Theor Appl Genet (2002) 104:1078–1085
DOI 10.1007/s00122-001-0804-1

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Comparison of homoeologous group-6 short arm physical maps of wheat and barley reveals a similar distribution of recombinogenic and gene-rich regions

Received: 20 March 2001 / Accepted: 8 September 2001 / Published online: 6 February 2002

Abstract Eighty two new loci, mapped with 51 DNA clones, were added to the earlier deletion maps of the homoeologous group-6 short arms of hexaploid wheat (*Triticum aestivum* L. em Thell., 2n = 6*x* = 42, AABBDD). There are now 41, 56 and 52 loci mapped on deletion maps of 6AS, 6BS and 6DS, respectively. The linear order of orthologous loci in all three arms appears to be identical. The majority of the loci are located in the distal one-half of the three arms. There seems to be an increased marker/gene density from the centromeric to the telomeric regions in each arm, and the marker density in comparable physical regions is similar on all three maps. Recombination is not uniformly distributed along the chromosome arms; 60% of recombination occurs in the distal one-third of each arm. Recombination increases from the proximal region to the distal end in a nonlinear pattern. The distribution of loci and recombination along each of the three chromosome arms is highly correlated. Comparison of the 6BS deletion map from this study and a 6HS physical map of barley (*Hordeum vulgare* L., 2n = 2*x* = 14, HH) reveals a remarkably similar distribution of recombinogenic and gene-rich regions between the two chromosome arms, suggesting that the distribution patterns of genes may be conserved in the homoeologous group-6 chromosome short arms of wheat and barley. A consensus map of wheat group-6 short arms containing 46 orthologous loci was constructed. Comparison of the consensus map with published linkage maps of Triticeae group-6 chromosome short arms indicates that the linear order of the loci on the maps has been largely conserved. Evidence from this study does not support the existence of a 2BS–6BS reciprocal terminal translocation.

Communicated by J. Dvorak

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Keywords Wheat · Barley · Comparative mapping · Deletion mapping · Recombination

Introduction

The use of rice as a reference genome in the isolation of genes from barley and wheat has shown the limits of colinearity, with the presence of rearrangements within colinear regions (reviewed by Bennetzen 2000). It was proposed that, for map-based cloning of genes, a model species as closely related as possible to the species of interest should be considered (Feuillet and Keller 1999). One example of this notion is the cloning of the candidate gene for the leaf rust resistance locus *Lr10* in common wheat (*Triticum aestivum* L., 2n = 42, AABBDD) using *Triticum monococcum* L. (2n = 14, A^m A^m) as the reference genome (Stein et al. 2000). *T. monococcum* is a close relative of common wheat, and chromosomes of the two species are highly colinear (Dubcovsky et al. 1996).

Barley was also thought to be a desirable candidate of the reference genome for map-based cloning of genes in wheat (Feuillet and Keller 1999). The high colinearity of molecular markers between wheat and barley genomes at the genetic-map level has been well documented (Devos et al. 1993; Van Deynze et al. 1995; Dubcovsky et al. 1996). Construction of physical maps using deletion stocks in wheat (Werner et al. 1992; Hohmann et al. 1994; Delaney et al. 1995a,b; Mickelson-Young et al. 1995; Gill et al. 1996a,b; Weng et al. 2000) or translocation lines in barley (Kunzel et al. 2000) has revealed some common characteristics in the distribution of mapped loci and genetic recombination among these genomes. However, it is not known how similar the physical organization and distribution of orthologous loci is between wheat and barley genomes. Meanwhile, although deletion maps for all 21 chromosomes of wheat are available, the number of loci placed on most maps is very limited.

In earlier work, we reported the construction of deletion maps of group-6 chromosomes of wheat (Weng et

al. 2000). Here we report the placement of 82 more RFLP loci on the earlier maps of the group-6 short arms of wheat. The distribution of genes and recombination along homoeologous group-6 short arms of wheat and barley is compared.

Materials and methods

Plant materials and DNA clones

Fourteen homoeologous group-6 short-arm deletion lines of the hexaploid wheat cv Chinese Spring (CS) were analyzed. Ten of them were homozygous for the deletion-containing chromosomes, three (6AS-2, 6AS-3 and 6DS-5) were heterozygous, and one (6DS-3) was hemizygous. Fraction length (FL) values of 6AS and 6DS deletion lines were based on those posted at http://www.ksu.edu/WGRC. To make the results comparable, FL values of 6BS deletion stocks were converted from the data at the above web site assuming that the FL value of the NOR region is about 0.68 (Gill et al. 1993).

DNA clones known to hybridize to Triticeae homoeologous group-6 chromosome short-arm segments were used. For comparative physical mapping, most of the clones that were employed by Kunzel et al. (2000) in barley 6HS mapping were analyzed. The sources and nature of DNA clones used were described in detail in Weng et al. (2000).

Map construction

DNA manipulation and Southern hybridization follow of the procedure of Weng et al. (2000). Three restriction enzymes (*Hin*dIII, *Eco*RI or *Eco*RV) were used. The 6AS, 6BS and 6DS deletion maps were constructed according to Werner et al. (1992). The method described in Weng et al. (2000) was used to construct a consensus map of the homoeologous group-6 short arms.

Characterization of the distribution of mapped loci and recombination

The percentage of mapped loci per unit of arm length, the percentage of recombination per unit of arm length, and the physical-togenetic ratio were used to characterize a deletion breakpoint-defined region. Calculation of the percentages of mapped loci and recombination per unit of arm length will be described in the next section.

The physical-to-genetic ratio in a chromosomal region is measured by a million base pairs per centiMorgan (Mb/cM). The haploid genome DNA content of common wheat is 16,980 Mb (Bennett and Smith 1976), and the total length of the genetic maps of the ITMI (International Triticeae Mapping Initiative) hexaploid wheat mapping population is about 3,700 cM (Van Deynze et al. 1995; Nelson et al. 1995a, b, c; Marino et al. 1996). Assuming a constant DNA density along the chromosomes, the average physical-to-genetic ratio for the wheat genomes is about 4.6 Mb/cM. The physical length and arm ratio data of a chromosome was used in calculating the Mb/cM values in deletion breakpoint-defined regions. The total length of all 21 chromosomes at mitotic metaphase is about 235.4 μm, and the physical length for 6AS, 6BS and 6DS was 4.67 μm, 5.77 μm and 4.5 μm, respectively (Gill et al. 1991). The DNA content per μm is thus 72.13 Mb.

Results and discussions

Deletion maps of 6AS, 6BS and 6DS

In the present study, 71 loci were mapped to the three group-6 short arms using 42 new clones and 11 new loci were mapped by nine clones used previously (Weng et al. 2000). On average, 1.69 loci were mapped per clone. Twenty three, 24, and 24 loci were mapped in 6AS, 6BS and 6DS, respectively. Of the 42 clones, 14 clones each detect three orthologous loci, 11 clones each detect two orthologous loci, and 17 clones each detect only one locus.

The 82 loci from this study were combined with those on the earlier maps of Weng et al. (2000), bringing the total number of loci on the three deletion maps to 149, with 41, 56 and 52 loci on 6AS, 6BS and 6DS, respectively (Fig. 1). Of the 149 total loci mapped by 77 clones, 28 are not present on any published linkage map of the homoeologous group-6 short arms of common wheat, durum wheat (*Triticum turgidum* (L.) Thell. covar. *durum* (Desf.) MK.), *Triticum monococcum* or *Aegilops tauschii* (Coss.) Schmal. (Hart 1997; Blanco et al. 1998; Boyko et al. 1999). However, some loci on these linkage maps were not identified in this study. Locations of three loci, *Xcdo534-6AS*, *Xfba344-6BS* and *XksuI28-6DS*, mapped in Weng et al. (2000), were corrected and placed in new positions based on the results of the present study.

As shown in Fig. 1, of the 15 regions on the three short-arm deletion maps defined by 14 deletion breakpoints, 12 were molecularly tagged by mapped loci, with four in each of the three arms. A characteristic common to the three deletion maps is the uneven distribution of mapped loci. This can be expressed by the percentage of mapped loci per unit of physical length in the deletion breakpoint-defined regions. For example, the region distal to deletion breakpoint 6AS-4 (the FL value is 0.67) is physically about 33% of the short arm, but 68.3% (28/41) loci were mapped within this region. Assuming the physical length of 6AS is 100 units, then the ratio of mapped loci per unit of arm length in this region is 2.07 (68.3%/33%). The ratios of mapped loci per unit of arm length for all deletion breakpoint-defined regions are summarized in Table 1. Three deletion lines, 6AS-5, 6BS-8 and 6DS-6, were not considered in the calculation because their FL values are uncertain.

From Table 1, it is clear that in each arm the density of mapped loci per unit of arm length increases from the centromeric region to the distal end, which seems to be nonlinear. On each of the three group-6 short-arm maps, while about 60% of loci were in the distal one-third, 5% or less of the mapped loci were in the proximal one-third of the chromosome arms. This distribution pattern of mapped loci seems to be true on the deletion maps of groups 1, 5 and 6 chromosome arms of wheat where an adequate number of loci has been placed (Gill et al. 1996a,b; Faris et al. 2000; Weng et al. 2000). However, a significant portion (18% to 36%) of loci has been placed

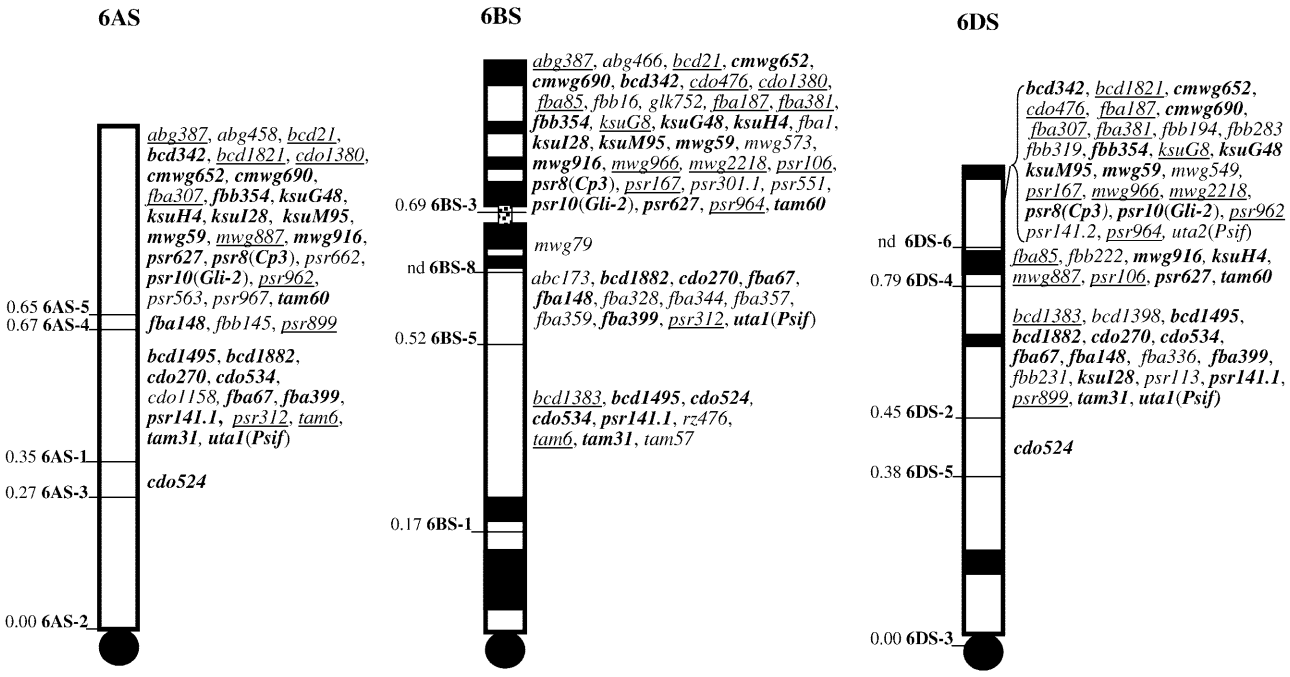

Fig. 1 Deletion maps of wheat chromosome arms 6AS, 6BS and 6DS. The *black circles* indicate centromeres. Deletion-line breakpoints and fraction lengths (*FLs*) are indicated, respectively, by the *horizontal line to the right* and the *numbers to the left* of each deletion-line symbol. The breakpoint positions are drawn appropriately to scale. The prefix 'X' has been omitted in the name of each locus on each map. *Darkened areas* within chromosome arms are C-bands (Endo and Gill 1996). Symbols for orthologous loci mapped in 6AS, 6BS and 6DS are in *boldface type*, those for orthologous loci mapped in two of the three arms are *underlined*, and those for loci mapped in one chromosome arm only are in *plain text*. The *dotted block* on the 6BS map is the NOR. *nd* = not determined

in the proximal one-fourth of the centromeric regions of all six group-7 chromosome arms (Hohmann et al. 1994).

Forty percent of the clones (31/77) used for constructing the three arm maps were cDNAs or known-function clones. The majority of the remainder are genomic *Pst*I probes, most of which are thought to represent genes (Michalek et al. 1999). Therefore, the uneven distribution of mapped loci may reflect the distribution of genes along the chromosome arms. However, because of the limited number of deletion lines used in this study, it is not clear whether the increased density of markers or genes fiom the centromeric region to the distal end is disrupted by gene-poor regions. Some mapping studies of wheat and barley chromosomes (e.g., Hohmann et al. 1994; Faris et al. 2000; Kunzel et al. 2000; Weng et al. 2000) have indicated the existence of marker-rich regions that are separated by marker-poor ones. In this study, the segment delimited by deletion breakpoints 6BS-3 and 6BS-8 seems to be a marker-poor region (Fig. 1), which is near the nucleolus organizer region (NOR) and is rich in C-banded heterochromatin (Endo and Gill 1996). It is possible that more gene-rich and gene-poor sub-regions may be identified if more deletion lines are available within each deletion breakpoint-defined region of the three short arms.

Table 1 Distribution of mapped loci and genetic recombination along 6AS, 6BS and 6DS

Arm	BP-defined regions[a]	% Of arm length	Ratios of mapped loci[b]	Ratios of recombination[b]	Estimated Mb/cM
6AS	Distal to 6AS-4	33	2.07	2.23	1.76
	6AS-4 to 6AS-1	32	0.91	0.60	6.53
	6AS-1 to 6AS-3	8	0.31	0.00	N/A[c]
	Proximal to 6AS-3	27	0.00	0.00	N/A[c]
6BS	Distal to 6BS-3	31	1.96	1.75	1.11
	6BS-3 to 6BS-5	17	1.37	0.66	11.8
	6BS-5 to 6BS-1	35	0.46	0.51	15.3
	Proximal to 6BS-1	17	0.00	0.00	N/A[c]
6DS	Distal to 6DS-4	21	3.11	3.02	1.29
	6DS-4 to 6DS-2	34	0.96	0.51	7.61
	6DS-2 to 6DS-5	7	0.27	0.00	N/A[c]
	Proximal to 6DS-5	38	0.00	0.00	N/A[c]

[a] BP: deletion breakpoint
[b] In per unit of physical arm length, assuming each arm has 100 units of physical length. See text
[c] N/A: data not available because no recombination occurs in this region

A 2BS–6BS reciprocal translocation was hypothesized by Devos et al. (1993) in a RFLP mapping study based on: (1) mapping of RFLP loci near the distal ends of the linkage maps of 2AS and 2DS with five clones (PSR566, PSR649, PSR908, PSR928, PSR933) that did not detect any 2BS locus, and (2) mapping of a locus near the distal end of the 2BS linkage map with clone PSR899 that also detects loci located in the distal ends of 6AS and 6DS. Evidence supporting the translocation of a 2BS fragment to the distal end of 6BS was not found in the present study.

In this study, the single-copy cDNA clone PSR899 detected one locus each in 6AS and 6DS, and none in 6BS; however, *Xpsr899-6A* and *Xpsr899-6D* were deletion-mapped in the interstitial regions of both arms (Fig. 1). In linkage mapping, loci detected by clone PSR899 were mapped in 6AS and/or 6DS of common wheat (Jia et al. 1996; Marino et al. 1996) and durum wheat (Blanco et al. 1998; Du and Hart 1998); but they were not always mapped at the most-distal regions on linkage maps (Marino et al. 1996; Du and Hart 1998).

If the reciprocal 2BS/6BS translocation does exist, loci mapped in the region distal to loci detected by clone PSR899 would be missing from the 6BS deletion and linkage maps. Meanwhile, at least some loci that are orthologous to the loci mapped in the distal ends of both 2AS and 2DS should be mapped at the distal end of 6BS. From Fig. 1, it is obvious that most loci mapped in 6AS and 6DS that are distal to *Xpsr899-6AS* or *Xpsr899-6DS* have their orthologs in 6BS at comparable locations (distal to breakpoint 6BS-3). No loci have been detected in 2BS by clones such as BCD1821, FBA307 and MWG887 (see Fig. 1) that detected loci in 6AS and 6DS, but not in 6BS (Hart 1997). Clones CDO456, PSR649, PSR908, PSR928 and PSR933 that detected loci at the distal ends of 2AS and 2DS, but not in 2BS (Devos et al. 1993; Nelson et al. 1995a), were analyzed in this experiment. None of them detected any locus in the group-6 chromosome short arms using two enzymes, *Eco*RI or *Hin*dIII (data not shown).

Comparison between genetic and deletion maps of 6AS, 6BS and 6DS

The group-6S deletion maps of this study and the corresponding genetic maps of Marino et al. (1996) were compared. Comparison of the 6BS genetic and deletion maps is shown in Fig. 2 (A and B). Fifteen orthologous loci are shared between the two maps and the orders of all but one, *Xfba359-6BS* that was mapped in the centromeric region, are colinear.

Most loci (19 of 22) on the linkage map of 6BS are located in the proximal one-half of the map of the arm. In contrast, they are physically located in the distal one-half of the arm. Based on the loci shared between the two maps, about 54% of the recombination in the short arm (29 cM of a total 54 cM) occurs in the satellite region, which accounts for 31% of the arm 6BS. Therefore, the ratio of recombination per unit of arm length in the region distal to deletion breakpoint 6BS-3 is 1.75 (54%/31%), assuming the total physical length of 6BS is 100 units. The average DNA content for the whole genome of wheat is about 72.13 Mb/μm, so the DNA content of the 6BS satellite region (l.79 μm) is 129 Mb. The physical-to-genetic ratio in this region is estimated to be 4.45 Mb/cM (129 Mb/29 cM) (1.11 Mb/cM in Table 1, see below for explanation). The ratios of recombination per unit of arm length and Mb/cM ratios for all deletion breakpoint-defined regions were estimated and are listed in Table 1.

It can be seen from Table 1 that recombination per unit of physical length increases from the proximal region to the distal end in each arm. This increase seems to be nonlinear. While the distal ends are highly recombinogenic, there is practically no recombination in the proximal one-third of the three arms. In 6BS, 54% of recombination occurs in the distal 31%. By comparing Fig. 1 and Marino et al. 1996, it was revealed that 74% (63/85.5) and 64% (53/83.5) of recombination occurs in the distal 35% and 21% of 6AS and 6DS, respectively. The distribution of mapped loci and recombination seems to be highly correlated. Based on the data in Table 1, the correlation coefficient between the percentages of mapped loci and recombination in breakpoint-defined regions of each arm is 0.98, 0.92 and 0.99 for 6AS, 6BS and 6DS, respectively. This correlation has also been found in some other mapping studies in wheat and barley (e.g., Kunzel et al. 2000; Weng et al. 2000), implying that most recombination in a chromosome arm probably occurs in gene-rich regions.

Recombination and loci are absent from the centromeric regions; however, this does not mean that there are no active genes around the centromeres. In *Arabidopsis thaliana*, of the total of 25,498 genes identified, at least 47 expressed genes were found in the genetically defined centromeres. Some of these genes reside in islands of unique sequence flanked by repetitive arrays (AGI 2000).

The physical-to-genetic ratios in the distal regions of 6AS and 6DS have been estimated to be 1.76 and 1.29 Mb/cM, respectively (Table l), which are well below the whole-genome average of 4.6 Mb/cM, suggesting that these regions are highly recombinogenic. Nevertheless, the Mb/cM ratios in Table 1 may still be underestimates. First, some deletion-mapped loci may be outside of the linkage map intervals used for calculation (Marino et al. 1996). Second, each molecularly tagged region is still very large, and mapped loci in these regions should be further placed into smaller bins. For example, the estimated physical-to-genetic ratio in the satellite region of 6BS is about 4.45 Mb/cM. However, this region is usually heavily C-banded (Gill et al. 1991), and the C-banded constitutive heterochromatic regions are thought to be composed mainly of repetitive DNA sequences and lacking in recombination (Flavell et al. 1987). Recombination may also be suppressed in the vicinity of the ribosomal RNA gene locus within the NOR

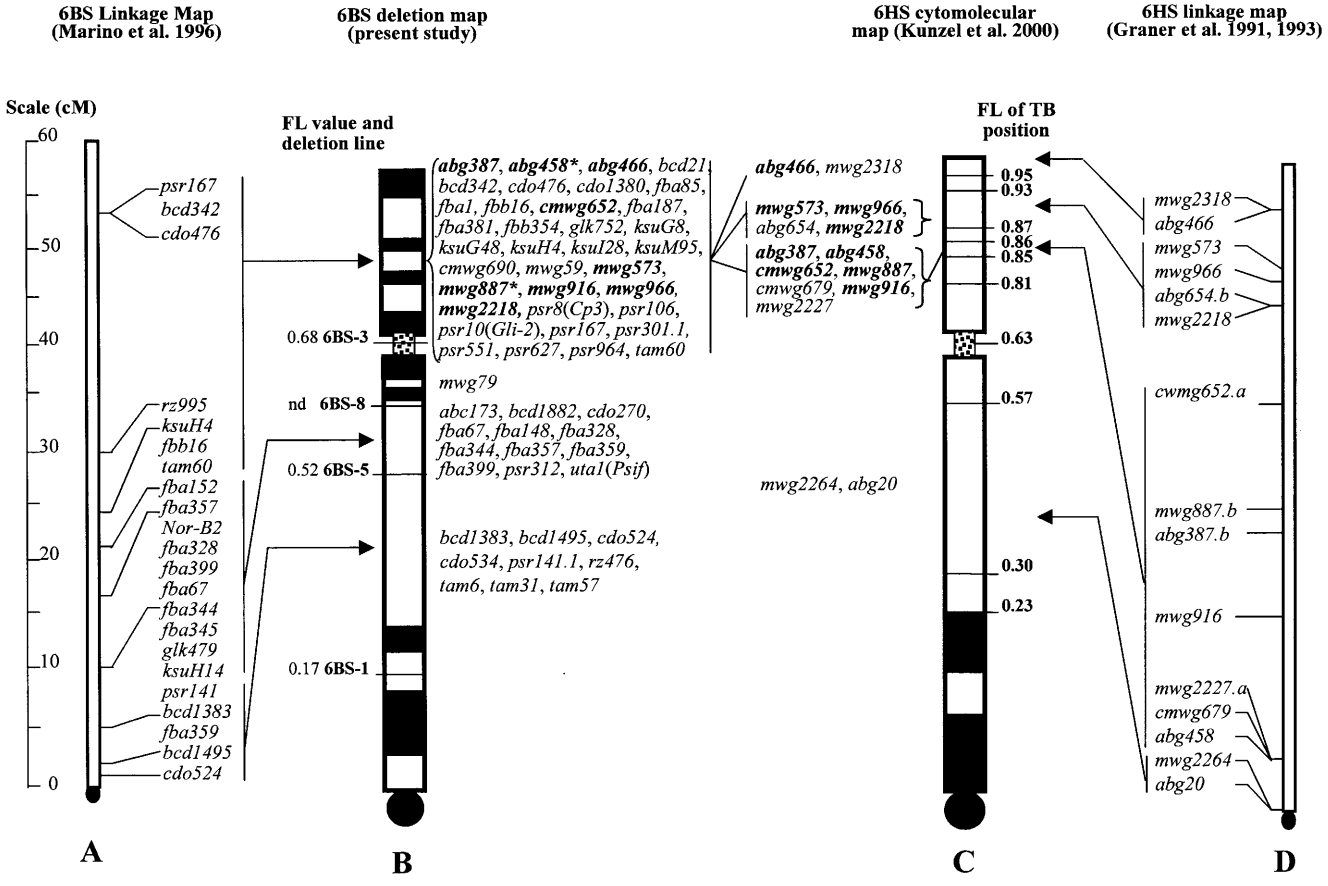

Fig. 2 Comparison of genetic (**A**) and deletion (**B**) maps of wheat 6BS, physical (**C**) and genetic (**D**) maps of barley 6HS. **A** was redrawn from Marino et al. (1996). **C** and **D** were redrawn from Kunzel et al. (2000). All maps were drawn to scale. The prefix 'X' has been omitted in the name of each locus on each map. *Solid lines* between **B** and **C** connect colinear loci. Regions pointed to by *arrows* connecting maps **A** and **B**, as well as **C** and **D**, are where loci on linkage maps were physically mapped. *Vertical bars* delimit blocks of loci mapped on the linkage or physical maps. *Darkened circles* desig**C**nate centromeres. Orthologous loci on maps **B** and are in *boldface type*. In **B** and **C**, *dotted blocks* designate NORs; *darkened blocks* designate C-bands (**B**) or N-bands (**C**). *Asterisks* in **B** designate loci which were not mapped in 6BS and whose locations were inferred from Fig. 1. *TB* = translocation breakpoints

of 6BS (Luo et al. 1998). Therefore, just as found in the satellite regions of wheat chromosome 1BS (Gill et al. 1996a) or barley 6HS (Kunzel et al. 2000, see below), it is possible that the 58% of total recombination in 6BS may occur in less than one-fourth of the satellite region. If this is true, the physical-to-genetic ratio will be roughly 1.11 Mb/cM, which is comparable to the Mb/cM estimate in the 6AS and 6DS distal ends.

Comparison of physical maps of wheat 6BS and barley 6HS

Recently, cytogenetically based physical maps of the seven barley chromosomes were constructed using translocation stocks (Kunzel et al. 2000). The physical map and a linkage map of 6HS were compared with the deletion map of 6BS fiom this study (Fig. 2). Both 6BS and 6HS have a NOR, and the satellite attached to each arm comprises about one-third of the physical arm length (Gill et al. 1991; Jensen and Linde-Laursen 1992). The genetic length of the 6BS and 6HS linkage maps is also comparable (53.5 cM vs 61.6 cM) (Graner et al. 1991, 1993; Marino et al. 1996).

The distribution of mapped loci along arms 6HS and 6BS is very similar (Fig. 2B, C). Eighty seven percent (13/15) and 64% (34/56) of loci were mapped in the satellite region of 6HS and 6BS, respectively. All nine orthologous loci shared between the two maps are in the satellite region of each arm and are colinear. As shown in Fig. 2, the distribution of recombination is highly uneven in both 6BS and 6HS. While 87% (54.2 of 61.6 cM) of recombination occurs in the satellite region of 6HS, the satellite region of 6BS accounts for 54% (29/53.5) of all the recombination in this arm.

If the satellite region of 6HS is treated as a whole, the ratios of mapped loci and recombination per unit of arm length are 2.34 and 2.35, respectively, which are comparable with those of the distal ends of the three group-6 short arms of wheat (Table 1). The DNA content per haploid genome of barley is about 5,350 Mb (Bennett and Smith 1976). The total length of the seven chromosomes of barley at mitotic metaphase is about 64.6 μm, and the satellite region is estimated to be 1.5 μm (Jensen

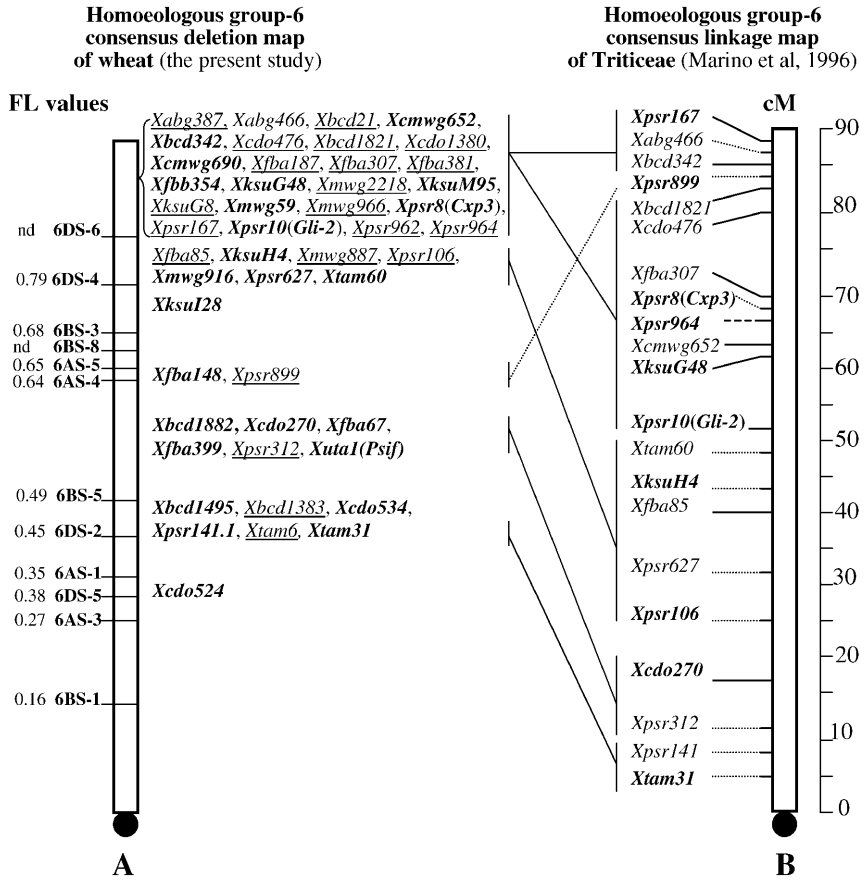

Fig. 3 Consensus deletion map of the group-6 chromosome short arms of hexaploid wheat (**A**) from this study, and comparison with the consensus *Triticeae* group-6S linkage map (**B**) from Marino et al. (1996). Both maps are drawn to scale. *Solid lines* between the maps connect colinear loci and the *dashed line* between the maps connects loci mapped with the same clone that are not colinear. *All symbols* in **A** have the same meaning as in Fig. 1. In **B**, the *black circle* designates the centromere. *Boldface type* designates markers whose orientation relative to each other was determined across two or more Triticeae genomes. Loci connected to the map with *solid lines* were placed on the hexaploid wheat 6AS linkage map of Marino et al. (1996) at a LOD score ≥ 3.0

and Linde-Laursen 1992). Based on these data, the physical-to-genetic ratio within the 6HS satellite region is calculated to be 2.29 Mb/cM, but it would be 0.73 Mb/cM if only the three marker-tagged regions were considered (see Fig. 2C). The average physical-to-genetic ratio for the whole barley genome is almost the same as wheat (4.4 Mb/cM) (Kunzel et al. 2000). This estimation of the physical-to-genetic ratio suggests that some sub-regions within the 6HS satellite may be more recombinogenic than others.

The resolution of the group-6s deletion maps generated in this study is relatively low. The number of loci mapped on the physical and linkage maps of barley 6HS is also very limited (Fig. 2C, D), which may be one possible reason leading to the differences in the calculated ratios of mapped loci and recombination per unit of arm length between 6BS and 6HS. Nevertheless, the above comparison does indicate that the order of loci in homoeologous group-6 short arms of wheat and barley is highly colinear, and the distribution of marker-rich, recombinogenic regions is quite similar.

The nine orthologous loci shared between the 6BS and 6HS physical maps (Fig. 2B, C) were mapped in the satellite of 6BS. In 6HS, they were further mapped into three non-consecutive bins which together make up 12% physical length of the short arm (or about one-third of the satellite region) (Fig. 2C). This gives us some clue as to the locations of the loci mapped in the satellite region of 6BS. It is possible that they may be further mapped into two or more smaller bins if more deletion stocks in this region become available.

Consensus deletion map of homoeologous group-6 short arms of wheat

Because many clones detected two or three orthologous loci among the three group-6 chromosome short arms and the loci appear to be colinear, it is possible to construct a consensus deletion map of the three arms. It contains a total of 46 orthologous loci from the three deletion maps (Fig. 3A). This consensus map provides better resolution in the relative positions of mapped orthologous loci than each individual map does. The group-6S consensus map was compared with the Triticeae homoeologous group-6S consensus linkage map of Marino et al. (1996) (Fig. 3B). Of 21 shared loci between the two maps, all but one (*Xpsr899*) are colinear (Fig. 3). This was also true when the order of loci was compared between this consensus map and other homoeologous group-6S linkage maps, such as the consensus genetic map of common wheat (Jia et al. 1996) and barley (Qi et al. 1996), and the 6A and 6B linkage maps of durum wheat (Du and Hart 1998) (data not shown).

Although constructed according to the relative order of orthologous loci in the three chromosome arms rather than FL values (Weng et al. 2000), the resulting consensus map shows a quite consistent order of FL values (in-

creasing FL values from proximal to distal ends) with the exceptions of 6AS-1/6DS-5 and 6AS-4/6AS-5 (Fig. 3A). Deletion breakpoint 6BS-8 (its FL value is 0.56 according to http://www.ksu.edu/WGRC/) is probably also out of order. The reversed order of 6AS-4 and 6AS-5 is based on deletion mapping data, and may be attributed to the limited resolution power of the light microscope in measuring FL values with only a 0.01 difference (Weng et al. 2000). The positions of breakpoints 6BS-8 and 6AS-1 on the consensus map are reasonable because 6BS is the longest (5.77 μm) of the three arms, and 6AS is slightly longer than 6DS (4.67 μm vs 4.5 μm) (Gill et al. 1991). As shown in Fig. 3A, 65% (30/46) of the orthologous loci were located in the distal 20% of the consensus map. Figure 3 was drawn to scale, so this suggests that the locations containing orthologous loci are comparable and highly conserved among the three group-6 chromosome short arms.

Acknowledgments We are grateful to Dr. B. S.Gill at Kansas State University (Manhattan, Kan.) for supplying us with seed stocks of the deletion lines used in this study. We are in debt to Drs. Gary E. Hart of Texas A & M University (College Station, Tex.), Wanlong Li of Kansas State University (Manhattan, Kan.) and two anonymous reviewers for critical comments and suggestions of the manuscript. We thank Mr. Gary Peterson for technical help. This research was supported by the Texas Agricultural Experiment Station.

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