Theor Appl Genet (1994) 88: 1043–1049

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Metaphase I-bound arms frequency and genome analysis in wheat-*Aegilops* hybrids. 3. Similar relationships between the B genome of wheat and S or S^l genomes of *Ae. speltoides*, *Ae. longissima* and *Ae. sharonensis*

Received: 22 November 1993 / Accepted: 12 January 1994

Abstract The meiotic behaviour of *Triticum aestivum* × *Aegilops speltoides*, *T. aestivum* × *Ae. sharonensis* and *T. aestivum* × *Ae. longissima* tetraploid hybrids (genome constitution ABDS, ABDS^l, and ABDS^l, respectively) has been analysed by the C-banding technique. Of the six types of pairing normally occurring, at metaphase I three were recognized: A-D, AD-BS/AD-BS^l and B-S/B-S^l. The relative order observed in the low pairing hybrid, A-D> B-S^l>AD-BS^l, as well as that found in high-pairing 'Chinese Spring' × *Ae. speltoides* hybrids, A-D>AD-BS>B-S, revealed the existence of preferential pairing patterns among the different genomes that are in competition. In all of the hybrids analysed the mean number of bound arms per cell for the A-D type was significantly higher than the mean number of associations between the B and S/S^l genomes. Usually the relative contribution of each type of pairing is maintained among hybrids with different *Aegilops* species. These results indicate that the genomes of *Ae. speltoides*, *Ae. sharonensis* and *Ae. longissima* show a similar affinity with the genomes of hexaploid wheat; therefore none of these species can be considered to be a distinct donor of the B genome of wheats.

Key words Genome analysis · C-banding · Wheat × *Aegilops* hybrids · B genome · Evolutionary relationships

Introduction

The diploid ancestors of the A and D genomes of wheats are well established as being *Triticum monococcum* and *Aegilops squarrosa*, respectively (Kerby and Kuspira 1987). However, identification of the progenitor of the B genome has remained unclear and controversial, althought numerous studies using biochemical, cytological, geographical, meiotic pairing and morphological approaches have been made. On many occasions one or more of the *Aegilops* species of Sitopsis section namely, *Ae. speltoides*, *Ae. sharonensis*, *Ae. longissima*, *Ae. searsii* and *Ae. bicornis*, have been proposed to be the donor(s) of the B genome of cultivated wheats (see Kerby and Kuspira 1987 for a review). However, these studies did not provide convincing evidence for either the acceptance or rejection of any one of the five species as the probable donor of the B genome of the polyploid wheats.

Genome analysis has been considered to be the main method for studying evolutionary relationships in the Triticineae group (Kimber and Sears 1987). This technique is based on measurements of the total amount of pairing per cell observed at metaphase I in interspecific hybrids. Generally, most of these genome analyses have been carried out using traditional staining methods that do not allow a direct analysis of the type of chromosome associations produced in meiosis of the hybrids. Therefore, the interpretation of data derived from different hybrid combinations is often complicated and equivocal.

The utilization of differential staining procedures enables a more direct and detailed analysis of genomic affinities since the genomes that are implicated in each meiotic configuration can be determined (Cermeño et al. 1985; Cuñado et al. 1986; Orellana et al. 1989; Fernández-Calvín and Orellana 1991, 1992; Naranjo 1992).

The investigation presented here was an attempt to obtain more information on the phylogeny of wheats. Meiotic associations between different genomes at metaphase I in *T. aestivum* × *Aegilops* tetraploid hybrids (genome constitution ABDS or ABDS^l) were studied using the C-banding procedure.

Materials and methods

Tetraploid hybrid plants (genome constitution ABDS/ABDS^l) were obtained from crosses between hexaploid wheat *Triticum aestivum* L. cv 'Chinese Spring' ('CS', genome constitution AABBDD) as female and three species of *Aegilops*, *Ae. speltoides* Tausch (genome

Communicated by K. Tsunewaki

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constitution SS), *Ae. sharonensis* Eig (S^lS^l) and *Ae. longissima* Schw. et Musch. (S^lS^l), as males.

Hybrid seeds were germinated at 20 °C on moist filter paper in petri dishes. Primary roots 1 cm long were excised and immersed in tap water at 0 °C for 24–30 h to accumulate metaphase cells and shorten the chromosomes. The tips were then fixed in acetic ethanol (1:3) and stored at 0–4 °C for several months. In order to obtain meiotic cells, anthers of hybrids were fixed in acetic ethanol (1:3) and stored for 1–4 months at 0–4 °C. The fixed material was squashed and stained following the Giemsa C-banding technique described by Giráldez et al. (1979).

Results

The application of the C-banding technique revealed the existence of three different identifiable chromosome groups:

(1) the A and D genomes of wheat were characterized by the absence of prominent C-bands;

(2) the B genome of 'Chinese Spring' showed prominent pericentromeric C-bands as well as some disperse and intercalary heterochromatin. The chromosomes of this genome are characterized by the absence of telomeric C-heterochromatin, except for chromosome 1B, which possesses a telomeric C-band located on the long arm (Gill et al. 1991; Fernández-Calvín and Orellana 1993);

(3) the S/S^l genomes of the three *Aegilops* species analysed had telomeric heterochromatin as well as scattered, intercalary and pericentromeric bands in almost all of the chromosomes (see Fig. 1).

In the tetraploid hybrids (genome constitution ABDS/$ABDS^l$) six different types of homoeologous association (A-B, A-D, A-S/A-S^l, B-D, B-S/B-S^l and D-S/D-S^l) at metaphase I can occur. Chromosomes of the A and D genomes were pooled because they possessed an indistinguishable C-banding pattern, likewise the chromosomes of the B and S/S^l genomes could not be identified in all meiotic cells due to the fact that the degree of condensation always makes it difficult to detect telomeric C-bands in metaphase I cells. Consequently, these also were considered as a whole. Thus, only three types of pairing were unequivocally distinguished, namely associations between the A and D genomes (A-D), A or D chromosomes and B or S/S^l genomes (AD-BS/AD-BS^l) and between B and S/S^l chromosomes (B-S/B-S^l).

Table 1 shows the different meiotic configurations observed for the three distinguishable types of pairing in all combinations analysed. The 'CS' × *Ae. sharonensis* and 'CS' × *Ae. longissima* hybrids had a low-homoeologous-pairing frequency (Fig. 2), whereas the presence of the *Ae. speltoides* genotype promoted an increase in the level of pairing with multivalents being frequently observed (Fig. 3).

It has been known for some time that in hybrids between polyploid wheats and *Ae. speltoides* pairing between homoeologous chromosomes is not prevented. Kimber (1974) described a range of variation in this species, which he divided into groups of low, intermediate, high and super-high pairing. The accession employed in the present work can be classified as high pairing.

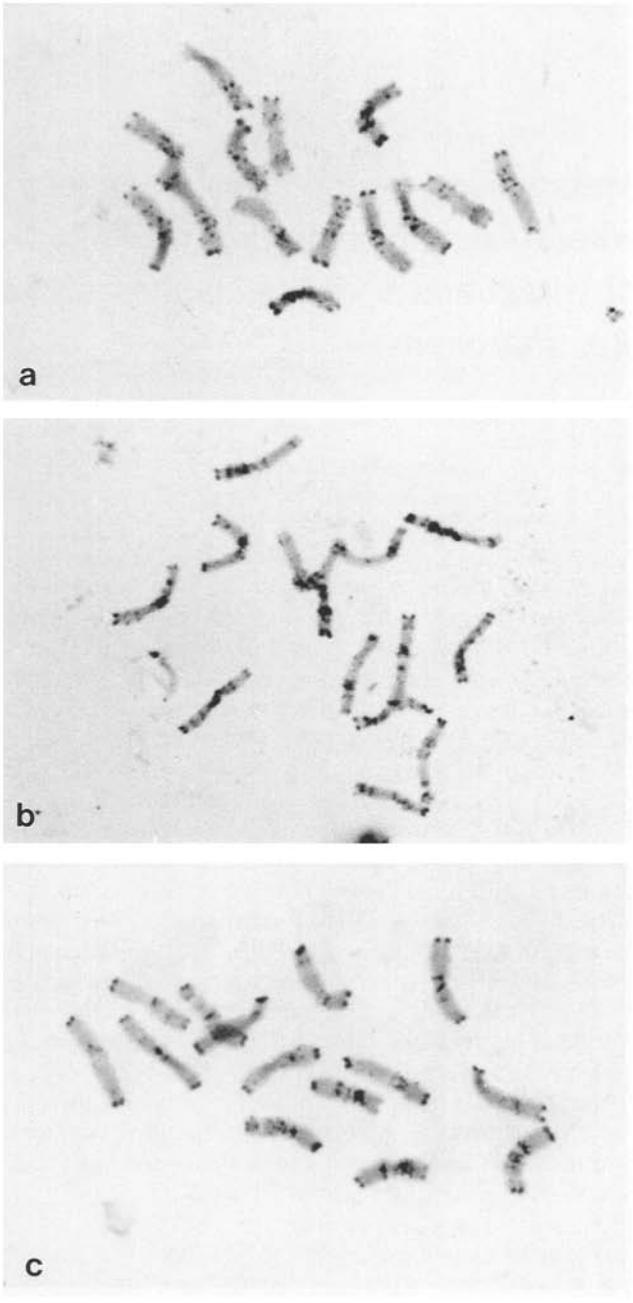

Fig. 1a–c Mitotic metaphase cells of *Aegilops* species. **a** *Ae. speltoides*, **b** *Ae. sharonensis*, **c** *Ae. longissima*

If all of the chromosomes for a given homoeologous group were associated, the largest meiotic configuration to be expected would be a quadrivalent; however, pentavalents and even hexavalents were found in 'CS' × *Ae. speltoides* hybrids (Fig. 3b, c). This type of configuration can only be explained by the existence of translocation between the different genomes of the hybrids. The existence of reciprocal translocations involving different homoeologous groups has been described in *Aegilops* (Tanaka 1955;

Table 1 Number of the different meiotic configurations observed for the three distinguishable types of pairing in 'Chinese Spring' × *Ae. speltoides*, 'Chinese Spring' × *Ae. sharonensis* and 'Chinese Spring' × *Ae. longissima* hybrids (*O* open bivalents, *R* ring bivalents, *III* trivalents, *IV* quadrivalents, *V* pentavalents, *VI* hexavalents)

Hybrid	No. of Cells	Meiotic configuration											
		Bivalents						Univalents		Multivalents			
		A-D		AD-BS		B-S		AD	BS	III	IV	V	VI
		R	O	R	O	R	O						
CS × *Ae. spel*-1	50	106	57	15	68	21	52	107	306	53	45	2	–
CS × *Ae. spel*-2	50	124	65	18	60	29	87	85	275	53	26	1	1
CS × *Ae. spel*-3	50	122	61	13	69	34	104	90	188	65	25	3	1
CS × *Ae. spel*-4	50	104	70	6	82	20	88	108	271	57	25	2	–
Total	**200**	**456**	**253**	**52**	**279**	**104**	**331**	**390**	**1040**	**228**	**121**	**8**	**2**
CS × *Ae. shar*-1	100	1	56	–	22	–	36	1264	1306	–	–	–	–
CS × *Ae. shar*-2	100	3	110	–	45	–	57	1120	1235	5	–	–	–
CS × *Ae. shar*-3	100	4	100	–	50	–	56	1132	1233	5	–	–	–
CS × *Ae. shar*-4	100	5	82	–	14	–	50	1210	1285	1	–	–	–
CS × *Ae. shar*-5	100	–	40	–	17	–	11	1303	1361	–	–	–	–
Total	**500**	**13**	**388**	**–**	**148**	**–**	**210**	**6029**	**6420**	**11**	**–**	**–**	**–**
CS × *Ae. long*-1	100	1	60	–	22	–	24	1256	1330	–	–	–	–
CS × *Ae. long*-2	100	2	55	–	29	–	25	1256	1319	1	–	–	–
CS × *Ae. long*-3	100	2	51	–	27	–	26	1267	1321	–	–	–	–
CS × *Ae. long*-4	100	1	46	–	28	1	35	1278	1300	–	–	–	–
Total	**400**	**6**	**212**	**–**	**106**	**1**	**110**	**5057**	**5270**	**1**	**–**	**–**	**–**

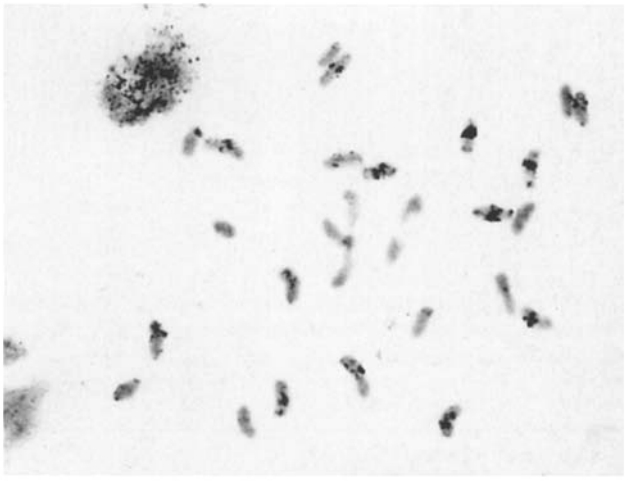

Fig. 2 Metaphase I cell of 'Chinese Spring' × *Ae. sharonensis* hybrid. All the associations are of the A-D type

Cuñado et al. 1986) and in wheat (Kobrehel and Feillet 1975; Benito and Pérez de la Vega 1979; Naranjo et al. 1987, 1988; Naranjo 1990), and it is well known that this cytogenetic mechanism has accompanied the evolutionary process of the Triticineae group.

The number of bound arms per cell for the different kinds of homoeologous associations at metaphase I has been estimated to be the minimun number of chiasmata that can explain each meiotic configuration. In those configurations where three chromosome arms were associated at the same point, as in the frying pan and Y-shaped trivalent or quadrivalent (see Fig. 3d, e), the type of association could not be ascertained and, subsequently, they were considered as undetermined (Un).

Table 2 shows the number of bound arms for each type of specific association observed in all of the hybrids analysed. In both 'CS' × *Ae. sharonensis* and 'CS' × *Ae. longissima*, the frequencies of bound arms per cell at metaphase I were very similar, since no significant deviation was detected when a *t*-test was performed ('CS' × *Ae. sharonensis*=1.59, 'CS' × *Ae. longissima*=1.11; t=1.362; df=7). Obviously, the mean number of bonds per cell observed in 'CS' × *Ae. speltoides* was significantly higher than that found in low-homoeologous-pairing crosses ('CS' × *Ae. sharonensis* and 'CS' × *Ae. longissima*).

If pairing takes place at random among the different genomes that are in competition to pair, one would expect the following relative order: AD-BS/AD-BS^l>B-S/B-S^l=A-D, in a ratio 4:1:1; that is, the meiotic pairing would depend only on the number of genomes implicated in each kind of association. However, in the low pairing hybrids the three types of specific associations showed the relative order A-D>B-S^l>AD-BS^l, whereas in high-pairing hybrids the relative order observed was A-D>AD-BS>B-S.

The type of association in which an equal number of genomes are involved could provide additional information about the genome affinities expressed, because the same mean number of bound arms per cell at metaphase I is expected for all of those types if preferential pairing does not occur.

The comparisions carried out among the three distinguishable types of associations revealed that the associations between the A and D genomes of wheat were always

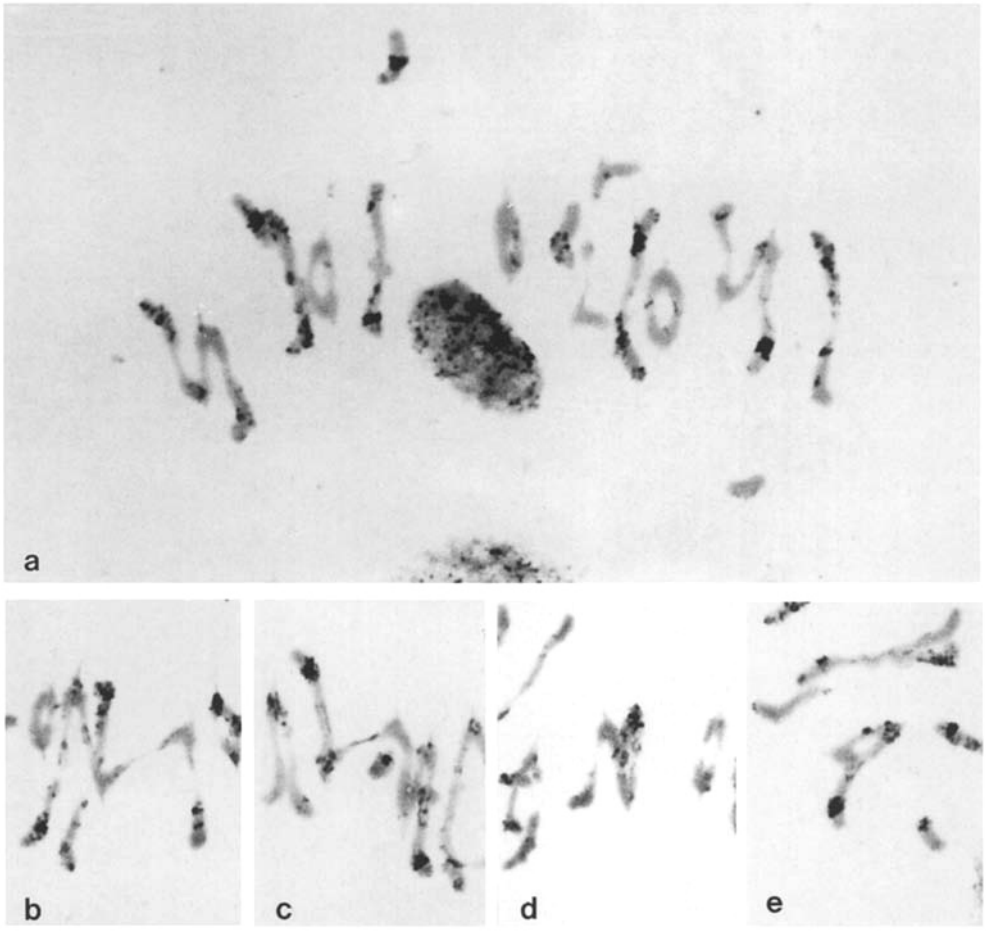

Fig. 3a Metaphase I cell of 'Chinese Spring' × *Ae. speltoides* high pairing hybrid. **b** Pentavalent. **c** Hexavalent. **d** Frying pan quadrivalent. **e** Frying pan trivalent

Table 2 Numbers of bound arms observed for each type of specific association at metaphase I in all hybrids analysed. Undetermined associations are also included (*Un*) (*B.A./cell* mean number of bound arms per cell)

Hybrid	Number of association					
	A-D	AD-BS	B-S	Total	Un	B.A./cell
CS × *Ae. spel*-1	340	236	138	714	2	14.32±0.33
CS × *Ae. spel*-2	383	191	173	747	2	14.98±0.34
CS × *Ae. spel*-3	370	211	217	798	2	16.00±0.27
CS × *Ae. spel*-4	345	194	155	694	2	13.92±0.31
Total	**1438**	**832**	**683**	**2953**	**8**	**14.81±0.17**
CS × *Ae. shar*-1	58	22	36	116	–	1.16±0.09
CS × *Ae. shar*-2	120	49	59	228	–	2.28±0.13
CS × *Ae. shar*-3	113	54	57	224	–	2.24±0.13
CS × *Ae. shar*-4	93	15	50	158	–	1.58±0.12
CS × *Ae. shar*-5	40	17	11	68	–	0.68±0.07
Total	**424**	**157**	**213**	**794**	**–**	**1.59±0.04**
CS × *Ae. long*-1	62	22	24	108	–	1.08±0.04
CS × *Ae. long*-2	59	30	26	115	–	1.15±0.09
CS × *Ae. long*-3	55	27	26	108	–	1.08±0.08
CS × *Ae. long*-4	48	28	37	113	–	1.13±0.07
Total	**224**	**107**	**113**	**444**	**–**	**1.11±0.04**

Table 3 Comparisons by paired *t*-tests between the mean number of bound arms per cell observed for the different types of pairing in all of the crosses analysed

Hybrid	Comparisons	*t*-value	*df*
CS × *Ae. spel*	A-D/AD-BS		
	7.19/4.16	8.347**	3
	A-D/B-S		
	7.19/3.42	14.974***	3
	AD-BS/B-S		
	4.16/3.42	1.675	3
CS × *Ae. shar*	A-D/AD-BS^l		
	0.85/0.31	5.123**	4
	A-D/B-S^l		
	0.85/0.43	5.622**	4
	AD-BS^l/B-S^l		
	0.31/0.43	0.539	4
CS × *Ae. long*	A-D/AD-BS^l		
	0.56/0.27	7.116**	3
	A-D/B-S^l		
	0.56/0.28	4.720*	3
	AD-BS^l/B-S^l		
	0.27/0.28	1.635	3

*, **, *** Significant at the 5%, 1% and 0.1% level, respectively

Table 4 Comparisons of the relative contribution for all types of distinguishable associations between tetraploid hybrids with different parental *Aegilops*. In all cases *t*-tests were performed

Comparison	Type of pairing	Relative contribution	*t*-value	*df*
CS × *Ae. spel* – CS × *Ae. shar*	A-D	0.49–0.54	2.215	
	AD-BS/AD-BS^l	0.28–0.20	2.425*	7
	B-S/B-S^l	0.23–0.26	0.877	
CS × *Ae. spel* – CS × *Ae. long*	A-D	0.49–0.51	0.546	
	AD-BS/AD-BS^l	0.28–0.24	1.998	6
	B-S/B-S^l	0.23–0.25	0.812	
CS × *Ae. shar* – CS × *Ae. long*	A-D	0.54–0.51	1.034	
	AD-BS^l	0.20–0.24	1.272	7
	B-S^l	0.26–0.25	0.163	

* Significant at the 5% level

significantly higher than those of B-S/B-S^l and AD-BS/AD-BS^l types (Table 3).

The differences between the hybrid combinations analysed with respect to the levels of pairing (low and high) made it necessary to develop a method that takes into account the amount of pairing relative to the total associations. Thus, the mean number of associations per total number of bonds represents the "relative contribution" of each type of association (Fernández-Calvín and Orellana 1991). In order to study whether the three different *Aegilops* species employed in this work exhibited differential behaviour in their affinities with respect to wheat genomes, the relative contribution for each type of pairing was compared between different tetraploid hybrid crosses. It is apparent from the data in Table 4 that the relative contribution was generally maintained in the different hybrid combinations.

Discussion

The levels of pairing observed in our low tetraploid hybrids ('CS' × *Ae. sharonensis* and 'CS' × *Ae. longissima*) similar to the meiotic behaviour previously described by various authors for 'Chinese Spring' × *Ae. sharonensis* and 'Chinese Spring' × *Ae. longissima* hybrid combinations (Riley et al. 1961; Mello-Sampayo 1971; Mello-Sampayo and Canas 1973; Yu and Jahier 1992; Fernández-Calvín and Orellana 1993).

Traditionally, the study of meiotic behaviour in hybrids has been carried out on the basis of the mean number of bound arms per cell or the mean number of bivalents per cell. The degree of associations between the chromosomes in a hybrid is generally a good indication of the degree of genome relatedness. In this way, high levels of pairing have been associated with strong genome affinities in wheat-*Ae. speltoides* hybrids (Riley et al. 1958), although this interpretation was later rejected on the premise that the high homoeologous pairing was a reflection of strong promoters of meiotic pairing in the *Ae. speltoides* genotype (Riley et al. 1961). Likewise, Kushnir and Halloran (1981) suggested that *Ae. sharonensis* could be the ancestor of the B genome of wheats, based on the high homoeologous pairing observed in 'Chinese Spring' (*ph1b* mutant) × *Ae. sharonensis* hybrids. In this case, the high level of pairing found was due to the effect of *Ph* gene inactivation. Kimber and Sears (1987) pointed out that in wheat-*Ae. speltoides* hybrids (with a high level of homoeologous pairing) there was no way of distinguishing homologous from homoeologous pairing and, consequently, it was not possible to carry out genome analysis in these combinations. All of these problems appeared in these studies due to the fact that meiotic pairing had to be considered as a whole as there was no cytological marker available for the determination of genome-specific association in the hybrids.

The utilization of such differential staining methods as the C-banding allows a more detailed study of the different chromosomes that are implicated in each meiotic configuration to be carried out and therefore provides unequivocal evidence of the genomic affinities that are expressed in hybrid combinations, independently of the level of pairing. Using telocentric chromosomes as markers, Riley and Chapman (1966) studied 'Chinese Spring' × *Ae. speltoides* hybrids. They found that the association of the 5B chromosome with the 5D was much more frequent than any of the other possible associations, with the next most common pairing being between chromosome 5B and 5S. However, Belfield and Riley (1969) reported that the three wheat genomes were similarly related to the S genome of *Ae. speltoides* in *Ae. speltoides* × *T. aestivum* hybrids. On the other hand, Feldman (1978) described a preferential pairing between the B genome of wheat and the S^l genome of *Ae. longissima*, whereas the A and D genomes paired only slightly. The results of the present study are in disagreement with those of the above reports. The associations between the A and D genomes of wheat were significantly more frequent than any of the two other distinguishable classes (AD-BS/AD-BS^l and B-S/B-S^l) in all of the tetraploid hybrids analysed (see Table 3).

If any S/S^l genome of *Aegilops* species were the ancestral B-genome donor, one should expect that the associations between both genomes (B-S/B-S^l type) would be the most frequent. In low-pairing tetraploid hybrids the associations between the B and S^l genomes were more frequent

than AD-BS^l pairing, but when the *t*-test was performed no deviation was detected. Therefore, there is a preferential pairing among B and S^l genomes, since if the pairing was at random the most frequent type should be the AD-BS^l.

Recently, a certain degree of preferential pairing between chromosomes of both the A and D genomes has been detected by means of C-banding in such different situations as the haploids of wheat (Jauhar et al. 1991), wheat-rye hybrids (Hutchinson et al. 1983; Naranjo et al. 1987, 1988) and in wheat-*Aegilops* hybrids (Fernández-Calvín and Orellana 1991, 1992, 1993). Kimber and Alonso (1981) studied hybrids between *T. aestivum* and *Ae. speltoides* and observed that the pairing pattern tends to be in two clusters of two. Subsequently, Alonso and Kimber (1983) showed that in *T. aestivum* × *Ae. speltoides* and *T. aestivum* × *Ae. longissima* tetraploid hybrids, involving telocentric chromosomes, these clusters are AD and BS/BS^l, and that the relative affinity of the A genome for the D genome is about the same as that of the B genome for the S/S^l genomes. If pairing frequencies can be taken as a measure of the relationships between the genomes that are in competition, the results obtained in this work indicate that the A and D genomes of wheat are more closely related to each other than is the B genome with the S/S^l genomes of the *Aegilops* species employed.

If two genomes have originated from different diploid species, such as the A and D genomes of wheat, one would expect that the affinity between these genomes would be smaller than the relationship between one genome and its possible ancestral donor. With this kept in mind and on the basis of the pairing pattern observed in the tetraploid hybrids analysed here (with low and high pairing level) it seems unlikely that either S^l genome of *Ae. sharonensis* and *Ae. longissima* or the S genome of *Ae. speltoides* can be considered to be the source of the B genome of wheat.

On the other hand, *Ae. sharonensis* and *Ae. longissima* are closely related, so much so that they are even taken as varieties of the same species (Lilienfeld 1951; Tanaka 1955; Kihara and Yamashita 1956; Yen and Kimber 1990), therefore one should expect a similar meiotic behaviour in hybrid combinations. The results obtained when the relative contribution of each type of association was compared among hybrids with different *Aegilops* species indicate that all of them show similar relationships with the genomes of wheat; only the AD-BS type does not contribute in the same way in 'CS' × *Ae. sharonensis* and 'CS' × *Ae. speltoides* hybrids. The excess of this type of pairing might be due to the high multivalent frequency observed at metaphase I while the remainder types are maintained.

In conclusion, our study demonstrates that the genomes of *Ae. speltoides*, *Ae. sharonensis* and *Ae. longissima* are equally related to wheat genomes and that at present there is no strong reason for believing that one of them is the diploid ancestor of the B genome.

Acknowledgements This work has been supported by Grant No. AGR90-0090 from the Comision Interministerial de Ciencia y Tecnología (CICYT) of Spain.

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