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Homoeologous relationships of *Triticum sharonense* chromosomes to *T. aestivum*

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Abstract Homoeologous pairing at metaphase I was analyzed in standard-type, *ph2b*, and *ph1b* hybrids of *Triticum aestivum* (common, bread or hexaploid wheat) and *T. sharonense* in order to establish the homoeologus relationships of *T. sharonense* chromosomes to hexaploid wheat. Chromosomes of both species, and their arms, were identified by C-banding. Normal homoeologous relationships for the seven chromosomes of the S^{sh} genome, and their arms, were revealed, which implies that no apparent chromosome rearrangement occurred in the evolution of *T. sharonense* relative to wheat. All three types of hybrids with low-, intermediate-, and high-pairing level showed preferential pairing between A-D and B-S^{sh}. A close relationship of the S^{sh} genome to the B genome of bread wheat was confirmed, but the results provide no evidence that the B genome was derived from *T. sharonense*. Data on the pairing between individual chromosomes of *T. aestivum* and *T. sharonense* provide an estimate of interspecific homoeologous recombination.

Key words C-banding · Homoeologous pairing · Homoeologous relationships · Wheat · *Triticum sharonense*

Introduction

Bread wheat-alien chromosome addition and substitution lines have been produced from related species (Shepherd and Islam 1988). These lines were used to determine homoeologous (genetic) relationships of alien chromosomes to those of bread wheat, either by means of compensation-substitution tests or by the location of marker genes on the alien chromosomes. However, this approach was unsuccessful in *Triticum sharonense* due to the exclusive preferential transmission of chromosome $4S^{sh}$ in wheat (Maan 1975). This chromosome compensated well for the deficiency of chromosome 4B (after the nomenclature adopted at the 7th International Wheat Genetics Symposium, Cambridge, UK, 1987) and 4D (Miller et al. 1982). Isolation of the remaining chromosomes of *T. sharonense* as addition lines was conditioned by the presence of chromosome $4S^{sh}$ (Miller 1982).

In alternate approaches, C-banding has been used to determine cytogenetic relationships between wheat and alien chromosomes. As *T. sharonense* chromosomes show a distinctive C-banding pattern (Teoh and Hutchinson 1983), Friebe and Gill (1996) were able to assign the S^{sh} genome chromosomes to the seven homoeologous groups on the basis of similarities in the morphology and C-banding pattern to *T. longissimum* chromosomes, the latter having been cytogenetically identified by means of compensation-substitution tests (Friebe et al. 1993).

C-banding analysis of homoeologous pairing at the metaphase I of interspecific hybrids provides another approach, as was demonstrated for the arm homoeology of most bread wheat chromosomes (Naranjo et al. 1987, 1988a, b) and those of rye with wheat (Naranjo and Fernández-Rueda 1991; Naranjo 1992). A double translocation involving the arms 5AL, 4AL and 7BS and a pericentric inversion of chromosome 4A that arose during the evolution of wheat were detected. Likewise, different evolutionary translocations were detected in rye. The cytogenetic identification of *T. longissimum* chromosomes (Hart and Tuleen 1983; Friebe et al. 1993) and a translocation between $4S^{l}L$ and $7S^{l}L$ were also confirmed by homoeologus pairing (Naranjo 1995). This method of analysis also provides

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information on the degree of affinity between genomes and the frequency of recombination between alien chromosomes and wheat chromosomes (Naranjo et al. 1989; Naranjo and Maestra 1995; Naranjo and Fernández-Rueda 1996).

The aim of the work presented here was to establish the homoeologous relationships of *T. sharonense* chromosomes to *T. aestivum* and to determine the degree of affinity between the S^{sh} genome with A, B and D genomes of hexaploid wheat by an analysis of homoeologous pairing.

Material and methods

Plants of *Triticum aestivum* (AABBDD, $2n = 6x = 42$) cv 'Chinese Spring' standard-type, *ph2b* (Wall et al. 1971; Sears 1984) and *ph1b* (Sears 1977) mutant lines were crossed with *T. sharonense* ($S^{sh}S^{sh}$, $2n = 14$) accession TH01 (kindly supplied by M. Feldman, The Weizmann Institute of Science, Rehovot, Israel). One standard-type hybrid, three *ph2b* hybrids and four *ph1b* hybrids were used for this study. All hybrids were grown in a greenhouse.

Metaphase-I anthers of the hybrids were fixed in acetic acid-alcohol (1:3) and stored at 0°–4°C for a minimum of 2 months. The fixed material was squashed and stained according to the C-banding technique of Giráldez et al. (1979). A total number of 250 pollen mother cells (PMCs) in the standard-type hybrid, 300 PMCs (176, 83 and 41 PMCs per plant, respectively) in the *ph2b* hybrids, and 300 PMCs (30 + 70 + 100 + 100) in the *ph1b* hybrids were scored. The chromosomes of *T. aestivum*, and their arms, were identified according to Naranjo et al. (1987), which is in agreement with the standard karyotype of wheat reported by Gill et al. (1991).

For somatic chromosome identification, *T. sharonense* seeds were germinated on moist filter paper in petri dishes. Growing-roots 1–2 cm long were excised and immersed in tap water at 0°–4°C for 24–36 h to accumulate metaphase cells and shorten the chromosomes. The tips were fixed in acetic acid-alcohol (1:3), stored at 0°–4°C for 2 months and stained with the C-banding procedure. Each homologous pair of the chromosome complement showed a distinctive C-banding that could be recognized in the cells at metaphase I of the hybrids. The assignment of *T. sharonense* chromosomes according to the seven homoeologous groups and the arm designation, S or L, were carried out by virtue of pairing with *T. aestivum* chromosomes in the hybrids.

Results

All chromosome arms of *T. sharonense* associated with *T. aestivum* chromosomes at metaphase I in the three types of hybrids were identified in all of the PMCs scored (Fig 1). Chromosomes 2A and 2D, and their arms, could not be distinguished from one another. The arms 2AS, 2BS and 2DS are homoeologous, as are 2AL, 2BL and 2DL (Naranjo 1994). Because $2S^{sh}S$ paired with 2BS and $2S^{sh}L$ paired with 2BL, a similar pairing pattern was assumed with the short and long arms of chromosomes 2A and 2D.

The frequency of association between the arms of *T. sharonense* chromosomes and *T. aestivum* chromosomes in the three types of hybrids analyzed is given in Table 1. Associations involving 2AS-$2S^{sh}S$ and 2DS-$2S^{sh}S$ and associations 2AL-$2S^{sh}L$ and 2DL-$2S^{sh}L$ were pooled. In group-5 chromosomes, long arm, pairing combination A-S^{sh} includes both an intercalary association 5AL-$5S^{sh}L$ and a distal association 7BS-$5S^{sh}L$, since 7BS carries a translocated segment from 5AL (Naranjo et al. 1987, 1988a, b). In the short arm of group-7 chromosomes, combination B-S^{sh} corresponds to association 4AL-$7S^{sh}S$ in standard-type and *ph2b* hybrids and to associations 4AL-$7S^{sh}S$ (58.3% of PMCs) and 7BS-$7S^{sh}S$ (1.7% of PMCs) in *ph1b* hybrids, since 4AL carries a translocated segment from 7BS.

All chromosomes of *T. sharonense* except $5S^{sh}$ paired with their homoeologues of the B genome more frequently than with those of the A and D genomes. In group 5, combinations D-S^{sh} and B-S^{sh} showed similar frequencies of pairing in both the short and the long arms.

The frequency of pairing for the different combinations of wheat homoeologous arms are shown in Table 2. These frequencies were calculated according to Naranjo and Maestra (1995). Association of the A-D type was the most frequent in all groups except the short arm of group 4 and the long arm of group 5. Chromosome arm 4AS seldom pairs owing to the structural modification of chromosome 4A by a pericentric inversion (Naranjo 1990). The structural modification of 5AL, which carries a translocated segment from 4AL, and the small size of the segment of 5AL translocated to 7BS account for the low frequency of A-D associations in the long arm of group 5.

Table 3 shows the mean number of univalents, bivalents and multivalents per cell and the proportion of A-D and B-S^{sh} pairing with regard to the total number of chromosome associations. The A-D pairing ratio was higher than the B-S^{sh} pairing ratio in the *ph1b* and *ph2b* hybrids. According to Feldman (1978) the frequency of bonds per cell in the standard-type hybrid suggests that the accession TH01 of *T. sharonense* used is a low-pairing genotype.

Discussion

Chromosome pairing in interspecific hybrids has been traditionally used as a method of assessing genomic affinities among species. The degree of pairing at metaphase I between chromosomes of different genomes has been considered to be a good indicator of their degree of relatedness. Chromosome size differences between genomes and marked chromosomes have been used in conventional studies to ascertain intergenomic chromosome associations. The usefulness of the analysis of homoeologous pairing for resolving genome relationships between wheat and related species has been greatly enhanced with the application of C-banding

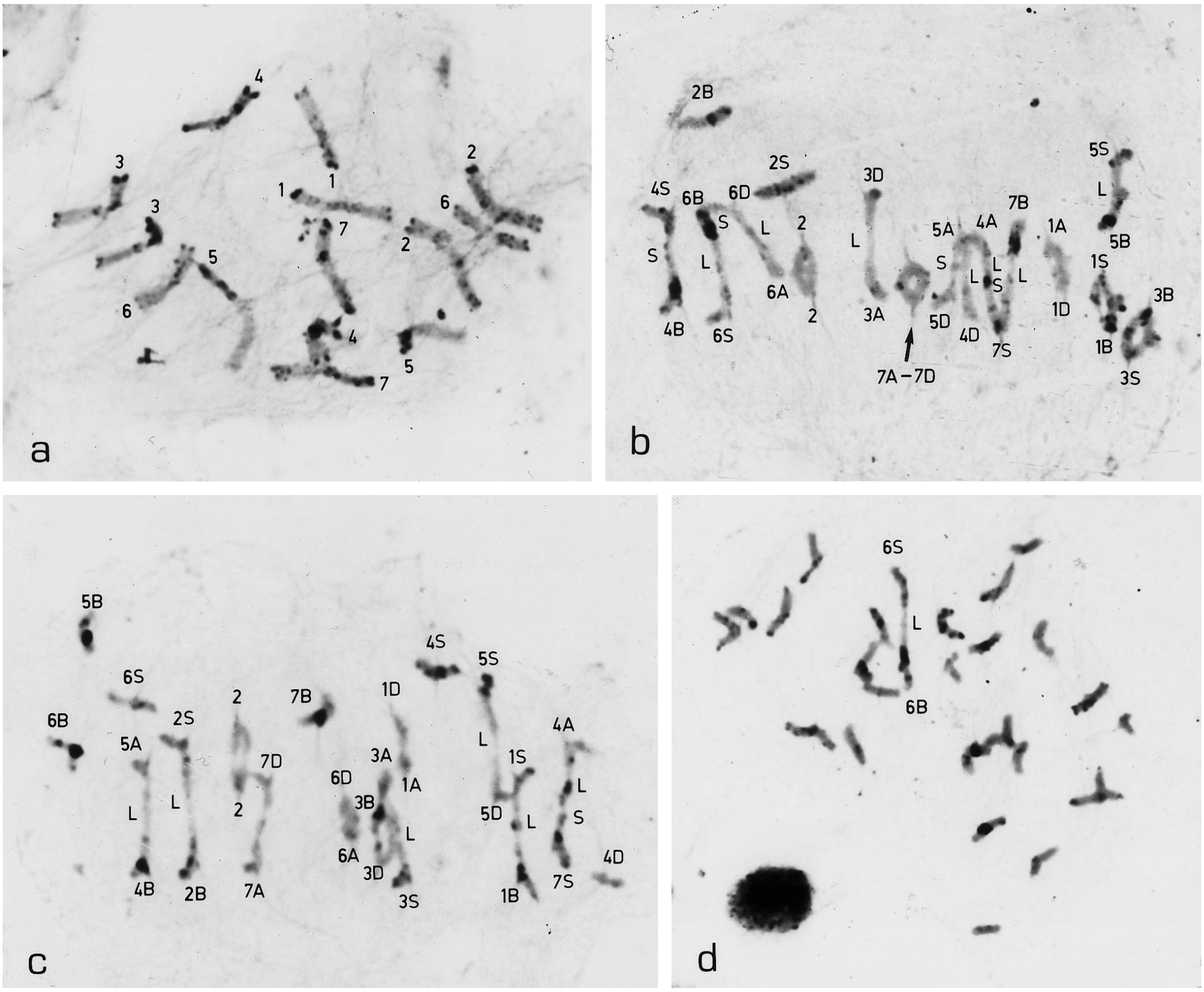

Fig. 1a–d Identification of *T. sharonense* chromosomes by C-banding and homoeolgous pairing. **a** Mitotic metaphase of *T. sharonense*. *Numbers* indicate the homoeologous group and are located close to the telomere of the S arm. **b–d** Metaphase I cells of *ph1b*, *ph2b* and standard *T. aestivum* × *T. sharonense* hybrids, respectively. Chromosomes of bread wheat and *T. sharonense* (S), and the arms associated, are identified. Chromosomes 2A and 2D that could not be distinguished from one another are indicated by *number 2.* In **b**, the ring bivalent 7A–7D is indicated (*arrow*), but individual chromosomes 7A and 7D could not be identified

at meiosis. Not only can differential affinity between genomes be evidenced, but the pairing specificity between individual chromosome arms can also be revealed, from which elucidations on the chromosome structure of homoeologues can be inferred (see review by Jauhar and Joppa 1996).

On the basis of the results of homoeologus pairing between chromosomes of *T. sharonense* and *T. aestivum*, we were able to identify normal homoeologous relationships for all of the chromosomes of the S^{sh} genome to bread wheat. The homoeology of chromosome $4S^{sh}$ to wheat chromosomes of group 4 reported by Miller et al. (1982) is confirmed. The C-banding pattern of *T. sharonense* chromosomes reported by Friebe and Gill (1996) for accession TH01 is the same as shown here (Fig. 1a). Their assignment of the S^{sh} genome chromosomes to the seven homoeologous groups, and the arm designation, based on morphology and C-banding, are consistent with our results from homoeologous pairing.

The pattern of pairing of chromosome arms involved in evolutionary translocations of durum and bread wheat, rye and *T. longissimum* and in the pericentric inversion of chromosome 4A was different from that of the arms showing normal homoeologous relationships in interspecific hybrids. The arms with some structural change paired with chromosomes from a different homoeologous group and/or showed a very low frequency of pairing compared to that of completely homoeologous arms (Naranjo et al. 1987, 1988a,b;

Table 1 Frequency (%) of association at metaphase I between chromosome arms of *T. sharonense* and *T. aestivum* in standard, *ph2b* and *ph1b* ABDS^{sh} hybrids

Group	Genotype	Short arm				Long arm			
		WWS^{sh}	AS^{sh}	DS^{sh}	BS^{sh}	WWS^{sh}	AS^{sh}	DS^{sh}	BS^{sh}
1	Standard	0.0	0.0	0.0	0.8	0.0	1.2	0.8	7.1
	ph2b	0.0	2.3	0.3	3.3	0.7	9.7	7.3	53.7
	ph1b	0.0	6.0	3.0	15.7	1.7	12.3	12.3	57.7
2	Standard	0.0	0.8[a]		0.0	0.0	2.3[a]		4.7
	ph2b	0.0	20.0[a]		12.7	0.3	25.3[a]		29.3
	ph1b	2.3	25.3[a]		35.7	1.0	33.0[a]		39.0
3	Standard	0.0	0.0	0.4	1.9	0.0	0.4	0.4	5.5
	ph2b	0.0	2.3	1.3	18.3	1.3	7.3	8.0	25.0
	ph1b	0.7	7.7	5.7	42.3	1.0	8.7	8.0	55.0
4	Standard	0.0	0.0	0.0	1.9	0.0	0.0	0.8	1.2
	ph2b	0.0	0.0	3.7	23.0	0.0	0.3	1.7	22.7
	ph1b	0.0	0.0	8.0	20.7	1.3	2.7	8.0	32.3
5	Standard	0.0	0.0	0.0	0.0	0.0	0.0	9.8	14.5
	ph2b	0.0	0.3	0.7	1.7	5.0	0.3	30.0	30.3
	ph1b	0.0	0.7	4.7	3.7	6.3	2.0	28.3	35.7
6	Standard	0.0	0.0	0.0	0.8	0.0	0.0	0.0	4.3
	ph2b	0.0	1.3	1.3	16.3	0.0	2.0	0.7	48.3
	ph1b	1.0	6.3	5.7	34.0	1.0	3.7	3.7	64.7
7	Standard	0.0	0.0	0.0	5.5	0.0	0.0	0.0	0.0
	ph2b	0.0	1.0	0.3	37.0	0.0	3.7	1.0	14.7
	ph1b	0.3	0.7	1.7	60.0	0.3	2.7	5.3	47.0

W = A, B or D genomes

[a] AS^{sh} + DS^{sh}

Table 2 Frequency (%) of association at metaphase I between chromosome arms of *T. aestivum* in standard, *ph2b*, and *ph1b* *T. aestivum* × *T. sharonense* hybrids

Group	Genotype	Short arm				Long arm			
		ABD	AD	AB	BD	ABD	AD	AB	BD
1	Standard	0.0	1.6	0.0	0.0	0.0	6.0	0.4	0.8
	ph2b	0.0	27.7	1.0	3.7	0.0	56.0	8.3	8.7
	ph1b	0.0	69.0	3.7	5.0	1.7	64.0	10.3	10.3
2	Standard	0.0	5.7	0.0[a]		0.0	4.9	3.1[a]	
	ph2b	0.3	43.0	16.3[a]		1.3	40.3	35.0[a]	
	ph1b	0.3	53.3	22.0[a]		3.3	46.7	41.7[a]	
3	Standard	0.0	0.8	0.4	0.4	0.0	3.5	1.2	0.8
	ph2b	0.0	29.3	1.7	2.7	0.7	37.0	5.3	20.0
	ph1b	1.0	53.3	4.0	7.3	1.0	73.3	7.3	8.7
4	Standard	0.0	0.0	0.0	1.2	0.0	1.9	0.0	1.2
	ph2b	0.0	0.0	0.0	10.3	0.3	31.3	3.3	13.0
	ph1b	0.0	0.0	0.0	26.3	0.0	46.7	2.0	18.0
5	Standard	0.0	1.6	0.4	0.0	0.0	0.0	0.0	3.5
	ph2b	0.0	17.6	3.7	1.0	0.0	1.0	1.0	17.7
	ph1b	0.0	30.7	7.3	4.7	0.0	0.0	2.7	23.3
6	Standard	0.0	2.8	0.4	0.4	0.0	6.7	0.4	0.0
	ph2b	0.0	42.0	1.7	2.7	0.0	63.7	2.7	4.0
	ph1b	0.7	66.0	5.3	5.0	0.7	76.0	5.3	5.7
7	Standard	0.0	4.1	0.0	0.0	0.0	4.1	0.0	0.0
	ph2b	0.0	38.2	0.7	1.3	0.3	31.2	5.7	1.7
	ph1b	0.3	87.0	4.3	2.0	1.0	81.7	6.3	1.3

[a] AB + BD

Table 3 Mean values per cell of metaphase-I configurations and ratios of the A-D and B-S^{sh} pairing types in standard, *ph2b* and *ph1b* *T. aestivum* × *T. sharonense* hybrids

Configuration	Type of hybrids		
	Standard	*ph2b*	*ph1b*
I	25.21 ± 0.14	10.16 ± 0.21	4.37 ± 0.12
II (open)	1.18 ± 0.07	5.58 ± 0.09	3.74 ± 0.10
II (ring)	0.03 ± 0.01	1.42 ± 0.07	3.79 ± 0.09
III	0.03 ± 0.01	0.71 ± 0.05	1.14 ± 0.05
IV		0.40 ± 0.04	1.16 ± 0.05
V + VI + VII		0.02 ± 0.01	0.09 ± 0.01
Bonds/cell	1.29 ± 0.08	11.17 ± 0.17	17.93 ± 0.12
Pairing ratio			
A-D/total bonds	0.35	0.40	0.41
B-S^{sh}/total bonds	0.38	0.31	0.30

Naranjo and Fernández-Rueda 1991; Naranjo 1990, 1992, 1995). Because no alteration in the arm specifity and frequency of pairing between chromosomes of *T. sharonense* and *T. aestivum* was detected, the conclusion can be drawn that no apparent chromosome rearrangement occurred in the evolution of the S^{sh} genome, which preserves the chromosome structure of the ancestral genome from which genomes A, B and D were derived.

Among the genomes that are in competition for pairing in the ABDS^{sh} hybrids analyzed, combinations A-D and B-S^{sh} showed preferential pairing (Tables 1 and 2). However, A-D pairing occurred at a higher frequency than B-S^{sh} pairing in the *ph2b* and *ph1b* hybrids. Only in the short arm of group-4 chromosomes and in the long arm of group-5 chromosomes was B-S^{sh} pairing much more frequent than A-D pairing, which was a result of the structural modification of 4AS and 5AL. The existence of A-D and B-S^{sh} preferential pairing types in hybrids of *T. sharonense* and the standard line of 'Chinese Spring' had been reported by Fernández-Calvín and Orellana (1993, 1994).

Preferential pairing between chromosomes of the A and D genomes has also been detected in haploids of bread wheat (Jauhar et al. 1991), wheat-rye hybrids (Hutchinson et al. 1983; Naranjo et al. 1987, 1988a, b; Naranjo and Fernández-Rueda 1996) and hybrids between bread wheat and different *Triticum* (*Aegilops*) species (Alonso and Kimber 1983; Fernández-Calvín and Orellana 1991, 1992, 1993, 1994; Naranjo and Maestra 1995). The very close relationships between the A and D genomes might facilitate pairing between alien and B-genome chromosomes in hybrids of *T. aestivum* and related species. Naranjo and Maestra (1995) concluded that preferential pairing between the B and S^{l} genomes in hybrids of hexaploid wheat and *T. longissimum* is a result of the greater affinity of S^{l} to B than to A or D. This conclusion was based on the behavior of the short arm of group 4 chromosomes. In the absence of preferential A-D pairing, 4S^{l}S paired more frequently with 4BS than with 4DS. Because the S genomes of *T. longissimum* and *T. sharonense* show a similar pairing pattern with *T. aestivum* chromosomes in the interspecific hybrids (Naranjo and Maestra 1995; present work), we may conclude that the S^{sh} genome is also more closely related to the B genome than to the A or D genomes. Chromosome 5S^{sh}, like chromosome 5S^{l}, is the only exception; it appears to be almost equally related to 5B and 5D. Yen and Kimber (1990a, b) investigated the phylogenetic relationships among the S-genome diploid species of the genus *Triticum* by analyzing chromosome pairing in triploid hybrids with two genomes from one species and the third genome from the other species. They found that *T. sharonense* and *T. longissimum* are very closely related. Nevertheless, these two species differ by translocation 4L/7L that occurred in the evolution of *T. longissimum.*

Species of the *Sitopsis* section of *Triticum* have been implicated as putative donors of the B genome of wheat (see review by Kerby and Kuspira 1987). Based on a conventional analysis of homoeologous pairing in *ph1b T. aestivum* × *T. sharonense* hybrids, Kushnir and Halloran (1981) assumed that bivalents found at metaphase I were mainly formed by homoeologous chromosomes of the B and S^{sh} genomes. Under this assumption and other lines of evidence they proposed *T. sharonense* as the donor of the B genome. Fernández-Calvin and Orellana (1993) studied homoeologous pairing in standard-type ABDS^{sh} hybrids by means of C-banding. They did not identify individual chromosomes but recognized three types, A-D, B-S^{sh} and AD-BS^{sh}, of chromosome associations. Because B-S^{sh} pairing was less frequent than A-D pairing, they rejected the hypothesis that the B genome derived from *T. sharonense.* Subsequently, Fernández-Calvín and Orellana (1994) reported a similar C-banding analysis of metaphase-I pairing in hybrids between standard 'Chinese Spring' and *T. sharonense*, *T. longissimum* and *T. speltoides.* They concluded that the genomes of these three species show a similar affinity with the B genome of hexaploid wheat and that none of them can be considered to be the ancestor donor of the B genome.

Although our results indicate that the S^{sh} genome preserves the chromosome structure of the original B genome of polyploid wheats, this evidence is not sufficient to consider *T. sharonense* as the donor of the B genome. The S^{sh} and S^{l} genomes of *T. sharonense* and *T. longissimum* show a similar pairing behavior in hybrids with bread wheat. *T. longissimum* was excluded, however, as donor of the B genome because of its 4S^{l}L/7S^{l}L translocation (Naranjo 1995). Chromosome pairing provides no evidence to support the proposal of Kushnir and Halloran (1981). From the C-banding pattern and the location of major nucleolar organizing regions and 5S rRNA genes in the species of the *Sitopsis* section, Friebe and Gill (1996) suggested that the S genome of *T. speltoides* is more closely related to the B genome than the other S genomes.

The frequencies of pairing listed in Table 1 may be used to estimate recombination between chromosomes of *T. sharonense* and *T. aestivum*, which may be of importance for the introgression of useful agronomic traits from *T. sharonense* into bread wheat. The *ph1b* mutation induces the highest level of interspecific recombination. Gene transfer from the S^{sh} to the B genome should be much easier than to the A or D genomes except in group 5. On the other hand, the frequency of recombination between 4BL and $4S^{sh}L$ should be much higher than between 4BL and $4S^{l}L$ of *T. longissimum* because of the $4S^{l}L/7S^{l}L$ translocation (Naranjo and Maestra 1995).

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