Physical characterization of the homoeologous Group 5 chromosomes of wheat in terms of rice linkage blocks, and physical mapping of some important genes

R.N. Sarma, L. Fish, B.S. Gill, and J.W. Snape

Abstract: The wheat homoeologous Group 5 chromosomes were characterized physically in terms of rice linkage blocks using a deletion mapping approach. All three chromosomes, 5A, 5B, and 5D, were shown to have a similar structure, apart from the 4A–5A translocation on the distal end of chromosome arm 5AL. The physical mapping of rice markers on the deletion lines revealed that the whole of rice chromosome 9 is syntenous to a large block, proximal to the centromere, on the long arm. Likewise, a small segment of the distal end of the long arm showed conserved synteny with the distal one-third end of the long arm of rice chromosome 3. In between those conserved regions, there is a region on the long arm of the Group 5 chromosomes which shows broken synteny. The proximal part of the short arms of the Group 5 chromosomes showed conserved synteny with a segment of the short arm of rice chromosome 11 and the distal ends showed conserved synteny with a segment of rice chromosome 12. The physical locations of flowering time genes (*Vrn* and earliness per se) and the gene for grain hardness (*Ha*) on the Group 5 chromosomes were determined. These results indicate that comparative mapping using the deletion mapping approach is useful in the study of genome relationships, the physical location of genes, and can determine the appropriate gene cloning strategy.

Key words: wheat, rice, comparative mapping, deletion lines.

Résumé : Les chromosomes homéologues du Groupe 5 chez le blé ont été caractérisés physiquement en fonction des linkats du riz à l'aide d'une approche de cartographie par délétion. Il a été trouvé que les trois chromosomes (5A, 5B et 5D) présentent une structure chromosomique semblable à l'exception de la translocation 4A–5A sur l'extrémité distale du bras chromosomique 5AL. La cartographie physique de marqueurs du riz sur les lignées à délétion a révélé que tout le chromosome 9 du riz est en synténie avec un grand segment du bras long, à proximité du centromère. Pareillement, un petit segment de l'extrémité distale du bras long montre une synténie avec le tiers distal du bras long du chromosome 3 du riz. Entre ces deux régions conservées, le bras long des chromosomes du Groupe 5 présente une région de synténie brisée. La portion proximale des bras courts des chromosomes du Groupe 5 s'est avérée syntène avec un segment du bras court du chromosome 11 du riz tandis que les extrémités distales montraient de la synténie avec un segment du chromosome 12 du riz. L'emplacement physique de gènes contrôlant le moment de la floraison (*Vrn* et la hâtivité en soi) et la dureté des grains (*Ha*) sur les chromosomes du Groupe 5 a été déterminé. Ces résultats indiquent que la cartographie comparée réalisée à l'aide de délétants est utile pour l'étude des relations entre les génomes, pour la cartographie physique et peut aider à choisir une approche de clonage appropriée.

Mots clés : blé, riz, cartographie comparée, lignées à délétion.

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Introduction

A better understanding of the genetic architecture of agronomically useful traits in wheat through the use of molecular markers is starting to have an impact on wheat breeding. Additionally, comparative mapping, using a set of cross-hybridizing markers, now allows a new approach to the genetic analysis of wheat by utilizing the advantages of information from other cereal species. The extensive conservation of marker synteny for different chromosomal regions has been reported among cereals, including those of rice and wheat (Ahn et al. 1993; Kurata et al. 1994). Utilizing such information, Moore et al. (1993) have described the chromosomes of wheat, and other major cereals, in terms of rice linkage blocks. This facilitates the use of rice as a model species for revealing the gene content of the Triticeae, and defines a strategy for gene isolation in these large genomes. However, linkage mapping, indeed comparative mapping in wheat, is greatly hampered by a lack of polymorphism in

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wheat intervarietal crosses. Such a lack of polymorphism often hinders the examination of orthologous relationships between genes of rice and wheat.

Deletion lines, a novel aneuploid series containing subarm deletions, have been developed in wheat using the gametocidal chromosome of *Aegilops cylindrica*. These have been found more effective in mapping the wheat genome since a presence–absence polymorphism can be revealed for all markers (Gill and Gill 1994; Endo and Gill 1996). These have been used to develop physical maps of various wheat chromosomes at the cytogenetic level (Gill et al. 1996; Gill and Gill 1994), but can also be used effectively in comparative mapping, by mapping heterologous probes into various deletion regions. Thus, one can compare the location of different markers from different species in the same deletion bin without the need to look for polymorphism (Sarma et al. 1998).

The homoeologous Group 5 chromosomes of wheat are known to carry some agronomically important genes, such as vernalization response, frost resistance (Galiba et al. 1995), grain hardness (Mattern et al. 1973), plant form (Roberts 1989), response to environmental stress (Quarrie et al. 1994), and yield (Snape et al. 1985). Most of these genes have been mapped through linkage mapping. However, in wheat as well as in other cereals, it has been demonstrated that linkage mapping is not an efficient method for determining the physical location of those genes, due to variation in recombination along the length of a chromosome (Snape et al. 1985; Werner et al. 1992; Gill et al. 1996). Comparative mapping with heterologous probes also does not measure actual physical syntenic relationships between two genomes. This investigation was therefore conducted to provide insight into the structural syntenic relationships of the wheat homoeologous Group 5 chromosomes with various rice chromosomes, and to physically locate genes for flowering time and grain hardness using the Group 5 deletion lines.

Materials and methods

Materials

Sixty-four deletion lines for the Group 5 chromosomes of wheat, produced in the background of *Triticum aestivum* 'Chinese Spring', using the gametocidal chromosome of *Aegilops cylindrica* (Endo and Gill 1996; Gill et al. 1996), were used in this study. Of those lines, there were 14 deletion lines for the short arm and 20 deletion lines for the long arm of chromosome 5A; 10 deletion lines for the short arm, and 9 deletion lines for the long arm of chromosome 5B; and 6 deletion lines for the short arm, and 5 deletion lines for the long arm of chromosome 5D. Additionally, 'Chinese Spring' and it's nullisomic–tetrasomic lines and ditelosomic lines (Sears 1954; Sears and Sears 1978) were used to define the chromosomal locations of loci.

Southern blot analysis

Genomic DNA was extracted from each deletion line, the nullisomic–tetrasomic lines and ditelosomic lines, digested with the restriction enzymes *Bam*HI, *Dra*I, *Eco*RI, *Eco*RV and *Hin*dIII; electrophoresed and blotted to membranes (Devos et al. 1993). A selection of rice, wheat, barley, and oat probes available from the John Innes Centre, Norwich (prefixed with PSR), Rice Genome Program, Japan (prefixed with C, G, L, R, and Y), and Cornell University (prefixed with BCD, CDO, RZ) were used. The FBA and MTA clones were available from INRA (Institut National de la Recherche Agronomique), France (Nelson et al. 1996; Gautier et al. 1994). The markers were selected on the basis of their known map positions on rice linkage groups. A locus detected by RFLP (restriction fragment length polymorphism) markers was assigned to a chromosome arm by Southern analysis of nullisomic–tetrasomic lines and ditelosomic lines. Each Group 5-specific band was mapped to the chromosomal region defined by the breakpoint of the largest deletion lacking the band and the next largest deletion possessing the band.

Trait analysis

Seeds of the 64 deletion lines as well as the nullisomic–tetrasomic lines were germinated on filter paper in Petri dishes, soaked in distilled water at 21°C for 24 h in the dark. Seedlings were transplanted into 12-cm pots in a controlled environment cabinet, without vernalization, following a randomized block design with 4 replications. During growth, a temperature of 20°C with a relative humidity of 65–70% and a 16-h day length were maintained. Flowering time was recorded for each plant as the number of days from transplanting to ear emergence of the first spike.

Grain hardness was assessed on the deletion lines for the short arms, nullisomic–tetrasomic and ditelosomic lines only. Ten grams of seed from each line, harvested from single plants, was cleaned, and then milled using a Tecator mill. The flour samples were analysed for grain hardness using NIR spectroscopy on an Oxford Analytical Instrument (Oxford, model QN 1000). Since the quantity of flour available was low for some samples, a small cup of 5 mL was selected for the measurement of grain hardness using an appropriate calibration as per the manufacturer's instructions.

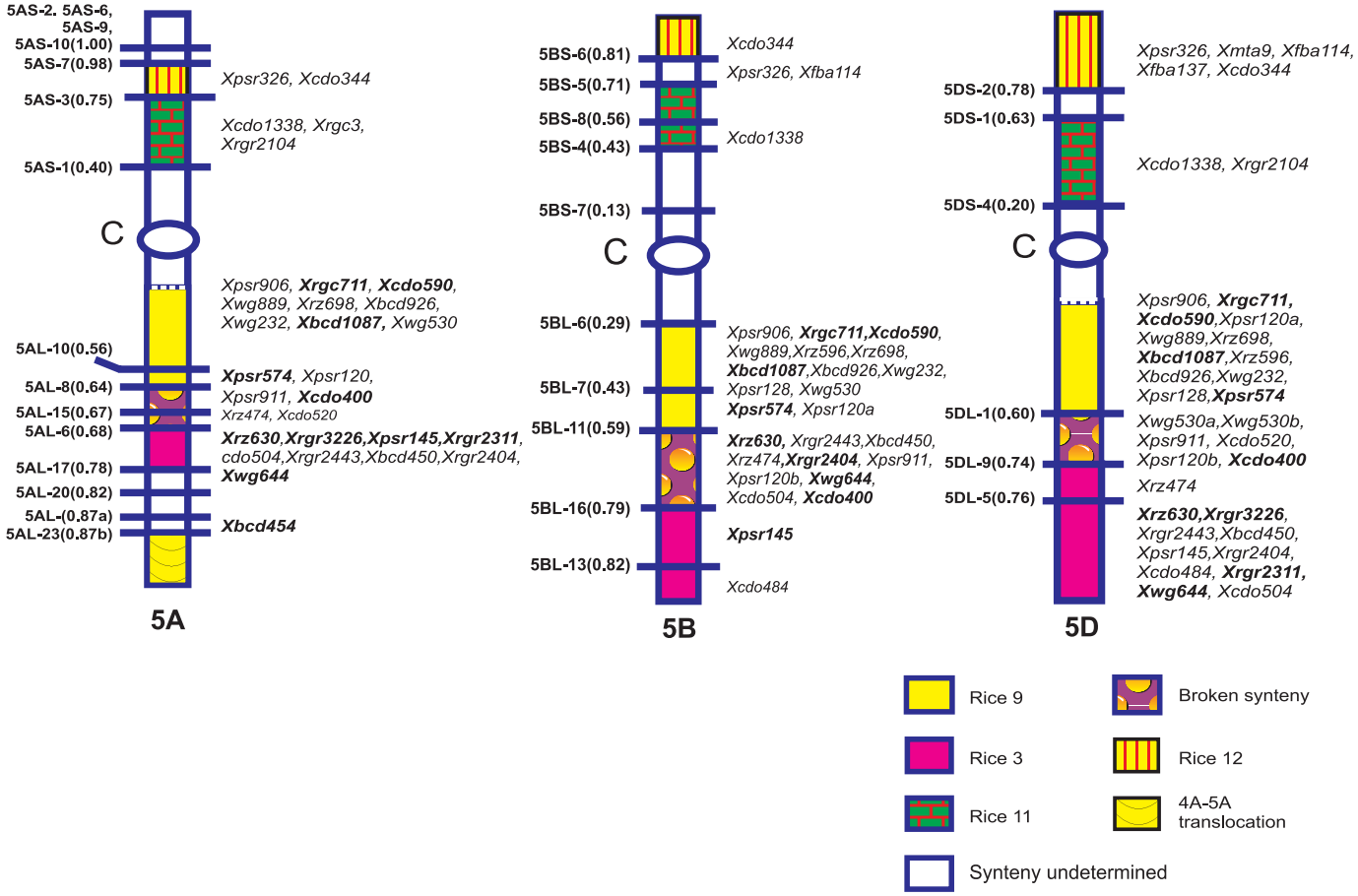
Results

Physical mapping of the Group 5 chromosomes by deletion mapping of RFLP probes from rice revealed that, out of the 80 probes tested, only 35 (43%) revealed a presence–absence polymorphism suitable for deletion mapping. When bands did not show polymorphism, this either indicated that they mapped on another homoeologous group or that there were overlapping bands. The physical maps of the Group 5 chromosomes are presented in Fig. 1, and there were 30 loci mapped on chromosome 5A, 29 loci on chromosome 5B and 36 loci on chromosome 5D.

Characterization of chromosome 5A

Out of nine markers mapped onto the long arm of chromosome 5A between the centromere and breakpoint 0.56, seven were linked to rice chromosome 9 (Causse et al. 1994; Harushima et al. 1998). Two markers were mapped in the deletion region between breakpoints 0.56–0.64. The markers, *Xrgc711*, *Xcdo590*, *Xpsr574*, and *Xbcd1087* were also mapped onto rice chromosome 9 in the IR20 × 63–83 mapping population at the John Innes Centre, Norwich (Quarrie et al. 1997; Sarma et al. 1998). Thus, physical mapping of rice markers onto the deletion lines revealed that most, if not all of the chromosomal region between the centromere and breakpoint 0.64 shows conserved synteny with rice chromosome 9. Out of the two markers mapped in the deletion region bracketed by breakpoints 0.64–0.67, the marker *Xcdo400* has been mapped to rice chromosome 2 (Quarrie et al. 1997; Causse et al. 1994). Likewise, out of the two markers mapped on the small deletion region between breakpoints 0.67–0.68, one each was linked to rice chromosomes 3 (*Xrz474*) and 11 (*Xcdo520*) on the Cornell map (Causse et

Fig. 1. Proposed physical map of wheat chromosomes 5A, 5B, and 5D in terms of rice linkage blocks. Deletion lines are shown in the left with deletion breakpoint in brackets (markers shown in bold are mapped in the IR20 × 63–83 mapping population of rice).



al. 1994). Thus, no clear-cut syntenic relationship of the region of chromosome arm 5AL with rice chromosomes was observed between breakpoints 0.64–0.68. Nine markers were mapped in the deletion region between breakpoints 0.68–0.78. Among these, seven markers were mapped on the long arm of rice chromosome 3 (Causse et al. 1994; Harushima et al. 1998). By comparing the linkage map of rice chromosome 3, this deletion region can be considered as showing conserved synteny with the distal one-third of the long arm of rice chromosome 3.

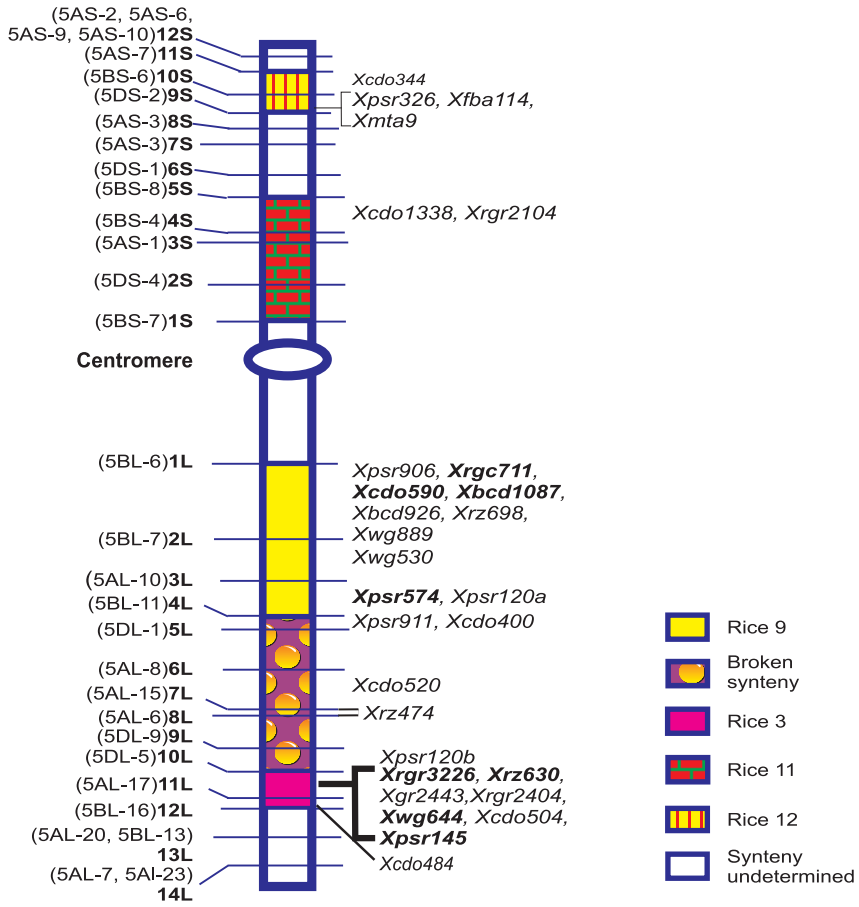
For the short arm, no marker was mapped between the centromere and breakpoint 0.40. The three markers mapped between breakpoints 0.40–0.75 were linked to the short arm of rice chromosome 11 (Causse et al. 1994; Harushima et al. 1998), indicating orthology of this region with the short arm of rice chromosome 11. Out of the two markers mapped on the deletion lines distal to breakpoint 0.75, the marker *Xcdo344* was linked to the long arm of rice chromosome 12 (Causse et al. 1994), so the region distal to breakpoint 0.75 can be considered to be orthologous to a segment of the long arm of rice chromosome 12.

Characterization of chromosome 5B

No marker was mapped on either arm of chromosome 5B in the regions immediately proximal to the centromere. Out of the 11 markers mapped in the deletion region 0.29–0.43 on the long arm, there were six markers linked to rice chromosome 9 (Causse et al. 1994; Harushima et al. 1998; Quarrie et al. 1997). Likewise, the marker *Xpsr574* mapped in this deletion region was also linked to rice chromosome 9 (Quarrie et al. 1997). Thus, it can be inferred that the chromosome region between breakpoints 0.29–0.59 shows conserved synteny with rice chromosome 9. Ten loci were mapped in the largest deletion region between breakpoints 0.59–0.79. Out of those, markers linked to the long arm of chromosome 3 (*Xrz630*, *Xrgr2443*, *Xrz474*, *Xrgr2404*) were mapped (Causse et al. 1994; Harushima et al. 1998; Sarma *et al.* 1998). However, mapping of a marker from rice chromosome 2 (*Xcdo400*) in this region showed that there is a disruption of synteny, and the availability of smaller deletions within this region will be necessary to be able to separate the syntenic regions from the non-syntenic region. The marker *Xpsr145*, mapped between breakpoints 0.79–0.82, was linked to the long arm of rice chromosome 3 (Sarma et al. 1998), and the marker, *Xcdo484*, mapped distal to breakpoint 0.82, and is linked to the long arm of rice chromosome 3 (Sagai Maroof et al. 1996). Thus, the chromosomal region distal to breakpoint 0.79 showed conserved synteny with the long arm of rice chromosome 3.

The short arm of chromosome 5B showed conserved synteny with the short arm of rice chromosome 11 by mapping a marker from rice chromosome 11 on the deletion region between breakpoints 0.43–0.56. Likewise, the chromosome region distal to the breakpoint showed con-

Fig. 2. A consensus physical map of the Group 5 chromosomes in terms of rice linkage blocks. Deletion lines are shown on the left.



served synteny with a segment of the long arm of rice chromosome 12, as revealed by mapping a marker from rice chromosome 12, *Xcdo344*.

Characterization of chromosome 5D

Out of the 12 loci mapped on the deletion region between the centromere and breakpoint 0.60 on chromosome arm 5DL, four markers (*Xrgc711*, *Xcdo590*, *Xbcd1087*, *Xpsr574*) were mapped to rice chromosome 9 in the IR20 × 63–83 mapping population (Sarma et al. 1998; Quarrie et al. 1997). Thus, this region shows conserved synteny with rice chromosome 9. However, the deletion region between breakpoints 0.60–0.74 on chromosome 5DL showed broken synteny by mapping markers linked to rice chromosomes 2 (*Xcdo400*) and 11 (*Xcdo520*) from the Cornell map (Causse et al. 1994). Only one marker from rice chromosome 3 (Causse et al. 1994) was mapped on the deletion lines between breakpoints 0.60–0.74. Similarly, markers from the long arm of rice chromosome 3 in the IR20 × 63–83 population as well as the Cornell and RGP maps were mapped on the deletion lines distal to breakpoint 0.76, so the chromosome region distal to breakpoint 0.74 on the long arm of chromosome 5D can be considered as showing conserved synteny with the long arm of rice chromosome 3.

For the short arm, the two markers linked to the short arm of rice chromosome 11 mapped on the deletion lines between breakpoints 0.23–0.63 (Causse et al. 1994; Harushima et al. 1998), so the proximal region of the short arm of chromosome 5D, up to breakpoint 0.63, can be considered as showing conserved synteny with the short arm of rice chromosome 11. Likewise, the deletion region distal to breakpoint 0.78 showed conserved synteny with the long arm of rice chromosome 12 by mapping a marker, *Xcdo344*, from the Cornell map (Causse et al. 1994). As no marker was mapped between breakpoints 0.63–0.78, the orthology of this deletion region with rice chromosomes cannot be established from the present study.

A consensus comparative Group 5 chromosome deletion map

The conservation of gene synteny among the three homoeologous chromosomes of wheat is well established. The results here show that this extends to structure in terms of rice linkage blocks, and predates the speciation of the ancestral genomes. The information from physical mapping of each homoeologous chromosome can thus be combined to generate better resolution by producing a single consensus physical map of the wheat Group 5 chromosomes, based on the relative positions of breakpoints with respect to markers across the three homoeologues (Gill and Gill 1994; Werner et al. 1992). Thus, on the basis of a single consensus map, each deletion breakpoint from the centromere can be represented as 1L, 2L, etc. on the long arm, and 1S, 2S, etc. on the short arm (Fig. 2). A comparison of the consensus physical map with the linkage map of rice revealed that most of the markers from rice chromosome 9 were mapped on the

deletion region between breakpoints 1L–4L. It can therefore be concluded that this region on the long arm of the wheat Group 5 chromosomes, between breakpoints 1L–4L, shows conserved synteny with rice chromosome 9 as a single unit. Again, the markers linked to the long arm of rice chromosome 3 were concentrated between breakpoint 11L–12L, excepting the marker *Xrz474*, so the deletion region between breakpoints 10L–12L can be considered orthologous to the long arm of rice chromosome 3. However, no syntenic relationship was observed between the deletion regions 4L–10L on the long arm. On the short arm, the proximal part up to breakpoint 5S showed conserved synteny with the short arm of rice chromosome 11, and the telomeric end distal to breakpoint 9S showed conserved synteny with rice chromosome 12.

Physical mapping of flowering time genes

Phenotypic variation for a trait among the deletion lines can be used to establish the physical locations of genes affecting that trait. The vernalization response genes on the Group 5 chromosomes have been mapped on the long arms and shown to form a homoeologous series (Galiba et al. 1995; Snape et al. 1998). Aneuploid analysis has shown that removal of chromosomes 5A, 5B, and 5D delays flowering under unvernalized conditions (Flood and Halloran 1986). Thus, any deletion lines lacking the vernalization response genes would be expected to show a similar late flowering phenotype. Analyses of variance showed significant differences for flowering time among the sets of deletion lines for the long arms of chromosomes 5A, 5B, and 5D, respectively (data not shown). The variation among the deletion lines is represented as histograms in Figs. 3*a*, 3*b*, and 3*c* for the chromosome arms 5AL, 5BL, and 5DL, respectively.

The deletion lines for chromosome arm 5AL can be grouped into three classes (A, B, and C) between breakpoints 0.56–0.64 and 0.68–0.78 (Fig. 3*a*). Sarma et al. (1998) showed the physical location of *Vrn-A1* between deletion breakpoints 0.68–0.78, and this represents the difference between the B and C groups, as shown previously. However, another effect is apparent in this case; a difference of 7.5 days between the A and B groups, which was statistically significant. This implies the presence of a gene not previously found. In barley, in addition to the well-known *Vrn-H1 (Sh2)* effect, Laurie et al. (1995) mapped an earliness per se gene (*eps–5H*) for flowering on chromosome 7 (5H), near to the centromere. Moreover, the markers associated with the *eps–5H* locus of barley (*Xpsr906*, *Xwg889*, *Xwg530*) also mapped onto the deletion lines between the centromere and breakpoint 0.64. Therefore, the gene near to the centromere may be a homoeologue of *eps–5H*. Previously, conventional aneuploid analysis and other genetic mapping efforts have failed to detect such a locus on chromosome 5A, probably because of limitations of the experimental populations used, and an apparent lack of polymorphism.

Although the long arm of chromosome 5B is known to carry the *Vrn-B1* gene for vernalization response, there is no published report of the linkage mapping of this gene. Flowering time analysis for the deletion lines of chromosome arm 5BL revealed that the deletion lines can also be grouped into three classes, A, B, and C, between breakpoints 0.29–0.43 and 0.59–0.79, respectively (Fig. 3*b*). The difference between (A + B) and C was 5 days, which is statistically significant. The markers associated with the *Vrn-A1* locus (*Xbcd450*, *Xwg644*) also mapped in this region. Therefore, such a big difference in the flowering time in the deletion region between breakpoints can be attributed to the *Vrn-B1* locus. However, there is a complication. The deletion lines, 5BL–13–1, 5BL–13–2 with breakpoint 0.82, are homozygous but contain deletions for chromosomes 2BS, 5DS, and 7AL, which may affect the flowering time analysis for these lines. However, the effect is likely to be for later, rather than earlier flowering, so the differences are consistent with the absence of *Vrn-B1* being the main effect.

Although the difference between the A and B groups was not statistically significant, the markers associated with the *eps–5H* locus of barley (Laurie et al. 1995) mapped between breakpoints 0.29–0.43, suggesting a homoeologue of the 5A

Fig. 3. Physical mapping of flowering time on the deletion lines for the long arm of the Group 5 chromosomes of wheat. *(a)* Variation in flowering time among the deletion lines for the long arm of chromosome 5A. (*b*) Variation in flowering time among the deletion lines for the long arm of chromosome 5B. (*c*) Variation in flowering time among the deletion lines for the long arm of chromosome 5D.

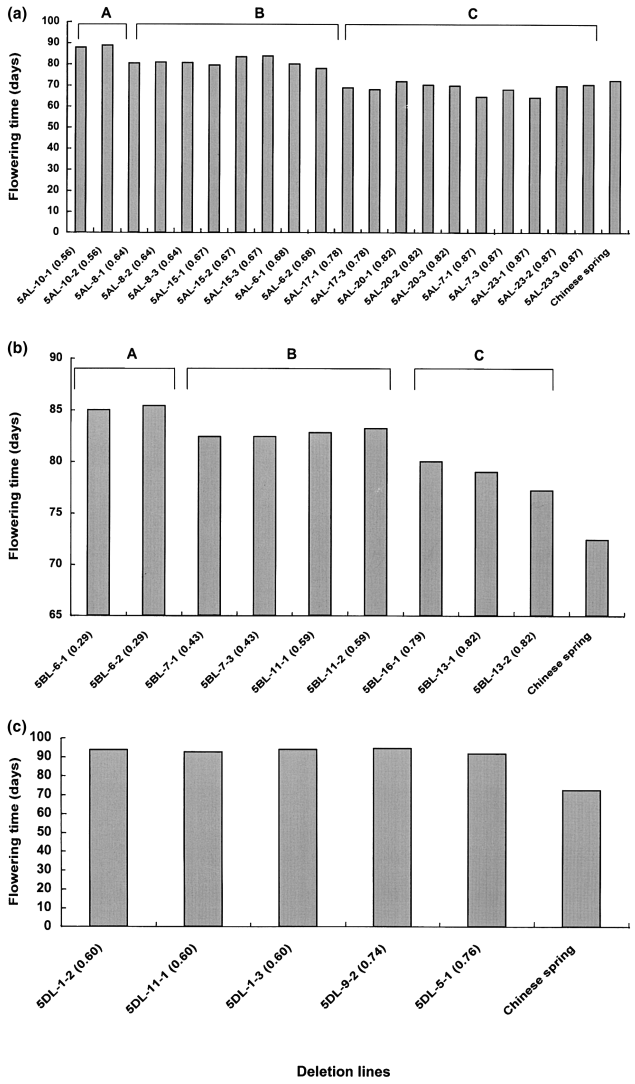
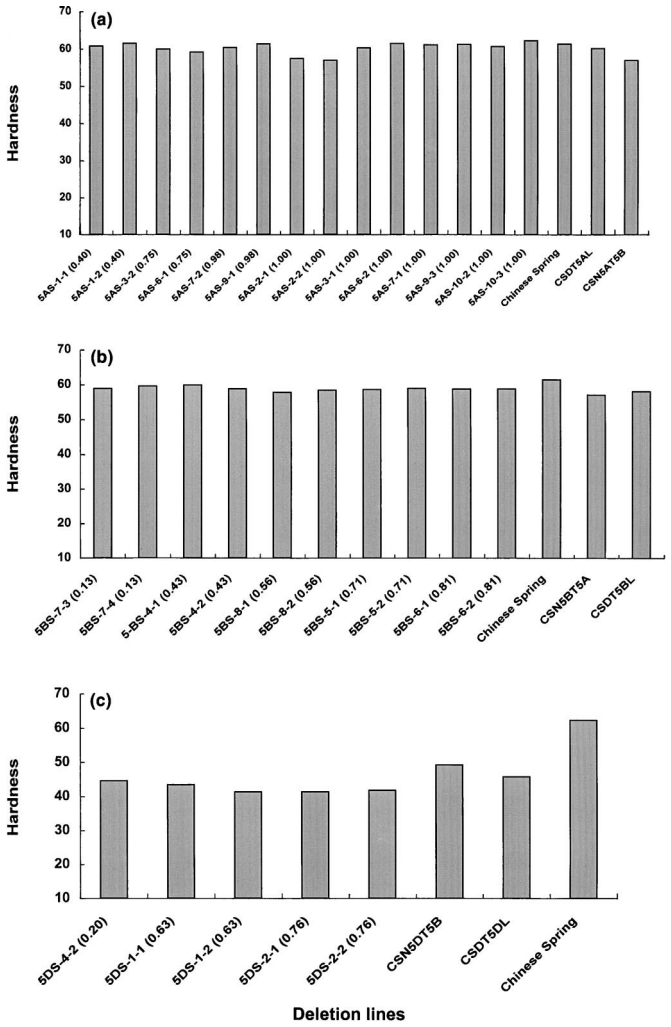


Fig. 4. Physical mapping of the grain hardness gene on the deletion lines for the short arms of the Group 5 chromosomes. (*a*) Variation in grain hardness for the deletion lines for the short arm of chromosome 5A. (*b*) Variation in grain hardness for the deletion lines for the short arm of chromosome 5B. (*c*) Variation in grain hardness for the deletion lines for the short arm of chromosome 5D.



and *Eps–5H* loci. There is also a complication here; the two deletion lines (5DL–6–1, 5BL–6–2) with a breakpoint of 0.29 are also trisomic for chromosome 5A. Trisomic and tetrasomic lines, however, for chromosome 5A in 'Chinese Spring' flower at the same time as the euploid (Dr. T.E. Miller, personal communication). Following this, one should expect them to flower earlier, if increased dosage has any effect. This study revealed that the deletion lines 5DL–6–1 and 5BL–6–2 took a longer time to flower. This result does, therefore, imply the presence of another locus in a similar location as on chromosome 5A, possibly homoeologous to the *eps–5H* gene of barley.

The histogram showing variation for flowering time among the deletion lines for chromosome arm 5DL (Fig. 3*c*) revealed that there was no significant difference between the deletion lines, and all the deletion lines took longer time to flower than euploid 'Chinese Spring'. The markers associated with the vernalization response gene, *Vrn-A1* (*Xbcd450*, *Xwg644*), mapped distally to breakpoint 0.76. Thus, the difference between the deletion lines and 'Chinese Spring' is probably due to the deletion of the *Vrn-D1* locus present in the deletion region distal to breakpoint 0.76. The deletion lines 5DL–1–1, 5Dl–12, and 5DL–1–3, are homozygous but trisomic for chromosome 5A, but this should not influence the analysis unduly, as stated above.

The deletion lines for the short arms of the homoeologous Group 5 chromosomes did not show any differences from 'Chinese Spring', indicating the absence of genes controlling flowering time on the short arms of this group (data not shown).

Physical mapping of the grain hardness gene (*Ha*) on chromosome 5D

Analysis of variance for grain hardness revealed that the deletion lines for chromosome arm 5DS differed significantly, whereas no statistically significant difference was observed for the deletion lines for chromosome arms 5AS and 5BS (Figs. 4*a* and 4*b*). These results reveal that a gene controlling grain hardness is present on the short arm of chromosome 5D. The cultivar 'Chinese Spring' is a soft-grained variety due to the *ha* allele at the *Ha* locus on the short arm of chromosome 5D (Law et al. 1978). The *ha* allele promotes softness as aneuploids for 5D tend to be harder than the euploid. Thus, deletion lines lacking the *ha* allele should behave as hard-grained genotypes. The variation for grain hardness for 5DS is represented as a histogram in Fig. 4*c*. It is seen from the figure that the CSN5DT5B and CSditelo5DL lines behaved as hard-grain types. Again, all the deletion lines also behaved as hard grain types, showing much lower readings than 'Chinese Spring'. This clearly indicates that such a difference is due to the deletion of the *Ha* gene present on the deletion region distal to the breakpoint 0.78. Sourdille et al. (1996) mapped a grain hardness locus on chromosome arm 5DS, close to the markers *Xmta9* and *Xfba114*. These markers also mapped in this region of chromosome arm 5DS. These results confirm the physical location of *Ha* on the distal end of the short arm of chromosome 5D.

Discussion

This study has clearly demonstrated the utility of the wheat deletion lines for revealing the syntenic relationships of various rice chromosomes along the physical length of the Group 5 chromosomes. Hohmann et al. (1995) also demonstrated the utility of the deletion lines of wheat in constructing the physical map of barley, based on the colinearity of markers. The wheat Group 5 chromosomes were previously indicated to be composed of parts of rice chromosomes 3, 9, 11, and 12 (Moore et al. 1993; Van Deynze et al. 1995), as was confirmed here. Also, the disruption of synteny on the wheat Group 5 chromosomes relative to rice chromosome 9 was reported by the insertion of markers from rice chromosomes 2, 8, and 11 (Foote et al. 1997). Moore et al. (1997) also reported extensive disruption of synteny around the centromeric region of rice linkage block 9 by insertion of parts of several linkage groups of rice to constitute a part of the wheat Group 5 chromosome. The present study also clearly revealed a specific region with a disruption of

synteny with rice chromosomes, in confirmation of those findings. A major implication of these results is that the use of the rice genome as a tool for revealing the genetic content of the Triticeae is limited to those regions that have been identified as showing clear, conserved synteny to a specific rice chromosome. For those regions with broken synteny, it may be inappropriate to use rice as an intergenomic vehicle to clone the genes present on this region. This will require a more extensive analysis of wheat itself and the availability of large insert libraries. Unfortunately, to date, these are not available, although a BAC library of *Triticum monococcum* is presently under construction (Dubcovsky, personal communication). This thus limits the potential for gene isolation in wheat in such regions until appropriate libraries become available.

Within rice, chromosome 9 shows a high level of polymorphism, which is not characteristic of the syntenous region of the group 5 chromosomes of wheat. In wheat, there is a great discrepancy between genetic distance and physical distance, due to variation in the distribution of chiasmata, which tend to be distally located, resulting in low recombination frequencies in the proximal estimated two-thirds of each chromosome arm (Snape et al. 1985). The region on the Group 5 chromosomes syntenous to rice chromosome 9 is proximal to the centromere, and thus in a region in wheat of reduced recombination, and hence also tends to show low levels of molecular marker polymorphism. Clearly, during the evolution of the genomes of rice and wheat from a common ancestor, there have been drastic changes in the levels of polymorphism due to evolutionary differences in genome organization. Hence, the different evolutionary pathways of the genomes not only influences chromosome number and genome size, but also the distribution of recombination. This will have implications on the rate of evolution within the different species for such regions, and genes in rice will tend to be more polymorphic in certain regions than the syntenous regions of wheat. This could also influence the responses to selection for genes in such regions.

This difference in frequencies of recombination in syntenous regions will also have important implications for gene cloning strategies in wheat, and will reinforce the use of rice as a tool for gene isolation in the Triticeae. Thus, in rice there will be an almost constant ratio between physical distances and mapping distances (bp/cM) but in wheat this will vary greatly, and possibly increase exponentially, in regions proximal to the centromere. Fine-mapping in such regions in wheat will be extremely difficult, if not impossible. From the data presented here, there is a flowering time QTL (quantitative trait locus) on chromosome 5A in the region proximal to the centromere. It will be very difficult to fine-map and clone this in wheat, even if large inset libraries are available. Clearly, it will have to be fine-mapped in rice and the information used to locate an appropriate rice BAC or YAC for the syntenous region, which could then be sequenced to detect a candidate gene. Such a strategy is being used for cloning the *Ph1* gene that is proximal to the centromere on chromosome 5B, for homoeologous pairing in wheat (Moore, personal communication). This difference in recombination distribution between wheat and rice will apply to all the other regions of the wheat genome proximal to the centromeres. Thus, it will be very important to characterize, in detail, the syntenous relationships of all homoeologous groups of wheat for these regions. For the distal regions of wheat chromosomes, where there are high levels of recombination, it should be possible to fine-map directly and use wheat large insert libraries for chromosome walking and (or) landing. There will need to be different gene-cloning strategies in wheat relative to the physical locations of genes on chromosome arms.

All three *Vrn–1* regions of wheat have been demonstrated to show conserved synteny with the long arm of rice chromosome 3, so it may be possible to clone the orthologue of the vernalization response gene from rice. Similarly, a region proximal to the centromere on each Group 5 chromosome was shown to contain a flowering time effect in a region showing conserved synteny to rice chromosome 9. Interestingly, Sarma et al. (1998) have shown that there are at last two QTL on rice chromosome 9 controlling flowering time. It will be useful to establish the detailed orthology of these regions. Likewise, this study has demonstrated that the chromosome region associated with the *Ha* locus is orthologous to rice chromosome 12, indicating the possibility of having found an orthologue of the *Ha* gene from rice. This information is an important step in developing strategies for cloning-out these agronomically important loci.

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