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Comparative mapping of the wheat chromosome 5A *Vrn-A1* region with rice and its relationship to QTL for flowering time

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Abstract The vernalization gene *Vrn-A1* on chromosome 5A is the predominant gene determining the spring/winter habit difference in bread wheat. *Vrn-A1* was physically mapped using a set of deletion lines which located it to the region of chromosome 5A flanked by deletion breakpoints 0.68 and 0.78. This interval was shown to be homoeologous to a region of rice chromosome 3 that contains the flowering-time QTL *Hd-6*, previously mapped in a Nipponbare × Kasalath cross, and *FLTQ1*, a novel QTL identified by analysis of 78 F_3 families derived from a cross of 'IR20' × '63–83'. Possible relationships between *Vrn-A1* and rice QTL are discussed. Analysis of the chromosome 5A deletion lines showed evidence for a second, more proximal flowering-time effect located between deletion breakpoints 0.56 and 0.64. The proximal part of chromosome 5A is homoeologous to rice chromosome 9, on which two QTL were detected in the 'IR20 × '63–83' cross. The possible relationship between these effects is also discussed.

Key words Comparative trait mapping · Deletion mapping · Flowering time · QTLs · Vernalization response

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Introduction

Flowering time is an important criterion for regional adaptation and yield in all cereals. In rice (*Oryza sativa* L., 2n = 2x = 24) flowering time has been shown to be determined by the basic vegetative growth phase (BVG) and photoperiod sensitivity (PS). Two genes conferring PS, *Se-1* and *Se-2*, have been mapped onto rice chromosomes 6 and 7, respectively (Kinoshita and Takahashi 1991; Mackill et al. 1993). Several other genes conferring PS (*Se-3*, *Se-4*, *E-1*, *E-2*, *E-3*) have been reported, but their chromosomal locations are still uncertain (Sato et al. 1988; Tsai 1995; Kinoshita and Takahashi 1991; Yokoo and Okuno 1993). Flowering-time quantitative trait loci (QTL) mapped in relation to restriction fragment length polymorphism (RFLP) markers include loci *Hd-1*, *Hd-2*, *Hd-3*, *Hd-4*, *Hd-5* and *Hd-6* mapped in a Nipponbare x Kasalath population (Yamamoto et al. 1996; Yano et al. 1997).

In bread wheat (*Triticum aestivum* L., 2n = 6x = 42), an initial need for a period of growth at low temperature to initiate flowering (vernalization response) distinguishes winter wheats from spring wheats, which have little or no vernalization response. Several loci for vernalization response have been identified, and their chromosomal locations have been established (Law 1976; Snape et al. 1985). Among these, the *Vrn-A1* (formerly *Vrn1*) locus has been found to predominate and has been mapped onto the long arm of chromosome 5A (Galiba et al. 1995). This locus has been shown to form a homoeologous series with *Vrn-B1* (formerly *Vrn2*) on chromosome 5B and *Vrn-D1* (formerly *Vrn3*) on chromosome 5D (Snape et al. 1997). A comparison of a common set of RFLP markers suggests that the *Vrn-A1* locus is homologous to Sh_2 (*Sgh2*), the vernalization gene of barley mapped on chromosome 5H by Laurie et al. (1995), and to *Sp1*, another vernalization-response locus mapped on to the 5R chromosome of rye (Plaschke et al. 1993).

A remarkable level of synteny has been observed between the genomes of a number of cereals including rice and wheat (Kurata et al. 1994a) and rice and maize (Ahn and Tanksley 1993) despite differences in chromosome number and genome size. Based on the conservation of marker synteny between rice and the *Triticeae*, Moore et al. (1993) suggested the possibility of revealing the gene content of *Triticeae* species using rice as a tool. Consequently, such conservation of marker synteny has opened up a new vista for comparative trait mapping across large taxonomic distances. This can identify and help to clone homologous genes that might have an equivalent function or share sequence similarity and evolutionary relationships. It is necessary to establish a homoeologous relationship of the *Vrn-A1* locus of wheat with a chromosomal region of rice to take advantage of the latter for positional gene cloning, and it could be hypothesized that this region would be associated with allelic variation for flowering time in rice.

The low level of polymorphism in wheat due to its polyploidy and the recent origin of the hexaploid wheat genome has hampered the genetic mapping of wheat to a great extent. To overcome this, Endo and Gill (1996) have proposed the use of deletion lines produced by the use of the gametocidal chromosome of *Aegilops cylindrica* to map the probes from different species intrachromosomally. Using these deletion lines, two genes of agronomic importance (*Q* and *Ph1*) have been mapped precisely onto the long arm of the group 5 chromosomes of wheat (Gill et al. 1993, 1996). Here we report the physical location of the *Vrn-A1* locus on the long arm of wheat chromosome 5A and its possible homology with a region on rice chromosome 3, using a comparative mapping approach.

Materials and methods

RFLP mapping in rice

A mapping population was developed by crossing two rice cultivars, 'IR20' (Indica) and '63–83' (Japonica) (Quarrie et al. 1997). Seventy-eight F_3 families derived from individual F_2 plants were used for the present study. Genomic DNA from the parents as well as from the mapping population was extracted using a modified CTAB method (Murray and Thompson 1980) and digested with restriction enzymes *Bam*HI, *Dra*I, *Eco*RI, *Eco*RV and *Hin*dIII (Northumbria Biochemical). Electrophoresis and Southern blotting were carried out using standard procedures. A range of cDNA and genomic DNA clones from rice, wheat and barley available from the Cereals Research Department, John Innes Centre, Norwich (PSR and PSB clones), the Rice Genome Program (RGP), Japan (prefixed with G, C, R, Y and L) and Cornell University, USA (prefixed with RG, RZ, BCD and CDO) were used as probes for hybridization after labelling with ^{32}P. Probes detecting polymorphism in the parents were used to characterize the genotype of each line of the mapping population. The linkage map was generated using MAPMAKER version 3.0 (Lincoln et al. 1992) using the Kosambi mapping function. This map was compared with published wheat maps for chromosomes 5A, 5B and 5D (Gill and Raup 1997).

Wheat physical mapping

Sixty-four deletion lines for the group 5 chromosomes of wheat were produced in the background of 'Chinese Spring' using the gametocidal chromosome of *Aegilops cylindrica* (Gill et al. 1996). Fourteen deletion lines for the short arm of chromosome 5A and 20 for the long arm were used for the present study. Genomic DNA was extracted from each deletion line, digested with restriction enzymes *Bam*HI, *Dra*I, *Eco*RI, *Eco*RV and *Hin*dIII, electrophoresed and blotted to membranes (Devos et al. 1993). Nullisomic–tetrasomic lines and ditelosomic lines (Sears 1954) for the group 5 chromosomes of wheat were used to assign the DNA fragments of the mapped probes to different arms. Each group 5-specific band of the different probes was mapped to the chromosomal region defined by the breakpoint of the largest deletion lacking the band and next largest deletion possessing the band. RFLP marker loci were prefixed by X, followed by laboratory probe designation, following the nomenclature of McIntosh et al. (1995).

Flowering-time analysis

Four plants of each rice F_3 family were grown in pots in a controlled environment cabinet using a randomized block design. During growth, a temperature of 28°C during the day and 24°C at night along with a relative humidity of 80% and 13 hours of day–length were maintained. Flowering time was recorded for each plant as the emergence of the first panicle from the tiller. QTL analysis was performed on the mean values over replications for each line using the software QTL CARTOGRAPHER (Zeng 1994; Basten et al. 1996). Out of six options given in the programme, option 3 (equivalent to the interval mapping of Lander and Botstein, 1989) and option 6 (composite interval mapping taking markers as a co–factor to control background) were employed for the study. The number of background parameters for option 6 was determined by running the subprogram SRMAPQTL. The threshold value of LR (likelihood ratio) was considered as 10, which is equivalent to a LOD score of 2.0, to detect the presence of a QTL.

Four plants of each of the wheat group 5 deletion lines were grown in pots in a controlled environment cabinet without vernalization under a regime of 16 h light at a temperature of 20°C using a randomized block design. Ear emergence time was recorded on each plant at the heading time of the first tiller. Similar experiments were performed in the phytotron of the Hungarian Academy of Agricultural Sciences, Martonvasar, Hungary during 1996 and 1997.

Results and discussion

Rice linkage map construction

The linkage map was constructed for the set of 78 F_3 lines with 91 markers distributed over the 12 linkage groups of rice with an average inter-marker distance of 11.7 cM. The markers were selected from the F_2 map of the same cross (Quarrie et al. 1997). The marker order was in agreement with the map of Kurata et al. (1994b) except for some probes which detected several bands. Marker coverage in the map is within the optimum level for initial QTL studies required for the objective of the present study (Darvasi et al. 1993). Long arm and short arms of rice chromosomes were identified using the markers mapped by Singh et al. (1996). The centromere of rice chromosome 3 is defined by RFLP markers *Xrgc136* and *Xbcd454*, while for

chromosome 9, the centromere is defined by markers *Xrgc711* and *Xcdo590*.

QTL mapping for flowering time in rice

There was a difference of 14 days in flowering time between the parents, 'IR20' being later in flowering. The distribution of means for flowering time was nearly normal, and transgressive segregation was observed, indicating polygenic inheritance of flowering time (data not shown). Based on the results of both simple and composite interval mapping, three QTLs for flowering time (*FLTQ1* to *FLTQ3*) with significant effects were identified. For the *FLTQ1* on chromosome 3 (Fig. 1) and *FLTQ3* on chromosome 9 (Fig. 2), 'IR20' alleles contributed additive effects of 7 days and 3 days for early flowering, respectively. For *FLTQ2*, also on chromosome 9 (Fig. 2), there was an additive effect of 7 days, with the '63–83' allele conferring early flowering. The identification of early and late-flowering alleles in both parents accounts for the transgressive segregation observed.

Simple and composite interval mapping suggested that there may be a second QTL in the *Xrgr2311* to *Xrgc136* interval (Fig. 1). Yamamoto et al. (1996) showed that the *Hd-6* QTL in the Nipponbare × Kasalath population was in the *Xrgc393* to *Xrgc595* interval, which overlaps with both the QTL regions in the 'IR20' × '63–83 cross. *Hd-6* might be allelic to either effect in the 'IR20' × '63–83' cross or may be a different locus. Li et al. (1996) also mapped one QTL for flowering time on rice chromosome 3. Based on the comparison of the published map (Causse et al. 1994), this QTL lies at the end of the short arm of rice chromosome 3, whereas the QTL identified in this study lies on the long arm of rice chromosome 3. However, it is not possible to relate these QTLs more precisely due to a lack of common markers.

Physical mapping of the *Vrn-A1* gene

The deletion lines for the homoeologous group 5 chromosome of wheat were produced in the 'Chinese Spring' background. Aneuploid analysis showed that removal of the 5A chromosome from 'Chinese Spring' delayed flowering under unvernalized condition (Flood and Halloran 1986), and any deletion line lacking *Vrn-A1* would therefore be expected to show a similar late flowering. Analysis of variance for flowering time revealed significant differences for flowering time among the deletion lines for wheat chromosome 5A (data not shown), and this variation is represented in Fig. 3. The deletion lines for chromosome 5A divide into three groups (A, B and C) between the breakpoints 0.56 and 0.64 and the breakpoints 0.68 and 0.78. The mean difference between A and B was 7.5 days, while the mean difference between B and C groups was 12.2 days. Both differences were statistically significant. This experiment was repeated in Martonvasar, Hungary, during 1996 and 1997 and revealed similar results with a mean difference of 15 days between the B and C groups in both experiments.

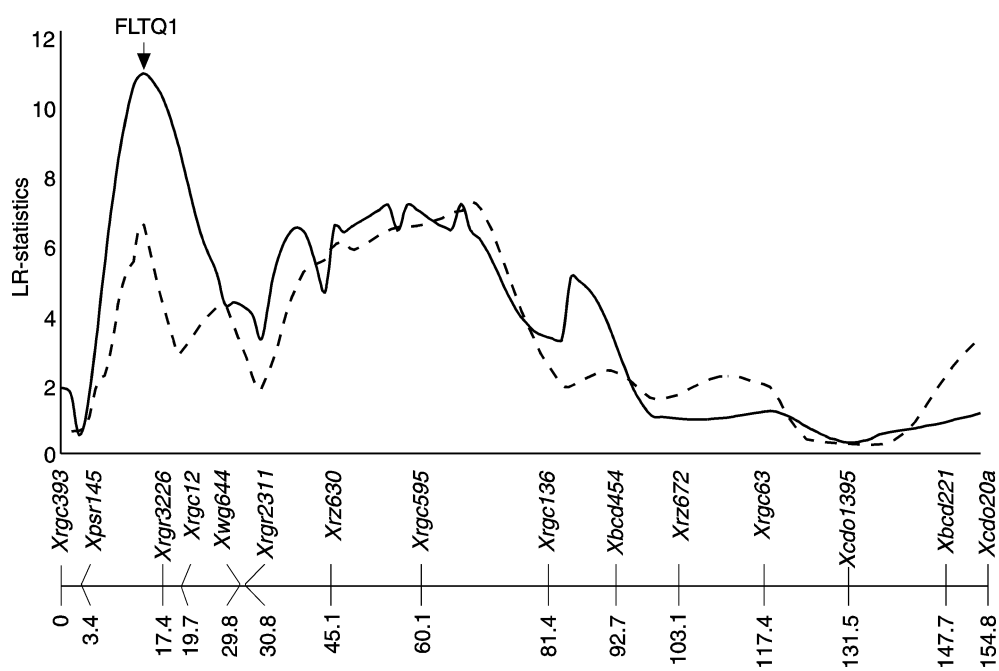


Fig. 1 QTL-likelihood curve of LR statistics for flowering time on chromosome 3 of rice. Markers on the map are shown along the *X-axis*. The distances are shown in centiMorgans from the *left marker*

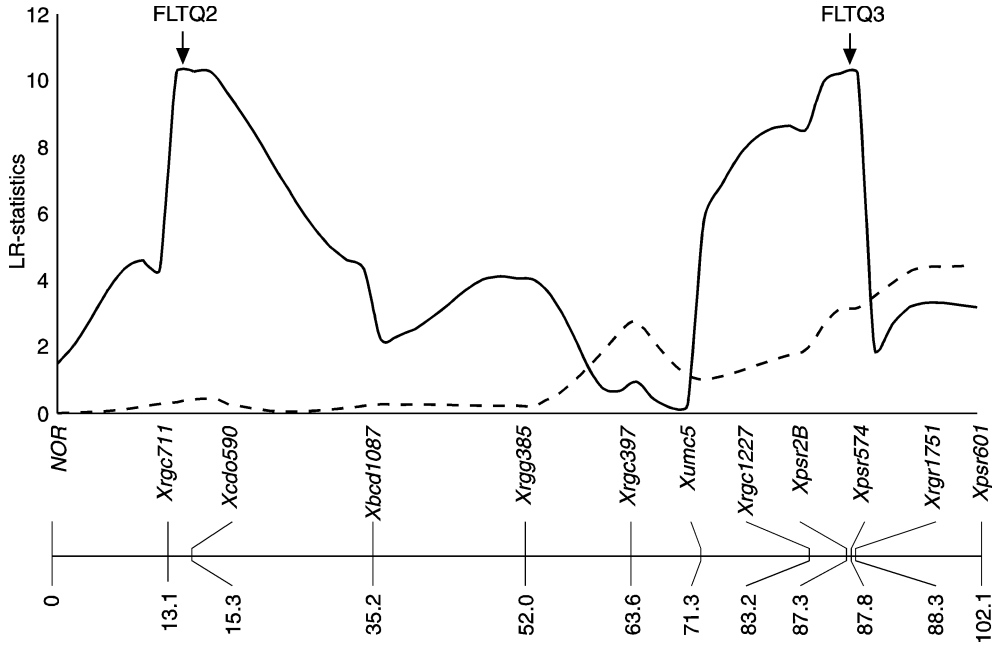


Fig. 2 QTL-likelihood curve of LR statistics for flowering time on chromosome 9 of rice. Markers on the map are shown along the *X-axis*. The distances are shown in centiMorgans from the *left marker*

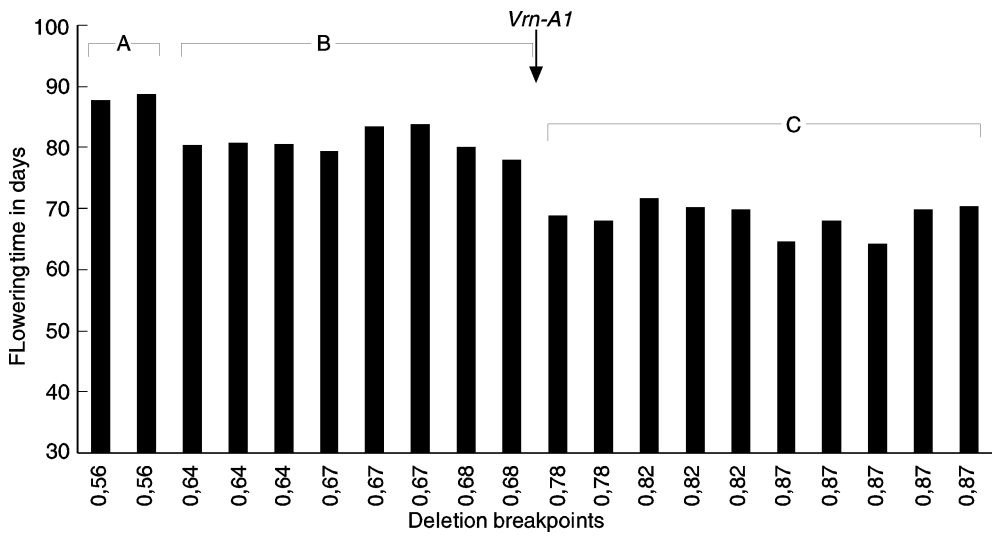
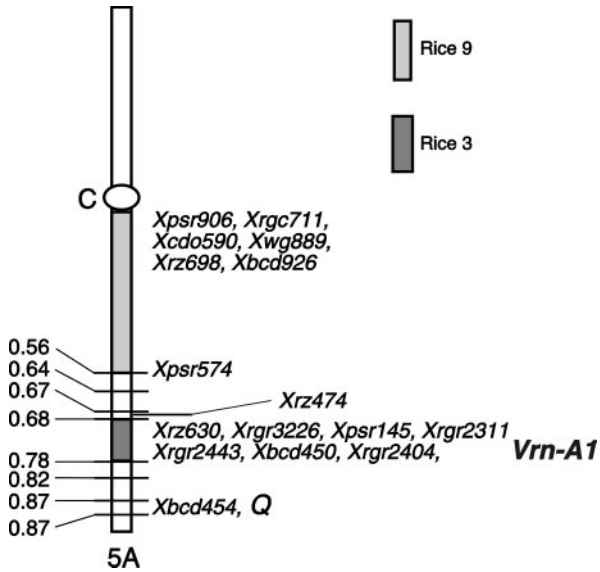


Fig. 3 Histogram of the flowering-time differences of the deletion lines for wheat chromosome 5A. The location of the *Vrn-A1* locus is shown on the basis of the variation in flowering time of the deletion lines

Physical mapping of RFLP markers linked to the *Vrn-A1* gene and comparative mapping with rice

Hybridization of RFLP probes to the deletion lines showed that probes linked to *Vrn-A1*/*Sh*$_2$/*Sp1* (WG644, BCD450 and PSR145) were located in the region between breakpoints 0.68 and 0.78 (Fig. 4; Nelson et al. 1996; Gill et al. 1996). This clearly indicates that the difference in flowering time observed between the B and C groups of the deletion lines (Fig. 3) was due to the deletion of *Vrn-A1*, locating the gene in the 0.68 and 0.78 interval. This confirms the work of Gill et al. (1996) who predicted the location of *Vrn-A1* by hybridization of linked RFLP markers to the deletion lines.

The wheat group 5 chromosomes contain regions homoeologous to rice chromosome 9 and part of rice chromosome 3 (Van Deyne et al. 1995; Moore 1995). Physical mapping of rice probes onto the deletion lines of wheat clearly supports this view (Fig. 4). Markers from chromosome 9 were located in the region between the centromere and breakpoint 0.56, with the exception of *Xpsr574* which was in the 0.56–0.64 interval. Markers from the distal third of the long arm of rice chromosome 3 (Causse et al. 1995; Kurata et al. 1994b) were located in the region of wheat 5A bracketed by the 0.68 and 0.78 interval, except for the marker *Xrz474* which was located in the 0.67–0.68 interval (Fig. 4). These data show that the region of chromosome 5A

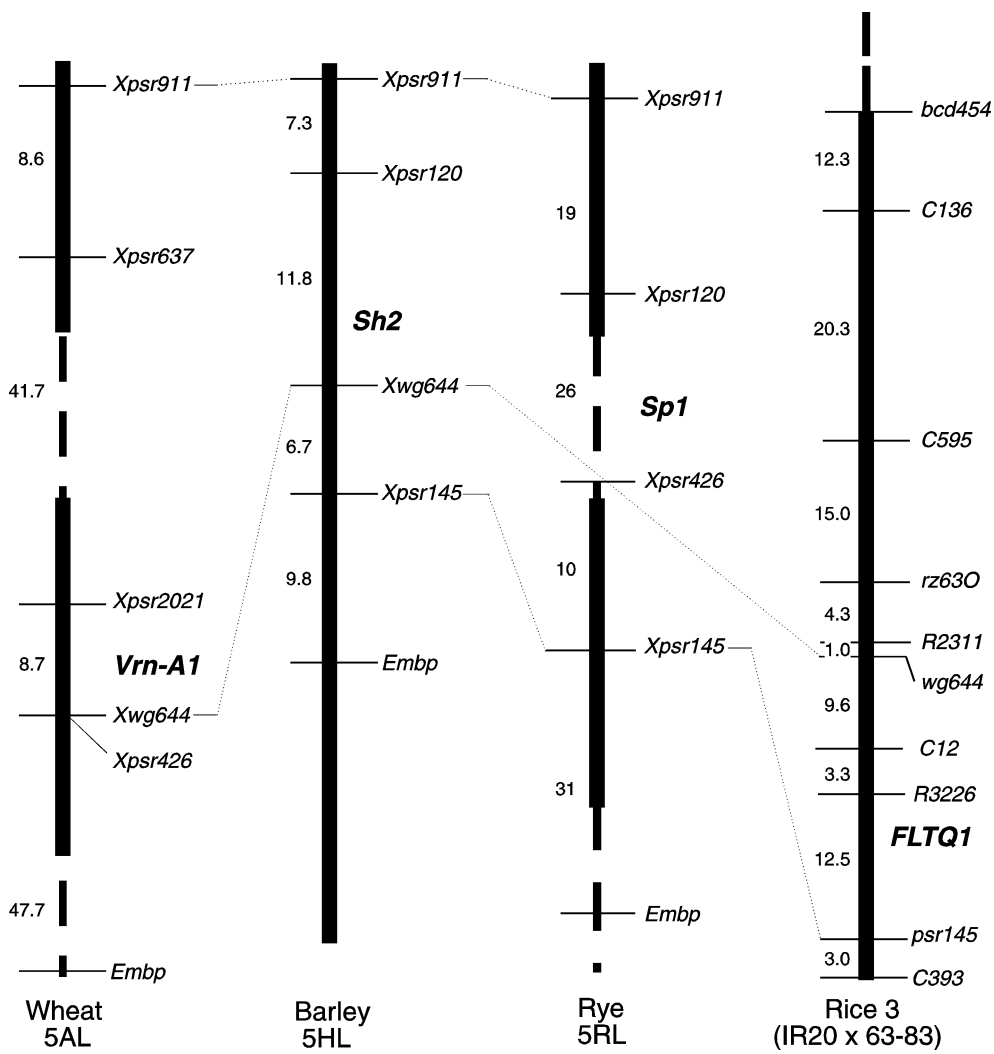


containing the *Vrn-A1* gene is homologous to a region of chromosome 3 of rice.

The relevent region of rice 3 contains at least one flowering-time QTL in the 'IR20' × '63–83' population (Fig. 1), but neither of the graph peaks corresponds to the location of *Xwg644*, the closest RFLP marker to *Vrn-A1* (Fig. 5). The *Hd-6* QTL was found in the same chromosomal region in the Nipponbare x Kasalath population (Yamamoto et al. 1996). Although there is no strong evidence to suggest that either of the rice QTL are orthologues of *Vrn-A1*, they provide valuable candidates that can be tested by further analysis.

Fig. 4 Physical mapping of wheat chromosome group 5A in relation to linkage blocks from rice chromosome 9 and 3. *Numbers* to the *left* of the chromosome are the deletion breakpoints. *Q* Gene for spike type, *C* centromere. The location of *Vrn-A1* is shown based on the mapping of RFLP markers associated with this locus

Fig. 5 Comparative mapping of flowering time showing the possible homoeologous relationship of the *FLTQ1* QTL of rice with vernalization response genes of the *Triticeae*. *Numbers* to the *left* of the chromosomes are the distances in centiMorgans (not to scale). Only part of rice chromosome 3 is shown. The maps of wheat 5AL, barley 5HL and rye 5RL are from Galiba et al. (1995), Laurie et al. (1995) and Plascheke et al. (1993), respectively



The second flowering-time effect detected in the analysis of the wheat 5A deletion lines was in the interval defined by the 0.56 and 0.64 breakpoints. This region contained the probe *Xpsr574* which mapped close to the *FLTQ3* peak on rice chromosome 9 (Fig. 2). The relationship between these effects is worthy of further investigation which will be facilitated by the detailed physical map of this region of rice (Foote et al. 1997).

Holland et al. (1997) reported an association between *Xcdo484b* on linkage group 24 of oats and vernalization response. This marker has been mapped onto the subterminal region of the long arm of rice chromosome 3 and barley chromosome 5H by Sagai Maroof et al. (1996). This suggests that the oat vernalization response may be controlled by the homoeoallele of *Vrn-A1*.

Conclusions

The progressive divergence of cereals from a common ancestor implies that related species can retain similarities in genome organization and the genetic control of characters. Genome studies and sequence database comparisons suggest that taxonomic variation between related species is essentially due to allelic variation rather than the creation of novel genes (Dorweiler et al. 1993; Doebley et al. 1994).

Allelic variation at the vernalization-response loci produces variation in flowering time in spring wheats (Quarrie et al. 1995) and spring barleys (Takahashi and Yasuda 1971). Analysis of a spring barley cross by Bezant et al. (1996) also revealed QTL for flowering time in the *Sh* and Sh_2 regions. This suggests that if vernalization-response genes arose before the divergence of wheat from rice they may retain a role in the latter as regulators of flowering time. The present work shows that candidate QTL exist in the relevent region of rice chromosome 3, and their further analysis will increase our understanding of the comparative genetics of flowering time. Identification of a rice orthologue of *Vrn-A1* would greatly facilitate the cloning of vernalization response genes of the *Triticeae*.

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