.001; *** < 0.001

logues for flowering time is a pleiotropic effect of the *Vrn1* locus from this sowing. There may still be an additional effect of *q* but this variation cannot be separated from the larger effect of *Vrn1*. The height difference previously associated with *Vrn1* from the winter sowing is not expressed from the spring sowing, and in contrast an effect linked to *q* is apparent. This may be a consequence of the larger difference in ear length.

A significant effect associated with *Vrn1* on tiller number reinforces the previous suggestion that this is a pleiotropic effect of this locus, with a large interaction with sowing time. Presumably the increased tiller number of *vrn1* genotypes is a response to the shorter vernalisation treatment. The effect of the second locus on tiller number is not apparent from this sowing.

4) Estimation of recombination between quantitative trait loci (qtl) and markers

The above data indicate several quantitative trait loci (qtl) affecting important agronomic characters located on the long and short arms of chromosome 5A. Some of these effects are due to pleiotropy of the major genes and/or to the effects of closely linked loci. These alternatives cannot be unequivocably separated. Nevertheless, on the assumption of only one locus affecting each character, recombination frequencies between the qtl's and the major gene loci can be calculated from the differences between the means of the two parental classes (Table 4) and the differences between the means of the marker allelic groups (Table 5) using the following model:

Let A/a be the marker gene locus, B/b the qtl and p, the recombination frequency between them. Let d be the additive effect of the qtl defined from an origin m, using the terminology of Mather and Jinks (1971). Then the frequencies of the two parental and two recombinant classes and the genotypic mean of each for the qtl are:

Genotype	Frequency	Mean
AB	½ (1–p)	m + d
Ab	½ p	m–d
aB	½ p	m + d
ab	½ (1–p)	m–d

The difference between the two parental classes (AB and ab), P = 2d. This can be estimated in the present experiment from the difference between the unrecombined marker classes *Vrn1 q b1* and *vrn1 Q B1*. The difference between the mean of the marker allele groups (AB + Ab, aB + ab), R = 2 (1 - 2p) d. This can be calculated using the data in Table 5. Combining these two equations produces a solution for the recombination frequency between the marker and the qtl, of p = (1 - R/P)/2. Appropriate errors can also be calculated for the estimates of p using the variances of R and P.

Recombination frequencies calculated using this formula are shown in Table 7 for both the winter and the spring sown experiments. These values can be used to augment the genetic map of chromosome 5A based on the major gene loci. The presumed positions of the qtl's relative to the marker loci are given in Fig. 1. These values reinforce the suggestions that the effects on ear emergence time (em2), ear length (erlth) and grain weight/ear (egnwt) from the winter sowing are a pleiotropic effect of *q* whilst the effect on height (htl) is a pleiotropic effect of *Vrn1*. However these values also suggest that more than one locus affecting tiller number and spikelet number are present since for both characters R > P. Examination of the means for tiller number in Table 4 and Table 5 would suggest one locus (*tn1*) located near to *Vrn1* with the *T. spelta* allele increasing expression and the other locus (*tn2*) located near to *b1*

Table 7. Recombination frequencies between qtl's and Marker loci

Locus	Experiment	qtl for characters							
		Ear emergence time	Height	Tiller no./plant	Grain weight/ plant	Spikelet no./ear	Ear length	Grain weight/ ear	50 grain weight
Vrn1	Winter sowing	0.23*	0.03	[a]	0.15*	[a]	0.21*	0.31*	–
	Spring sowing	0.09	0.33*	[a]	0.35*	[a]	0.26*	0.28*	0.21*
q	Winter sowing	0.05	0.21*	[a]	0.10	[a]	0.13	0.08	–
	Spring sowing	0.21*	0.00	[a]	0.02	[a]	0.06	0.09	0.12
b1	Winter sowing	0.22*	0.43*	[a]	0.34*	[a]	0.27*	0.16*	–
	Spring sowing	0.36*	0.24*	[a]	0.14*	[a]	0.24*	0.20*	0.27*

[a] Values not calculated because R > P suggesting more than one qtl present
* Values significantliy different from zero

with the Hobbit allele increasing expression. Similarly for spikelet number, an allele (*spn1*) located near to or possibly a pleiotropic effect of *Vrn1* increases spikelet number whilst *q* or an allele (*spn2*) linked to it decreases spikelet number. These dispersed alleles in the parents give rise to recombinant lines with alleles associated, producing phenotypes which transgress the non-recombinant classes.

The recombination frequencies between the *qtl's* and the marker loci for the spring sown material is shown in Table 6 and their relative positions mapped in Fig. 1. In addition to the loci already located the qtl affecting 50 grain weight (*gnsz*) is closely associated with *q*.

Discussion

These results have general consequences for strategies for the breeding of both winter and of spring sown wheat varieties.

Firstly in breeding winter sown varieties they illustrate that the presence of a vernalisation requirement per se may not be necessary for good agronomic performance. If the sowing is carried out late in autumn then varieties without a vernalisation requirement show equivalent yielding abilities and general agronomic performance to their vernalisation requiring counterparts. In the present material there was even a yield advantage in possessing the spring allele which appeared to be due to linkage of a "yield increasing" gene. Thus a strategy of assessing material for agronomic performance from a winter sowing regardless of the level of vernalisation requirement could increase the amount of genetical variation available for selection. Indeed, varieties such as Fenman are reaching the recommended list of varieties in the UK which have unconsciously been selected from such a strategy (Kirby et al. 198). However caution has to be exercised in the choice of sowing date. Sowings early in autumn will cause precocious development of genotypes lacking a vernalisation requirement with the danger of damage to the initiated spike from winter frosts (Snape and Parker, unpublished). Nevertheless the absence of a vernalisation requirement enables varieties to be winter sown or if field conditions are adverse, seed may be kept over winter for spring sowing. A requirement for vernalisation need only be maintained for varieties designed to be sown very early in the autumn.

For the breeding of spring wheat varieties these results reinforce the conclusion of Law et al. (1981) that genes selected for high yielding ability from winter sowings also produce high yields from spring sowings. Thus the genetical differences between winter wheats and spring wheats in the U.K. environment are a function of vernalisation genes alone and not of more fundamental differences determined by a range of genes determining adaptation. Thus the approach used here could be extended to other high yielding winter genotypes, particularly those with good bread making quality, to produce high yielding spring genotypes which could be marketed as spring varieties in their own right or used as parents in spring wheat breeding programmes. This could enlarge the gene pool available in spring wheat and increase potential yields.

In terms of genetical analysis in wheat these results again demonstrate the power of single-chromosome recombinant lines as a means of locating and identifying loci controlling important quantitative characters and also as a means of chromosome engineering. Chromosome 5A has been shown to carry alleles affecting important yield components and also at least two loci affecting height. Indeed, allelic variation at these height loci is probably responsible for the wide range of whole chromosome effects of 5A previously detected by Snape and Law (1980). The extent of this variation could be of significance in breeding for reduced height phenotypes.

The dispersed nature of the proposed genes affecting yield on this chromosome means that recombinant 5A chromosomes can be selected which increase yield over that of both parental homologues. These could be introduced into breeding programmes to give improved performance. Such useful recombinants would lack *q*, which affects threshability adversely, but contain the genes which increase yield linked to it. This would involve simultaneous crossovers between *q* and the proposed yield genes *gnwt* and *egnwt* (Fig. 1) located either side of it. The appropriate double-cross-over types would be expected to give higher yields than any of the single cross-overs, distal or proximal to *q*. Evidence that such derivatives have already been produced, were given by yield studies of spring 'Hobbit' recombinants derived from earlier generations of the substitution line described by Law et al. (1978) and Law et al. (1981).

In addition to genetical analysis, these single chromosome recombinant lines used here provide a tool for assessing the physiological and biochemical basis of variation for these agronomic traits. For example, studies of the effect of *Vrn1* allelic variation on aspects of primordia development and ear initiation are in progress to characterise growth responses from different sowing dates. In future studies the availability of genotypes such as these with defined single gene differences will provide suitable material for identifying the biochemical basis of variation for agronomic traits, a prerequisite for the successful application of molecular techniques of plant transformation in plant breeding.

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