Origin, structure, and behavior of a highly rearranged deletion chromosome 1BS-4 in wheat

Lili Qi, Bernd Friebe, and Bikram S. Gill

Abstract: Wheat (*Triticum aestivum* L.) deletion (del) stocks are valuable tools for the physical mapping of molecular markers and genes to chromosome bins delineated by 2 adjacent deletion breakpoints. The wheat deletion stocks were produced by using gametocidal genes derived from related *Aegilops* species. Here, we report on the origin, structure, and behavior of a highly rearranged chromosome 1BS-4. The cytogenetic and molecular marker analyses suggest that 1BS-4 resulted from 2 breakpoints in the 1BS arm and 1 breakpoint in the 1BL arm. The distal segment from 1BS, except for a small deleted part, is translocated to the long arm. Cytologically, chromosome 1BS-4 is highly stable, but shows a unique meiotic pairing behavior. The short arm of 1BS-4 fails to pair with a normal 1BS arm because of lack of homology at the distal ends. The long arm of 1BS-4 only pairs with a normal 1BS arm within the distal region translocated from 1BS. Therefore, using the 1BS-4 deletion stock for physical mapping will result in the false allocation of molecular markers and genes proximal to the breakpoint of 1BS-4.

Key words: Triticum aestivum, wheat, deletion–translocation, physical mapping.

Résumé : Les collections de délétions chez le blé (*Triticum aestivum* L.) constituent des outils précieux pour la cartographie physique de marqueurs moléculaires et de gènes en permettant d'assigner ceux-ci à des segments chromosomiques définis par 2 points de cassure adjacents. Ces délétions chez le blé ont été produites à l'aide de gènes gamétocides provenant d'*Aegilops* apparentés. Les auteurs rapportent ici l'origine, la structure et le comportement d'un chromosome IBS-4 très fortement remanié. Les analyses cytogénétique et à l'aide de marqueurs moléculaires suggèrent que IBS-4 résulte de 2 cassures au sein de IBS et d'une cassure dans le bras IBL. Le segment distal de IBS, à l'exception d'une petite délétion, a été transloqué sur l'autre bras. Un examen cytologique révèle que le chromosome IBS-4 est très stable mais qu'il présente un appariement méiotique unique. Le bras court de IBS-4 ne s'apparie pas avec un bras IBS normal en raison du manque d'homologie aux extrémités distales. Le bras long de IBS-4 s'apparie uniquement avec un bras IBS normal au sein de la région transloquée. Ainsi, la cartographie physique à l'aide de cette lignée les auteurs induiront en erreur quant à l'emplacement de marqueurs et de gènes qui sont proximaux à la cassure chez IBS-4.

Mots clés : Triticum aestivum, blé, délétion-translocation, cartographie physique.

[Traduit par la Rédaction]

Introduction

Gametocidal (*Gc*) genes introduced from related *Aegilops* species into common wheat, *Triticum aestivum* L. ($2n = 6x = 42$, AABBDD), are known to induce chromosome breaks in the 1st postmeiotic interphase in gametophytes lacking them (Finch et al. 1984; Endo 1988, 1990; Nasuda et al. 1998). *Gc* genes were used to develop deletion stocks in wheat (Endo and Gill 1996); barley, *Hordeum vulgare* L. ($2n = 2x = 14$) (Shi and Endo 1999, 2000); and rye, *Secale cereale* L. ($2n = 2x = 14$, RR) (Friebe et al. 2000). These deletion stocks are valuable tools for studies on basic chromosome biology, such as the healing of broken ends (Werner et al. 1992; Friebe et al. 2001) and physical genome mapping (Qi et al. 2003; Qi et al. 2004). The majority of the deletions originated from a single break followed by the loss of the distal segment and healing of the broken end by the addition of telomeric repeats, whereas other deletions were shown to be more complex (Ogihara et al. 1994; Hohmann et al. 1995; Qi et al. 2003). The use of such complex deletion stocks in mapping studies can result in the false allocation of markers and genes along the chromosome length. Here, we document the complex breakage–deletion–fusion events in the origin of deletion–translocation chromosome 1BS-4, which may explain some of the mapping discrepancies reported for the 1B deletion bin map (Sandhu et al. 2001; Sandhu and Gill 2002; Dilbirligi et al. 2004; Wheat expressed sequence tag (EST) mapping project (http://wheat.pw.usda.gov/cgi-bin/westsql/map_locus.cgi)).

Received 18 October 2004. Accepted 18 February 2005. Published on the NRC Research Press Web site at http://genome.nrc.ca on 6 August 2005.

Corresponding Editor: J.P. Gustafson.

L. Qi, B. Friebe,[1] and B.S. Gill. Wheat Genetics Resource Center, Department of Plant Pathology, Throckmorton Plant Sciences Center, Kansas State University, Manhattan, KS 66506-5502, USA.

[1]Corresponding author (e-mail: friebe@ksu.edu).

Materials and methods

Genetic stocks

The genetic stocks used are listed in Table 1, including 3 group-1 nullisomic–tetrasomic (NT) lines (Sears 1954,

 doi: 10.1139/G05-020

Table 1. List of wheat genetic stocks used in the study.

TA No.*	Stock	Fraction length†
3008	CS	—
3258	N1AT1D	—
3260	N1BT1D	—
3262	N1DT1B	—
3112	Dt1BS	—
3113	Dt1BL	—
4512L10	1BS-10	0.50
4512L9	1BS-9	0.84
4550L3	1BS-2/7DL-3	1.06
4544L4	1BS-19/6DS-4	0.31‡
4533L9	1BS-18/4DL-9	0.50‡
4524L9	1BS-4/3BS-9	0.52‡
4512L4	1BS-4	0.52‡
4513L6	1BL-6	0.32
4513L1	1BL-1	0.47
4541L8	1BL2/6AL8	0.69
4534L10	1BL-3/5AS-10	0.85

*WGRC collection accession numbers.
†In double deletion lines, the fraction length values related to the deletions of chromosome 1B are listed.
‡The deletion breakpoint is located in the satellite of the 1BS arm.

1966), 2 ditelosomic (Dt) lines (Sears and Sears 1978), 10 deletion (del) lines of chromosome 1B (Endo and Gill 1996), and the hexaploid wheat cultivar *Triticum aestivum* L. 'Chinese Spring' (CS). Six 1B deletions are also present in deletion stocks involving different wheat chromosomes (double deletions) (TA4550 L3, TA4544 L4, TA4533 L9, TA4524 L9, TA4541 L8, and TA4534 L10). An extra pair of 1BL telosomes is present in TA4533 L9 (del1BS-4/del3BS-9). The fraction length (FL) value of each deletion identifies the position of the breakpoint from the centromere relative to the length of the complete arm. The FL values involving SAT chromosome arms 1BS and 6BS were calculated independently for the region between the centromere and the secondary constriction, and for the satellite. Thus, deletions with a breakpoint within the secondary constrictions have FL values greater than 1 (Table 1, del1BS-2). All genetic stocks listed in Table 1 except del1BS-4 (TA4512 L4) were verified previously by RFLP analysis with more than 500 EST clones (Qi et al. 2003). All genetic stocks are maintained at the Wheat Genetics Resource Center at Kansas State University, Manhattan, US.

Cytogenetic analysis

The deletion stock 1BS-4 (TA4512 L4) was crossed with Dt1BS (TA3112) and Dt1BL (TA3113), and meiotic metaphase I pairing was analyzed in pollen mother cells (PMCs) after C-banding. C-banding and chromosome identification were according to Gill et al. (1991). Table 2 shows metaphase I pairing frequencies in different testcross combinations involving wheat chromosomes 1B and 1BS-4 (TA4512 L4), telosomes t1BS and t1BL.

RFLP analysis

Genomic DNAs were isolated from selected genetic stocks and digested with restriction enzymes *Eco*RI and *Hin*dIII. The RFLP and EST clones used are listed in Table 3. These clones were kindly provided by Dr. M.E. Sorrells (BCD and CDO clones) (Cornell University Ithaca, NY, USA) and Dr. O. Anderson (EST clones) (USDA-ARS-WRRC Albany, California, USA). Protocols for Southern hybridization were as described by Qi et al. (2003).

Results and discussion

The deletion chromosome 1BS-4 (identified as del1BS-4, hereafter) previously was reported to be present in 2 deletion stocks, TA4524 L9 and TA4512 L4 (Endo and Gill 1996). The C-banding pattern of del1BS-4 was identical in both lines, indicating a common origin. The distal 48% of the satellite was missing, including the terminal C-band 1BS3.4, band 1BS3.3, and part of the distal C-band 1BS3.2 (Figs. 1*a* and 1*b*; C-band nomenclature is according to Gill et al. 1991). The size of C-band 1BS3.2 in chromosome 1BS-4 was smaller than the corresponding C-band in a normal 1BS arm, suggesting that this deletion arose from a break within region 1BS3.2. The long arm of del1BS-4 also was aberrant (Fig. 1*b*). Endo and Gill (1996) also reported that the long arm of del1BS-4 was shorter than the normal 1BL arm. The C-banding pattern of the proximal half of the long arm of chromosome 1BS-4 up to C-band 1BL2.3 was similar to that of a normal 1BL arm. However, the telomeric C-band in the long arm of 1BS-4 is larger than the 1BL2.5 C-band of a normal 1BL arm (Fig. 1*b*), which suggested that this deletion arose from a break within the region 1BL2.4 and concomitant loss of the distal acentric segment of 1BL2.4 to the telomere. The telomeric C-band in the long arm of del1BS-4 was probably translocated from either the 1BS or a different wheat chromosome arm.

To test this hypothesis, we analyzed meiotic metaphase I pairing in testcrosses of del1BS-4 and the Dt1BS (t1BS) and Dt1BL (t1BL) stocks. In the control, crosses with normal CS, t1BS maintained MI chiasmate association with its homologous 1BS arm of 1B in 87% of PMCs. The t1BL formed chiasmate association with 1BL arm of 1B in 97% of PMCs (Table 2). In homozygous del1BS-4 plants, the short and long arms of chromosome 1BS-4 paired in 76% and 71% of the PMCs, respectively. In comparison, we observed no chiasmate association of t1BL with either arm of del1BS-4 in 147 PMCs. The data confirmed the aberrant nature of 1BL arm of del1BS-4. Surprisingly, t1BS formed chiasmate association with aberrant 1BL arm of del1BS-4 in 56% of PMCs as a heteromorphic rod bivalent (Figs. 1*c* and 1*d*). Thus, our meiotic pairing data suggested that the distal region of the long arm of del1BS-4 actually was derived from the distal region of the satellite of the 1BS. The telomeric C-band in the long arm of del1BS-4 actually corresponded to band 1BS3.4 (Fig. 1*a*). The t1BS did not pair with remnant 1BS arm of del1BS-4, because homology at the telomeric ends is required for pairing (Qi et al. 2002).

To further verify the cytological data, ESTs previously mapped to different chromosome bins of 1B (http://wheat.pw.usda.gov/cgi-bin/westsql/map_locus.cgi) were selected to analyze the structure of 1BS-4 (Table 3). Five ESTs (BE445834, BE446240, BE442876, BE443905, and BE445579) mapping to bin 1BL1–0.47–0.69 were present in all 3 stocks, del1BS-4, del1BS-4/del3BS–9, and del1BS–18. One EST (BF200980) mapping to the bin 1BL1–0.47–0.69

Table 2. Metaphase I pairing frequencies in different testcross combinations involving wheat chromosomes 1B and 1BS-4 (TA4512 L4), telosomes t1BS and t1BL. PMC, pollen mother cell.

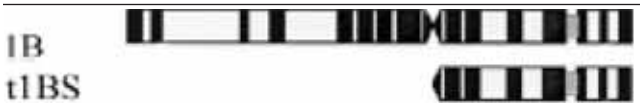
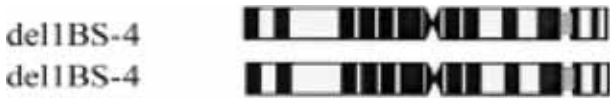
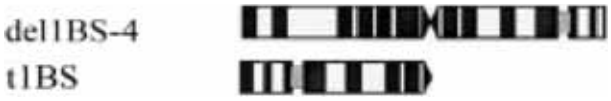
Pairing combination	No. of PMCs	Metaphase I pairing frequency (%)		Reference
		1BS	1BL	
	—	87	0	Dvorak and McGuire (1981)
	—	0	97	Gill and Friebe (1998)
	46	76	71	Present study
	64	0	56	Present study
	147	0	0	Present study

Table 3. List of clones used to test the structure of del1BS-4. –, specific 1B fragment missing; +, specific 1B fragment present.

Clones	Location	Enzymes	del1BS-18 $2n$ = 20″ + 1BS-18″	del1BS-4/del3BS-9* $2n$ = 19″ + 1BS-4″ + t1BL″ + 3BS-9″	del1BS-4 $2n$ = 20″ + 1BS-4″
BF474758	1BS.sat18–0.50–1.00[†]	*Eco*RI	–	–	–
BF291787	1BS.sat18–0.50–1.00	*Eco*RI	–	–	–
BE399213	1BS.sat18–0.50–1.00	*Eco*RI	–	–	–
BCD98	1BS.sat18–0.50–1.00	*Hin*dIII	–	–	–
CDO99	1BS.sat18–0.50–1.00	*Hin*dIII	–	–	–
CDO580	1BS.sat18–0.50–1.00	*Eco*RI	–	+	+
BE490041	1BS.sat18–0.50–1.00	*Eco*RI	–	+	+
BE445834	1BL1–0.47–0.69	*Eco*RI	+	+	+
BE446240	1BL1–0.47–0.69	*Hin*dIII	+	+	+
BE442876	1BL1–0.47–0.69	*Eco*RI	+	+	+
BE443905	1BL1–0.47–0.69	*Eco*RI	+	+	+
BE445579	1BL1–0.47–0.69	*Eco*RI	+	+	+
BF200980	1BL1–0.47–0.69	*Eco*RI	+	+	–
BE444305	1BL2–0.69–0.85	*Eco*RI	+	+	–
BE443020	1BL2–0.69–0.85	*Eco*RI	+	+	–

*Del3BS-9/1BS-4 line has a pair of 1BL telocentric chromosomes.
[†]Chromosome bin is delineated by 2 adjacent deletion breakpoints. For distal deletions, the bin is delineated by a deletion breakpoint and the terminus.

and 2 ESTs (BE444305 and BE443020) mapping to the chromosome bin 1BL2–0.69–0.85 were missing in del1BS-4 but present in del1BS-18 and del1BS-4/del3BS-9 that has a t1BL (Fig. 2*a*). Previously, the EST BF200980 was located in the bin 0.61–0.69 in the consensus physical map of homoeologous group 1 (Peng et al. 2004). The mapping data confirmed that a break occurred in the 1BL arm of 1BS-4 in the region of FL 0.61–0.69 with a concomitant loss of the distal 40% of the 1BL arm.

Our cytological data showed that most of the presumed deleted segment in the short arm of chromosome 1BS-4 was present as a translocated segment at the terminus of 1BL. However, previous reports indicated that 3 RFLP clones, BCD98, CDO99, and CDO580 (Sandhu et al. 2001) detected

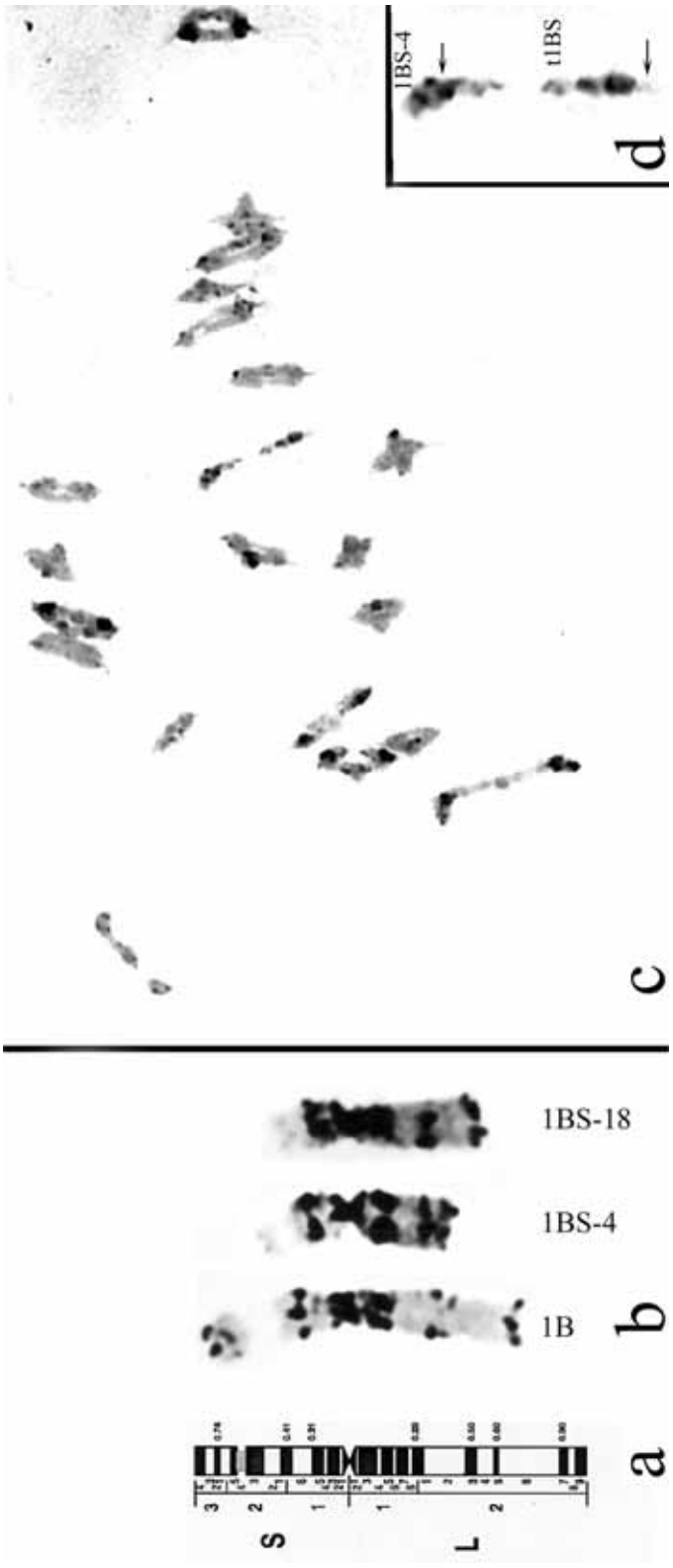
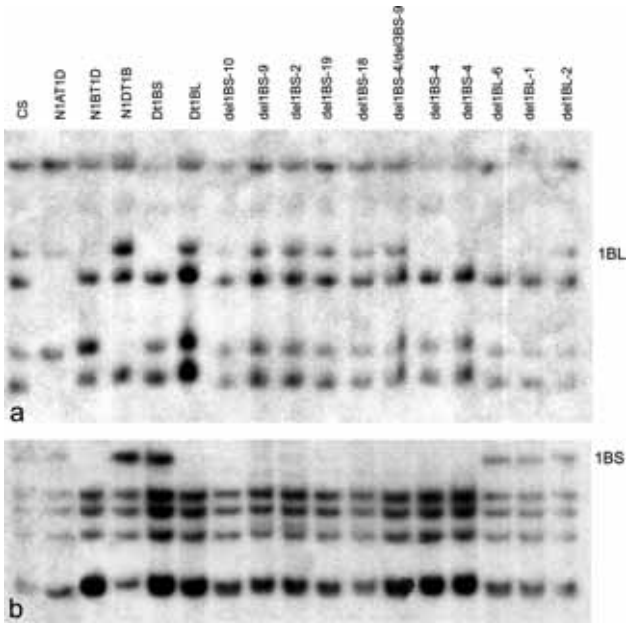


Fig. 1. C-banding pattern and meiotic metaphase I pairing of chromosome del1BS-4. (*a*) C-band nomenclature of chromosome 1B according to Gill et al. (1991); (*b*) C-banding patterns of chromosome 1B and the deletions del1BS-4 and del1BS-18 (taken from Endo and Gill 1996); (*c*) C-banded meiotic metaphase of the testcross del1BS-4 × Dt1BS. Note that the long arm of del1BS-4 is paired with the 1BS telosome in form of a heteromorphic rod bivalent (enlarged view in (*d*)). Arrows point to the centromeres.

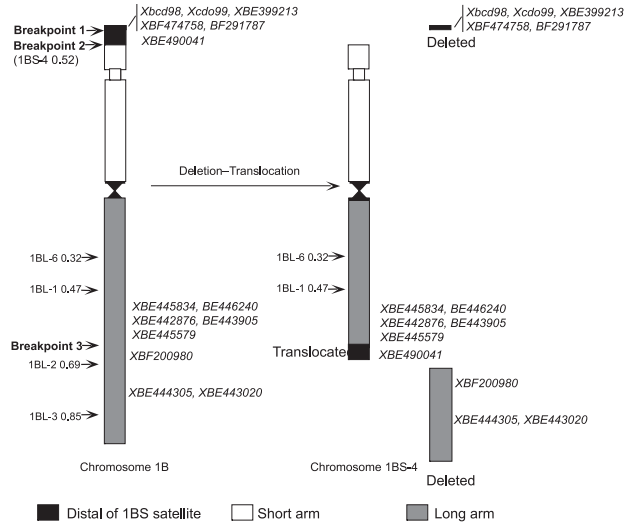
Fig. 2. Autoradiographs of Southern hybridizations. (*a*) EST clone BF200980 hybridized with genomic DNAs digested with *Eco*RI of selected genetic stocks. The specific 1BL fragment was absent in N1BT1D, Dt1BS, del1BS-4, del1BL-6, and del1BL-1. This fragment was present in del1BS-4/del3BS-9, because the line has an extra pair of 1BL telosome. (*b*) RFLP clone BCD98 hybridized with genomic DNAs digested with *Hin*dIII of selected genetic stocks. The specific 1BS fragment was absent in N1BT1D, Dt1BL, and all 1BS deletions including del1BS-4 and del1BS-4/del3BS-9. This marker is located in the part of the distal 1BS arm that was deleted during the production of 1BS-4 (see Fig. 3).



specific 1BS fragments that were missing in del1BS-4. In the wheat EST mapping project, 3 EST clones, BF474758, BF291787, and BE399213, detected specific 1BS fragments that were missing in del1BS-4/del3BS-9 (http://wheat.pw.usda.gov/cgi-bin/westsql/map_locus.cgi). These 6 clones were used to check both lines in the present study. Our results agreed with previous data for all clones (Table 3; Fig. 2*b*) except CDO580. Five of 6 clones had 1BS fragments that were missing in both lines. These data confirmed that the 1BS-4 chromosomes present in del1BS-4 and del1BS-4/del3BS-9 are identical, as also indicated by cytological data. Furthermore, chromosome 1BS-4 has a small deletion at the 1BS terminus. As to the clone CDO580, Sandhu et al. (2001) showed that it detected 2 loci; 1 proximal to del1BS-4 (4 fragments present) and 1 distal to del1BS-4 (1 fragment missing). Using the same probe/*Eco*RI combination in our experiment, CDO580 detected 1BS fragments in del1BS-4 and del1BS-4/del3BS-9. No 1BS fragment was missing in either line (data not shown). This discrepancy is caused by 1 of 5 fragments and may be due to technical reasons.

A model for the origin of chromosome 1BS-4 is presented in Fig. 3. Chromosome 1BS-4 originated from 2 breakpoints in the 1BS and 1 breakpoint in the 1BL arm. The segments distal to the breakpoints 1 and 3 were lost, and the segment flanked by the breakpoints 1 and 2 was translocated to the

Fig. 3. Structural changes involved in the origin of chromosome 1BS-4. The deletion lines with fraction-length values are listed on the left of a chromosome. The segments distal to breakpoints 1 and 3 were deleted. The segment between breakpoints 1 and 2 was translocated to the long arm of chromosome 1BS-4. The EST clone BE490041 is used to explain why a 1BS-specific fragment was missing in del1BS-18 (FL 0.50), but present in del1BS-4 (FL 0.52). The segment where the EST BE490041 resides was translocated to the long arm of del1BS-4 (Table 3).

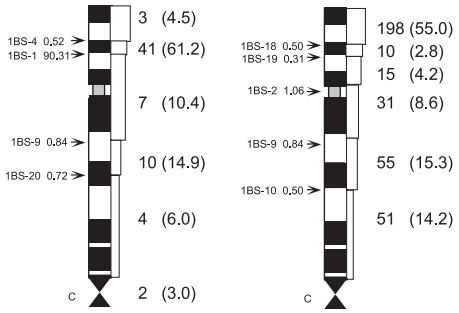


long arm. The broken ends were probably healed by the de novo addition of telomeric sequences. The newly rearranged chromosome 1BS-4 is cytologically highly stable, but fails to pair with the normal 1B long arm. The long arm of 1BS-4 is capable of pairing only with the short arm of normal 1B. The short arm of 1BS-4 fails to pair with a normal 1BS arm because of lack of homology at the distal ends.

The loss of a small 1BS segment distal to the breakpoint 1 in del1BS-4 also was confirmed by the metaphase I pairing data. The 1BS segment translocated to the 1BL arm in chromosome 1BS-4 is missing the segment distal to the breakpoint 1 (Fig. 3). As a result, the 1BS telosome paired with the translocated 1BS segment in the long arm of chromosome 1BS-4 in 56% of the PMCs as compared with 87% in the 1B/t1BS testcross combination (Table 2).

Wheat deletion stocks are valuable tools for the physical mapping of molecular markers and genes to chromosome bins delineated by 2 adjacent deletion breakpoints. A marker or gene is assigned to a chromosome bin according to the presence or absence of a restriction fragment in a series of deletion lines after Southern hybridization (Qi et al. 2003, 2004). Thus, using the correct deletion stocks is a prerequisite for precise mapping. As described previously, chromosome 1BS-4 is a highly rearranged deletion–translocation chromosome. The clones that map in the interval of breakpoints 1 and 2 have the 1BS-specific fragments present in the del1BS-4, because this segment is present as a translocated fragment in the long arm of del1BS-4. Using del1BS-4 for physical mapping can result in the false allocation of molecular markers to the region proximal to breakpoint 2 of del1BS-4 if this line is treated as a simple deletion. Our data explain the discrepancies reported for the 1B deletion bin map (Sandhu et al. 2001; Sandhu and Gill

Fig. 4. Discrepancies in physical mapping results with del1BS-4. The numbers on the left of a chromosome indicate the individual deletion lines and the faction-length values of each deletion. The numbers on the right are the mapped loci in each chromosome bin. The numbers in parentheses are the percentage of mapped loci; 61.2% of the RFLP loci mapped proximal to the breakpoint of del1BS-4 in group 1 physical map, whereas 55% of EST loci mapped to distal region of 1BS arm. (Sources: RFLP physical map, Sandhu et al. 2001; Wheat EST physical map (http://wheat.pw.usda.gov/cgi-bin/westsql/map_locus.cgi.)).



2002; Dilbirligi et al. 2004; Peng et al. 2004; Qi et al. 2004; Wheat EST mapping project (http://wheat.pw.usda.gov/cgi-bin/westsql/map_locus.cgi)). In the physical map of chromosome 1BS, del1BS-4 (FL 0.52) was used as a simple deletion. The fact that part of the segment deleted from 1BS is present in the long arm of 1BS-4 was not recognized. As a result, the majority of the RFLP loci (61.2%) were falsely assigned to bin 1BS.sat19–0.31–0.52 based on the specific 1BS fragments missing in del1BS-19 and present in del1BS-4 (Fig. 4; Sandhu et al. 2001). In wheat EST mapping, a confirmed deletion line 1BS-18 with a FL value of 0.50, in the satellite of 1BS, was used to replace del1BS-4 (FL 0.52). The chromosome bin 1BS.sat19–0.31–0.50 delineated by the deletion breakpoints of del1BS-19 and del1BS-18 is almost identical in size to chromosome bin 1BS.sat19–0.31–0.52 delineated by the deletion breakpoints of del1BS-19 and del1BS-4 (Fig. 4). However, the EST mapping results indicated that chromosome bin 1BS.sat19–0.31–0.50 is in a gene-poor region. Only 2.8% (10/360) of EST loci mapped to bin 1BS.sat19–0.31–0.50 compared with 61.2% of RLFP loci that mapped to bin 1BS.sat19–0.31–0.52 when del1BS-4 was used (Fig. 4). The distal bin of 1BS.sat18–0.50–1.00 accounts for 55% of the mapped EST loci (Fig. 4). These results are consistent with the results obtained for the corresponding region in 1AS and 1DS (Peng et al. 2004; Qi et al. 2004; Wheat EST mapping project (http://wheat.pw.usda.gov/cgi-bin/westsql/map_locus.cgi)). In contrast, only 4.5% of RFLP loci were mapped to the distal bin of 1BS.sat1BS4–0.52–1.00 in the 1BS physical map (Fig. 4).

Gc genes can cause random chromosome breakage across the entire genome as well as affect only a single chromosome, as shown in the present study. Cytologically, chromosome 1BS-4 is highly stable, but the short arm fails to pair with a normal 1BS arm because of lack of homology at the distal end; and the long arm fails to pair with a normal 1BL arm, because of the presence of the translocated segment from 1BS.

Acknowledgements

We thank John W. Raupp for critical reading of the manuscript. The research was supported by a special United States Department of Agriculture grant to the Wheat Genetics Resource Center. It was supported by National Science Foundation Cooperative Agreement Number DBI-9975989. This paper is contribution number 05–119J from the Kansas Agricultural Experiment Station, Kansas State University, Manhattan, Kansas, USA.

References

Dilbirligi, M., Erayman, M., Sandhu, D., Sidhu, D., and Gill, K.S. 2004. Identification of wheat chromosome region containing expressed resistance genes. Genetics, **166**: 461–481.

Dvorak, J., and McGuire, P.E. 1981. Nonstructural chromosome differentiation among wheat cultivars, with special reference to differentiation of chromosomes in related species. Genetics, **97**: 391–414.

Endo, T.R. 1988. Induction of chromosomal structural changes by a chromosome from *Aegilops cylindrica* L. in common wheat. J. Hered. **79**: 366–370.

Endo, T.R. 1990. Gametocidal chromosomes and their induction of chromosome mutations in wheat. Jap. J. Genet. **65**: 135–152.

Endo, T.R., and Gill, B.S. 1996. The deletion stocks of common wheat. J. Hered. **87**: 295–307.

Finch, R.A., Miller, T.E., and Bennett, M.D. 1984. 'Cuckoo' *Aegilops* addition chromosome in wheat ensures its transmission by causing chromosome breaks in meiospores lacking it. Chromosoma (Berlin), **90**: 84–88.

Friebe, B., Kynast, R.G, and Gill, B.S. 2000. Gametocidal factor-induced structural rearrangements in rye chromosomes added to common wheat. Chromosome Res. **8**: 501–511.

Friebe, B., Kynast, R.G, Zhang, P., Qi, L.L., Dhar, M., and Gill, B.S. 2001. Chromosome healing by addition of telomeric repeats in wheat occurs during the first mitotic divisions of the sporophyte and is a gradual process. Chromosome Res. **9**: 137–146.

Gill, B.S., and Friebe, B. 1998. Plant cytogenetics at the dawn of the 21st century. Curr. Opin. Plant Biol. **1**: 109–115.

Gill, B.S., Friebe, B., and Endo, T.R. 1991. Standard karyotype and nomenclature system for description of chromosome bands and structural aberrations in wheat (*Triticum aestivum*). Genome, **34**: 830–839.

Hohmann, U., Endo, T.R., Hermann, R.G., and Gill, B.S. 1995. Characterization of deletions in common wheat induced by an *Aegilops cylindrica* chromosome: detection of multiple chromosome rearrangements. Theor. Appl. Genet. **91**: 611–617.

Nasuda, S., Friebe, B., and Gill, B.S. 1998. Gametocidal genes induce chromosome breakage in the interphase prior to the first mitotic cell division of the male gametophyte in wheat. Genetics, **149**: 1115–1124.

Ogihara, Y., Hasegawa, K., and Tsujimoto, H. 1994. High-resolution cytological mapping of the long arm of chromosome 5A in common wheat using a series of deletion lines induced by gametocidal genes of *Aegilops speltoides*. Mol. Gen. Genet. **244**: 253–259.

Peng, J.H., Zadeh, H., Lazo, G.R., Gustafson, J.P., Chao, S., Anderson, O.D., Qi, L.L., Echalier, B., Gill, B.S. et al. 2004. Chromosome bin map of expressed sequence tags in homoeologous group 1 of hexaploid wheat and homoeology with rice and *Arabidopsis*. Genetics, **168**: 609–623.

Qi, L.L., Friebe, B., and Gill, B.S. 2002. A strategy for enhancing recombination in proximal regions of chromosomes. Chromosome Res. **10**: 645–654.

Qi, L.L., Echalier, B., Friebe, B., and Gill, B.S. 2003. Molecular characterization of a set of wheat deletion stocks for use in chromosome bin mapping of ESTs. Funct. Integr. Genomics, **3**: 39–55.

Qi, L.L., Echalier, B., Chao, S., Lazo, G.R., Butler, G.E., Anderson, O.D., Akhunov, E.D., Dvorák, J., Linkiewicz, A.M., Ratnasiri, A., et al. 2004. A chromosome bin map of 16 000 EST loci and distribution of genes among the three genomes of polyploid wheat. Genetics, **168**: 701–712.

Sandhu, D., and Gill, K.S. 2002. Structural and functional organization of the '1S0.8 gene-rich region' in the Triticeae. Plant Mol. Biol. **48**: 791–804.

Sandhu, D., Champoux, J.A., Bondareva, S.N., and Gill, K.S. 2001. Identification and physical localization of useful genes and markers to a major gene-rich region on wheat 1S chromosomes. Genetics, **157**: 1735–1747.

Sears, E.R. 1954. The aneuploids of common wheat. Univ. Mo. Agric. Exp. Stn. Bull. **572**: 1–58.

Sears, E.R. 1966. Nullisomic–tetrasomic combinations in hexaploid wheat. *In* Chromosome manipulations and plant genetics. *Edited by* R. Riley and K.R. Lewis. Oliver and Boyd, Edinburgh, Scotland. pp. 29–45.

Sears, E.R., and Sears, M.S. 1978. The telocentric chromosomes of common wheat. *In* Proceedings of the 5th International Wheat Genetics Symposium. *Edited by* S. Ramanujam. Indian Society of Genetics and Plant Breeding, New Delhi, India. pp. 389–407.

Shi, F., and Endo, T.R. 1999. Genetic induction of structural changes in barley chromosomes added to common wheat by a gametocidal chromosome derived from *Aegilops cylindrica*. Genes Genet. Sys. **74**: 49–54.

Shi, F., and Endo, T.R. 2000. Genetic induction of chromosomal rearrangements in barley chromosome 7H added to common wheat. Chromosoma (Berlin), **109**: 358–363.

Werner, J.E., Kota, R.S., Gill, B.S., and Endo, T.R. 1992. Distribution of telomeric repeats and their role in the heating of broken chromosomes in wheat. Genome, **35**: 844–848.