



A strategy for enhancing recombination in proximal regions of chromosomes

L. L. Qi, B. Friebe* & B. S. Gill

Wheat Genetics Resource Center, Department of Plant Pathology, Throckmoton Plant Science Center, Kansas State University, Manhattan, KS 66506-5502, USA; Tel: 785-532-1108; Fax: 785-532-5692; E-mail: friebe@ksu.edu

*Correspondence

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Abstract

As a rule, recombination in bread wheat (*Triticum aestivum* L.) is low in proximal and high in distal regions of chromosomes. Recombination may be enhanced in proximal regions by using deletion (del) chromosomes deficient for a distal part of a chromosome arm. The chromosome del5BL-11 derived from Chinese Spring (CS) is missing 41% of the distal long arm. This line was made polymorphic by crossing with a stock in which chromosome 5B of CS (5B^{CS}) is substituted for chromosome 5B of *T. turgidum* ssp. *dicoccoides* origin (5B^{T.dic}). Three recombinant del5BL-11 (del5BL-11^{rec}) lines were isolated, all resulting from localized recombination between loci *Xbcd926* and *XksuH1*. In del5BL-11^{rec}, the centromere to fraction length (FL) 0.53 (C-FL0.53) segment is derived from 5B^{T.dic} and the distal region of FL 0.55–0.59 is from 5B^{CS}. Genetic recombination for the C-FL 0.53 interval was assayed in segregating progenies from 5B^{CS}/5B^{T.dic} and del5BL-11/del5BL-11^{rec} crosses using polymorphic markers and for the FL 0.55–0.59 interval in del5BL-11/del5BL-11^{rec} cross from chiasma counts. The pairing data and comparative mapping of normal 5B and del5BL-11 indicated that the increase in recombination was restricted to the FL 0.55–0.59 interval of the del5BL-11 chromosome. No significant increase in recombination in more proximal regions was observed although the order of several markers that cosegregated in the normal 5B map was resolved in the del5BL-11 map. The presented data show that recombination in proximal, usually low-recombination, regions can be increased by placing them close to the chromosome end.

Introduction

Several features of eukaryotic chromosome biology and behavior, especially those related to euchromatin and heterochromatin, are now well understood. Many of these properties are related to the chromosome compartments of euchromatin and heterochromatin. However, evidence is accumu-

lating that individual chromosome size and specific regions adjacent to major chromosome landmarks, centromeres, telomeres and intervening (interstitial) regions also are structurally and functionally specialized. As a rule, shorter chromosomes derived from longer chromosomes have a higher recombination per unit length (Kaback *et al.* 1989). There are upper and lower limits on chromosome size;

larger chromosomes interfere with mitotic division and smaller chromosomes fail to form chiasmata and are eliminated during meiosis (Schubert & Oud 1997, Schubert 2001).

Bread wheat (*Triticum aestivum* L.) ($2n = 6x = 42$, AABBDD) is hexaploid and has a large genome size, 1.6×10^{10} bp/1C. Because of its highly buffered polyploid genome, wheat tolerates a certain level of aneuploidy, and an unparalleled array of aneuploid (Sears 1954, 1966, Sears & Sears 1978) and deletion stocks (Endo & Gill 1996) have been produced. Cytogenetically engineered chromosomes allow the observation of individual chromosome behavior during mitotic and meiotic cell cycles. The majority of the deletion chromosomes are terminal deficiencies that arise from single breakage, followed by loss of the acentric terminal fragment and the *de-novo* addition of a functional telomere (Werner *et al.* 1992, Friebe *et al.* 2001). Extensive physical mapping studies using the deletion stocks have revealed gene-rich and high-recombination regions at the chromosome ends, whereas the proximal halves of the chromosome arms are mainly devoid of genes and low in genetic recombination (Gill KS *et al.* 1993, 1996a, 1996b). Further studies on homo- and heterozygous deletion stocks revealed that homology at the chromosome ends is crucial for the formation of a chiasmate association at meiotic MI (Curtis *et al.* 1991, Endo *et al.* 1991, Lukaszewski 1995, Gill BS *et al.* 1997). Even the loss of a small distal segment in an otherwise homologous and identical chromosome drastically reduces the amount of chiasmate MI association between deficient and normal chromosome arms. However, MI pairing is restored to a normal level when the deficient chromosome is homozygous, indicating that an overall mechanism ensures formation of one chiasma per arm even in chromosome regions where normally chiasmata rarely form and recombination is suppressed.

In the present study, we analyzed recombination in chromosome del5BL-11, where the distal 41% of the arm that is gene rich and where chiasma usually form, has been deleted. Our hypothesis was that recombination in the previously genetically inert proximal 59% of the 5BL arm would be enhanced because of the fact that at least one chiasma (formed as a result of reciprocal recombination) per arm usually form in terminal regions that share

complete homology. The results of the test of this hypothesis are presented herein.

Materials and methods

Genetic stocks

A disomic substitution line of *Triticum turgidum* L. subsp. *dicoccoides* (Körn. ex Asch Grachn) chromosome 5B for chromosome 5B of *T. aestivum* L. cv. Chinese Spring (CS), designated DS5B^{*T. dic*} (5B^{CS}), was developed by Dr. E. R. Sears. The 5B^{*T. dic*} and 5B^{CS} chromosomes are considered homologous because *T. aestivum* arose from a hybridization between *T. turgidum* and *Aegilops tauschii* Coss. approximately 8000 years ago (McFadden & Sears 1946). The deletion line 5BL-11 (del5BL-11) of CS, which is deficient for the distal 41% of chromosome arm 5BL, was described in Endo & Gill (1996). All materials are maintained at the Wheat Genetics Resource Center, Kansas State University, Manhattan, USA.

Experimental design

To measure recombination in the deficient arm of del5BL-11, we created a polymorphic 5BL-11 chromosome. This was achieved by crossing DS5B^{*T. dic*} (5B^{CS}) with del5BL-11 of CS, and crossing the F₁ as a female with a homozygous del5BL-11 line. The BC₁ progeny was analyzed by N-banding to identify plants disomic for del5BL-11. Three recombinant del5BL-11 (del5BL-11^{rec}) chromosomes are derived from female gametes, detected by polymorphic N-bands, and confirmed by scoring a number of RFLP loci. Three BC₁ plants containing a del5BL-11 and a del5BL-11^{rec} chromosome were used to produce an F₂ mapping population. The crossing scheme is shown in Figure 1. One hundred and seventeen recombinant substitution lines (RSLs) of chromosome 5B from the cross CS/DS5B^{*T. dic*} (5B^{CS}) (Gill KS *et al.* 1996a; Figure 1) were used as a mapping population for the normal chromosome 5B.

Cytogenetic analysis

N- and C-banding analyses and chromosome identification were according to Gill BS *et al.*

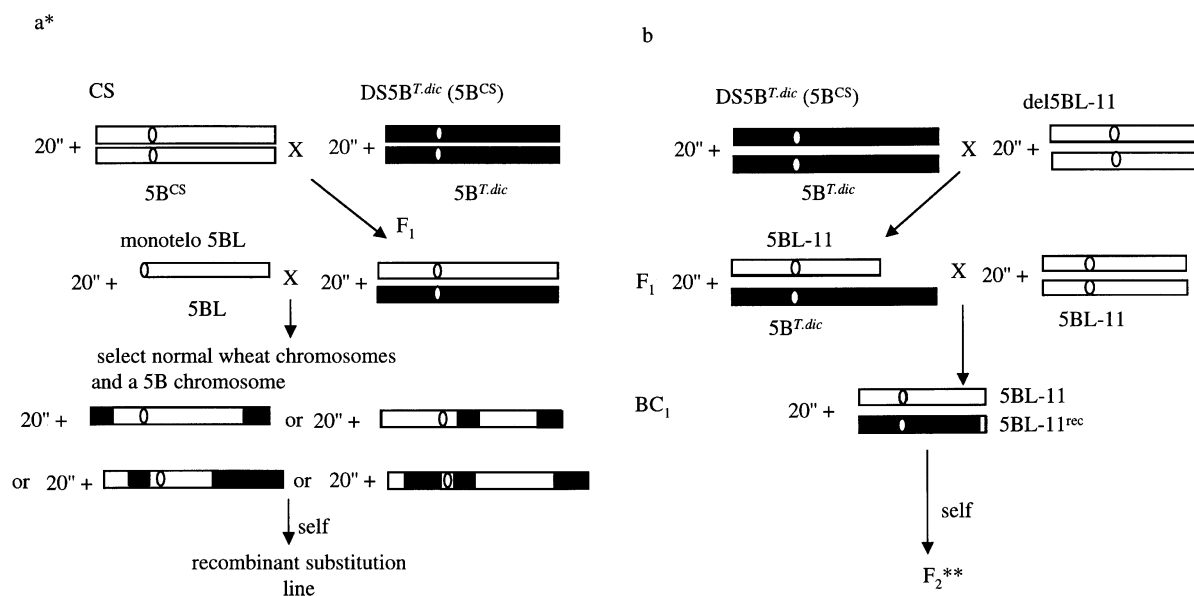


Figure 1. Scheme for production of the two mapping populations: (a) recombination substitution lines population of chromosome 5B; (b) F₂ population of del5BL-11. *modified after Gill KS *et al.* 1996a; **the progeny from the plants del5BL-11/del5BL-11^{rec} is similar to an F₂ population.

(1991). Meiotic metaphase I (MI) pairing was analyzed in pollen mother cells (PMCs) after C-banding. The fraction length (FL) value indicates the breakpoint in the deleted chromosome and the length of the remaining arm from the centromere relative to the length of the complete arm (Endo & Gill 1996).

RFLP analysis

The method for gel-blot DNA hybridization was described previously by Qi *et al.* (1997). Fifteen-microgram samples of total genomic DNA were digested with *EcoRI*, *EcoRV*, *HindIII*, and *DraI* restriction endonucleases. RFLP probes were generously provided by Dr. M. E. Sorrells, Ithaca, NY, USA (designated BCD, CDO, and WG); Dr. A. Graner, Grünbach, Germany (designated MWG); and Dr. M. D. Gale, Norwich, UK (designated PSR). KSU probes were developed by Gill KS *et al.* (1991). Mapping data were analyzed using the computer program Mapmaker (Lander *et al.* 1987) with Kosambi function at LOD of 3.0 (Kosambi 1944). The Z-test was used to determine the significance of the difference in the

recombination frequencies of markers between the two populations.

Results

Development of a recombinant del5BL-11

A total of 387 BC₁ plants from the cross CS del5BL-11 with DS5B^{T.dic} (5B^{CS}) were screened by N-banding. Eighty-eight plants were identified as disomic del5BL-11 and three had recombinant del5BL-11 chromosomes identified by their different N-banding patterns compared to CS del5BL-11 (Figure 2).

Twelve DNA markers for the long arm of chromosome 5B, previously mapped in the proximal 59% of chromosome 5BL (Gill KS *et al.* 1996a), were used to further confirm the crossover point in the recombinant del5BL-11. The markers that mapped in the region of FL 0.29–0.55 detected heteroloci in these three plants, whereas markers in the region of FL 0.55–0.59 detected homoloci. These results indicated that the segment from the centromere to FL 0.55 of the long arm in the recombinant del5BL-11 is derived from 5B^{T.dic},

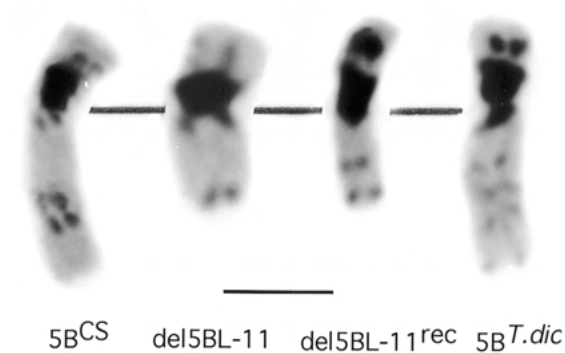


Figure 2. N-banded chromosomes of $5B^{CS}$, $CS\ del5BL-11$, $del5BL-11^{rec}$, and $5B^{T.dic}$. The banding pattern in 5BL arm of *T. dicoccoides* is different from that in the 5BL arm of CS. Scale bar = 5 μ m.

and the distal part of FL 0.55–0.59 is of Chinese Spring origin. All three crossovers were located in the FL 0.53–0.55 interval between marker loci *Xbcd926* and *XksuH1*.

Pairing data in the F_1 and BC_1 plants from the cross between $DS5B^{T.dic}$ ($5B^{CS}$) and $del5BL-11$

Meiotic pairing of F_1 plants with one $5B^{T.dic}$ and one $del5BL-11$ chromosome was analyzed by C-banding. Among 120 pollen mother cells (PMCs) analyzed, 46.7% had $5B^{T.dic}$ and $del5BL-11$ univalents (Figure 3a), in 50.0% of the cells the short arms of $5B^{T.dic}$ and $del5BL-11$ paired, and, in 3.3%

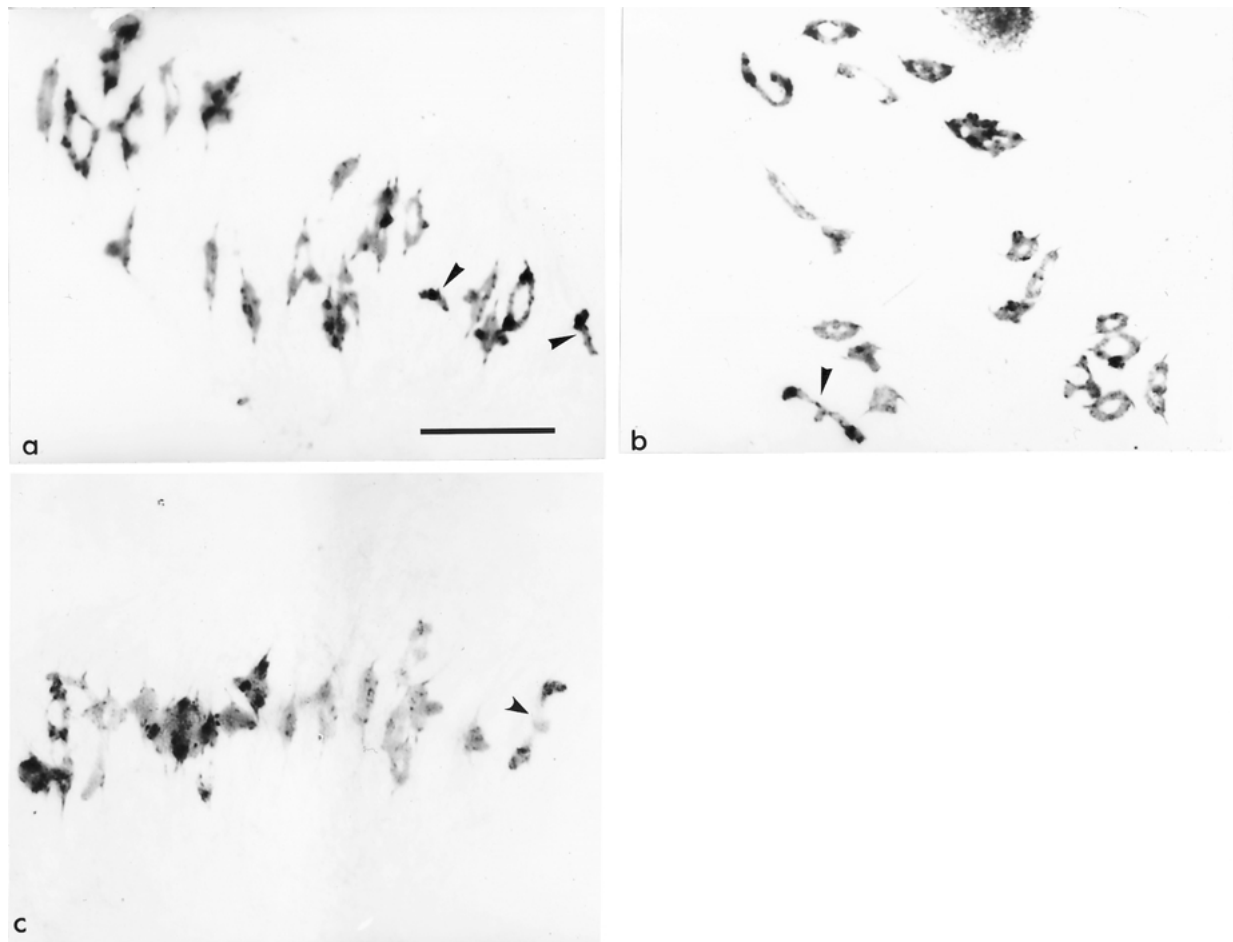




Figure 3. C-banded chromosomes at meiotic metaphase I in the F_1 and BC_1 of $CS\ del5BL-11/DS5B^{T.dic}$ ($5B^{CS}$). (a) Metaphase I pairing in the F_1 , arrows indicate two univalents of 5BL-11 and $5B^{T.dic}$. (b) Metaphase I pairing in the F_1 , arrow indicates a rod bivalent formed by long arms of $5B^{T.dic}$ and 5BL-11. (c) Metaphase I pairing in the BC_1 , arrow indicates a rod bivalent formed by the long arms of CS 5BL-11 and the recombinant 5BL-11. Scale bar = 20 μ m.

Table 1. Metaphase I pairing frequencies of chromosome 5B in F₁ and BC₁ of wheat.

Combination	No. of PMCs	Metaphase I Pairing frequency (%)	
		5BS	5BL
F ₁ 20'' +  5BL-11 5B ^{T.dic}	120	50.0	3.3
BC ₁ 20'' +  5BL-11 5BL-11 ^{rec}	55	49.1	89.1

of the PMCs, rod bivalents were formed resulting from pairing between the long arms of 5B^{T.dic} and del5BL-11 (Table 1, Figure 3b).

Chiasmate associations were largely restored in the homomorphic del5BL-11/del5BL-11^{rec} BC₁ plants as they formed a ring bivalent in 45.5% of the PMCs. Rod bivalents resulting from the pairing of the deficient long arms and from complete short arms of the del5BL-11/5BL-11^{rec} pair were observed in 43.6% and 3.6% of the PMCs, respectively (Figure 3c) and two univalents were observed in only 7.3% of the cells. Thus, the deficient 5BL arms of del5BL-11 and del5BL-11^{rec} paired in 89.1% of the PMCs (45.5% ring bivalent

plus 43.6% rod bivalent pairing in the long arm) (Table 1).

Comparison of recombination frequencies between chromosome 5BL and del5BL-11

A comparative map was constructed from the two separate populations, one for the intact 5BL arm and another for the deficient 5BL arm. Thus, we could compare recombination in the region, which is proximal in the intact 5B chromosome but distal in del5BL-11. To map the intact 5BL arm, 117 RSLs derived from the cross CS/DS5B^{T.dic} (5B^{CS}) were analyzed. For mapping of the del5BL-11 arm,

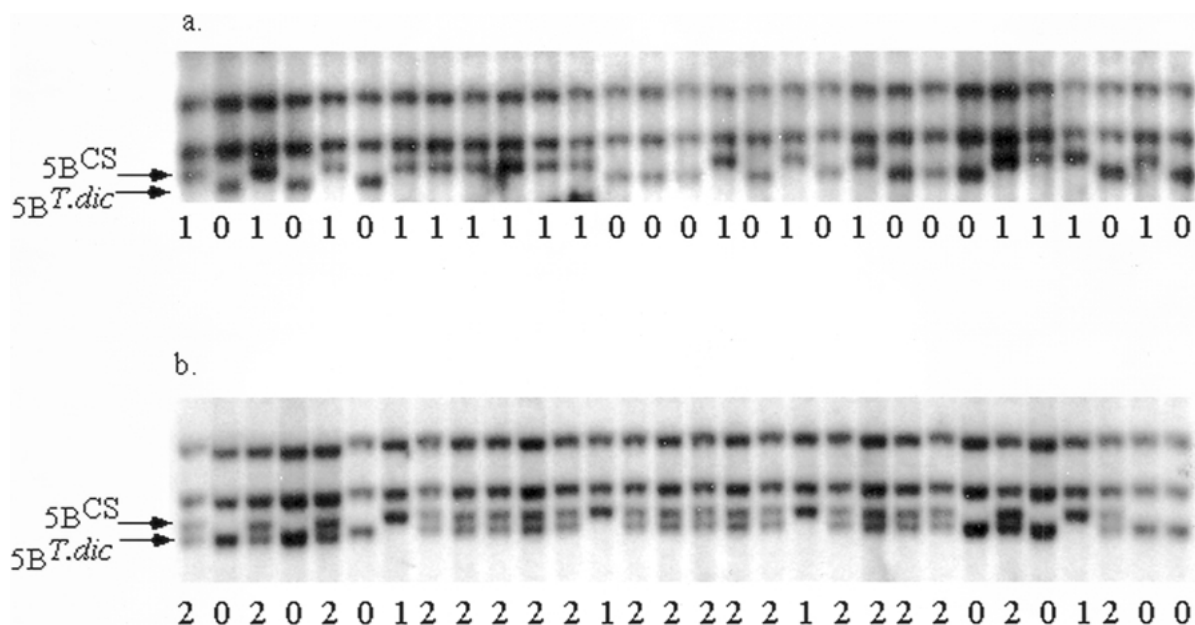


Figure 4. Hybridization of marker BCD157 with DraI-digested genomic DNA from the 5B RSLs (a) and del5BL-11 F₂ (b) populations. 1 = CS type, 0 = *T. dicoccoides* type, and 2 = heterozygous. Segregation ratios are 1:1 and 1:2:1 in the 5B RSLs (a) and del5BL-11 BC₁F₂ (b) populations, respectively.

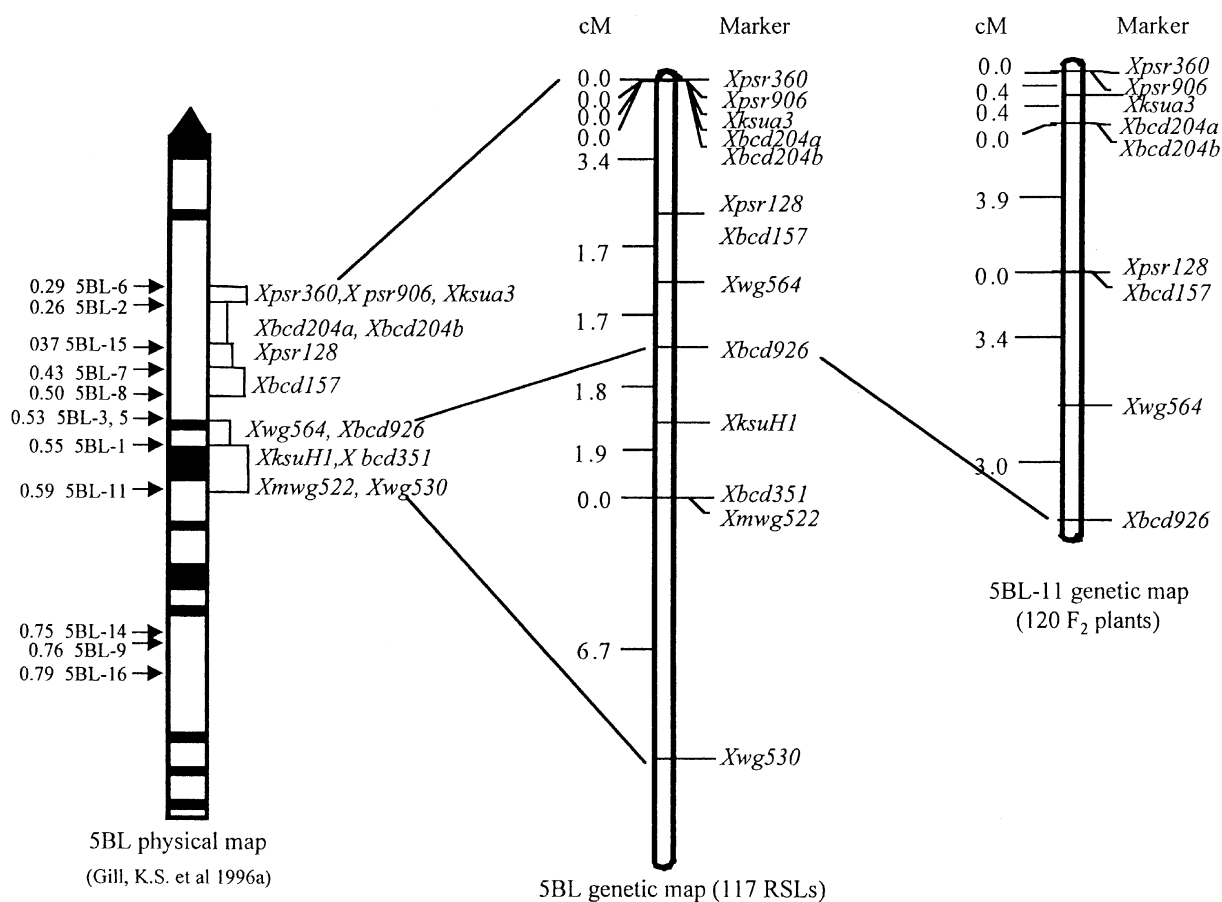


Figure 5. Comparative map of the long arms of normal 5B and 5BL-11. The 5BL arm physical map was taken from Gill KS *et al.* 1996a. The 5BL arm genetic map was constructed from 117 RSLs, and the 5BL-11 arm genetic map was constructed from 120 F₂ plants.

120 F₂ progeny derived from del5BL-11/del5BL-11^{rec} plants (Figure 1) were analyzed. The genetic composition of these two populations was similar, differing only in the structure of the targeted chromosome. Segregation for each marker in F₂ population of the del5BL-11/del5BL-11^{rec} cross fits the expected 1:2:1 ratio ($\chi^2 = 0.23-0.41$; $0.90 > p > 0.75$). The markers in the RSL population showed a 1:1 ratio (Figure 4).

The genetic length of the shared interval (FL 0.29 to FL 0.55) between 5BL and del5BL-11 can be determined from the 5BL and the del5BL-11 maps (Figure 5). For the FL 0.29–0.55 interval, the 5BL genetic map was 6.8 cM compared to 11.1 cM length of the del5BL-11 genetic map, a 1.6-fold increase in genetic recombination in the shorter (del5BL-11) chromosome. Moreover, genetic recombination was observed between markers

PSR360/PSR906-KSUA3 and KSUA3-BCD204a/BCD204b in the del5BL-11 map, whereas these markers mapped to a single locus in the 5BL map. Although there is a tendency towards enhanced recombination frequency in the regions and intervals tested between the 5BL and del5BL-11 maps, the differences were not statistically significant (Table 2). However, del5BL-11 and 5BL-11^{rec} share perfect homology in the extreme telomeric region because of the strategy used to produce the recombinant chromosome (see Figure 1, right bottom pair of chromosomes). When recombination in this region is taken into account (see below), we observe a statistically significant, very high recombination in the del5BL-11 chromosome.

In the region of FL 0.55–0.59, the markers KSUH1, BCD351, MWG522, and WG530

Table 2. Comparison of recombination frequency (RF) in the long arms of the normal 5B and 5BL-11.

FL	Interval	5BL RF	5BL-11 RF
0.26–0.29	<i>Xpsr360-Xpsr960</i>	0.00	0.00
	<i>Xpsr960-XksuA3</i>	0.00	0.40
0.29–0.37	<i>XksuA3-Xbcd204a</i>	0.00	0.40
	<i>Xbcd204a-Xbcd204b</i>	0.00	0.00
0.37–0.53	<i>Xbcd204a-Xpsr128</i>	3.40	3.90
	<i>Xpsr128-Xwg564</i>	1.70	3.40
0.53–0.55	<i>Xwg564-Xbcd926</i>	1.70	3.00
Total		6.80	11.10
0.55–0.59	<i>Xbcd926-XksuH1</i>	1.80	
	<i>XksuH1-Xbcd351</i>	1.90	
	<i>Xbcd351-Xmwg522</i>	0.00	
	<i>Xmwg522-Xwg530</i>	6.70	
Total		10.40	33.40*

*Calculated from chiasma counts (0.89 chiasma in del5BL-11 = 44.5 cM).

detected 10.4% recombination in the normal 5B-mapping population (Figure 5). These markers could not detect recombination in the FL 0.55–0.59 intervals in the del5BL-11 population because this region of del5BL-11^{rec} was identical to that of CS del5BL-11 (Figure 1). Instead, the recombination frequency of this region in del5BL-11 was estimated from pairing data at MI of the BC₁ plants. We observed an average of 0.89 chiasmata in the long arm between del5BL-11/del5BL-11^{rec} chromosomes. Based on chiasmata data, the calculated recombination in the long arm of del5BL-11 is 44.5 cM. The observed recombination in the region of centromere to the FL 0.55 in del5BL-11 was 11.1 cM. The difference in genetic length between the two estimates is 33.4 cM, which reflects the increased recombination in the region of the FL 0.55–0.59 interval in del5BL-11 (Table 2). This value (33.4 cM) is three times higher than the recombination frequency of the same region in a normal 5BL arm (11.5 cM).

Discussion

Previous studies in wheat suggest that homology at the telomeric regions is essential for initiating synapsis that leads to chiasmate MI associations (Curtis *et al.* 1991, Endo *et al.* 1991, Lukaszewski 1995). Even the loss of a small distal segment drastically reduces the frequency of MI pairing

between the deficient chromosome arm and the corresponding arm of the complete chromosome. The reduction in pairing frequency is not caused by the inability of the deficient chromosome arm to undergo chiasma formation, which is indicated by the nearly normal MI pairing frequency of deficient chromosome arms in homozygous condition. Telomeric regions also play an important role in the pairing of homologous chromosomes in barley (Kasha & Burnham 1965, Linde-Laursen 1982), maize (Burnham *et al.* 1972, Doyle 1990), and in fission and budding yeast (see review of Walker & Hawley 2000). The data presented in this paper strongly support the notion that homology alignment leading to chiasmate association at MI is initiated in the telomeric region, and that lack of homology in these regions leads to pairing failure. Plants with a 5B^{*T. dic*}/5B^{CS} chromosome showed 1.1 chiasmata in the 5BL arm (B. Friebe unpublished data). In the plant with the 5B^{*T. dic*}/del5BL-11 chromosome constitution, the distal 41% of the 5BL arm lacks a pairing partner, and only 3.3% pairing was observed in the 5BL arm at MI (Table 1). However, in plants with a del5BL-11/del5BL-11^{rec} combination, homology in the telomeric region is restored, and the long arm of the 5BL-11 paired with that of 5BL-11^{rec} in 89.1% of the PMCs. This pairing frequency is similar to that of the normal 5BL arm (0.89 vs. 1.10).

The observation that the amount of chiasmate association is restored to a normal level in a homozygous deletion indicates that recombination frequencies in a region usually low in recombination can be increased by placing them at the chromosome ends. Whether the increase in recombination frequency is restricted to only the chromosome ends or whether it also affects the adjacent proximal regions is unknown. Previously, more than 30 DNA markers have been mapped in the region from the centromere to FL 0.59 of the 5BL arm (Gill KS *et al.* 1996a), providing an opportunity to study the physical distribution of recombination in this region using molecular markers. In the present study, a recombinant del5BL-11 chromosome was developed in which the proximal region from the centromere to FL 0.55 was from *T. dicoccoides* and the distal end of FL 0.55–0.59 was of Chinese Spring origin. Data from this population of del5BL-11^{rec} and CS del5BL-11 are comparable to those from recombinant

substitution lines of the normal chromosome 5B from the cross CS/DS5B^{T.dic} (5B^{CS}). The recombination frequencies detected by eight markers in the region between the centromere and FL 0.55 were 6.8 cM and 11.1 cM in the normal 5BL arm and deficient 5BL arm respectively, indicating a tendency for higher recombination (however, the difference was not statistically significant). Compared with recombination in the proximal 55% of normal 5BL arm, the deletion interval of FL 0.55–0.59 is a region of high recombination. Four markers detected 10.4% recombination in this small region in the normal 5BL arm. A three-fold increase in recombination frequency was observed in the region of FL 0.55–0.59 when it was placed at the end of the 5BL chromosome arm in del5BL-11 (Table 2). These data indicate that the increase in recombination is restricted mainly to the very distal homologous end of the 5BL-11 arm, and does not affect more the proximal region of the deficient 5BL arm.

Jones *et al.* (2002) analyzed the recombination pattern in a midsize chromosome derived from 1BL of wheat. They reported that recombination frequencies increased in individual chromosome segments when they were placed closer to the telomere, whereas recombination decreased when segments were placed closer to the centromere. These results also are in agreement with previous reports showing that recombination in wheat preferentially occurs in the distal regions of chromosome arms (Dvorak & Chen 1984, Dvorak & Appels 1986, Lukaszewski 1992, Lukaszewski & Curtis 1993, Gill KS *et al.* 1993, 1996a, 1996b).

Our data indicate that the region of FL 0.53 and 0.55 (proximal to a large C-band) in the normal 5BL arm is also a region of high and localized recombination. Chiasmata were formed preferentially in this region in the F₁ of 5B^{T.dic}/CS 5BL-11. All three 5BL-11 recombinants recovered from the above F₁ occurred in the region of FL 0.53–0.55 between markers BCD926 and KSUH1.

In wheat, the long arm of chromosome 5B is the longest of all chromosome arms. The 5BL arm of CS shows 1.92 chiasmata at MI, one always at a terminal and a second often at a subtelomeric location (Sallee & Kimber 1978). Chromosome pairing is reduced in the 5B^{T.dic} and 5B^{CS} chromosomes of interspecific origin that had 1.1 chiasmata in the 5BL arm (B. Friebe unpublished

data). This indicates significant differentiation in the chromosome 5B between *T. aestivum* and *T. turgidum* ssp. *dicoccoides* although they are considered as homologous. The deficient 5BL arm in the plants del5BL-11/del5BL-11^{rec} formed 0.89 chiasma as compared to 1.1 chiasmata for the complete 5BL arm even though del5BL-11 arm is 41% shorter than normal 5BL arm. Thus, the frequency of chiasmata per unit of relative arm length is greater in the 5BL-11 arm. Similar results have been observed in bread wheat where the chiasma frequency in smaller chromosomes of the D genome is similar to that of larger chromosomes of the A and B genomes (Sallee & Kimber 1978).

Chromosome size-dependent control of meiotic recombination has been investigated in detail in *Saccharomyces cerevisiae* (Kaback *et al.* 1989, 1992, 1999). Recombination frequencies were inversely related to chromosome size. Further studies demonstrated that crossover interference plays a role in recombination frequencies on different-sized chromosomes. The amount of chiasmata interference increases with chromosome size. High levels of interference occur in larger chromosomes, and much lower levels of interference were observed in smaller chromosomes (Kaback *et al.* 1999). In the present study, the region between the centromere and FL 0.55 is identical in a normal 5BL chromosome arm and the deficient 5BL-11 arm, although they have different chromosome sizes. Only one double crossover was observed in the region of FL 0.26–0.55 in the 5BL arm of the physically longer 5B chromosome. Three double crossovers were observed in the same region of the physically shorter chromosome del5BL-11. Therefore, higher recombination in the del5BL-11 chromosome may be due to a reduced amount of interference compared to normal chromosome 5B.

The enhanced recombination in a proximal region placed at the telomeric end, as demonstrated here for chromosome del5BL-11, has practical applications. Recombination is suppressed in proximal regions especially in wheat where it may not exceed 10 cM (Gill KS *et al.* 1996a, 1996b). Therefore, genes located in proximal regions are not amenable to map-based cloning (Qi & Gill 2001). The strategy used here for del5BL-11 should be of general application for accessing genes located in regions of poor recombination. The disadvantage of the strategy is the presence of the

distal homologous region in the recombined deletion chromosome, so that most enhanced recombination is confined to the non-informative homologous region. New methods are needed for introducing polymorphism into physically shorter chromosomes, perhaps similar to the one used in yeast (Kaback *et al.* 1999).

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