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Mapping genes affecting flowering time and frost resistance on chromosome 5B of wheat

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Abstract Two populations of single chromosome recombinant lines were used to map genes controlling flowering time on chromosome 5B of wheat, and one of the populations was also used to map a new frost resistance gene. Genetic maps were developed, mainly using microsatellite markers, and QTL analysis was applied to phenotypic data on the performance of each population collected from growth-room tests of flowering time and frost tolerance. Using a recombinant substitution-line mapping population derived from a cross between the substitution-line 'Chinese Spring' ('Cheyenne' 5B) and 'Chinese Spring' (CS), the gene *Vrn-B1*, affecting vernalization response, an *earliness* per se locus, *Eps-5BL1*, and a gene, *Fr-B1*, affecting frost resistance, were mapped. Using a 'Hobbit Sib' ('Chinese Spring' 5BL) × 'Hobbit Sib' recombinant substitution line mapping population, an *earliness* per se locus, *Eps-5BL2* was mapped. The *Vrn-B1* locus was mapped on the distal portion of the long arm of chromosome 5B, to a region syntenous with the segments of chromosomes 5A and 5D containing *Vrn-A1* and *Vrn-D1* loci, respectively. The two *Eps-5BL* loci were mapped close to the centromere with a 16-cM distance from each other, one in agreement with the position of a homoeologous locus previously mapped on chromosome 5H of barley, and suggested by the response of 'Chinese Spring' deletion lines. The *Fr-B1* gene was mapped on the long arm of chromosome 5B, 40 cM from the centromeric marker. Previous comparative mapping data with rice chromosome 9 would suggest that this gene could be orthologous to the other *Fr* genes mapped previously by us on chromosomes 5A or 5D of wheat, although in a more proximal position. This study completes the mapping of these homoeoallelic series of vernalization requirement genes and frost resistance genes on the chromosomes of the homoeologous group 5 in wheat.

Keywords Wheat · Vernalization response · Frost resistance · Microsatellites · Flowering time

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Introduction

Bread wheat (*Triticum aestivum* L.) is the most widely grown cereal in the world due to its ability to survive under different agronomic regimes in different eco-geographical conditions. Genes that control the flowering time are critical to this wide adaptation. The determination of flowering time in wheat is complex, controlled by three major groups of genes, photoperiod response genes (*Ppd* genes), vernalization response genes (*Vrn* genes) and developmental rate genes ('earliness per se', *Eps* genes) (see review by Snape et al. 2001). Specific *Vrn* genes have already been mapped on the long arms of chromosomes 5A (Galiba et al. 1995) and 5D (Snape et al. 1997). These genes are homoeologous to each other and to the vernalization genes on chromosomes 5H of barley (called *Vrn-H1*, formerly *Sgh2*) (Laurie et al. 1995; Cattivelli et al. 2002) and 5R of rye (called *Sp1*) (Plaschke et al. 1993). Other *Vrn* genes have also been mapped on chromosome 4H in barley (Laurie et al. 1995). Sarma et al. (2000) reported the physical mapping of flowering-time genes on the chromosomes of homoeologous group 5 in wheat, and they found two possible loci affecting flowering time on the long arm of the 5B chromosome, one distal, presumed to be *Vrn-B1*, and the other a possible *Eps* locus close to the centromere. To-date, only very few *Eps* loci have been mapped in wheat, such as on chromosomes of homoeologous group 2, and on the short

arm of chromosome 3A (Shah et al. 1999). However, several of them have been provisionally mapped in barley (Laurie et al. 1995), and taking account of the high level of synteny between barley and wheat, many more are predicted to exist in wheat, but remain to be discovered (Snape et al. 2001).

A further requirement for the successful adaptation of winter wheats to different eco-geographical conditions is the ability to survive low winter temperatures. Frost resistance is a complex quantitative character in wheat, but it can be accurately evaluated under controlled experimental conditions. Genes influencing frost resistance have been located on chromosomes of homoeologous group 5, 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).

On the homoeologous group 5 chromosomes, the genes *Fr-A1* (formerly *Fr1*) and *Fr-D1* (formerly *Fr2*) have been mapped on chromosomes 5A (Galiba et al. 1995) and 5D (Snape et al. 1997), and they are closely linked to the *Vrn-A1* and *Vrn-D1* genes. The *Fr-A1* and *Fr-D1* genes appear homoeologous to each other and to a frost resistance gene mapped on barley chromosome 7(5H) (Hayes et al. 1993). As yet, however, the homoeologous locus *Fr-B1* has not been reported, and this paper reports the mapping of this locus and genes for flowering time on chromosome 5B.

Materials and methods

Mapping populations

Two populations of recombinant substitution lines were studied. The first of 61 lines was derived from the cross between the single chromosome substitution line 'Chinese Spring' ('Cheyenne' 5B) and 'Chinese Spring' (CS). The second of 76 lines was derived from the cross between the single chromosome substitution line 'Hobbit Sib' ('Chinese Spring' 5BL) and 'Hobbit Sib', a UK semi-dwarf winter wheat.

Determination of flowering-time variation

In the absence of vernalization, it can be assumed that differences in flowering time in these materials were mainly attributable to allelic variation at *Vrn-B1*, where the 'Chinese Spring' 5B chromosome carries an allele, *Vrn-B1a*, that is vernalization insensitive (being a spring wheat), and 'Cheyenne' (a winter wheat) is vernalization sensitive and carries the allele *Vrn-B1b*. Ten unvernalized plants of each recombinant, and the parental controls, were grown in pots in a controlled environment room (16 h/8 h light/dark period; 20 °C) using a randomised block design for each population. In contrast, following full vernalization, differences in flowering time are expected to be attributable to the effect of loci insensitive to vernalization. To detect the presence of such earliness per se loci, five vernalized plants (treated at 6 °C for 6 weeks, 8-h days) of each of the 'Hobbit Sib' ('Chinese Spring' 5B) recombinant substitution lines were grown in pots in a controlled environment room (16 h/8 h light/dark period; 20 °C) using a randomised block design. Ear emergence time was recorded for each plant when the first tiller headed, measured from the time of sowing.

Freezing test

A test of the frost resistance of the 'Chinese Spring' ('Cheyenne' 5B) and 'Chinese Spring' mapping population was carried out using the procedure 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 –2 °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 –11 °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 for15 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 illumination for 18 days. After recovery, the plants were scored from 0 to 5 depending on the recovery rate (Sutka 1981).

Molecular marker analysis

Genetic maps of the populations were developed using simple sequence repeat (SSR) markers on the 'Chinese Spring' (CS) × CS ('Cheyenne' 5B) population, and SSR and RFLP markers on the 'Hobbit Sib' ('Chinese Spring' 5BL) × 'Hobbit Sib' population. DNA was extracted from the parents and recombinant lines using standard procedures. Primer pairs for SSR polymorphisms known to be on chromosome 5B from a variety of sources were tested on the parental DNA for the two crosses. PCR was performed in 15 μl final volume using 1.5 μl of 10 × PCR buffer (Invitrogen), 0.45 μl of 50 mM $MgCl_2$ (Invitrogen), 1 μl of 2 mM dNTP (Invitrogen), 1.5 μl of 2 mM microsatellite primers, 0.35 units of *Taq* polymerase (Invitrogen) and 100 ng of template DNA. The PCR parameters and the annealing temperatures were applied according to published data (Röder et al. 1998; Wheat Microsatellite Consortium. Agrogene S.A.). The separations of the PCR products were done by sequencing gels (Savant Instruments, Inc.) and visualised by silver staining using a standard protocol. For the 'Hobbit Sib' × 'Hobbit Sib' ('Chinese Spring' 5BL) population, RFLP data from earlier studies were also used (Zhang et al. 1998).

Linkage maps were constructed using JoinMap (Stam 1993), and the recombination frequencies were converted to centimorgans (cM) using the Kosambi mapping function (Kosambi 1944).

QTL Analysis

QTL analysis was initially performed using QTL Cafe (http://sun1.bham.ac.uk/g.g.seaton). Using this programme, marker means ANOVA, simple interval mapping (Haley and Knott 1992) and marker regression (Kearsey and Hyne 1994) approaches were implemented. When putative QTLs were found, these locations were further confirmed using MQM mapping (Jansen and Stam 1994) implemeted using the programme MapQTL. All QTLs found were confirmed to be at the same location (±2 cM) by the different methods.

Nomenclature

In a recent study, a frost tolerance locus independent of the gene *Fr1* was mapped on the long arm of chromosome 5A (G. Galiba and J. Dubcovsky, personal communication). The presence of more than one frost resistance locus on the long arm of chromosome 5A and of genes with similar effects on chromosomes 5B and 5D complicates the use of a sequential number for *Fr* gene nomenclature. In agreement with J. Dubcovsky (University of California, Davis), we propose a homoeologous system of nomenclature similar to the one currently in use for the vernalization genes in wheat (McIntosh et al. 1998). We will refer to *Fr1* as *Fr-A1*, to *Fr2*

as *Fr-D1*, and to the new locus described in this study on the 5B chromosome as *Fr-B1*.

Results and discussion

Mapping of *Vrn-B1*

The mean flowering times of the two parents of the first cross, raised under non-vernalization conditions, were 70.6 ± 2.97 days for 'Chinese Spring' and 75.6 ± 1.08 days for 'Chinese Spring' ('Cheyenne' 5B). The range of flowering times of the recombinant substitution lines was 66.4 to 88.4, where the transgressive segregation suggests the presence of two loci in repulsion. Nine SSR markers were found to be polymorphic on the long arm of chromosome 5B and tested on the recombinant lines of this mapping population. The map (Fig. 1) covers 92 cM with an average of 12 cM distance between the SSR markers. The biggest gap (21 cM) was found between *Xgwm408* and *Xgwm604*.

The map positions of two QTLs affecting flowering time were localised using QTL Café, and confirmed by composite interval mapping (Table 1). The main one was situated distally on the long arm of chromosome 5B (78 cM from the centromeric markers), closely linked to the SSR locus *Xgwm604* and distal to *Xgwm408*. This had an additive effect of 1.76 days and accounted for 10.7% of the phenotypic variation, the late allele coming from Chey 5B. Previously, Röder et al. (1998) have shown that both these SSR loci are closely linked (9.7 cM, and 4.5 cM, respectively) to *Xcdo504-5B*, a RFLP locus on the long arm of the group-5 chromosomes. A homoeologous RFLP locus, *Xcdo504-5A*, was found to be closely linked to *Vrn-A1* on the long arm of chromosome 5A (Galiba et al. 1995). Taking account of the synteny among the homoeologous group-5 chromosomes, the QTL found here on 5B should thus equate to *Vrn-B1*.

Mapping of *Eps* loci

The other QTL segregating in the 'CS/Chey' 5B population had a less pronounced, but still significant effect ($P < 0.03$), on flowering time, with an additive effect of 1.49 days, accounting for 8.2% of the phenotypic variation. This was linked to the SSR locus *Xwmc73*, close to the centromere. Previous mapping data in barley showed the existence of an *Eps* QTL at a homoeologous position (Laurie et al. 1995; Snape et al. 2001). Consequently, we

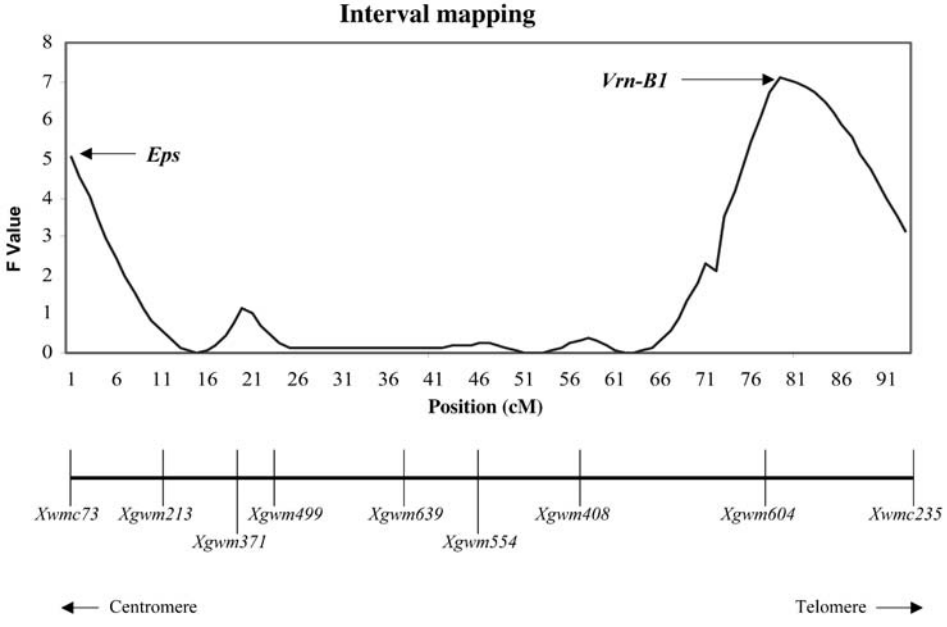

Fig. 1 QTL-likelihood curve (*F*-value variance ratio) for flowering time on the long arm of chromosome 5B of the 'CS' × 'CS ('Cheyenne'5B) mapping population The plants were grown under unvernalized conditions. Distances are shown along the *X-axis* in centimorgans from the left marker. Markers are shown below the *X-axis*

Table 1 QTL analysis on the 'CS' × 'CS' ('Chey' 5B)' and 'Hobbit Sib' × 'Hobbit Sib' ('5B)' recombinant substituion line populations: the nearest marker, the additive effect and the proportion of variance accounted for MQM mapping

Character	Nearest marker	Additive effect	% Variance accounted
'CS' × CS' ('Chey' 5B) population (* 'Chey' allele promotes later flowering or greater frost tolerance)			
Flowering time	Xgwm604	1.76 days*	10.7
	Xwmc73	1.49 days*	8.2
Frost tolerance (–11 °C)	Xgwm639	0.53 units*	31.4
(–12 °C)	Xgwm639	0.33 units*	12.0
'Hobbit Sib' × 'Hobbit Sib' ('CS' 5B) population (Hobbit allele promotes later flowering)			
Flowering time	Xgwm499	1.21 days*	5.7

hypothesise that this QTL represents an *Eps* locus. To examine this hypothesis further, the flowering time of the fully vernalized population from the 'Hobbit Sib' × 'Hobbit Sib'('Chinese Spring' 5BL) cross was analysed.

The mean flowering times of the two parents were 88.5 ± 2.6 days for 'Hobbit Sib' and 86 ± 3.7 days for 'Hobbit Sib' ('Chinese Spring' 5BL). The range of flowering times of the recombinant substitution lines was 77.6 to 102.7, again transgressive segregation being displayed, suggesting the segregation of at least two loci in repulsion. Nine microsatellite and five RFLP markers were found to be polymorphic on the parents, and the 'Hobbit Sib' × 'Hobbit Sib' ('Chinese Spring' 5BL) recombinant lines were genotyped for these. The map developed covers 68 cM and the average distance between the markers was 6.8 cM. (Fig. 2). There was a 22-cM gap proximal from the *Xcdo504* RFLP locus. In agreement with Röder et al. (1998) the linkage (2 cM)

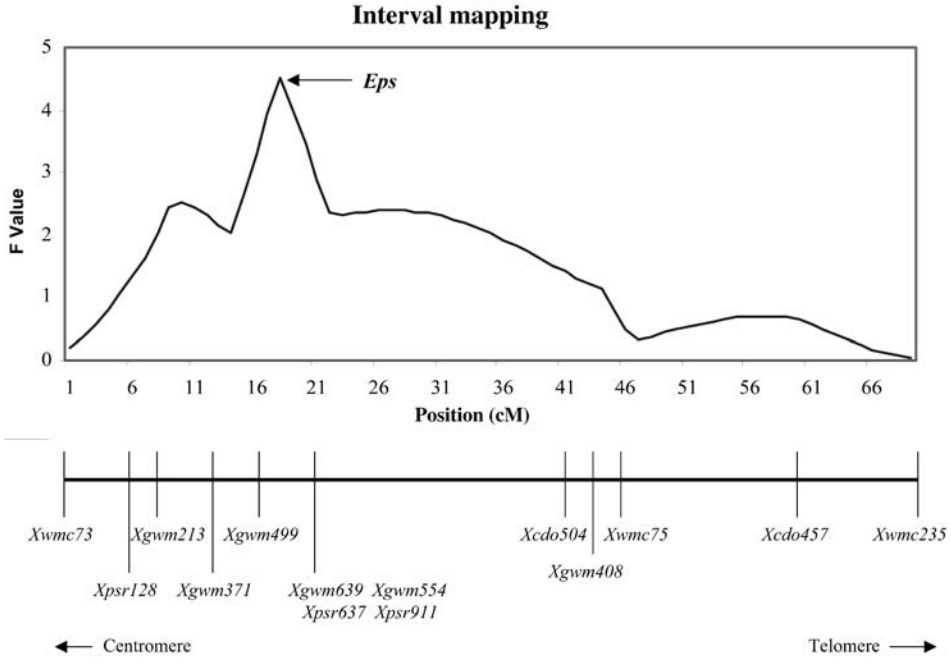

Fig. 2 QTL-likelihood curve (*F*-value variance ratio) for flowering time on the long arm of chromosome 5B of the 'Hobbit Sib' × 'Hobbit Sib' ('Chinese Spring' 5BL) cross. The plants were fully vernalized. Distances are shown along the *X-axis* in centimorgans from the left marker. Markers are shown below the *X-axis*

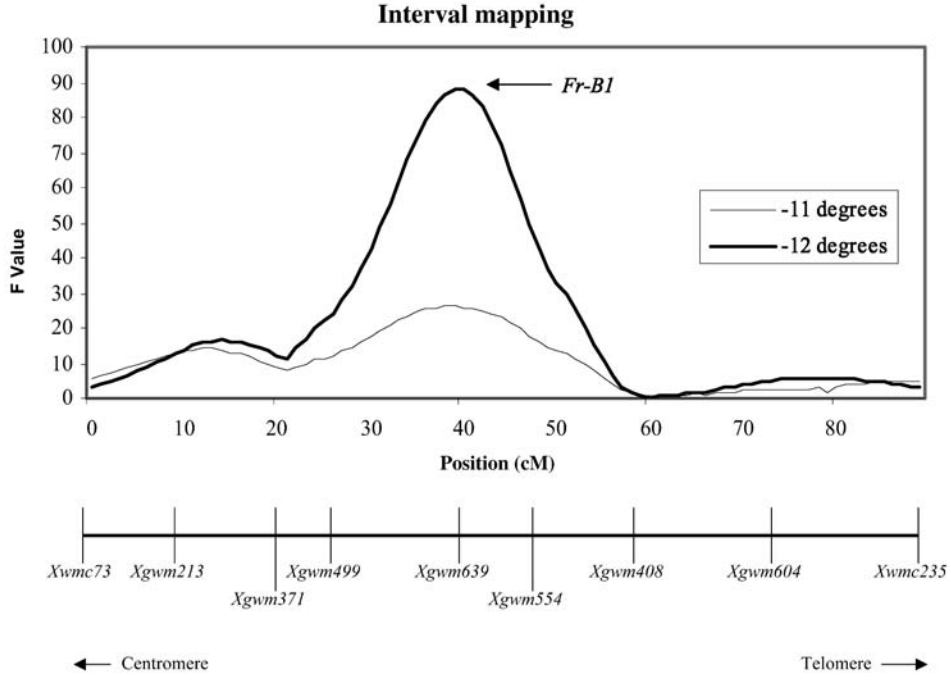

Fig. 3 QTL-likelihood curve (*F*-value variance ratio) for frost resistance on the long arm of chromosome 5B at –11 and –12 degrees using the 'CS' × 'CS' ('Cheyenne'5B) cross. Distances are shown along the *X-axis* in centimorgans from the left marker. Markers are shown below the *X-axis*

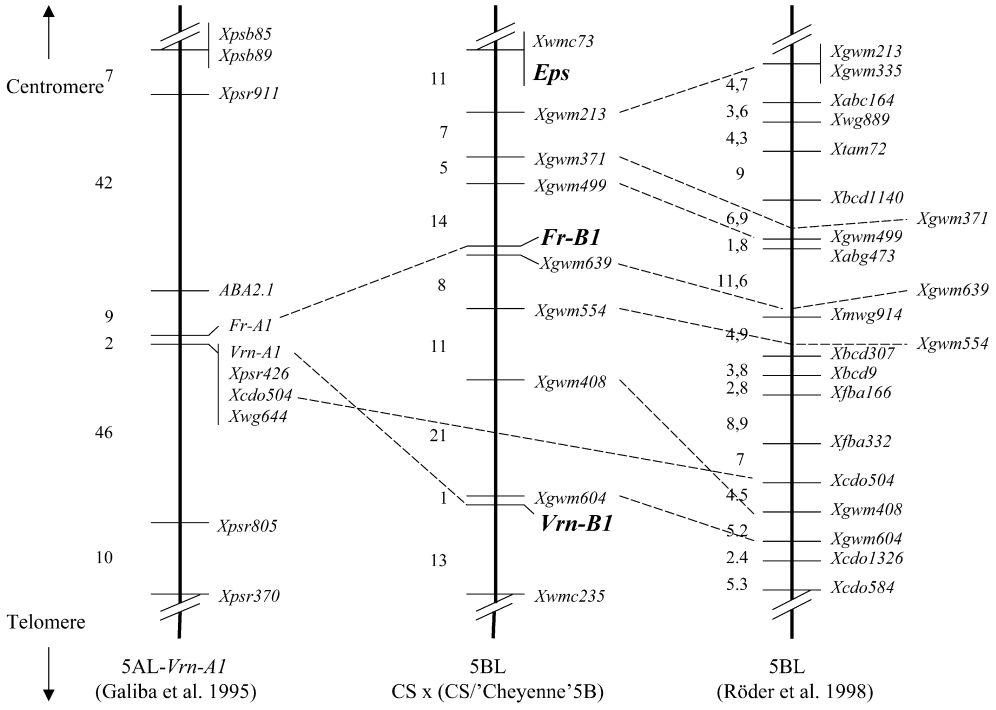

Fig. 4 Comparative mapping of flowering time and frost resistance genes showing the possible homoeologous relationship of the vernalization response gene (*Vrn-B1*) and the frost resistance gene (*Fr-B1*) on chromosome 5B, with the *Vrn-A1* and the *Fr-A1* on chromosome 5A. Numbers to the left are the distances in centimorgans (not to scale)

between *Xcdo504-5B* and *Xgwm408* was confirmed. *Xgwm604* was not mapped in this population due to a lack of polymorphism.

Although the presence of transgressive segregation suggests that probably two loci in repulsion were segregating, QTL analysis by interval mapping and composite interval mapping only detected the existence of a single QTL for flowering time (Table 1, Fig. 2), close to the centromere (approximately 16 cM away), near to the marker *Xgwm499*. This QTL had an additive effect of 1.2 days but only accounted for 5.7% of the variation in this cross. The positions of the *Eps* QTLs mapped on the two different mapping populations are suggested by these data to be different. It may be that both *Eps* loci were polymorphic in the 'Hobbit Sib' × 'Hobbit Sib' ('Chinese Spring' 5BL) crosses, one of which was homoeoallelic to that in the 'Chinese Spring' × 'Chinese Spring' ('Cheyenne' 5B) cross, although this second locus could not be located, possible because of the repulsion linkages making detection difficult.

Mapping of *Fr-B1*

The means of the frost scores of the parents were 1.8 for 'Chinese Spring', 2.8 for 'Chinese Spring' ('Cheyenne' 5B) at a –11 °C test temperature, and 0.5 for 'Chinese Spring', and 2.0 for 'Chinese Spring' ('Cheyenne' 5B) at a –12 °C test temperature. The range of frost scores of the recombinant substitution lines was 0.9 to 3.4 at –11 °C and 0.05 to 3.0 at –12 °C. For the QTL analysis the same map was used as for the mapping of *Vrn-B1*, except for four missing lines.

Using the mapping data and the frost scores, a single QTL was localised 40 cM from the centromeric marker using interval mapping, marker regression and composite interval mapping, and this mapped at the same position at both test temperatures. This QTL was closely linked to the SSR locus *Xgwm639* (Fig. 3), with additive effects of 0.53% and 0.33% at –11 °C and –12 °C, respectively (Table 1). At –11 °C, this QTL accounted for 31.4% of the variation, so clearly it is a major effect.

Comparative maps

Our maps covered the long arm of chromosome 5B, and the similarity in the order of the markers with the map published by Röder et al. (1998) is obvious (Fig. 4). A comparison of these maps to other maps of chromosomes 5A and 5D was difficult due to the lack of the common markers, but the similar localisation of the *Vrn* genes on the long arms distal from the centromeres is clearly noticeable. *Vrn-B1* was mapped closely linked to the SSR marker*Xgwm604*. Although this marker was not mapped on the 5A chromosome previously (Galiba et al. 1995), the *Xcdo504* RFLP locus links both to *Vrn-A1* and *Xgwm604* (Fig. 4). Additionally, Sarma et al. (2000) characterised the chromosomes of homoeologous group 5 of wheat in terms of rice linkage blocks. RFLP analysis shows that both 5A and 5B *Vrn* regions map to syntenous regions on rice chromosome 3.

In the case of the *Fr* genes, there is less obvious similarity concerning the positions on chromosomes 5A and 5B. However, comparative mapping with rice again suggests a link. These results reveal that rice chromosome

9 is syntenous to a large part of the long arms of the wheat homoeologous group-5 chromosomes, proximal to the centromere. In our case, the *Fr-B1* locus was mapped closely linked to the SSR locus *Xgwm639. Xgwm639* was also linked to the RFLP locus *Xpsr120* on the map developed from *Triticum turgidum ssp. durum*, 'Messapia' × *T. turgidum ssp. dicoccoides*, 'MG4343' (Korzun et al. 1999). This RFLP locus was localised on the 5B chromosome region which is syntenous with rice chromosome 9. Using deletion lines of 'Chinese Spring', Sutka et al. (1999) also showed that *Fr-A1* on 5A mapped to a region syntenous to rice chromosome 9, proximal to the rice chromosome-3 region. So, although *Vrn-B1* and *Fr-B1* are not as tightly linked on the long arm of chromosome 5B as *Vrn-A1* and *Fr-A1* are on 5A, nevertheless, they both appear to be homoeoallelic. Thus, *Fr-B1* is probably orthologous to the other *Fr* genes situated on chromosomes 5A and 5D.

This study thus completes the mapping of the homoeoallelic series of vernalization requirement genes and frost resistance genes on the chromosomes of the homoeologous group 5 in wheat.

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