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Genetic linkage between C-bands and storage protein genes in chromosome *1B* of tetraploid wheat

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Summary. Genetic mapping of polymorphic C-bands allows direct comparisons between genetic and physical maps. Eleven C-bands and two seed storage protein genes on chromosome *1B*, polymorphic between Langdon durum and four accessions of *T. dicoccoides*, were used to study the distribution of recombination along the entire length of the chromosome. Recombination in the short arm was almost completely restricted to the satellite, two-thirds of the arm's length from the centromere; the *Gli-B1* gene was found to be tightly linked to the telomeric C-band. In the long arm, the distal 51.4% of the arm accounted for 88% of recombination; the proximal half of the arm accounted for the remaining 12%. While the amount of crossing-over differed significantly between the four *T. dicoccoides 1B* chromosomes, there were no significant differences in the relative distributions of crossing-over along the chromosome. Consequently, the genetic maps obtained from the four individual *T. dicoccoides* chromosomes were combined to yield a consensus map of 14 markers (including the centromere) for the chromosome.

Key words: Emmer wheats – Chromosome *1B* – C-Bands – Seed storage protein genes – Mapping

Introduction

Genetic mapping in both *Triticum turgidum* L. (2n = 4x = 28, genomic constitution AABB) and *Triticum aestivum* L. em Thell. (2n = 6x = 42, genomic constitution AABBDD) has been limited by a paucity of markers, particularly those with easily screenable phenotypes. This is largely the result of the fact that they are allopolyploid species composed of related A, B, and D genomes, with many genes existing as duplicated or triplicated homoeoalleles. Consequently, both the isolation of mutant alleles and the identification of genotypic classes are complicated by multifactorial inheritance patterns. Though Cusick and McIntosh (1987) and Hart and Gale (1987) list over 250 loci for morphological, resistance, biochemical, and molecular traits in wheat, only about 100 have been located genetically of one of the 42 chromosome arms.

Far fewer genes in wheat have been physically located to specific chromosomal positions. In situ hybridization techniques have been utilized to determine the physical locations of highly repetitive DNA sequences (Hutchinson and Lonsdale 1982; Rayburn and Gill 1986) and the *Nor-B1*, *Nor-B2*, and 5S rDNA sequences (Appels et al. 1980; Miller et al. 1980; Mukai et al. 1990). Through analysis of a line of *T. aestivum* deficient for the satellite of chromosome *1B* and missing the *Gli-B1* gliadins, Payne et al. (1984) placed the *Gli-B1* gene on the short arm of chromosome *1B* distal to its secondary constriction. This was confirmed by genetic mapping within the satellite region (Snape et al. 1985). A 50% deficiency of the long arm of chromosome *1B* allowed the *Glu-B1* gene to be localized to that area (Payne 1987), while a 46% deficiency of the long arm of chromosome *5A* was utilized in localizing the speltoid suppression gene *Q* (Endo and Mukai 1988). In studying a chromosome *5BS* deficiency stock, Kota and Dvorak (1986) localized a pairing promoter gene and the *5S* rDNA genes to positions either at or distal to the interstitial C-band on the short arm.

Genetic mapping that implements the banding patterns of chromosomes as markers in effect integrates the genetic and physical maps, and can be used to physically

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localize genes to relatively small segments of chromosomes. Such banding patterns can also significantly increase the total number of markers along the length of a chromosome. Linde-Larsen (1979) combined differential banding patterns with biochemical markers in genetic mapping studies in barley, and simultaneously determined their positions on both genetic and physical maps. Jampates and Dvorak (1986) utilized variant banding patterns and duplication/deficiency stocks of chromosome *5B* to cytologically monitor the distribution of crossing-over throughout the long arm.

In all reports to date, a noncorrespondence was observed between the genetic and physical maps of wheat chromosomes. Typically, genes that map to genetic positions at or very near the centromere have been physically localized to the more distal chromosome regions. The genetic map distance between the centromere and the *Nor-B2* locus (located on the short arm of chromosome *6B*) is 0.3–2.2 cM, but, physically, the secondary constriction is two-thirds of the arm's length away from the centromere (Dvorak and Appels 1986). The *Ph1* gene on *5BL* mapped genetically by Sears (1984) to 0.9 crossover units from the centromere was physically located by Dvorak et al. (1984) no closer than 50% of the arm's length away from the centromere.

In this study, polymorphism for C-banding patterns among accessions of *T. dicoccoides* was used to study the distribution of recombination along chromosome *1B* and to determine the genetic linkage between C-bands and the storage protein genes *Gli-B1* and *Glu-B1*, located on the short and long arms, respectively, of the chromosome.

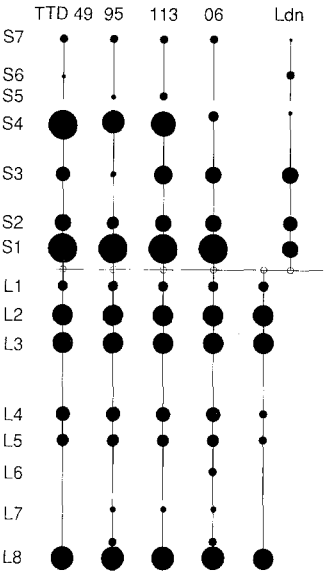

Fig. 1. Schematic diagram of C-band polymorphism for chromosome *1B* of *T. dicoccoides* accessions TTD49, TTD95, TTD113, and TTD06 and for the *1BS* and *1BL* telosomes of 'Langdon.' The double L8 band in TTD95 and TTD06 could not be used in analysis and was treated as a single unit

Materials and methods

Genetic stocks

T. dicoccoides accessions TTD49, TTD95, TTD113, and TTD06 were chosen for this study following screening for C-banding polymorphism among the collection of M. Feldman, The Weizmann Institute of Science, Rehovot, Israel. The four were collected in Israel near the Sea of Galilee and in the Golan Heights. They were included in this study because they exhibit several differences along their *1B* chromosomes for the presence and/or absence or size of C-bands compared to the *1B* telosomes in the double ditelosomic (*DDt*) *1B* line of *T. turgidum* var. *durum* cv 'Langdon' (Fig. 1). All stocks of 'Langdon' used in this study were obtained from L. R. Joppa, USDA-ARS, Fargo ND.

Crossing scheme

T. dicoccoides accessions TTD49, TTD95, and TTD113 were crossed to the 'Langdon' *DDt1B* (13″ + *1BS*″ + *1BL*″) line, and the resulting F_1 hybrids, carrying 26 chromosomes plus one *T. dicoccoides 1B* chromosome and 'Langdon' *1BS* and *1BL* telosomes, were backcrossed as males onto the 'Langdon' *1D*(*1B*) substitution line. Most backcross progeny (BC_1) would carry 13 pairs of chromosomes, a single *1D* chromosome, and either a complete *1B* chromosome or the *1BS* and *1BL* telosomes. Early in the analysis it became apparent that the size difference between the telomeric C-bands on the long arms of the selected *T. dicoccoides* complete chromosomes and the long-arm telosome of 'Langdon' was too small to accurately score for recombination in the distal region of the arm. Among a range of crosses between *T. dicoccoides* and various other 'Langdon' *DDt* lines, the hybrid between accession TTD06 × 'Langdon' *DDt6B* was included in the present study, as it fortuitously had sufficiently different telomeric C-bands in the long arms of the *1B* chromosomes to provide the best opportunity to study recombination in that particular segment of *1B*.

Cytological procedures

Individual seeds obtained from the backcross of the F_1 hybrids ('Langdon' *DDt1B* × TTD49, TTD95 or TTD113) to the 'Langdon' *1D*(*1B*) substitution line were numbered and cut in two. The larger germ portions were germinated, their root tips collected, fixed in 45% acetic acid, and C-banded as described by Lukaszewski and Gustafson (1983). On the basis of the parental *1B* banding patterns, the complete *1B* chromosome or the two *1B* telosomes in each BC_1 plant were identified as nonrecombinant or recombinant chromosome(s). The segment in which crossing-over occurred was determined by assuming the minimum number of crossover events necessary to produce the observed pattern of C-bands (Fig. 2). In the 'Langdon' × TTD06 combination, F_2 seeds carrying two complete *1B* chromosomes were used for C-banding. The position of crossover events was determined assuming the minimum number of most distal crossovers necessary to produce the observed pattern of C-bands.

For each accession, a physical map of the distribution of C-bands on chromosome *1B* was produced. The total length of the arms of chromosome *1B* and its telosomes and the distances between individual C-bands represent means of ten measurements per accession. The relative length of an interband distance represents the proportion of a region, as measured from the midpoint of one band to the midpoint of the adjacent band, to

Fig. 2. C-banding patterns of *1BS* and *1BL* telosomes and a complete *1B* chromosome in an F_1 hybrid between 'Langdon' *DDt1B* and *T. dicoccoides* accession TTD95, and several examples of recombined chromosomes. The regions in which recombination occurred are *arrowed*

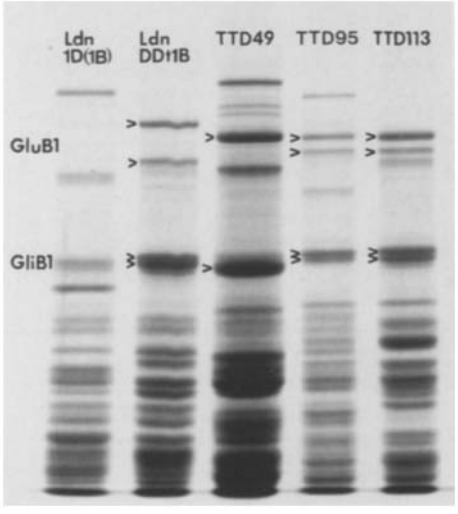

Fig. 3. SDS-PAGE migration pattern of total endosperm proteins extracted from seeds of 'Langdon' *DDt1B*, *T. dicoccoides* accessions TTD49, TTD95, and TTD113, and 'Langdon' *1D(1B)* substitution line. Allelic variation is *arrowed*

the total length of the chromosome arm. The measurements were taken directly from a TV camera monitor system attached to the Zeiss Axioscope 20 microscope.

To avoid any future confusion with the standard C-banding nomenclature for wheat chromosomes currently being prepared for publication (B. S. Gill, personal communication), the C-bands identified on the four *T. dicoccoides 1B* chromosomes in this study were sequentially numbered starting from the centromere. The C-bands on the short arm were assigned numbers S1-S7, those on the long arm L1-L8. The interband regions were identified by their delimiting C-bands, S1-S2, S2-S3, etc.

Meiotic pairing of the complete *1B* chromosome and the two telosomes in hybrids (Ldn *DDt1B* × TTD49, TTD95, TTD113) was analyzed on acetocarmine squashes of metaphase I anthers from sister plants of those F_1 hybrids that served as backcross parents. Unpaired short- and long-arm telosomes and the complete *1B* chromosome were easily identifiable on the basis of their length. The short telosome was also marked by its secondary constriction.

SDS-PAGE electrophoresis

The non-germ portions of the backcross seeds were used for SDS-PAGE electrophoresis of storage proteins. Given the absence of the *1B* telosomes in the 'Langdon'-TTD06 F_1 hybrid, *Gli-B1*- and *Glu-B1*-centromere mapping was not possible. The mapping of the *Glu-B1* and *Gli-B1* genes was consequently based on results derived from accessions TTD49, TTD95, and TTD113. The three accessions differed from the 'Langdon' *DDt1B* line in *Gli-B1* and *Glu-B1* alleles (Fig. 3).

The extraction of total endosperm proteins, SDS-PAGE electrophoresis, and the staining and destaining of gels were as described by Galili and Feldman (1983 a, b), with the following deviations: to ensure better separation of gliadins, the acrylamide percentage in the separating gel was decreased from 10 to 7%. Minigels (approximately 6 cm × 8.5 cm, 1 mm thickness) were prepared. Running time was decreased to 45 min.

Calculations

For each recombinant chromosome, the interband locations of the minimum number of crossovers necessary to generate its observed banding pattern were determined. On this basis, interband recombination frequencies (number of crossovers between two bands/number of chromosomes analyzed) were calculated for each of the four *T. dicoccoides* chromosomes. The conversion into map units (cM) was through the Kosambi mapping function (Kosambi 1944). Between-accession differences in percent recombination within homologous interband regions and in percent crossover events per chromosome were tested pairwise as differences between two proportions:

$$z = \frac{p_1 - p_2}{[p\,q(1/n_1 + n_2)]^{1/2}}$$

p_1 and p_2 = recombination frequencies being tested;
n_1 and n_2 = corresponding sample sizes

$$p = \frac{x_1 + x_2}{n_1 + n_2}; \quad q = 1 - p$$

where x_1 and x_2 = number of recombinants in both samples.

Chi-square tests of homogeneity were made for the four chromosome *1B* recombination distributions. Deviations in the male transmission frequency of complete *1B* versus *1BS* and *1BL* telosomes were also tested by Chi-square analysis. The eight BC_1 progeny aneuploid for chromosome *1B* were not included in this test of transmission frequencies.

Results

Pairing and transmission of complete chromosome and telosomes in F_1 hybrids

In the three F_1 hybrids involving Ldn *DDt1B* (Ldn *DDt1B* × TTD49, TTD95, TTD113), the level of metaphase I pairing ranged from 71.8 to 85.3% for *1BS* and

from 89.2 to 92.0% for *1BL* (Table 1). Pairing averaged 80.4% in the short arm and 90.7% in the long arm. No multivalents indicating the presence of translocations were observed in the hybrids, but in the Ldn *DDt1B* × TTD95 hybrid, two unpaired complete chromosomes other than *1B* were occasionally observed. Metaphase I pairing in the 'Langdon' *DDt6B* × TTD06 F_1 hybrid was not scored.

With full meiotic pairing, the normal transmission rate of the two telosomes versus complete *1B* would be 1 : 1. Assuming 50% transmission frequency, no significant differences in the male transmission rate were found between the complete *1B* and its telosomes in each of the F_1 hybrids between the *T. dicoccoides* accessions and 'Langdon' *DDt1B* (Table 2). However, when the frequencies from all three combinations were pooled, the complete *1B* chromosome had a significant advantage over the telosomes in the male transmission rate. This advantage of the complete chromosome was related to incomplete meiotic pairing, which favored the inclusion of the complete chromosome in the gametes. The complete chromosome was paired with at least one telosome in 93.6% of cells, while both telosomes were paired with the complete chromosome in only 77% of cells. This assured that a minimum 46.8% of gametes would receive a complete chromosome versus a minimum 38.5% gametes receiving both telosomes.

On the basis of the observed pairing frequencies, and assuming 25% inclusion rate of unpaired chromosomes in the gametes, the frequencies of all possible gametic constitutions were calculated as: 13 + *1B*, 47.7%; 13 + *1BS* + *1BL*, 40.2%; 13 + *1BS*, 2.5%; 13 + *1BL*, 7.6%; 13 + *1B* + *1BS*, 1.1%; 13 + *1B* + *1BL*, 0.6%; 13 + *1B* + *1BS* + *1BL*, 0.01% and 13, 0.3%. When these frequencies were used in Chi-square tests of the male transmission rate, no significant deviations were detected between the expected and observed classes of euploid gametes. However, the aneuploid-deficient classes were not represented among the recovered progeny.

The frequencies of recombinant complete chromosomes and recombinant telosomes in BC_1 progeny were similar. Therefore, for all further computations, results from both complete- and telosome-carrying plants were combined.

Table 1. Metaphase I pairing frequencies of complete *1B* chromosome of *T. dicoccoides* accessions TTD49, TTD95, and TTD113 with 'Langdon' *1BS* and *1BL* telosomes

T. dicoccoides accession	No. of cells analyzed	Pairing frequency of telosome (%)	
		1BS	*1BL*
TTD49	110	71.8	90.9
TTD95	100	85.0	92.0
TTD113	102	85.3	89.2

Table 2. Male transmission frequencies of complete *1B* chromosome versus *1BS* and *1BL* telosomes from F_1 hybrids between 'Langdon' double ditelosomic *1B* and *T. dicoccoides* accessions

F_1 hybrid	Gametic constitution			
	Aneuploid	Complete *1B* chromosome	*1BS* + *1BL* telosomes	χ^2-value (1 : 1)
(Ldn *DDt1B* × TTD49)	2	50	36	2.28
(Ldn *DDt1B* × TTD95)	3	33	21	2.67
(Ldn *DDt1B* × TTD113)	3	47	34	2.09
Pooled		130	91	6.88*

* Significant at $P < 0.05$

Table 3. Frequency of crossing-over for chromosome *1B* and crossovers per chromosome *1B* in *T. dicoccoides* accessions TTD49, TTD95, TTD113, and TTD06[a]

Interband region	Recombination frequency			
	TTD49	TTD95	TTD113	TTD06
S6-S7	Not scored	19.3[a]	32.1[b]	33.3[b]
S5-S7	34.1[ab]	26.3[a]	34.5[ab]	41.6[b]
S4-L4	14.7[ab]	17.5[a]	9.5[ab]	8.4[b]
L5-L7	Not scored	35.1[a]	25.0[b]	18.4[b]
Crossovers/ chromosome	0.6279[a]	0.5438[ab]	0.4938[b]	0.4833[b]

[a] Within each row, means with the same letter do not significantly differ according to the *z* test ($P < 0.01$)

Interband recombination frequencies

A total of 297 *1B* chromosomes was cytologically analyzed to determine the frequency of recombination between C-bands. These included chromosomes of 88 BC_1 plants from the hybrid Ldn *DDt1B* × TTD49, 57 BC_1 plants from Ldn *DDt1B* × TTD95, 84 BC_1 plants from Ldn *DDt1B* × TTD113, and 30 F_2 plants from Ldn × TTD06. Eight aneuploid BC_1 plants carrying a complete *1B* chromosome and either an additional *1BS* or *1BL* telosome were included in the total, since in the cytological analysis there could be no confusion as to the presence or location of crossovers in the disomic arm.

Recombination along the entire short arm could be monitored, since there was polymorphism for each band except S2 between 'Langdon' and at least one of the *T. dicoccoides* accessions (Fig. 1). Because there was no polymorphism between 'Langdon' and the four acces-

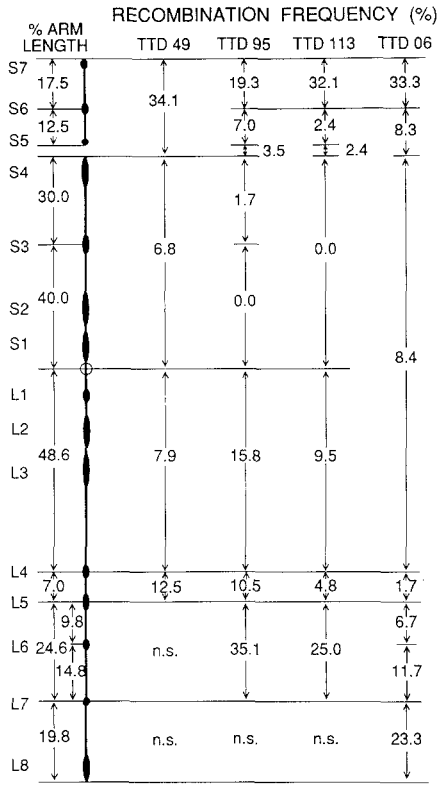

Fig. 4. Distribution of cytologically scored crossovers in chromosome *1B* in F_1 hybrids between the four *T. dicoccoides* accessions and 'Langdon.' Not scored = n.s.

sions at bands L1-L3 (Fig. 1), the centromere-L4 region was treated as a single unit. Recombination frequencies within individual interband regions differed significantly ($p<0.01$) among the four *1B* chromosomes (Fig. 4, Table 3). These included the satellite (both the entire S5-S7 region and its S6-S7 terminal region), the proximal region of the chromosome (S4-L4 region), and the long arm L5-L7 region. Differences in recombination frequencies in regions with fewer than five crossovers (S5-S6, S4-S5, L4-L5) were not statistically tested. Differences in the overall level of crossing-over between the four *1B* chromosomes were also observed. Accession TTD49 had a significantly higher amount of total crossing-over along chromosome *1B* than did accessions TTD113 and TTD06 ($p<0.01$, Table 3).

Chi-square tests of homogeneity for the entire length of chromosome *1B* indicated that the distribution of crossing-over did not significantly differ between the four accessions. Thus, while there were differences between accessions in the total amount of crossing-over, its apportionment along the chromosome length was similar. Consequently, the four individual frequency distributions (Fig. 4) were combined into a consensus distribution for chromosome *1B*. A direct compilation of results from the four individual distributions was not possible, since recombination could not be monitored in precisely the same interband regions in each of the four *T. dicoccoides*-'Langdon' hybrids (Fig. 1). A polymorphism at band L6 in accession TTD06 allowed a more precise determination of the distribution of recombination in the L5-L7 region than was possible in accessions TTD95 and TTD113, neither of which carried C-band L6. In order to derive a consensus recombination frequency for this region of the chromosome, the L5-L7 recombination frequencies obtained from TTD95 and TTD113 were partitioned into L5-L6 and L6-L7 segments, using as a proportion the L5-L6 and L6-L7 recombination frequencies from TTD06 (Fig. 4). Because the four individual recombination distributions were not statistically different, this reallotment of L5-L7 recombination frequencies was considered reasonable. Similarly, centromere-S4 and centromere-L4 subsets were proportioned from the S4-L4 recombination frequency of TTD06, using an average proportion derived from accessions TTD49, TTD95, and TTD113. Since accessions TTD49, TTD95, and TTD113 did not differ from the 'Langdon' *1BL* telosome in the terminal portion of the long arm (L7-L8), the recombination frequency for this region is derived from TTD06 alone.

Positioning of Glu-B1 and Gli-B1

The positions of the *Glu-B1* and *Gli-B1* genes on chromosome *1B* relative to their closest C-bands were determined by correlating the occurrence of cytological crossovers with *Glu-B1*-centromere and *Gli-B1*-centromere recombinational events. The mapping of *Glu-B1* and *Gli-B1* was based on results derived from accessions TTD49, TTD95, and TTD113. Results from monosomic arms of the eight aneuploid BC_1 plants (carrying complete *1B* and either a *1BS* or *1BL* telosome) were included in the genetic mapping of *Glu-B1* and *Gli-B1*. Results from disomic arms were excluded from the analysis. The *Glu-B1* or *Gli-B1* electrophoretic pattern of two non-crossover arms would be identical to that of two recombined arms. Consequently, chromosomes from 88 BC_1 hybrids involving TTD49, 56 BC_1 hybrids involving TTD95, and 84 BC_1 hybrids involving TTD113 were included in the mapping of *Glu-B1*, for a total of 228 chromosomes. Mapping of *Gli-B1* was based on results for chromosomes from 86 BC_1 plants from crosses involving TTD49, 55 BC_1 plants from TTD95, and 81 BC_1 plants from TTD113, for a total of 222 chromosomes.

Each chromosome with a cytological crossover between the centromere and band L5 had a corresponding genetic crossover between the centromere and *Glu-B1*, indicating that the gene was distal to the L5 band. However, only 21.8% of L5-L7 cytological crossovers had corresponding genetic crossovers between *Glu-B1* and the centromere, with the remainder (78.2%) being non-crossover for the *Glu-B1* locus. This indicated the gene

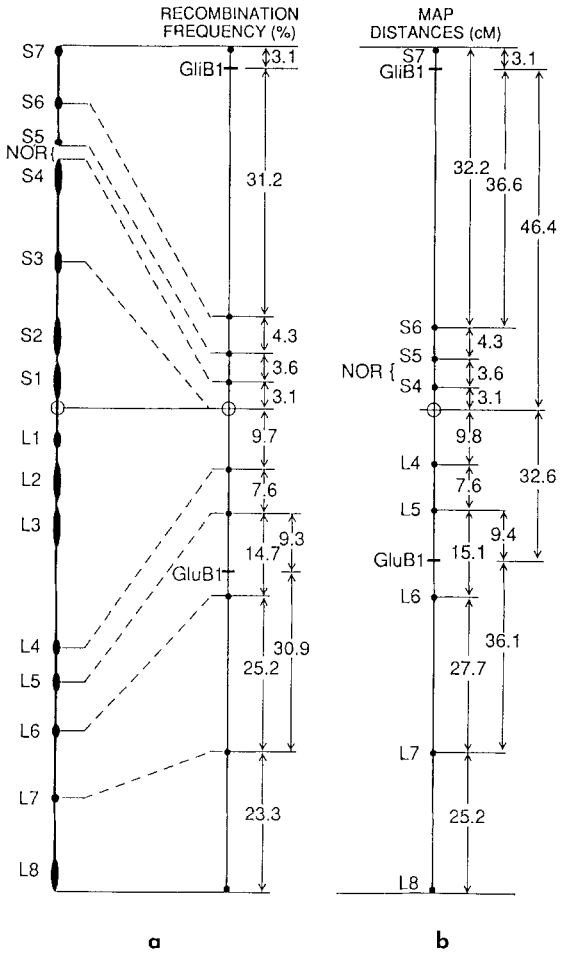

Fig. 5 a and b. Consensus distribution of recombination (**a**) and genetic linkage (**b**) between C-bands, *Gli-B1*, and *Glu-B1* on chromosome *1B*

was located between bands L5 and L7. Cytological crossovers in L5-L7 with corresponding *Glu-B1*-centromere crossovers were considered to have originated proximal to *Glu-B1*; cytological crossovers without corresponding *Glu-B1*-centromere crossovers were considered as originating distal to *Glu-B1*. Six chromosomes were found to have a parental banding pattern in the long arm, but were nonetheless recombined with respect to *Glu-B1*. These were interpreted as chromosomes in which a double crossover had occurred in the L5-L7 region, one proximal to *Glu-B1* and the second distal to it. *Glu-B1* was positioned on the genetic map within region L5-L7, relatively close to band L5, in agreement with a majority (78.2%) of the cytologically observed crossovers in this region being unrecombined for *Glu-B1*. The corresponding approximate physical location of the gene can thus be established in the long arm at 55–60% of the distance from the centromere.

Similar reasoning was employed for placing *Gli-B1* on the short arm of chromosome *1B*. All chromosomes with cytological crossovers between the centromere and the S6 band in the satellite also carried genetic crossovers between the centromere and *Gli-B1*. Similarly, 89.6% of the cytological crossovers observed in the terminal S6-S7 interband region had a genetic crossover between *Gli-B1* and the centromere. The remainder of the cytological crossovers (10.4%) did not have an analogous *Gli-B1*-centromere crossover, indicating that the gene was located between bands S6 and S7, probably in its more distal region. Accordingly, most of the interband crossing-over (89.6%) would originate proximal to the locus and be recombined both in the S6-S7 banding pattern and for the *Gli-B1* allele. The remainder of the crossing-over (10.4%) in this region would originate distal to the locus, so that a recombined banding pattern without an exchange of *Gli-B1* alleles would be expected. Seven chromosomes were identified that appeared unrecombined in their banding pattern, but that were recombined with regard to their *Gli-B1* alleles. These were again considered as double crossover events, one proximal and one distal to the gene. The corresponding physical location of the *Gli-B1* gene on chromosome *1B* is thus in the terminal half of its satellite, very close to the telomere, over 90% of the short arm distance from the centromere.

The additional crossovers detected through genetic mapping of *Gli-B1* and *Glu-B1* were combined with those obtained from the cytological analysis (Fig. 5a). These were then converted to map units to produce a genetic map for chromosome *1B* (Fig. 5b).

Discussion

The *Gli-B1*-centromere recombination frequency observed in this study (36.5%, 46.4 cM) indicates only a weak linkage between the two and is in the range reported previously (Payne et al. 1984; Galili and Feldman 1984; Snape et al. 1985; Singh and Shepherd 1988a). The *Glu-B1*-centromere map distance of 32.6 cM reported here, however, is much higher than that of 9.1 cM given by Payne et al. (1982) and the 18% recombination frequency reported by Curtis and Feldman (1988). Rather, it is in the range of the 28.1 ± 2.8 cM value given by Singh and Shepherd (1988b).

The physical localizations of *Glu-B1* and *Gli-B1* on chromosome *1B* are within the general regions of the two arms identified previously. Through deletion mapping of chromosome *1B*, *Gli-B1* had been localized to the satellite region (Payne et al. 1984), with *Glu-B1* in the distal half of the long arm (Payne 1987).

Comparisons between the physical map of chromosome *1B* and the four individual recombination distributions (Fig. 4) show proximal recombination to be an infrequent event. The proximal 70.0% of the short arm and the proximal 48.6% of the long arm support only low

levels of recombination. Crossing-over is instead concentrated in the distal regions of the arms. The satellite accounts for 30% of physical length of the short arm and is the site of 75.7% of the crossing-over in that arm (Fig. 5). Most of the remaining crossovers observed in the short arm appeared to occur within the S4 band itself; only one crossover between the centromere and S4 was detected. On the long arm, the distal 51.4% supports 88% of the recombination (Fig. 5).

It is evident that physical distances and genetic distances are not directly proportional. The probability of a crossover within a given physical distance depends more upon its location relative to the centromere than upon its actual length. Thus, in wheat, proximal regions on physical maps are telescoped into, and represented by, much shorter distances on genetic maps. Distal regions of the physical map that support high levels of crossing-over expand on the genetic map. Similar concentration of crossing-over in distal regions of chromosomes has been demonstrated in bread wheat by Dvorak and Chen (1984), Jampates and Dvorak (1986), and Snape et al. (1985).

No significant differences in the distribution of crossing-over along chromosome *1B* were observed between the four *T. dicoccoides* accessions tested. Significant differences, however, were found among the accessions in the overall level of recombination along chromosome *1B* (Table 3). Significant differences in the recombination frequencies observed in the individual chromosome segments (Table 3) are most likely related to the differences in the overall levels of crossing-over between the accessions. On the other hand, the differences in the overall level of crossing-over do not appear to result from differences in the metaphase I pairing frequencies between the *T. dicoccoides 1B* chromosomes and the 'Langdon' *1B* telosomes. The average level of pairing was 90.7% in the long arm and 80.4% in the short arm (Table 1), which is comparable to the 94.9% and 86.9% pairing observed between 'Chinese Spring' complete *1B* and 'Chinese Spring' *1B* long and short arm telosomes, respectively (Dvorak and McGuire 1981). The short arm of chromosome *1B* in accession TTD49 had the lowest pairing frequency (71.8%), but the highest recombination frequency (40.9%) of the three accessions tested. Fu and Sears (1973) noted poor correspondence between the levels of metaphase I pairing and recombination frequencies and suggested that chromosomes could recombine and separate in stages preceeding metaphase I. Lukaszewski (unpublished results) observed univalents recombined for C-banding patterns in metaphase I in rye. In addition, the strong selection for balanced gametes in tetraploid wheat (Joppa 1988) could result in a weak relationship between the frequency of metaphase I pairing and recombination. Gametes deficient for a chromosome or a chromosome arm, which frequently result from meiotic cells with unpaired chromosomes, were at a distinct competitive disadvantage at fertilization. Among the 229 BC_1 plants studied here, none resulted from such gametes although about 30 were expected. The eight aneuploids recovered resulted from gametes with an additional telosome.

The large amounts of proximal heterochromatin in chromosomes *1B* and *6B* have been implicated in forcing higher distal recombination in their short arms (Snape et al. 1985). However, the distribution of crossing-over in these arms is more likely to be influenced by the presence of a nucleolar organizing region (NOR) rather than heterochromatin. Gillies and Lukaszewski (1989) indicated that the NOR on rye chromosome *1R* may act as a barrier so that pairing initiated in the satellite cannot proceed into the proximal region. The distribution of recombination in *1BS* observed here is similar to that observed in *1RS* (Lawrence and Appels 1986). On the other hand, the distribution of recombination in the long arm of chromosome *1B* detected here is very similar to that reported in *5BL* (Jampates and Dvorak 1986) and observed in *2BS*, *2BL*, *3BS*, and *5BL* by A. J. Lukaszewski (unpublished results). It appears therefore that recombination in *1BL* shows a distribution more typical for wheat chromosomes than the NOR-carrying *1BS* and *6BS* arms studied earlier.

In the present study, a total of 14 markers, 7 on the short arm and 6 on the long arm and the centromere, was utilized to determine the distribution of recombination along the entire length of chromosome *1B*. In the process, the genes *Glu-B1* and *Gli-B1* were situated on chromosome *1B* in relation to its C-banding pattern. Until the development of in situ hybridization techniques for the localization of single-copy or unique DNA sequences on plant chromosomes, the mapping technique employed in this study can be utilized to physically locate genes to relatively small segments of chromosomes. In addition, the approach places a gene both physically and genetically for direct comparisons between both maps and so may have certain advantages over in situ hybridization.

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