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RFLP mapping of the vernalization (*Vrn1*) and frost resistance (*Fr1*) genes on chromosome 5A of wheat

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Abstract A population of single chromosome recombinant lines was developed from the cross between a frost-sensitive, vernalization-insensitive substitution line, 'Chinese Spring' (*Triticum spelta* 5A) and a frost-tolerant, vernalization-sensitive line, 'Chinese Spring' ('Cheyenne' 5A), and used to map the genes *Vrn1* and *Fr1* controlling vernalization requirement and frost tolerance, respectively, relative to RFLP markers located on this chromosome. The *Vrn1* and *Fr1* loci were located closely linked on the distal portion of the long arm of 5AL, but contrary to previous observations, recombination between them was found. Three RFLP markers, *Xpsr426*, *Xcdo504* and *Xwg644* were tightly linked to both. The location of *Vrn1* suggests that it is homoeologous to other spring habit genes in related species, particularly the *Sh2* locus on chromosome 7 (5H) of barley and the *Sp1* locus on chromosome 5R of rye.

Key words Wheat · Vernalization response · Frost resistance · RFLP mapping

Introduction

The existence of extensive allelic variation for genes controlling the time of flowering make bread wheat (*Triticum aestivum* L.) the most widely adapted major cereal crop in the world. Of particular importance for adaptation to autumn sowing are the genes for vernalization requirement (*Vrn* genes), which ensure the need for a period of growth at low temperatures before floral development can proceed. Spring-sown wheats either have no vernalization requirement, or have only a weak response, and the lack of vernalization requirement is generally dominant. Five loci are known to control spring/winter differences (Worland et al. 1987), and the chromosomal location of four of them has been established, namely *Vrn1*(5A), *Vrn3*(5D), *Vrn4*(5B) and *Vrn5*(7B) (Law 1966; Law et al. 1976; Snape et al. 1985). However, in European wheat varieties alleles at the *Vrn1* locus appear to be predominant in reducing vernalization requirement (Pugsley 1971; Snape et al. 1976). In a study carried out using a series of 5A substitution lines into 'Chinese Spring', the most insensitive *Vrn1* allele was found on chromosome 5A of an accession of *Triticum spelta* (Law et al. 1976). If this allele is substituted into winter wheat, the plants can be converted into spring wheats (Law et al. 1981).

A further requirement for the successful adaptation of winter wheats to many ecogeographic regions is the need to survive low winter temperatures. However, unlike vernalization requirement, frost tolerance in wheat appears to be a complex quantitative character determined by the plant genotype and the environment in which the plant is grown. Nevertheless, frost resistance can be evaluated under controlled experimental conditions, and genes influencing frost resistance have been located on the homoeologous group 5 chromosomes and chromosomes 4B, 4D and 7A through the study of monosomic and substitution lines (Law and Jenkins 1970; Puchkov and Zhirov 1978; Sutka 1981; Roberts 1986; Galiba and Sutka 1988; Veisz and Sutka 1989). Chromosomes 5A and 5D have been implicated most frequently, and they appear to carry major genes.

Sutka and Snape (1989) investigated the relative locations of the genes responsible for vernalization requirement and frost resistance on chromosome 5A using single chromosome recombinant lines developed from the cross between the substitution line 'Hobbit' 'sib' (*T. spelta* 5A) and 'Hobbit' 'sib'. In this sample of only 22 recombinant lines the locus for frost resistance, designated *Fr1*, was completely linked to the locus *Vrn1*. This result can be explained by pleiotropic action of the *Vrn1* locus or close genetic linkage between *Vrn1* and *Fr1*. In the present paper

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we report on the further mapping and tagging of the *Fr1* and *Vrn1* genes using restriction fragment length polymorphism (RFLP) techniques and a further population of single-chromosome recombinant lines.

Materials and methods

Mapping population

Substitution lines of chromosome 5A from a spring accession of *Triticum spelta* (Cambridge Laboratory accession number 1220017) and the North American winter wheat variety 'Cheyenne' into 'Chinese Spring' (CS), had been previously shown to be more cold sensitive and early flowering, and more resistant and late flowering, respectively, than their homologues from the recipient variety. Thus, to map *Fr1* and *Vrn1*, we developed single-chromosome recombinant lines from F_1s between these substitution lines using the technique first described by Law (1966). Briefly, the two substitution lines, CS (*T. spelta* 5A) and CS ('Cheyenne' 5A), were first intercrossed to produce a single chromosome (5A) heterozygote. These F_1s were grown and used in crosses as male parent to the monosomic line for chromosome 5A of CS. This produced a progeny generation segregating for chromosome number, where the monosomic (2n=41) plants each contained a hemizygous recombinant chromosome. These monosomics were identified morphologically and cytologically, grown to maturity and allowed to self-pollinate. Disomic recombinants for each family were then extracted cytologically from these progeny. Altogether, disomics were extracted from the selfed seed of 81 monosomic recombinants, where 31 recombinants were represented by duplicate or triplicate disomics and 50 recombinants by a single disomic.

These disomic recombinants were then used for mapping by characterizing the phenotype of each line for frost resistance, ear emergence time, ear type and isozyme and RFLP markers known to be located on chromosome 5A.

Characterization of recombinant lines

Freezing tests

Tests for frost resistance on each disomic line were carried out using the procedures described previously by Sutka (1981). Briefly, the plants were first treated for 5 weeks with a regime of decreasing temperature and illumination. During the 6th week, hardening was carried out using a day temperature of +2°C and a night temperature of 0°C with 20 h of illumination. After hardening, the boxes were transferred to a controlled environment where the temperature was reduced by 1°C/h to –4°C. Hardening was continued for a further 2 days in the dark, after which the frost treatment was carried out at –10°C and –12°C. After 24 h of freezing without illumination, the temperature was raised by 2°C/h to +1°C, and the plants were kept at this temperature for 15 h. The boxes were then transferred to a GB (Conviron) unit for recovery at a day temperature of 16°C and a night temperature of 15°C with a 14-h day for 18 days. The photosynthetic photon flux during the growth and hardening of the plants was 260 μmol m^{-2} s^{-1} (15 klux) using Sylvania Gro-Lux/WS fluorescent tubes.

Ear emergence time and ear type

In the absence of vernalization, differences in flowering time in this material are attributable to allelic variation at *Vrn1*, where the *T. spelta* 5A is vernalization insensitive and has the allele *Vrn1* and 'Cheyenne' 5A is vernalization-sensitive and has the allele *vrn1*. Recombinants and the parental controls were tested by growing 3 plants of each genotype randomized in a growth room experiment. Seed was germinated, and the seedlings were transplanted into soil in 10-cm-diameter pots and grown at 20°C under a regime of 16 h light, 8 h dark. Ears on the first plants emerged 32 days after transplanting, and flowering continued for a further 70 days.

T. spelta has a speltoid ear type, as the name implies, a character that is determined by the *Q* locus on chromosome 5A. Mature plants of each line were characterized visually as carrying the *q* (speltoid) or *Q* (square) alleles.

Isozyme variation

A gene coding for β-amylase, *β-amy-A1*, is located on chromosome 5A, and previous work has shown this gene to be polymorphic for alleles on CS (*T. spelta* 5A) and CS ('Cheyenne' 5A) (Ainsworth et al. 1987). Using the published procedures, we characterized each recombinant line for the alternative parental alleles at the *β-amy-A1* locus.

RFLP analysis

DNA was extracted from 60 different recombinant lines and the parents using a modified CTAB method (Murray and Thompson 1980). Polymorphisms were identified by hybridizing DNA of the parental lines digested with *Bam*HI, *Eco*RI, *Eco*RV, *Dra*I or *Hin*dIII with a range of cDNA and genomic DNA probes known from previous work (Xie et al. 1993; Devos and Gale 1993) to be located on chromosome 5A, using the methods of Devos et al. (1992). Some barley (PSB and WG) and oat (CDO) probes were also used that were known to hybridize to chromosome 7(5H) of barley (Heun et al. 1991; DA Laurie personal communication). Probes detecting polymorphisms between the parents were then used to analyze the recombinant population. Linkage maps were constructed using MAPMAKER (Lander et al. 1987), and the recombination frequencies were converted to centimorgans (cM) using the Kosambi mapping function (Kosambi 1944).

Results

Ear emergence time, ear type and frost tolerance classifications

One hundred and nineteen recombinant lines, representing the 81 different recombinant chromosomes, were characterized for ear emergence time, and examination of the mean ear emergence times for each line revealed that the recombinants essentially fell into two discontinuous groups based around the parental means. One family exhibited a difference between duplicates and was eliminated from the analysis. Of the remaining 80, 44 were classified as "late" and 36 as "early". These data indicate, as expected, segregation for a single gene, namely, *Vrn1*. Thus, each line was classified as carrying *Vrn1* or *vrn1*. Additionally, clear differences in ear morphology allowed each line to be classified as having a speltoid (44 lines) or square (37 lines) ear type, which is controlled by the segregation of alleles at the *Q* locus.

All 119 lines were initially tested in a freezing experiment, and most lines were classified as being tolerant or susceptible to freezing on the basis of their individual performances at different temperatures and by comparison with the parental controls within the different freezing temperatures. Some ambiguities were apparent, and 21 recom-

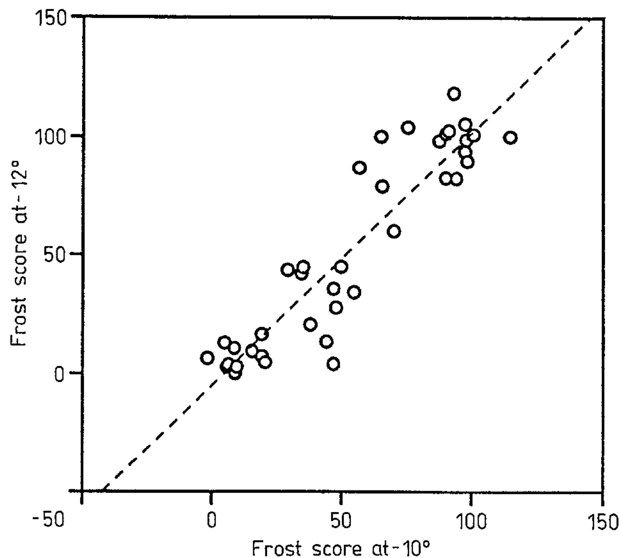

Fig. 1 Relationship between mean frost scores of 38 recombinant lines tested at –10°C and –12°C in the freezing tolerance test. Frost scores for the recombinant lines are given relative to scores for the CS (*T. spelta* 5A) substitution line (0%) and CS ('Cheyenne' 5A) (100%). The fitted regression line is shown (r, 36 df=0.92, P<0.001)

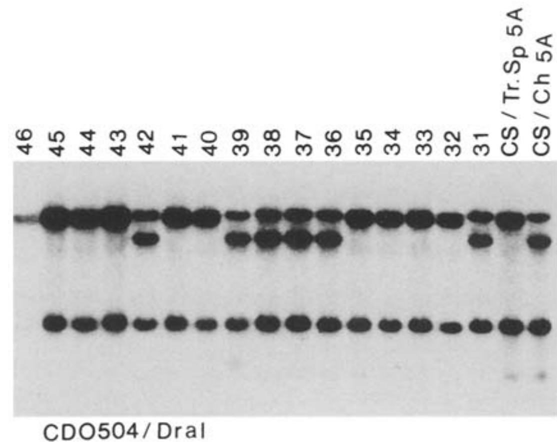

Fig. 2 Autoradiograph of *Dra*I-restricted DNA of the parental lines and a sample of recombinant lines probed with CDO504

binant lines representing 14 families were either inconsistent at different freezing temperatures or had a difference between their duplicates, and thus were not classifiable.

Of the 68 recombinant chromosomes provisionally classified, 12 appeared to be recombinants for the expected phenotypes for frost tolerance and flowering time, namely being either early and frost-tolerant, or late and frost-susceptible. These lines were retested in a further freezing experiment together with a sample of non-recombinants. Figure 1 shows the relationship between tolerances of individual lines at two temperatures, –10°C and –12°C, for the 38 lines retested in this second experiment. In this figure the distribution of phenotypes is essentially bimodal, thus enabling the classification of lines into tolerant or susceptible groups. Overall, of the 68 lines, 31 appeared to be tolerant and 37 susceptible, again suggesting segregation for a single gene, namely *Fr1*. Following this experiment, 11 presumptive recombinants were reclassified as non-recombinants, and only 1 was unambiguously confirmed as a recombinant between *Vrn1* and *Fr1*, which was characterized by being late and susceptible. Two other early lines had frost scores intermediate between those of the parents and need to be tested further to see if they are, in fact, early, tolerant recombinants.

RFLP and Isozyme analysis

From the range of genomic and cDNAs tested for polymorphism against restricted DNA of the two parental genotypes, CS (*T. spelta* 5A) and CS ('Cheyenne' 5A), and CS and 'Cheyenne', 11 suitable probe/restriction enzyme combinations showing easily scorable polymorphisms were identified for mapping the recombinant population. These were all located on 5AL, and from previous evidence (Xie et al. 1993), were considered to cover the majority of the arm. For example, Fig. 2 shows the polymorphism observed at *Xcdo504* in the parents and a sample of the recombinant lines. Clear differences for β-amylase isozymes were also observed, allowing unambiguous classification for this enzyme.

An unexpected problem arose during the genotypic classification of the recombinants for the RFLPs and β-amylase variation, where some of the recombinant lines were found to be segregating for CS alleles. Since all these aberrant lines had a mixture of CS and *T. spelta* alleles and not CS and 'Cheyenne' alleles, this suggested that in the development of the single-chromosome recombinants certain F_1s used in the subsequent backcrosses had been developed from a CS×CS (*T. spelta* 5A) cross and not solely the CS ('Cheyenne' 5A)×CS (*T. spelta* 5A) cross as originally planned. Because of this only 47 lines of the original 60 could be classified for all of the loci examined and subsequently used for map development.

Map development

The map presented in Fig. 3 was developed on the basis of the genotypic classifications for the 47 recombinant lines. This map covers about 80% of 5AL, as estimated from homologous and homoeologous maps (Xie et al. 1993, DA Laurie personal communication). The map length of approximately 180 cM is undoubtedly an overestimate due to the small population size, and the three large gaps are a result of a lack of polymorphisms both proximal and distal to the *Vrn1/Fr1* region of the arm. As found in a previous study (Law et al. 1976), *Vrn1* is located distally on the long arm of chromosome 5A, but proximal to the 5A/4A translocation break-point (Fig. 3). Although closely linked to *Vrn1*, *Fr1* can recombine with it to produce recombinant genotypes. Here, only a late susceptible

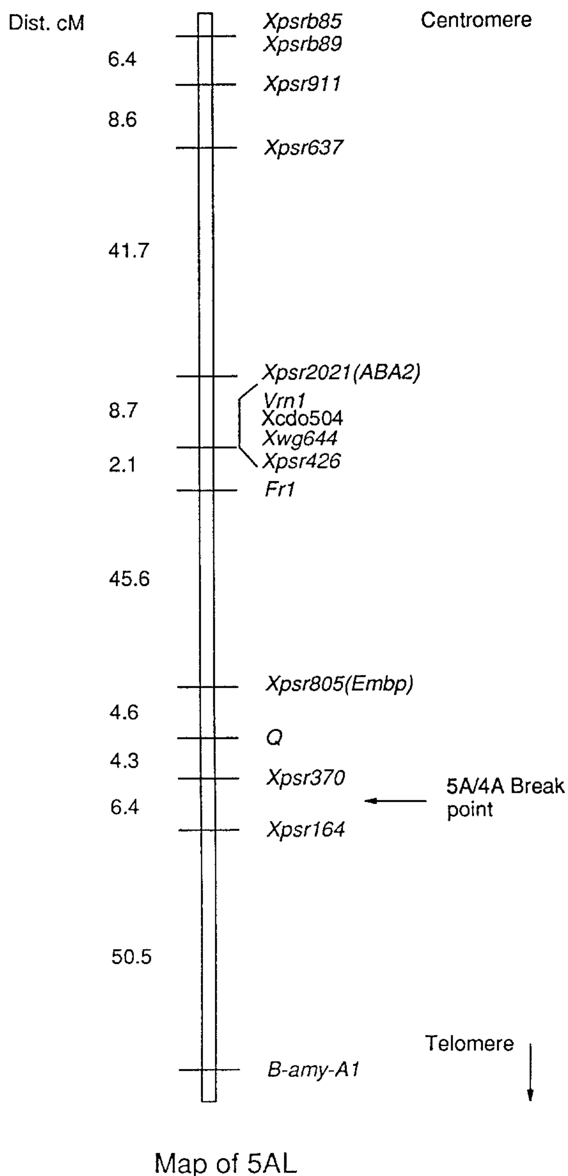

Fig. 3 Genetic map of wheat chromosome arm 5AL showing location of *Vrn1* and *Fr1* loci

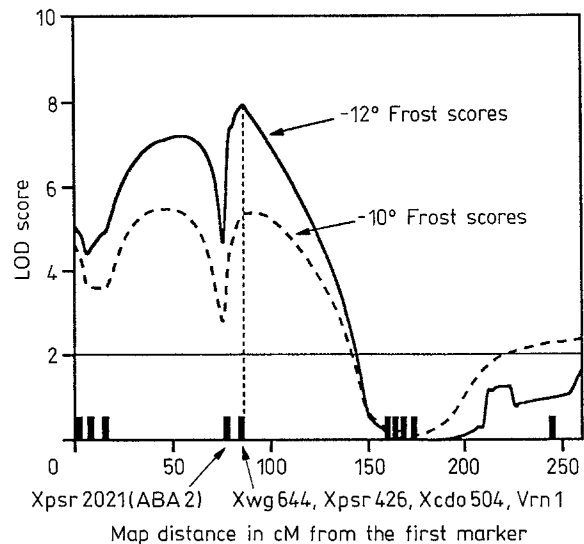

Fig. 4 MAPMAKER-QTL LOD score plot showing location of QTL for frost tolerance based on mean% survival scores of 37 recombinant lines at –10°C (*dashed line*) and –12°C (*solid line*). *Thick bars* on the axis show locations of markers. Map distances in cM are measured from the most proximal markers, *Xpsb85/Xpsb89*. The *dotted line* shows the maximum likelihood location for the QTL using frost scores at –12°C

recombinant was confirmed, although others were suspected. For plant breeding purposes an early and frost-tolerant recombinant would be desirable since this would have important consequences for the breeding of spring wheats. In addition, three RFLP markers are closely linked to both *Vrn1* and *Fr1*, namely *Xpsr426*, *Xwg644* and *Xcdo504*, allowing in the future the possibility of developing polymerase chain reaction (PCR)-based diagnostic markers for these loci. *Q* was shown to be distal to *Vrn1* on the long arm, and thus the gene order of *centromere-Vrn1-Q-B1* (the awn inhibitor locus that is closely linked to *β-amy-A1* (Snape, unpublished)) is the reverse of that presumed by Snape et al. (1985).

Frost tolerance was classified as a qualitative character in carrying out the genotypic classifications, although the original scoring system was quantitative. Thus, to provide additional evidence of the position of *Fr1*, the original quantitative frost scores at –10°C and –12°C were used in a quantitative trait loci (QTL) analysis using the program MAPMAKER/QTL (Lander and Botstein 1989). The results, shown in Fig. 4, confirm the close association between *Fr1* and *Vrn1* and the associated RFLP markers.

Discussion

Recombination between *Fr1* and *Vrn1* clearly shows that these are two major but independent genes on the long arm of chromosome 5A of wheat. Three RFLP loci were identified close to (within 3cM) these agronomically important genes. These results may provide opportunities for marker-mediated manipulation in breeding programmes and the isolation and positional cloning of the *Fr1* and *Vrn1* genes. This could eventually lead to detailed studies of their structure and function and make them available for transformation experiments.

The close genetic linkage (2.1cM) between the *Fr1* and *Vrn1* loci explains the failure of Sutka and Snape (1989) to separate these agronomically very important characters. However, there were some previous indications that the vernalization requirement and the frost resistance were affected by two separate genetic systems on the group 5 chromosomes. For example, Cahalan and Law (1979) found that although chromosome 5A of 'Chinese Spring' and 'Cheyenne' differed in cold resistance, both carried a recessive *vrn1* allele and thus had the same vernalization response. Moreover, Brule-Babel and Fowler (1988) re-

ported that lack of vernalization requirement did not necessarily mean a lack of cold hardiness. In contrast to the investigation of Roberts (1989), these two studies of frost resistance give no indication that more than one (*Fr1*) gene is involved with cold hardening on the long arm of chromosome 5A.

The spring growth habit gene (*Sp1*) in rye is phenotypically similar in effect to *Vrn1* and is located on the long arm of chromosome 5R (De Vries and Sybenga 1984; Melz 1989; Wricke 1991). Plaschke et al. (1993) mapped the *Sp1* locus using RFLP techniques, and based on the available genetic data they proposed that the wheat *Vrn1* and *Vrn3* loci, and possibly *Vrn4*, rye *Sp1*, and barley *Sh2*, form a homoeoallelic set. The results here strongly support this hypothesis. *Sp1* was shown by Plaschke et al. (1993) to be closely linked (6 cM) to the *Xpsr426-5R* locus on the rye map, and in our study the *Vrn1* locus co-segregated with *Xpsr426* (Fig. 3). The previously observed collinearity between the linkage maps of wheat and rye involving chromosome arms 5AL and 5RL (Devos et al. 1993), developed through using probes that hybridize to DNA of both species, clearly shows not only the same gene order but also the similarities in map distances.

In barley there are three genes that control vernalization response, *Sh*, *Sh2* and *Sh3*, located respectively on barley chromosomes 4(4H), 7(5H) and 5(1H) (Takahashi and Yasuda 1971; Laurie et al. 1995). Close linkage (about 4cM) has been found between the biochemical marker locus *βmy1* and the *Sh* locus on barley chromosome 4HL (Chojecki et al. 1989; Hackett et al. 1992). On the long arm of the wheat 5A chromosome the *β-amy-A1* locus (Ainsworth et al. 1987) is located on the 5AL.4AL non-homoeologous translocation segment (Liu et al. 1992; Xie et al. 1993). Thus, it was proposed by Forster and Ellis (1991) and by Hackett et al. (1992) that *Vrn1* is synonymous with *Sh*. However, since in our study *Vrn1* maps proximal (about 60 cM) to the break-point (which is located within the interval *Xpsr370-Xpsr164*), this is obviously not the case. *Sh2,* however, is on barley chromosome 7, which is homoeologous to the wheat group 5 chromosomes. Additionally, previous data on the *Sh2* intrachromosomal location (Sogaard and von Wettstein-Knowles 1987) is consistent with the position of *Vrn1*. Recent RFLP mapping data in barley (Laurie et al. 1995) confirms that this is the case and shows *Sh2* to be close to *Xwg644*.

QTL controlling traits associated with winter hardiness in barley (field survival, LT_{50}, growth habit (vernalization response) and crown fructan content) have also been mapped to chromosome 7(5H) by Hayes et al. (1993). The largest QTL effects for all traits were detected in a 21% recombination interval on the long arm. This interval should be homoeologous to the region surrounding the *Vrn1* and *Fr1* genes on wheat chromosome 5A because it contains both the *Xwg644* and *Xcdo504* RFLP marker loci (Heun et al. 1991; Kleinhofs et al. 1993). Hayes et al. (1993) concluded that the association between frost resistance and growth habit may be due to linkage rather than pleiotropy. Thus, these data support the proposition that an analogous adapted gene complex to *Vrn1-Fr1* is associated with *Sh2*.

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