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High-density physical maps reveal that the dominant male-sterile gene *Ms3* is located in a genomic region of low recombination in wheat and is not amenable to map-based cloning

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Abstract In wheat it is essential to know whether a gene is located in a high or low recombination region of the genome before initiating a map-based cloning approach. The objective of this study was to explore the potential feasibility of map-based cloning of the dominant male-sterile gene *Ms3* of wheat. High-density physical maps of the short arms of the group-5 chromosomes (5AS, 5BS, and 5DS) of *Triticum aestivum* L. were constructed by mapping 40 DNA markers on a set of 17 homozygous deletion lines. One hundred RFLP loci were mapped: 35 on 5AS, 37 on 5BS, and 28 on 5DS. A consensus physical map was colinearly aligned with a consensus genetic map of the group-5 short arms. Sixteen of the 17 markers in the consensus genetic map encompass a genetic distance of 25 cM and correspond to the distal region (FL 0.56–0.97) of the consensus physical map. Two rice probes, RG463 and RG901, previously identified to be linked to markers CDO344 and CDO749 (group-5 short arm of wheat), respectively, in the genetic map of rice chromosome 12, map between FL 0.56 and 0.63 in the consensus map. Thus at least a part of the group-5 short arm is homoeologous to a region of chromosome 12 of rice. The genetic map of chromosome arm 5AS was constructed using a population of 139 BC_1 plants derived from a cross between the euploid wheat "Chris" carrying a dominant male-sterile gene *Ms3* and a disomic substitution line in which chromosome 5A of *T. aestivum* cv Chinese Spring was substituted by chromosome 5A from *Triticum turgidum* ssp. *dicoccoides*. The map has a genetic length of 53.4 cM with 11 DNA markers. The initial map showed that the gene *Ms3* cosegregated with three markers, WG341, BCD1130 and CDO677. High-resolution mapping using an additional 509 BC_1 plants indicated that the marker WG341 was closely linked to *Ms3* at a genetic distance of 0.8 cM. The *Ms3* was mapped physically in the region spanning 40% of the arm length from the centromere of 5AS. Therefore, map-based cloning of the *Ms3* is not feasible, although WG341 can be used as a useful tag for the *Ms3* gene for breeding purposes.

Keywords *Triticum aestivum* · Physical map · Short arms · Group-5 · Genetic mapping ·*Ms3* gene

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Introduction

Physical maps of the 21 chromosomes of bread wheat (*Triticum aestivum* L.) incorporating more than 1,000 DNA RFLP loci have been constructed based on an array of deletion stocks in the wheat cultivar "Chinese Spring" (CS) (Werner et al. 1992; Gill et al. 1993, 1996a, b; Kota et al. 1993; Hohmann et al. 1994; Delaney et al. 1995a, b; Mickelson-Young et al. 1995; Faris et al. 2000; Weng et al. 2000). The physical maps when aligned with published genetic linkage maps (Chao et al. 1989; Devos and Gale 1993; Devos et al. 1993; Nelson et al. 1995; Jia et al. 1996; Marino et al. 1996) provide a wealth of data on the distribution of markers and recombination along the physical length of a chromosome. The proximal one-third to one-half of each chromosome arm surrounding the centromere has few markers and recombination is suppressed. The distal half of each arm is marker-rich and has high levels of recombination. The wheat genes are present in clusters interspersed by regions of low gene density. There are two to four gene clusters on each chromosome arm. Many agronomically important genes often map within gene clusters (Gill et al. 1996a, b; Faris et al. 2000). Development of high-density physical maps of specific regions may facilitate the map-based cloning of targeted genes.

A dominant gene conferring male-sterility, *Ms3*, induced by ethyl methanesulfonate (EMS) was reported in the alloplasmic wheat "Chris", which has the cytoplasm of *Aegilops tauschii* Coss. (Syn.: *Aegilops squarrosa* L.) (Franckowiak et al. 1976; Sasakuma et al. 1978). The

gene was later transferred to a euplasmic "Chris" wheat (Maan and Williams 1984). *Ms3* is located on the short arm of chromosome 5A with 3.1% recombination from the centromere (Maan et al. 1987). The dominant male-sterility gene has been utilized in wheat breeding programs, including recurrent selection for population improvement and in the pyramiding of useful genes (Sorrells and Fritz 1981; Deng and Huang 1993). Identification of tightly linked molecular markers to the dominant male-sterile gene will be useful in tagging male sterile plants in a breeding program. Knowledge of the recombination frequency and the distribution of markers near *Ms3* will help us to determine the feasibility of map-based cloning of the gene in wheat. Here we report the development of high-density physical maps of the short arms of the group-5 chromosomes and the genetic mapping of the dominant male-sterile gene *Ms3* in wheat.

Materials and methods

Plant materials

Seventeen, homozygous deletion (del) lines for chromosomes 5A, 5B and 5D of the group-5 short arms of Chinese Spring (Endo and Gill 1996) were used for mapping RFLP markers to deletion intervals (see Fig. 1 chromosome idiogram). Nullisomic-tetrasomic (NT) lines for each of the group-5 chromosomes and ditelosomics (Dt) for the long arm of each group-5 chromosome (Sears 1954, 1966; Sears and Sears 1978) were used to assign DNA fragments to individual chromosomes and chromosome arms. The *T. aestivum* cv Chris with the EMS-induced, dominant male-sterile gene *Ms3* was kindly provided by S. S. Maan. A disomic substitution (DS) line of Chinese Spring in which chromosome 5A is replaced by chromosome 5A of *Triticum turgidum* ssp. *dicoccoides* (Körn. Ex Asch. & Graebn) was developed by E. R. Sears. All of the genetic stocks are maintained by the Wheat Genetics Resource Center, Kansas State University, Manhattan, USA.

DNA markers

DNA probes for the short arms of the group-5 chromosomes were selected from published data (for a review, see McIntosh et al. 1998). These probes were kindly provided by A. Kleinhofs (ABG), Pullman, Wash., USA; M. E. Sorrells (BCD, CDO and WG), Ithaca, N.Y., USA; F. Quetier (FBA and FBB), Paris, France; A. Graner (MWG), Grünbach, Germany; M.D. Gale (PSR), Norwich, UK; S.R. McCouch (RG), Ithaca, N.Y., USA; G.E. Hart (TAM), College station, Tex., USA; K. Tsunewaki (TAG), Kyoto, Japan; and P. Spagnoletti (UBP), Potenza, Italy.

Physical mapping

Genomic DNA was extracted from deletion, NT, and Dt lines, digested with the restriction enzymes *Eco*RI, *Eco*RV, *Hin*dIII and *Dra*I, and electrophoresed and blotted to membranes as described by Qi et al. (1997). RFLP fragments were assigned to deletion intervals based on the presence or absence of bands in the series of chromosome deletion lines for each group-5 short arm.

Genetic mapping of the *Ms3* gene

The genetic linkage map of the *Ms3* gene was constructed using a population of 139 BC_1 plants derived from the cross euploid Chris/CS-*T. turgidum* ssp. *dicoccoides* DS5A. An additional population of 509 BC_1 plants was scored for flanking markers to construct a high-resolution map of the *Ms3* gene region. Goodness-of-fit for male sterile: fertile to a 1:1 segregation ratio in the BC_1 was tested by means of a chi-square analysis. The mapping data were analyzed at a LOD of 3.0 with the computer program Mapmaker V2.0 (Lander et al. 1987) using the Kosambi function (Kosambi 1944).

Table 1 The probe-enzyme combinations used to identify marker loci in Chinese Spring wheat, the number of DNA fragments generated, and/or their allocation to the 5AS, 5BS or 5DS chromosome arms of wheat

Clone	Total number of fragments	Number of fragments			Enzyme
		5AS	5BS	5DS	
Xabg497	6	0	1	0	*Eco*RV
Xabg705	4	1	1	1	*Hin*dIII
Xbcd873	5	1	0	1	*Hin*dIII
Xbcd873	8	0	1	0	*Eco*RV
Xbcd1130	5	1	1	1	*Dra*I
Xbcd1871	4	1	1	1	*Hin*dIII
Xcdo344	3	1	1	1	*Dra*I
Xcdo459	7	2	2	2	*Eco*RI
Xcdo677	4	1	2	1	*Eco*RI
Xcdo687	5	1	1	0	*Eco*RI
Xcdo749	4	1	1	1	*Eco*RV
Xcdo1335	4	1	1	1	*Eco*RI
Xfba114	2	0	1	0	*Eco*RV
Xfba232	6	1	1	1	*Eco*RI
Xfba342	7	1	1	0	*Dra*I
Xfba367	9	0	1	0	*Hin*dIII
Xfba393	4	0	1	1	*Hin*dIII
Xfbb121	12	0	1	0	*Eco*RI
Xfbb276	4	1	0	0	*Hin*dIII
Xmwg835	12	0	0	1	*Hin*dIII
Xmwg835	12	0	1	0	*Eco*RV
Xpsr118	3	1	1	1	*Hin*dIII
Xpsr170	8	1	1	0	*Dra*I
Xpsr326	6	1	1	1	*Hin*dIII
Xpsr628	3	1	1	1	*Dra*I
Xpsr903	6	0	0	1	*Dra*I
Xpsr929	3	1	0	0	*Eco*RI
Xpsr929	3	0	1	0	*Hin*dIII
Xpsr940	6	2	1	1	*Dra*I
Xpsr945	3	1	1	1	*Hin*dIII
Xpsr1204	3	1	1	1	*Eco*RV
Xrg463	5	1	1	0	*Dra*I
Xrg463	4	0	0	1	*Hin*dIII
Xrg901	3	1	1	1	*Hin*dIII
Xtam53	9	1	2	1	*Dra*I
Xtam54	6	1	1	1	*Hin*dIII
Xtag317	8	1	0	0	*Eco*RV
Xtag424	4	1	0	0	*Dra*I
Xtag629	6	1	0	1	*Hin*dIII
Xtag629	8	1	1	0	*Dra*I
Xubp3	3	1	1	1	*Hin*dIII
Xubp5	2	1	0	0	*Eco*RV
Xwg184	8	1	0	0	*Eco*RI
Xwg341	6	1	1	1	*Eco*RI
Xwg363	3	1	1	1	*Dra*I

Results

Physical maps

Sixty six DNA markers for the short arms of the group-5 homoeologous chromosomes and six rice genomic DNA

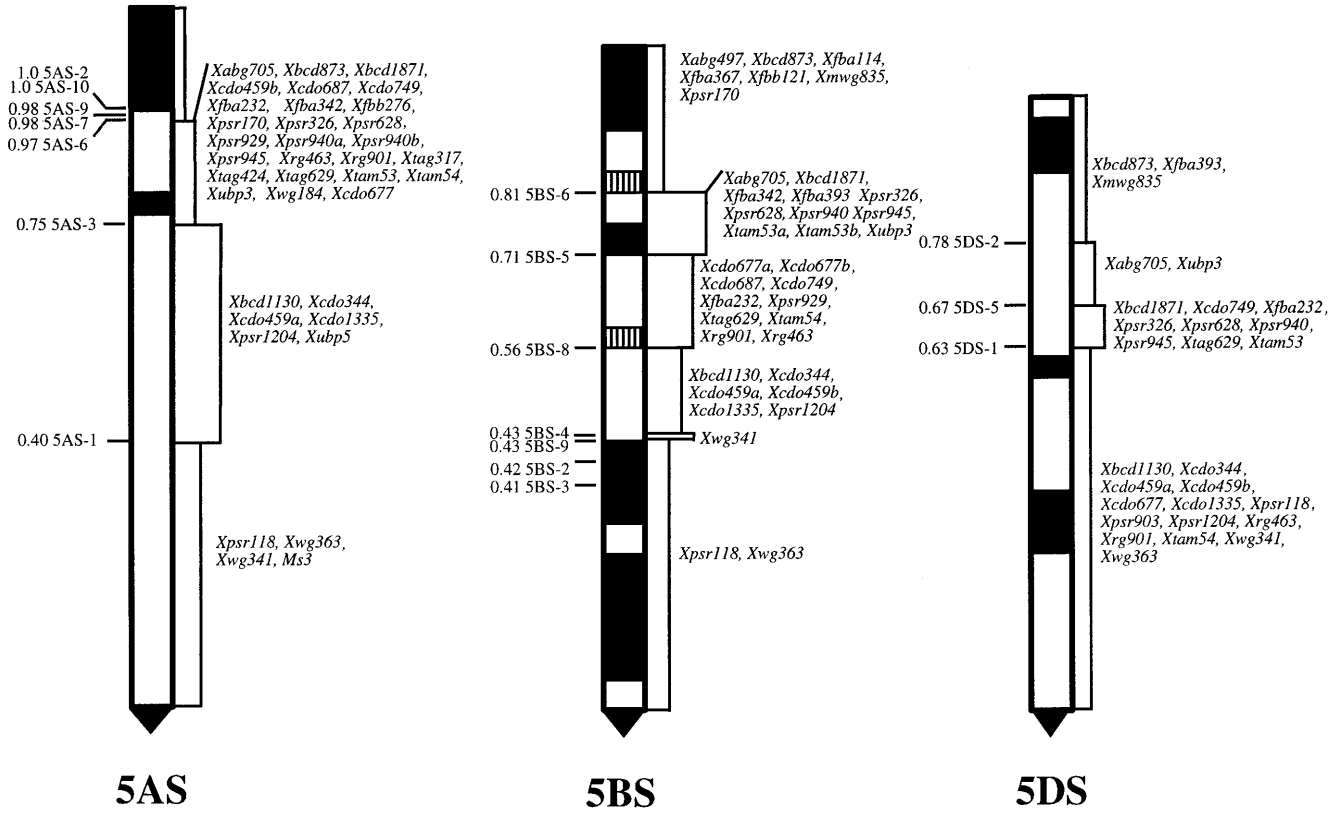

Fig. 1 The physical maps of the short arms of chromosomes 5A, 5B and 5D of wheat. Fraction-length values and deletion lines are indicated on the left and markers mapping in specific deletion intervals on the right. C-banding patterns of individual chromosomes of wheat were taken from Gill et al. (1991)

markers were selected and hybridized with genomic DNA of NT, Dt and 17 homozygous deletion lines of the group-5 short arm-chromosomes of bread wheat. Forty DNA markers were informative and subsequently used to construct high-density physical maps of the short arms of group-5 chromosomes (Fig. 1, Table 1). A total of 246 restriction fragments were detected using the 40 DNA clones in Southern hybridization (Table 1). Included were the data of five clones that were hybridized twice, each time with a different enzyme. One hundred RFLP loci were mapped: 35 on 5AS, 37 on 5BS, and 28 on 5DS. Using single probe/enzyme combinations, orthologous loci on all three chromosomes were detected by 21 markers. Two probe/enzyme combinations were needed to detect loci on all three chromosome arms for probes BCD873, RG463 and TAG629, and loci on two of three chromosome arms for probes MWG835 and PSR929 (Table 1). Four markers detected loci on two of three chromosome arms, and ten markers detected loci on one chromosome arm. Presumably, additional probe/enzyme combinations are needed to detect orthologous loci on all three chromosomes for these DNA markers.

The RFLP loci were nonrandomly distributed in the three chromosome arms (Fig. 1). In the 5AS arm, 74% of the markers mapped between deletion breakpoints 0.75–0.97. The proximal 43% of the 5BS arm had poor marker coverage. Deletion lines 5BS-4 and 5BS-9 have a similar FL value of 0.43, but the two lines were differentiated by the DNA marker WG341, i.e., a specific 5BS band of WG341 was absent in the del5BS-4, but present in the del5BS-9. The deletion interval between FL 0.63 and FL 0.67 in 5DS represents only 4% of the chromosome arm and contains 9 of the 28 (31%) loci mapped in the arm; a ten-fold increase in marker density (Fig. 1).

Consensus physical map versus genetic maps

A consensus map of a homoeologous group-5 short arm was constructed based on conserved colinearity among homoeologous chromosomes (Fig. 2). Individual loci were mapped to the shortest interval region in the consensus map by comparing the locations of the markers and fraction breakpoints on each chromosome arm map. For example, locus *Xfba393* maps between FL 0.71–0.81 in 5BS and FL 0.78–1.00 in 5DS. Therefore, it was placed between FL 0.78–0.81 on the consensus physical map. The relative positions of most DNA markers are the same among the three homoeologous chromosomes. Some markers hybridized to DNA fragments with different FL values on chromosomes 5AS, 5BS and 5DS. Seven marker loci, *Xcdo*677, *Xcdo*749, *Xfba2*32, *Xtag*629, *Xtam*54, *Xrg*463 and *Xrg*901, mapped to regions between FL 0.56–0.71 on 5BS and 5DS, but 0.75–0.97 on 5AS. On the consensus map, these markers were placed in the

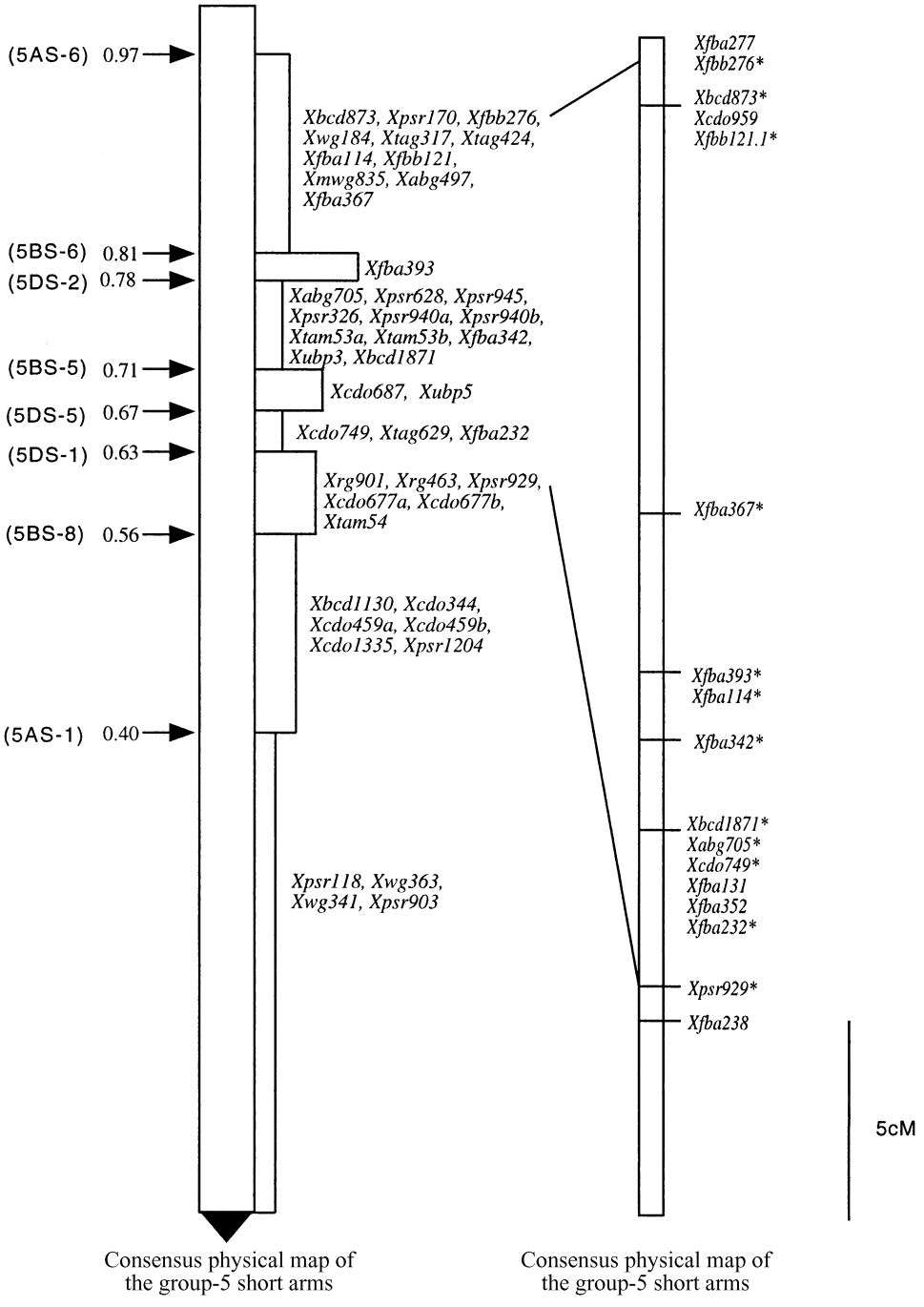

Fig. 2 Comparison of the consensus physical map and genetic map (Nelson et al. 1995) of the short arms of group-5 chromosomes. Markers in the consensus genetic map denoted with an *asterisk* (*) are also on the consensus physical map

interval of FL 0.56–0.67. Similarly, the marker loci *Xbcd1871*, *Xpsr326*, *Xpsr628*, *Xpsr940*, *Xpsr945* and *Xtam53*, which mapped to the interval of FL 0.75–0.97 on 5AS and 0.71–0.81 on 5BS but FL 0.63–0.67 on 5DS, were placed in FL 0.71–0.78 on the consensus map. The locus detected by *Xcdo459b* is placed in FL 0.43–0.56 interval on chromosome arms 5BS and 5DS but in FL 0.75–0.97 on chromosome arm 5AS. Two rice probes, RG463 and RG901 linked to the probes CDO344 and CDO749, respectively, in the chromosome-12 genetic map of rice (Causse et al. 1994; Saghai-Maroof et al. 1996; Wilson et al. 1999), map in the FL 0.56–0.63 region on the consensus map. The comparison between our consensus physical map and the genetic map of the group-5 short arms (Nelson et al 1995) indicated that the linear order on both maps is identical (Fig. 2). The locus *Xfba114* could be mapped either between *Xfba393* and *Xfba342* or between *Xfba393* and *Xfba367* on the genetic map. This locus is located between *Xfba393* and *Xfba367* according to our physical map (Fig. 2). Sixteen of 17 markers in the consensus genetic map encompass a genetic distance of 25 cM and correspond to the distal region (0.56–0.97) of the consensus physical map.

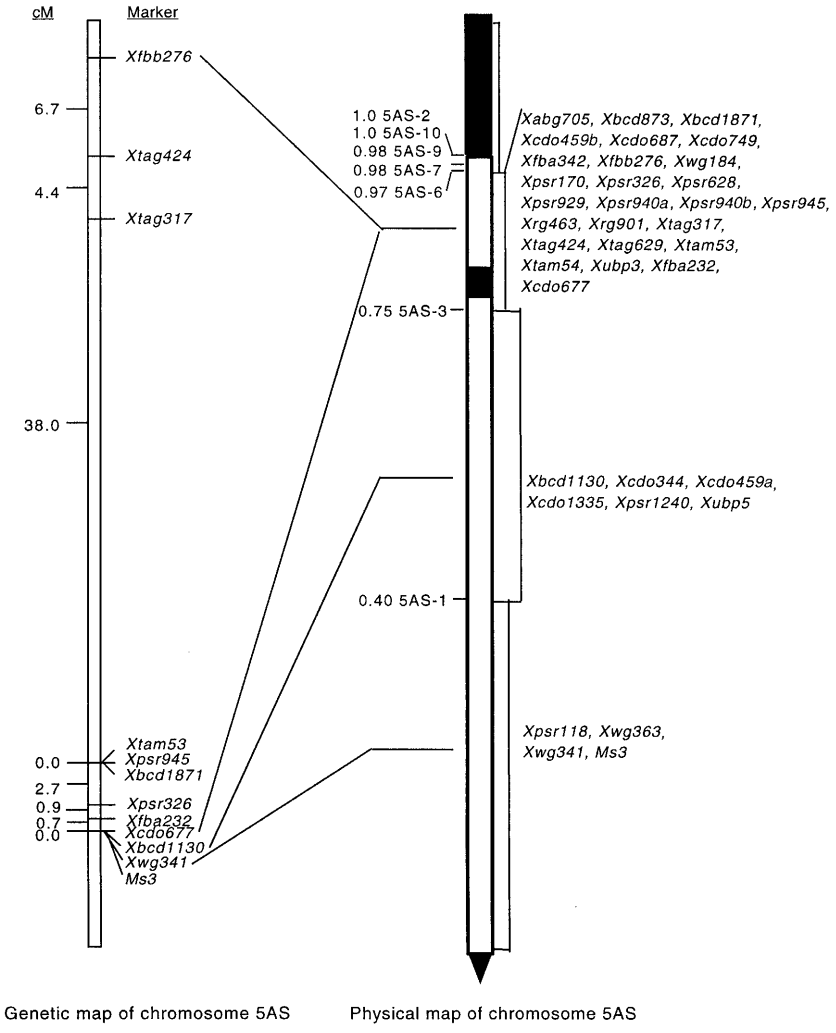

Fig. 3 Comparison of the physical map and genetic map of the short arm of chromosome 5 A. The genetic map was developed from the population of 139 BC_1 plants

Genetic mapping of *Ms3*

The euploid wheat cultivar Chris has the dominant male-sterile gene *Ms3*. Male-sterile plants with small aborted anthers are distinguishable from fertile plants at flowering. The analysis of 139 BC_1 plants gave a Mendelian segregation ratio of 66 (fertile): 73 (sterile) plants, and fits the expected 1:1 ratio (X^2 =0.3523, 0.75>*P*>0.50).

"Chris" and the CS-*Triticum dicoccoides* DS5A line were screened with RFLPs by digesting their DNA with five restriction enzymes (*Bam*HI, *Eco*RI, *Eco*RV, *Hin*dIII and *Dra*I). Membranes with the digested DNA were hybridized with 34 probes that detected loci on the physical map of the chromosome arm 5AS. Polymorphisms were detected between the parents by 13 probe/enzyme combinations. The genetic map of 5AS is 53.4 cM in length (Fig. 3). Eleven DNA markers were analyzed in 139 BC_1 plants from the cross euploid "Chris"/CS-*T. dicoccoides* DS5A. The loci *Xwg341*, *Xbcd1130* and *Xcdo677* cosegregated with *Ms3*, but they mapped in different intervals on the physical map (Figs. 3 and 4). Compared with the physical map of 5AS, nine marker loci on the genetic map were allocated to the distal region of FL 0.75–0.97, one marker in the FL 0.40–0.56 interval, and one marker in the proximal region of the chromosome arm 5AS (Fig. 3).

High-resolution mapping

The initial mapping established the possible location of the *Ms3* gene and markers, but the position of *Ms3* was not determined precisely because three markers cosegregated with *Ms3*. The three cosegregating markers and another marker BCD1871, which maps distal to *Ms3*, were selected and scored on a population of 509 BC_1 plants from the above cross. Four plants exhibited recombination events between *Ms3* and *Xwg341*. The *Xwg341* locus was linked to *Ms3* at a genetic distance of 0.8 cM (Fig. 5). This result combined with the physical location of *Xwg341* suggested that the *Ms3* gene was located physically in the proximal 40% of the chromosome arm 5AS (Fig. 1).

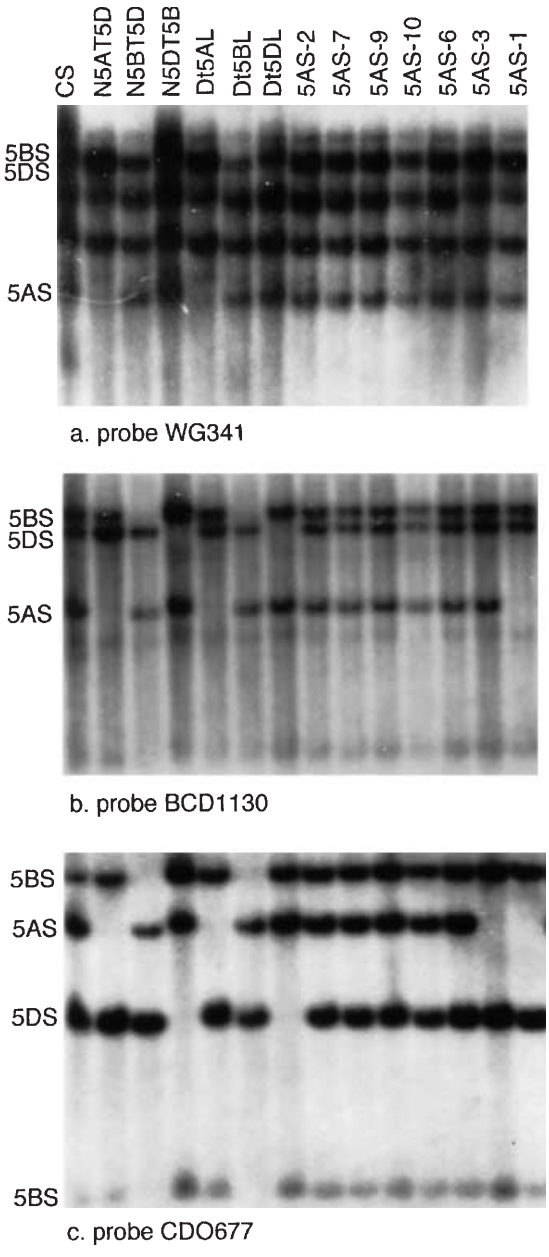

Fig. 4a–c Southern-blot hybridization of probes with restriction enzyme-digested genomic DNA of wheat cultivar Chinese Spring, nullisomic-tetrasomics, ditelosomics, and deletion lines of chromosome 5AS of CS. **a** Probe WG341/*Eco*RI, the 5AS specific band identified is absent in N5AT5D and Dt5AL respectively. This band is present in all of the deletion lines; **b** probe BCD1130/*Dra*I, the 5AS specific band identified is absent in N5AT5D, Dt5AL and del5AS-1; **c** probe CDO677/*Eco*RI, the 5AS specific band identified is absent in N5AT5D, Dt5AL, del5AS-3 and del5AS-1. Thus, these three markers were mapped in different deletion intervals, the centromere to FL 0.40, FL 0.40–0.75 and FL 0.75–1.00 of 5AS. All of them cosegregated with *Ms3* in the basic genetic map of 5AS

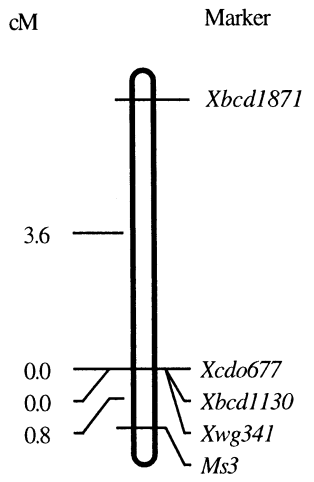

Fig. 5 The genetic map of the 5AS arm in the *Ms3* gene region developed from the population of 509 BC_1 plants

Discussion

Conservation of gene synteny in chromosomes of a homoeologous group in bread wheat is well known. Colinearity in the order of DNA markers among Triticeae species, rice, maize and oat has also been demonstrated (Ahn et al. 1993; Devos and Gale 1993; Devos et al. 1993; Gale and Devos 1998; Kurata et al. 1994; Namuth et al. 1994; Van Deynze et al. 1995; Sarma et al. 2000). In the present study, the relative positions of most DNA markers across homoeologous chromosomes appear to be conserved. The consensus physical map of the short arm of group 5 indicates that DNA markers are distributed preferentially in the distal regions of the chromosomes. Only four markers (9.7%) mapped in the proximal 40% of the arm. The markers that map in distal region between FL 0.56–0.97 contribute most to the genetic map length (Fig. 2). Seven DNA clones hybridized to chromosome segments with FL values 0.56–0.67 on 5BS and 5DS but to FL 0.75–0.97 on 5AS. One possible reason is the inaccuracy of the FL calculation of del5AS-3 (Fig. 1). Six markers mapped between FL 0.71–0.81 on 5AS and 5BS, but in 0.63–0.67 on 5DS. An alternative explanation is a small paracentric inversion on 5DS. It is worth noting that nine markers were assigned to the region of FL 0.63–0.67 on 5DS.

Comparative mapping of wheat and rice identified four marker loci from the wheat group-5 short arm, *Xcdo344, Xcdo459, Xcdo1335 and Xcdo749,* which mapped to rice chromosome 12 (Causse et al. 1994; Saghai-Maroof et al. 1996; Wilson et al. 1999). Recently, we placed two markers, RG463 and RG901 from rice chromosome 12, on the deletion lines of the wheat group-5 short arm. A comparison of the genetic map of rice chromosome 12 and our physical map revealed conservation of the marker order between corresponding rice and wheat chromosomes (Fig. 6). The four wheat and two rice marker loci that mapped to rice chromo-

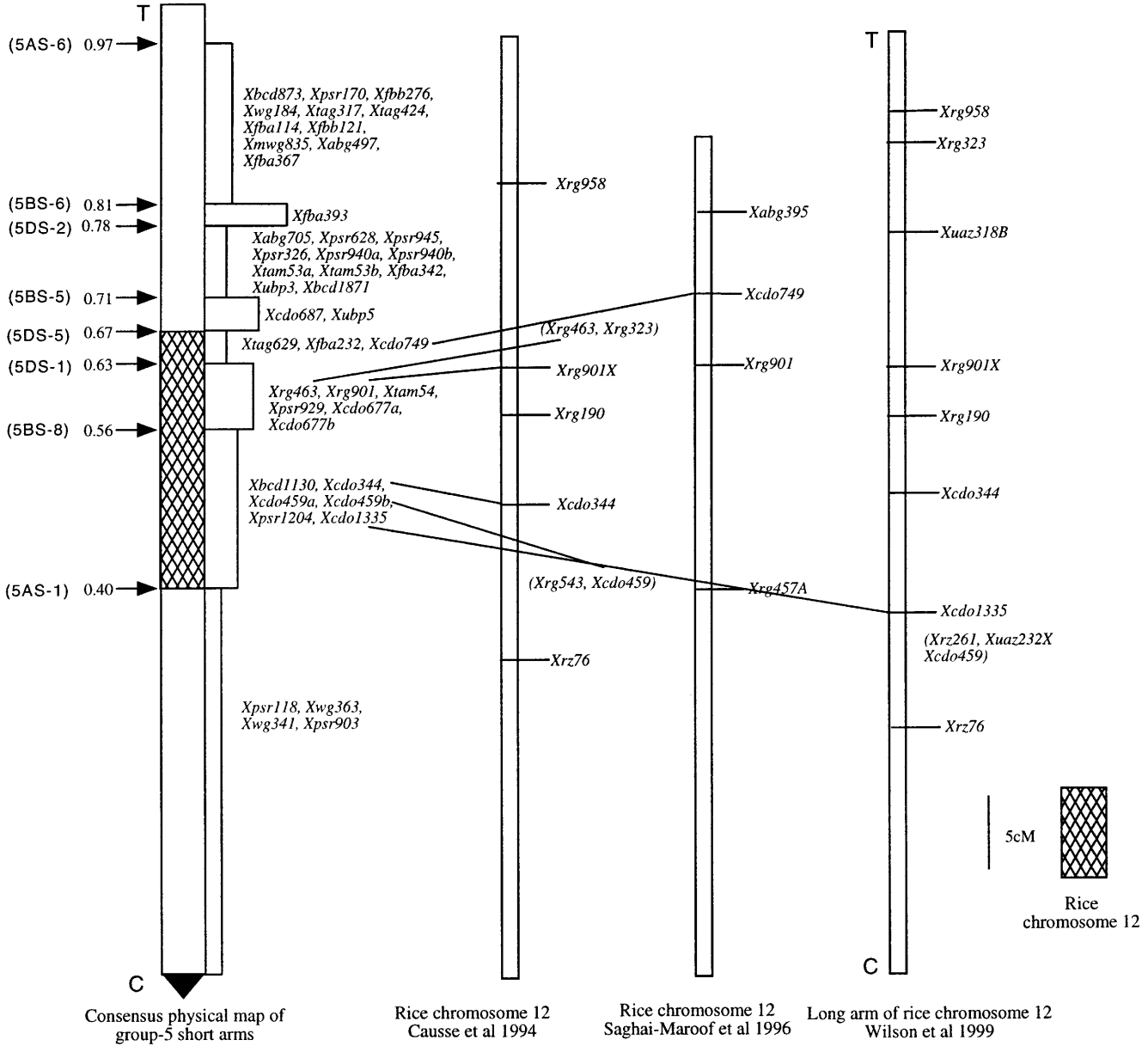

Fig. 6 Comparison of the genetic maps of rice chromosome 12 with the consensus physical map of group-5 short arms. *C* centromere, *T* telomere

some 12 were distributed within the FL 0.40–0.67 region in the consensus map of the group-5 short arm. This region of wheat is syntenic with the long arm of rice chromosome 12.

The dominant male-sterile gene *Ms3* was allocated previously to the short arm of chromosome 5A by cytogenetic analysis. The gene had 3.1% recombination with the centromere. (Maan et al. 1987). For molecular mapping of the *Ms3* gene, the marker WG341 closely linked to *Ms3* genetically (Fig. 5), and physical mapping indicated that it was located in the proximal 40% of the chromosome 5AS. The genetic map of chromosome 5AS revealed that 8 of the 11 markers were clustered near the centromeric region within a genetic distance of 4.3 cM (Fig. 3). The marker loci *Xwg341*, *Xcdo677* and *Xpsr326* were found to be completely linked to the centromere in the genetic map of *Triticum monococcum* L. (Dubcovsky et al. 1996), and the marker loci *Xcdo677* and *Xpsr326* were also tightly linked to centromere in the genetic map of *Ae. tauschii* (Boyko et al. 1999). These results indicate that the region encompassing *Ms3* may be a region of low recombination. Whether a gene is located in a high or low recombination region of the genome is essential information for the map-based cloning of genes in wheat. Cytologically based physical mapping in wheat has shown the distribution between the physical and genetic distances to be unequal (Gill et al. 1996a, b; Faris et al. 2000). Kilobase pair per centimorgans is about 110-fold in a region of low recombination (22 Mb/cM) compared to a recombination hot spot (118 Kb/cM) (Gill et al. 1996a). Besides *Ms3*, only three markers (3/33,

9.1%) mapped in same deletion intervals, indicating that the proximal 40% of 5AS is a marker-poor region. With the large genome and the amount of highly repetitive sequences in wheat, map-based cloning to isolate genes residing near regions of low recombination in wheat will be extremely difficult. This study established the colinearity of markers between segments of the long arm of rice chromosome 12 and the wheat group-5 short arm. Based on information provided by comparative mapping, rice may likely be chosen as the tool with which to isolate *Ms3* from wheat. However, there is only one report from China on a dominant male sterility gene in rice (D.S. Brar, personal communication). Among the mapped recessive male-sterile genes (Khush and Kinoshita 1991) and the photoperiod thermosensitive male-sterile genes (Zhang et al. 1994; Wang et al. 1995; Subudhi et al. 1997; Yamaguchi et al. 1997), none are located on chromosome 12.

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