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Homoeologous relationships of *Aegilops speltoides* chromosomes to bread wheat

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Abstract Homoeologous pairing at metaphase I was analysed in the standard-type, *ph2b* and *ph1b* hybrids of *Triticum aestivum* (AABBDD) and *Aegilops speltoides* (SS). Data from relative pairing affinities were used to predict homoeologous relationships of *Ae. speltoides* chromosomes to wheat. Chromosomes of both species, and their arms, were identified by C-banding. The *Ae. speltoides* genotype carried genes that induced a high level of homoeologous pairing in the three types of hybrids analyzed. All arms of the seven chromosomes of the S genome showed normal homoeologous pairing, which implies that no apparent chromosome rearrangements occurred in the evolution of *Ae. speltoides* relative to wheat. A pattern of preferential pairing of two types, A-D and B-S, confirmed that the S genome is very closely related to the B genome of wheat. Although this pairing pattern was also reported in hybrids of wheat with *Ae. longissima* and *Ae. sharonensis*, a different behaviour was found in group 5 chromosomes. In the hybrids of *Ae. speltoides*, chromosome 5B-5S pairing was much more frequent than 5D-5S, while these chromosome associations reached similar frequencies in the hybrids of *Ae. longissima* and *Ae. sharonensis*. These results are in agreement with the hypothesis that the B genome of wheat is derived from *Ae. speltoides*.

Key words Homoeologous pairing · Phylogenetic relationships · Wheat · *Ae. speltoides* · C-banding

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Introduction

Homoeologous (genetic) relationships between the chromosomes of bread wheat, *Triticum aestivum*, and those of related species can be established from the genetic and physiological compensation in wheat-alien substitution lines or by the location of marker genes on the added chromosomes of wheat-alien addition lines. These approaches were used to determine the homoeology of *Ae. longissima* and *Ae. searsii* chromosomes to hexaploid wheat (Hart and Tuleen 1983; Pietro et al. 1988; Friebe et al. 1993, 1995).

Chromosomes of species of the *Sitopsis* section of genus *Aegilops*, *Ae. longissima*, *Ae. sharonensis*, *Ae. speltoides*, *Ae. bicornis*, and *Ae. searsii* show a distinctive C-banding pattern (Teoh and Hutchinson 1983). Friebe and Gill (1996) established the homoeology of chromosomes of *Ae. sharonensis*, *Ae. bicornis*, and *Ae. speltoides* to those of *T. aestivum* on the basis of similarities in chromosome morphology and C-banding pattern with other species of the *Sitopsis* section.

C-banding analysis of homoeologous pairing at the metaphase I of interspecific hybrids provides another approach by which to establish the arm homoeology of most bread wheat chromosomes and those of alien chromosomes with wheat. This method of analysis revealed a double translocation 5A/4A/7B and a pericentric inversion of chromosome 4A which accompanied the evolution of polyploid wheat (Naranjo et al. 1987; Gill and Chen 1987; Naranjo 1990). Several translocations in rye relative to wheat were detected (Naranjo and Fernández-Rueda 1991). Later, the cytogenetic identification of *Ae. longissima* chromosomes (Hart and Tuleen 1983; Friebe et al. 1993) was confirmed (Naranjo 1995), and normal homoeology of *Ae. sharonensis* chromosomes to wheat was identified (Maestra and Naranjo 1997).

Quantification of pairing between different homoeologous combinations in interspecific hybrids by means of C-banding also provides information on the degree of affinity and the frequency of recombination between wheat and alien chromosomes (Naranjo et al. 1989; Naranjo and Maestra 1995; Naranjo and Fernández-Rueda 1996; Maestra and Naranjo 1997). The aim of the investigation presented here was to establish the homoeologous relationships of *Ae. speltoides* chromosomes to *T. aestivum* and to assess the degree of affinity between the S genome and A, B, or D genomes by analysis of homoeologous pairing in interspecific hybrids.

Material and methods

Plants of *Triticum aestivum* L. (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 *Aegilops speltoides* Tausch (*T. speltoides* Tausch) (SS, 2n = 2x = 14) from Askhelon (Israel). One standard-type hybrid, four *ph2b* hybrids and eight *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 100 pollen mother cells (PMCs) in the standard type, 100 PMCs (25 PMCs per plant) in the *ph2b* hybrids, and 200 PMCs (25 PMCs per plant) 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 (Gill and Kimber 1974; Gill et al. 1991).

For somatic chromosome identification, *Ae. speltoides* 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. The tips were fixed in acetic acid-alcohol (1 : 3), stored at 0°–4°C for 2 months, and stained using the C-banding procedure. Each homoeologous pair of the chromosome complement showed a distinctive C-banding pattern that could be recognized in the cells at metaphase I of the hybrids. The assignment of *Ae. speltoides* chromosomes to the seven homoeologous groups and the arm designation was carried out by virtue of pairing with *T. aestivum* chromosomes in the hybrids.

Results

The C-banding pattern of *Ae. speltoides* chromosomes is shown in Fig. 1. All of the chromosome arms of *Ae. speltoides* associated with *T. aestivum* chromosomes at metaphase I were identified (Fig. 2) in all PMCs of the three types of hybrids. 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 2SS paired with 2BS and 2SL paired with 2BL, a similar pairing pattern was assumed

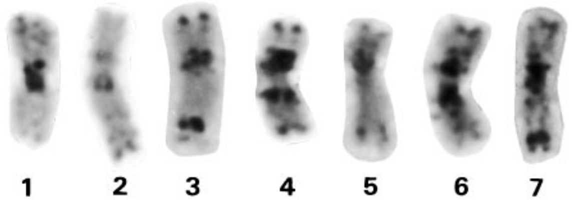

Fig. 1 The C-banding pattern of *Ae. speltoides* chromosomes

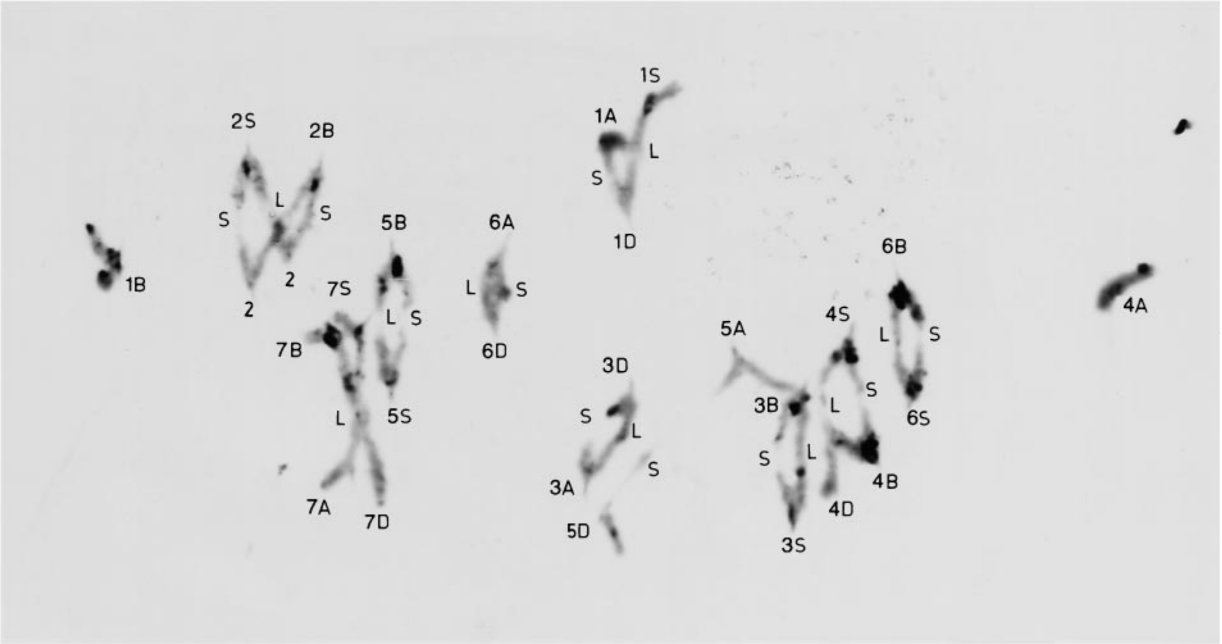

Fig. 2 C-banded metaphase-I cell from a *ph1b* wheat × *Ae. speltoides* hybrid. All chromosomes and the arms associated are identified with the exception of chromosomes 2A and 2D (*2*)

with the short and long arms of chromosomes 2A and 2D.

The frequency of association between the arms of *Ae. speltoides* chromosomes and the wheat chromosomes in the three types of hybrids analyzed is given in Table 1. Associations involving 2AS-2SS and 2DS-2SS and associations 2AL-2SL and 2DL-2SL, which could not be distinguished from one another, were pooled. All the remaining associations between wheat and *Ae. speltoides* chromosomes were identified. In the long arm of

Table 1 Frequency (%) of association at metaphase I between chromosome arms of *Ae. speltoides* and *T. aestivum* in standard, *ph2b* and *ph1b* ABDS hybrids

Group	Genotype	Short arm				Long arm			
		WWS[a]	AS	DS	BS	WWS[a]	AS	DS	BS
1	Standard	0.0	4.0	3.0	20.0	2.0	10.0	12.0	53.0
	ph2b	1.0	7.0	5.0	21.0	0.0	19.0	20.0	52.0
	ph1b	0.5	7.5	5.5	26.0	1.5	8.5	10.0	66.5
2	Standard	0.0	36.0[b]		29.0	1.0	32.0[b]		39.0
	ph2b	1.0	36.0[b]		34.0	0.0	35.0[b]		50.0
	ph1b	1.0	37.0[b]		32.0	0.5	37.0[b]		49.0
3	Standard	1.0	8.0	12.0	29.0	0.0	18.0	14.0	53.0
	ph2b	1.0	10.0	13.0	50.0	1.0	12.0	16.0	62.0
	ph1b	0.5	3.5	6.0	56.0	2.0	5.0	7.5	73.0
4	Standard	1.0	0.0	7.0	42.0	1.0	3.0	16.0	55.0
	ph2b	1.0	0.0	12.0	44.0	2.0	9.0	20.0	51.0
	ph1b	0.0	0.0	13.0	43.5	0.0	6.0	20.5	58.5
5	Standard	0.0	8.0	10.0	25.0	9.0	1.0	13.0	47.0
	ph2b	0.0	8.0	9.0	33.0	3.0	1.0	17.0	44.0
	ph1b	0.0	4.5	4.5	30.0	9.0	1.0	16.5	50.0
6	Standard	0.0	10.0	9.0	20.0	0.0	10.0	11.0	53.0
	ph2b	2.0	8.0	10.0	36.0	5.0	13.0	13.0	59.0
	ph1b	0.5	7.0	2.0	48.0	2.0	9.5	7.5	63.0
7	Standard	1.0	17.0	9.0	37.0	1.0	10.0	7.0	34.0
	ph2b	0.0	11.0	13.0	34.0	5.0	23.0	8.0	17.0
	ph1b	1.5	10.5	8.0	47.5	1.0	8.0	12.0	41.5

[a] W = A, B, or D genomes

[b] AS + DS

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

Group	Genotype	Short arm				Long arm			
		ABD	AD	AB	BD	ABD	AD	AB	BD
1	Standard	1.0	39.0	12.0	5.0	0.0	67.0	10.0	7.0
	ph2b	0.0	38.0	14.0	15.0	1.0	58.0	20.0	14.0
	ph1b	0.0	52.5	4.5	7.5	0.0	71.0	10.0	9.0
2	Standard	0.0	50.0	24.0[a]		4.0	41.0	48.0[a]	
	ph2b	1.0	49.5	27.0[a]		2.0	54.5	36.0[a]	
	ph1b	0.5	52.5	29.0[a]		2.0	52.5	37.0[a]	
3	Standard	0.0	43.0	8.0	7.0	1.0	57.0	15.0	18.0
	ph2b	1.0	54.0	7.0	12.0	2.0	62.0	14.0	11.0
	ph1b	0.5	58.5	3.5	3.5	0.0	81.5	7.5	4.5
4	Standard	0.0	0.0	0.0	15.0	0.0	50.0	14.0	12.0
	ph2b	0.0	0.0	2.0	20.0	0.0	45.0	14.0	14.0
	ph1b	0.0	0.0	0.5	16.5	0.0	54.5	11.5	9.5
5	Standard	0.0	25.0	6.0	7.0	0.0	4.0	0.0	26.0
	ph2b	1.0	39.0	4.0	9.0	0.0	1.0	2.0	27.0
	ph1b	0.0	44.5	3.5	8.0	0.0	2.0	1.0	22.5
6	Standard	0.0	58.5	10.0	9.0	1.0	69.0	10.0	8.0
	ph2b	0.0	62.0	9.0	10.0	2.0	62.0	12.0	11.0
	ph1b	0.5	81.0	1.0	5.0	0.5	76.5	6.0	7.0
7	Standard	0.0	50.0	8.0	5.0	0.0	56.0	5.0	8.0
	ph2b	0.0	50.0	9.0	5.0	1.0	27.0	8.0	11.0
	ph1b	0.5	72.5	5.5	7.0	1.5	73.0	7.5	4.5

[a] AB + BD

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

Configuration	Type of hybrids		
	Standard	*ph2b*	*ph1b*
I	3.97 ± 0.21	3.25 ± 0.18	2.53 ± 0.11
II (open)	4.09 ± 0.20	3.41 ± 0.20	3.36 ± 0.12
II (ring)	3.11 ± 0.17	3.28 ± 0.19	4.29 ± 0.13
III	1.05 ± 0.09	1.02 ± 0.09	0.99 ± 0.06
IV	1.36 ± 0.10	1.79 ± 0.11	1.39 ± 0.07
V	0.17 ± 0.04	0.15 ± 0.04	0.23 ± 0.03
VI + VII + VIII + IX	0.03 ± 0.02	0.06 ± 0.02	0.07 ± 0.02
Bonds per cell	17.79 ± 0.23	19.41 ± 0.20	20.08 ± 0.15
Pairing ratio			
A-D/total bonds	0.34	0.31	0.39
B-S/total bonds	0.30	0.30	0.34

group 4 chromosomes, combination A-S corresponds to association 5AL-4SL, since 5AL carries a translocated segment from 4AL. In the long arm of group 5 chromosomes, combination A-S includes both the intercalary 5AL-5SL association observed in 1 standard PMC and the distal 7BS-5SL association observed in 1 *ph2b* and 2 *ph1b* PMCs, since 7BS carries a translocated segment from 5AL. In group 7 chromosomes, short arm, combination B-S corresponds to association 4AL-7SS, since 4AL carries a translocated segment from 7BS. All chromosomes of *Ae. speltoides* paired with their wheat homoeologues of the B genome more frequently than with those of the A or D genomes.

The frequencies 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 group 4, short arm, and group 5, long arm. Chromosome arm 4AS seldom pairs owing to the pericentric inversion of chromosome 4A. 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 behaviour of the long arm of group 5 chromosomes.

The mean number of univalents, bivalents and multivalents per cell and the proportion of the A-D and B-S pairing with regard to the total number of chromosome associations are given in Table 3. The A-D pairing ratio and the B-S pairing ratio reached similar values in the three genotypes.

Discussion

Friebe and Gill (1996) reported the existence of polymorphism for the C-banding karyotype in *Ae. speltoides*. They assigned the chromosomes to the seven homoeologous groups according to their morphology and C-banding pattern. In the present investigation we could unambiguously identify the S-genome chromosomes at the metaphase I of the hybrids and assign them to the seven homoeologous groups by virtue of pairing with wheat chromosomes. Chromosomes 2S and 3S showed differences for the presence and size of some C-bands compared to those of Friebe and Gill (1996), which made it difficult to establish their correspondence. There was agreement, however, in the assignment of the five remaining chromosomes to homoeologous groups 1, 4, 5, 6, and 7.

The absence of *Ph* genes induces homoeologous pairing in interspecific hybrids of bread wheat and its relatives. Riley et al. (1961) reported a genetic system in *Ae. speltoides* that promoted homoeologous pairing by suppressing the activity of *Ph* genes. Genotypes of *Ae. speltoides* causing high, intermediate, and low levels of homoeologous pairing were detected (Dvořák 1972, Kimber and Athwal 1972). Chen and Dvořák (1984) suggested that two gene systems of *Ae. speltoides* were involved in the promotion of homoeologous pairing. One system was composed of two duplicate loci segregating independently each other, with the other system being composed of several minor genes modifying the effect of the major genes. Chen et al. (1994) transferred two major pairing promoter genes from *Ae. speltoides* to hexaploid wheat.

The level of homoeologous pairing in the standard-type hybrid analysed indicated that a high-pairing genotype of *Ae. speltoides* was used in the present work. Nevertheless, the *ph2b* and *ph1b* hybrids showed a higher frequency of chromosome associations than the standard-type hybrid (Table 3). This variation may be explained either by an effect of the minor genes system of *Ae. speltoides* or by incomplete inhibition of the activity of *Ph1* and *Ph2* by the two major suppressor genes.

Structural differences between chromosomes from different genomes can be detected by analysis of homoeologous pairing (Naranjo et al. 1987; Gill and Chen 1987; Naranjo 1990, 1995; Naranjo and Fernández-Rueda 1991, 1996). While homoeologous chromosome arms with the same genetic architecture do pair and recombine in hybrids where homoeologous pairing is not suppressed, the arms involved in translocations pair with arms from a different homoeologous group or show a very low frequency of association at metaphase I. Inversions involving distal chromosome segments, where chiasmata are formed, may also affect the frequency of pairing. This is the case of chromosome 4A—its short arm seldom pairs. However, inversions may also occur in chromosome segments rarely involved in chiasmata pairing and remain undetected after homoeologous pairing analysis. Chromosome 4B of ‘Chinese Spring’ has a pericentric inversion in its proximal part (Mickelson-Young et al. 1995) which did not affect B-S pairing (Table 1). Our results of pairing between wheat and *Ae. speltoides* chromosomes

(Table 1) allowed us to identify normal arm homoeology for the seven S-genome chromosomes relative to wheat. This finding suggests that no apparent chromosome rearrangement occurred in the evolution of the S genome, which preserves the chromosome structure of the ancestral genome from which the A, B, and D genomes of wheat were also derived.

Ae. sharonensis also preserves the ancestral chromosome structure (Maestra and Naranjo 1997), while *Ae. longissima* suffered a translocation between $4S^lL/7S^lL$ during its evolution (Friebe et al. 1993; Naranjo 1995). Earlier reports showing multivalents at metaphase I in hybrids of *Ae. longissima* and *Ae. sharonensis* or *Ae. speltoides* and only bivalents in the hybrids between *Ae. speltoides* and *Ae. sharonensis* (Feldman et al. 1979 and references therein) are consistent with the chromosome structure of these three species relative to wheat. Yen and Kimber (1990) concluded that *Ae. sharonensis* is almost equally related to both *Ae. longissima* and *Ae. speltoides* and that *Ae. longissima* and *Ae. speltoides* are more distant from each other than from *Ae. sharonensis.*

The pattern of pairing among the four genomes that were in competition in the ABDS hybrids was characterized by the existence of A-D and B-S preferential pairing types. The A-D pairing was more frequent than the B-D pairing (Tables 1 and 2), except in group 4 and in the long arm of group 5 chromosomes, most likely owing to the structural modification of chromosomes 4A and 5AL. The long arm of group 7 chromosomes showed an exceptional behaviour in the *ph2b* hybrids since the A-S association was more frequent than that of B-S. Preferential A-D and B-S pairing types were also found in hybrids of standard 'Chinese Spring' and *Ae. longissima*, *Ae. sharonensis*, and *Ae. speltoides* (Fernández-Calvín and Orellana 1994). Naranjo and Maestra (1995) and Maestra and Naranjo (1997) concluded that preferential B-S^l and B-S^{sh} pairing was not caused by the existence of preferential A-D pairing in the hybrids but that they were the result of a greater affinity of S^l and S^{sh} to B than to A or D. This conclusion can be extended to the S genome of *Ae. speltoides.*

Species of the *Sitopsis* section have been proposed to be the donors of the B genome of cultivated wheats (see review by Kerby and Kuspira 1987). Fernández-Calvín and Orellana (1994) studied homoeologous pairing in ABDS, $ABDS^l$, and $ABDS^{sh}$ hybrids by means of C-banding. They recognized three pairing types, A-D, B-S and AD-BS, but did not identify individual chromosomes. They concluded that the genomes of *Ae. speltoides*, *Ae. sharonensis* and *Ae. longissima* are equally related to bread wheat and that none of them can be considered to be the diploid ancestor of the B genome.

Different molecular approaches have suggested that the S genome of *Ae. speltoides* is more closely related to the B genome than to the other S genomes. Badaeva et al. (1996b) found that in *Ae. speltoides* there are two major ribosomal RNA loci on chromosomes of groups 1 and 6, like the B genome of bread wheat, whereas the other species of the *Sitopsis* section carry these loci on chromosomes 5 and 6. One minor NOR was also detected on chromosome arm 1BL of *T. aestivum* and 1SL of *Ae. speltoides* (Jiang and Gill 1994). The spacer sequences of *Ae. speltoides* were also more similar to those of the polyploid wheats than to the spacer sequences of the other S-genome species (Gill and Appels 1987). Daud and Gustafson (1996) isolated and cloned a genome-specific repetitive DNA sequence from *Ae. speltoides* which was also present in the genomes of polyploid wheats but barely detectable in any of the other four S-genome species. Results of chromosome banding (Friebe and Gill 1996) and the distribution of the highly repetitive DNA sequence pSc119 (Badaeva et al. 1996a) also support the contention that *Ae. speltoides* is the most probable B-genome progenitor of wheat.

The B-S pairing ratio yielded values in the hybrids of wheat and *Ae. speltoides* (Table 3) which were comparable to those obtained in hybrids of wheat with *Ae. longissima* and *Ae. sharonensis* (Naranjo and Maestra 1995; Maestra and Naranjo 1997). Qualitative differences in the degree of closeness of genomes S, S^l, and S^{sh} to the B genome were not apparent from the average B-S pairing ratios. However, significant differences between the three S genomes were observed when the behaviour of group 5 chromosomes was compared. Chromosomes $5S^l$ and $5S^{sh}$ from *Ae. longissima* and *Ae. sharonensis*, respectively, showed a similar frequency of pairing with chromosomes 5B and 5D of wheat, while chromosome 5S of *Ae. speltoides* paired with 5B more frequently than with 5D. Because chromosome 5B carries the *Ph1* gene, which is, at least in part, responsible for the diploidization of polyploid wheats, this chromosome had to develop some relevant role in the evolution. The existence of a closer relationship of 5B to 5S than to $5S^l$ or $5S^{sh}$ is consistent with the hypothesis that *Ae. speltoides* was the B-genome donor.

Strains of *Ae. speltoides* with genes that suppress the effect of *Ph1* have been used to transfer genetic material from this species to wheat (Knott and Dvořák 1981). Furthermore, Riley et al. (1968) were able to transfer a chromatin segment carrying the stripe rust resistence (*Yr8*) from *Ae. comosa* to wheat by first crossing a monosomic addition line carrying the alien chromosome with *Ae. speltoides* and then selecting for recombinants among the progeny from backcrosses to wheat. The results of ABD-S pairing provide an estimate of the frequency of recombination between wheat and *Ae. speltoides* chromosomes. The transfer of genes from the high-pairing genotype of *Ae. speltoides* to the B genome should be much easier than to the A or D genomes, regardless of the wheat genotype used. In hybrids of the *ph1b* mutant wheat with *Ae. longissima* and *Ae. sharonensis*, alien chromosomes also paired more frequently with chromosomes of the B genome than with those of the A or D genomes. The possiblity exists that pairing between wheat A- or D-genome chromosomes and alien chromosomes of species different from *Ae. speltoides* may be increased by using the high-pairing genotype of *Ae. speltoides* to induce homoeologous pairing, since *Ae. speltoides* chromosomes and the other alien chromosomes would compete on pairing with the B-genome chromosomes.

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