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The effect of ph mutations on homoeolgous pairing in hybrids of wheat with *Triticum longissimum*

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Abstract Homoeologous pairing at metaphase-I was analyzed in wild-type, *ph2b*, and *ph1b* hybrids of wheat and a low-pairing type of *T. longissimum* in order to study the effect of *ph* mutations on the pairing of *T. longissimum* chromosomes with wheat chromosomes. Chromosomes of both species, and their arms, were identified by C-banding. The three types of hybrids, with low-, intermediate-, and high-pairing levels, respectively, exhibited a very similar pairing pattern which was characterized by the existence of two types, A-D and B-S^l, of preferential pairing. These results confirm that the S^l genome of *T. longissimum* is closely related to the B genome of wheat. The possible use of *ph1b* and *ph2b* mutations in the transfer to wheat of genes from related species is discussed.

Key words C-banding · Homoeologous pairing · *ph1b* · *ph2b* · Wheat · *T. longissimum*

Introduction

Suppression of homoeologous pairing in wheat is largely under the control of a major gene (Riley and Chapman 1958; Sears and Okamoto 1958) located on the long arm of chromosome 5B. Another gene with an intermediate suppressor effect was located on 3DS (Upadhya and Swaminathan 1967; Mello-Sampayo 1971). These two genes were named *Ph1* and *Ph2*, respectively.

Mutants *ph1b* and *ph2a* conditioning a high- and an intermediate-pairing level, repectively, were recovered by Sears (1977, 1982, 1984). Mutant 10/13, obtained by Wall et al. (1971a), was formerly designated ph1a since it was believed to involve the *Ph1* locus (Wall et al. 1971b). Sears (1984) demonstrated that this mutation, which induces an intermediate-pairing level, involves the *Ph2* locus and was re-designated *ph2b*.

Homoeologous pairing induced by *ph1b* has been used to transfer genes from different related species to wheat (Islam and Shepherd 1991, 1992; Rogowsky et al. 1991). It was also employed to establish the arm homoeology of wheat chromosomes and of rye chromosomes to wheat (Naranjo et al. 1988a, b; Naranjo and Fernández-Rueda 1991; Naranjo 1992). A double translocation among the arms 5AL/4AL/7BS occurred in the evolution of wheat and several translocations in rye, relative to wheat, were detected.

Sears (1982) suggested that *ph2* mutants could be used for inducing the transfer to wheat of genes from alien chromosomes that are fairly closely related to one of the three genomes of wheat. In this way, the number of chromosome rearrangements resulting from homoeologous pairing between wheat chromosomes would be reduced with respect to that induced by *ph1b*.

Another possible use of *ph2* mutants suggested by Sears (1982) concerns the assessment of the degree of relatedness between certain alien chromosomes and their wheat homoeologues. Differences in the ability to pair for different homoeologous chromosome combinations might be more easily detected at the intermediate-pairing level than at the extreme low and high levels conditioned by the *Ph1Ph2* and *ph1b* genotypes, respectively.

Species of the Sitopsis section of genus *Triticum* (*T. bicorne*, *T. longissimum*, *T. searsii*, *T. sharonense*, and *T. speltoides*) are considered to be closely related to the B genome of wheat and have been implicated as putative donors of this genome (reviewed by Kerby and Kuspira 1987).

T. longissimum chromosomes and wheat chromosomes were identified by C-banding in hybrids between both species (Naranjo 1995). The study of homoeologous pairing at metaphase-I in wild-type and *ph1b* hybrids supported the existence of a translocation between the arms $4S^lL$ and $7S^lL$ of *T. longissimum* relative to wheat and normal homoeologous relationships for the remaining chromosomes previously established (Friebe et al. 1993, and references

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therein). However, the degree of affinity between the S^1 genome of *T. longissimum* and the A, B, and D genomes of wheat was not analyzed.

The aim of the present study was to determine the degree of pairing between *T. longissimum* chromosomes and their homoeologues of the A, B and D genomes of wheat in wild-type, *ph2b*, and *ph1b* hybrids in order to study the relationship between the S^1 genome and the wheat genomes as well as for assessing the effect of *ph1b*, and *ph2b* on the pairing of different homoeologous combinations.

Material and methods

Plants of *Triticum aestivum* (AABBDD, 2n=6X=42) of the wild-type, *ph2b*, and *ph1b* lines of cv Chinese Spring were crossed with *T. longissimum* (S^1S^1, 2n=14) accession TL01, which is a low-pairing genotype (Ceoloni et al. 1986). Three wild-type hybrids, six *ph2b* hybrids, and three *ph1b* hybrids were used for this study. Wild-type and *ph1b* hybrids were grown in a controlled environment chamber at 16–18°C after vernalization for 8 weeks at 6–8°C. Hybrids with the *ph2b* mutation 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). Chromosomes of wheat and *T. longissimum* were identified according to Naranjo (1995). On average, 100 pollen mother cells (PMCs) per plant in the wild-type and *ph1b* hybrids, and 50 PMCs per plant in *ph2b* hybrids, were scored.

Results

All chromosome arms of *T. longissimum* associated with wheat chromosomes were identified at metaphase-I (Fig. 1) in all PMCs scored in the three types of hybrids. Chromosomes 2A and 2D, and their arms, could not be distinguished from one another. The fact that 2AS, 2BS, and 2DS are homoeologous, as are 2AL, 2BL, and 2DL (Naranjo 1994), and the fact that $2S^1S$ paired with 2BS and $2S^1L$ paired with 2BL, suggested that associations of $2S^1S$ and $2S^1L$ with chromosomes 2A and 2D involved the short and long arms of these chromosomes, respectively.

The frequencies of pairing for the different combinations of wheat homoeologous arms are shown in Table 1. In group 2, associations 2AS-2BS and 2BS-2DS, as well as associations 2AL-2BL and 2BL-2DL, that could not be distinguished from one another, were pooled. When chromosomes 2A and 2D formed a ring bivalent, both arms were associated, but if they formed an open bivalent, the arm, S or L, being bound could not be determined. In multivalents formed by group 2 chromosomes, whether a given A-D association involved the short or the long arm was deduced from the arm of chromosome 2B or $2S^1$ that was bound to chromosome 2A or 2D. For instance, in chain trivalents 2BS-2A-2D or 2BS-2D-2A, 2AL and 2DL had to be bound since 2BS was associated with 2AS or 2DS, respectively. The frequencies of 2AS-2DS and 2AL-2DL associations given in Table 1 were calculated as the sum of

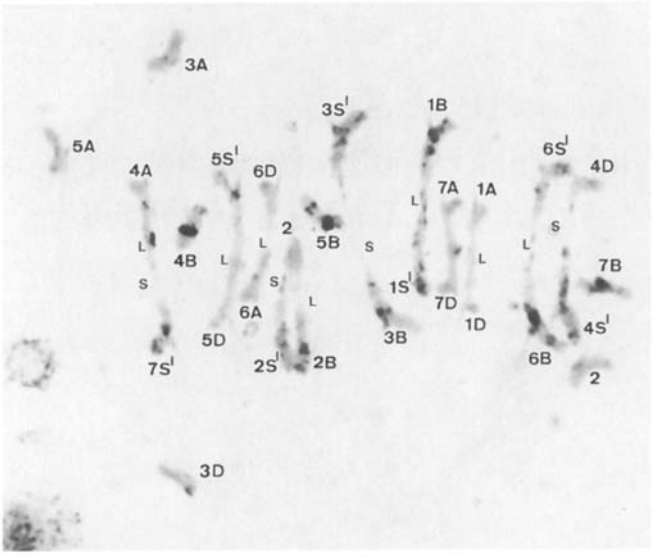

Fig. 1 C-banded metaphase-I cell from a *ph2b* wheat × *T. longissimum* hybrid. All chromosomes and the arms associated are identified with the exceptions of chromosomes 2A and 2D (*2*) and the arm being bound in the open bivalent 7A-7D

half the frequency of PMCs with an open 2A-2D bivalent, plus the frequency of PMCs with the ring 2A-2D bivalent, plus the frequency of PMCs with multivalents carrying such associations, respectively. In group 7, the frequencies of 7AS-7DS and 7AL-7DL associations were calculated as in group 2.

All associations between the remaining chromosome arms of wheat were identified. Because of the double translocation 5AL/4AL/7BS of wheat (Naranjo et al. 1987, 1988a, b), the frequencies of pairing for the long arms of group-4 and -5 chromosomes and for the short arms of group-7 chromosomes of Table 1 were obtained as follows: a terminal segment of 5AL translocated from 4AL pairs with 4BL and/or 4DL. In group 4, the long arm, triple association ABD corresponds to the association 5AL-4BL-4DL, and combinations AD, AB, and BD correspond to the associations 5AL-4DL, 5AL-4BL, and 4BL-4DL, respectively.

The arms 5BL and 5DL form intercalary bonds with 5AL and very distal bonds with 7BS, which carries a segment translocated from 5AL. Associations 5AL-5BL-5DL and 7BS-5BL-5DL, 5AL-5DL and 7BS-5DL, and 5AL-5BL and 7BS-5BL, were pooled in pairing combinations ABD, AD, and AB of group 5, long arm, respectively.

A terminal segment of 4AL translocated from 7BS pairs with 7AS and/or 7DS. Pairing combinations ABD, AD, AB, and BD of group 7, short arm, correspond to associations 7AS-4AL-7DS, 7AS-7DS, 7AS-4AL, and 4AL-7DS, respectively.

Association of the A-D type was the most frequent one in all groups except group 4, short arm, and group 5, long arm. In group 4, the 4AS arm seldom pairs owing to the

Table 1 Frequency (%) of association at metaphase-I between chromosome arms of wheat in wild-type, *ph2b*, and *ph1b* wheat×*T. longissimum* hybrids

Group	Genotype	Short arm				Long arm			
		ABD	AD	AB	BD	ABD	AD	AB	BD
1	Wild-type	0.0	5.0	0.3	0.0	0.0	11.0	0.7	0.3
	ph2b	0.0	16.7	1.0	0.0	0.3	54.0	3.7	4.7
	ph1b	0.7	29.7	7.7	11.7	1.7	57.7	9.3	11.3
2[a]	Wild-type	0.0	7.0	2.7[b]		0.0	6.0	6.7[b]	
	ph2b	0.0	33.7	4.3[b]		0.3	25.0	28.3[b]	
	ph1b	4.0	44.2	27.0[b]		7.3	35.8	45.3[b]	
3	Wild-type	0.0	4.3	0.0	0.3	0.0	5.3	0.7	0.3
	ph2b	0.0	6.0	1.0	1.0	0.0	26.3	5.3	10.0
	ph1b	1.0	58.7	3.7	7.7	2.3	63.0	9.3	11.3
4[a]	Wild-type	0.0	0.0	0.0	0.3	0.0	0.7	1.0	2.0
	ph2b	0.0	0.0	0.0	1.3	0.0	15.3	3.7	11.3
	ph1b	0.0	0.3	1.0	29.7	2.7	40.3	12.0	30.0
5[a]	Wild-type	0.0	2.7	0.7	0.7	0.0	0.0	0.0	1.7
	ph2b	0.0	7.7	1.0	0.3	0.0	0.7	2.7	20.7
	ph1b	0.3	43.3	8.3	7.7	0.3	6.0	3.7	21.3
6	Wild-type	0.0	6.7	0.0	0.3	0.0	12.3	0.3	0.3
	ph2b	0.0	34.7	1.7	0.3	0.0	43.0	0.0	1.3
	ph1b	1.7	70.0	3.7	6.0	1.7	87.3	2.3	3.0
7[a]	Wild-type	0.0	9.0	0.0	0.3	0.0	8.3	0.7	0.0
	ph2b	0.0	19.2	0.0	1.7	0.0	13.5	0.7	0.3
	ph1b	1.3	72.3	2.3	4.0	1.7	71.0	8.0	3.7

[a] See text
[b] AB+BD

structural modification of chromosome 4A by a pericentric inversion, which occurred in the primitive tetraploid wheat (Naranjo 1990). The behaviour of the long arm of group-5 chromosomes is explained by the structural modification of 5AL, and the small size of the segment of 5AL translocated to 7BS (Naranjo et al. 1987, 1988a, b).

The frequency of association between the arms of *T. longissimum* chromosomes and wheat chromosomes in the three types of hybrids analyzed is given in Table 2. Associations 2AS-2S^{1}S and 2DS-2S^{1}S and associations 2AL-2S^{1}L and 2DL-2S^{1}L, which could not be distinguished from one another, were pooled. All the remaining associations between the chromosome arms of *T. longissimum* and wheat were identified. In the long arm of group-5 chromosomes, pairing combination AS^1 includes both an intercalary association 5AL-5S^{1}L and a distal association 7BL-5S^{1}L. In the short arm of group-7 chromosomes, combination BS^1 corresponds to association 4AL-7S^{1}S, since 4AL carries a translocated segment from 7BS.

The arms 4S^{1}L and 7S^{1}L are involved in a translocation that arose in the evolution of *T. longissimum* (Friebe et al 1993; Naranjo 1995) in which segments of unequal length, a relatively long segment from 7S^{1}L and a very short segment from 4S^{1}L, were probably interchanged (Naranjo 1995). Pairing combinations DS^1 and BS^1 were only observed between the long arm of group-4 chromosomes (Table 2); they correspond to intercalary bonds of 4S^{1}L with 4DL or 4BL, respectively. In the long arm of group 7, the majority of associations involved the segment of 4S^{1}L translocated from 7S^{1}L and the arms 7AL, 7BL or 7DL. The frequency of these associations and that of 7AL-7S^{1}L, 7BL-7S^{1}L, and 7DL-7S^{1}L, which ranged from 0 to 2%, were pooled in each combination, AS^1, BS^1 and DS^1, of Table 2, respectively.

Chromosomes 1, 2, 3, 4, 6, and 7 of *T. longissimum* paired with their homoeologues of the B genome more frequently than with those of the A or D genomes. In group 5, the two association types B-S^1 and D-S^1 showed very similar frequencies in both the short and the long arms.

The rare associations, 2S^{1}L-4S^{1}L and 6S^{1}L-4BS, that were observed in only one PMC of the *ph1b* hybrids are not included in Table 2.

The mean numbers of univalents, bivalents and multivalents per cell and the proportion of A-D and B-S^1 pairing with regard to the total number of chromosome associations are shown in Table 3. The A-D and B-S^1 pairing ratios reached similar values in the three genotypes.

Discussion

Homoeologous pairing revealed the existence of A-D and B-S^1 preferential pairing types among the genomes that are in competition in wheat×*T. longissimum* hybrids. However, A-D pairing occurred with a higher frequency than

Table 2 Frequency (%) of association at metaphase-I between chromosome arms of *T. longissimum* and wheat in wild-type, *ph2b*, and *ph1b* hybrids

Group	Genotype	Short arm				Long arm			
		WWS[1]	AS[1]	DS[1]	BS[1]	WWS[1]	AS[1]	DS[1]	BS[1]
1	Wild-type	0.0	0.0	0.3	2.3	0.0	0.3	3.0	13.7
	ph2b	0.0	2.0	1.0	5.0	0.3	3.7	6.7	48.3
	ph1b	1.0	8.7	6.0	5.7	6.7	12.7	12.0	54.7
2	Wild-type	0.0	1.0[a]		1.0	0.3	4.7[a]		4.0
	ph2b	0.0	7.3[a]		8.7	0.3	13.7[a]		21.3
	ph1b	4.3	34.0[a]		23.0	4.0	35.3[a]		28.3
3	Wild-type	0.0	0.7	0.0	2.0	0.0	0.7	0.3	5.3
	ph2b	0.0	0.3	1.7	16.3	0.0	8.0	7.3	18.7
	ph1b	1.0	4.7	5.7	41.7	4.3	12.0	9.0	44.7
4[b]	Wild-type	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0
	ph2b	0.0	0.0	0.0	8.3	0.0	0.0	0.0	0.0
	ph1b	0.3	0.3	5.3	18.7	0.0	0.0	0.7	1.3
5[b]	Wild-type	0.0	0.0	0.7	0.7	0.0	0.0	8.3	12.0
	ph2b	0.0	0.3	1.0	0.0	1.3	0.0	21.0	19.0
	ph1b	0.0	4.3	12.7	13.7	9.3	4.3	37.3	26.0
6	Wild-type	0.0	0.0	0.3	1.7	0.0	0.0	0.3	3.0
	ph2b	0.0	1.7	1.0	16.0	0.0	0.7	1.3	36.7
	ph1b	1.7	4.0	6.3	32.0	0.3	2.0	1.0	71.3
7[b]	Wild-type	0.0	0.3	0.0	6.3	0.0	1.7	0.0	3.0
	ph2b	0.0	0.3	0.0	26.0	0.0	9.3	3.7	23.3
	ph1b	3.7	5.3	10.0	56.3	2.0	5.7	10.7	48.7

W=A, B or D genomes
[a] AS^1+DS^1
[b] see the text

Table 3 Mean values per cell of metaphase-I configurations and ratios of the A-D and B-S^1 pairing types in wild-type, *ph2b*, and *ph1b* wheat×*T. longissimum* hybrids

Configuration	Type of hybrids		
	Wild-type	*ph2b*	*ph1b*
I	24.55±0.18	14.93±0.21	3.48±0.13
II (open)	1.59±0.07	5.08±0.10	4.04±0.11
II (ring)	0.06±0.01	0.58±0.04	2.99±0.09
III	0.05±0.01	0.46±0.04	1.19±0.06
IV	0.003±0.003	0.08±0.02	1.49±0.06
V+VI+VII+VIII		0.007±0.005	0.18±0.02
Bonds/cell	1.81±0.08	7.44±0.14	18.28±0.29
Pairing ratio			
A-D/Total bonds	0.45	0.41	0.37
B-S^1/Total bonds	0.31	0.34	0.25

did B-S^1 pairing in most cases (Tables 1 and 2). In the short arm of group 3, and in the short and long arms of group-7, chromosomes, A-D pairing was less frequent than B-S^1 pairing but only in the *ph2b* hybrids. The ratio of A-D and B-S^1 pairing was similar in the three genotypes (Table 3), which indicates that the pattern of pairing was unaffected by the overall level of pairing.

Mathematical models simulating chromosome pairing, used by Kimber and Alonso (1981), indicated that the pairing pattern of wheat×*T. longissimum* hybrids tends to be in two clusters of two. Later, they marked wheat homoeologous chromosomes of group 3 with telocentrics in the hybrids and concluded that these clusters are A-D and B-S^1, 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^1 genome (Alonso and Kimber 1983; Kimber 1983). Fernández-Calvín and Orellana (1994), by means of C-banding, identified A-D and B-S^1 pairing in *Ph1Ph2* ABDS^1 hybrids; the four remaining pairing combinations could not be distinguished from one other and were pooled. They also found A-D and B-S^1 preferential pairing, the A-D type being more frequent than the B-S^1 type.

All of these results contradict those reported by Feldman (1978) on hybrids between ditelocentric lines of Chinese Spring and an intermediate pairing type of *T. longissimum*. Feldman concluded that most of the pairing occurred between chromosomes of the B and S^1 genomes while chromosomes of the A and D genomes paired relatively little. Although he could determine the pairing frequencies of the A-, B-, and D-genome telosomes, he could not ascertain with which genome they paired. Consequently, he grossly overestimated the B-S^1 pairing.

Preferential pairing between chromosomes of the A and D genomes was also detected using N- or C-banding techniques in haploids of wheat (Jaujar et al. 1991), wheat-rye hybrids (Hutchinson et al. 1983; Naranjo et al. 1987, 1988a, b), and hybrids between wheat and different Triticum (*Aegilops*) species (Fernández-Calvín and Orellana 1991, 1992, 1993, 1994).

Because of the very close relationship between the A and D genomes the question arises whether the pairing between B and S^1 is because A pairs with D and B remains unpaired, and is therefore, available for pairing with S^1, or there is a greater affinity between B to S^1 than between A or D to S^1.

Structural modification of chromosome arm 4AS strongly reduced its pairing frequency with 4DS or 4BS. In the absence of preferential A-D pairing, $4S^1S$ paired with 4BS more often than with 4DS. Furthermore, the level of D-S^1 pairing was lower in the short arm of group-4 chromosomes than in most of the remaining sets of homoeologous arms. This result indicates that the level of B-S^1 pairing versus A-S^1 or D-S^1 is a reflection of the degree of affinity between genomes. The conclusion can be drawn that the S^1 genome is closer to the B genome than A is to D.

Behaviour of $5S^1$ was in some respect different from that of the remaining *T. longissimum* chromosomes. In the long arm of group-5 chromosomes, A-D associations were less frequent than B-D associations because 5AL carries a translocated segment from 4AL. Pairing of $5S^1L$ with 5BL and 5DL showed comparable frequencies. In the short arm of group 5, the frequencies of B-S^1 and D-S^1 associations were similar, while preferential A-D pairing occurred. This suggests that the degree of relatedness between 5B and 5D to $5S^1$ is about the same.

The frequencies of pairing listed in Table 2 may be used as estimates of recombination between *T. longissimum* chromosomes and wheat chromosomes, which may be of importance for breeders interested in transferring useful agronomic characters from *T. longissimum* to wheat. Pairing between $4S^1L$ and 4BL or 4DL, and between $7S^1L$ and 7AL, 7BL or 7DL, is scarce because of the translocation $4S^1L/7S^1L$.

Wheat-S^1 pairing reached the highest level in the *ph1b* hybrids. These hybrids showed the lowest frequency of univalents and, therefore, they are expected to produce 14:14 balanced chromosome segregation at anaphase-I, and ultimately viable gametes, with a higher frequency than *ph2b* or wild-type hybrids. Consequently, from the backcross of the hybrid with wheat, interspecific recombinants may be recovered more easily using *ph1b* than *ph2b*. On the basis of the level of pairing conditioned by *ph1b* and *ph2b*, the last conclusion may extend to other derivatives, such as amphiploids, addition and substitution lines, and lines with interspecific translocations.

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References

Alonso LC, Kimber G (1983) A study of genome relationships in wheat based on telocentric chromosome pairing. II. Z Pflanzenzuecht 90:273–284

Ceoloni C, Straus I, Feldman M (1986) Effect of different doses of group-2 chromosomes on homoeologous pairing in intergeneric hybrids. Can J Genet Cytol 28:240–246

Feldman M (1978) New evidence on the origin of the B genome of wheat. In: Ramanujan S (ed) Proc 5th Int Wheat Genet Symp vol. 1. Kapoor Art Press, New Delhi, pp 120–132

Fernández-Calvín B, Orellana J (1991) Metaphase-I bound-arm frequency and genome anlysis in wheat-*Aegilops* hybrids. I. *Ae. variabilis*-wheat and *Ae. kotschyi*-wheat hybrids with low- and high-homoeologous pairing. Theor Appl Genet 83:264–272

Fernández-Calvín B, Orellana J (1992) Relationships between pairing frequencies and genome affinity estimations in *Aegilops ovata*×*Triticum aestivum* hybrid plants. Heredity 68:165–172

Fernández-Calvín B, Orellana J (1993) Metaphase-I bound-arm frequency and genome analysis in wheat-*Aegilops* hybrids. 2. Cytogenetical evidence for excluding *Ae. sharonensis* as the donor of the B genome of polyploid wheats. Theor Appl Genet 85: 587–592

Fernández-Calvín B, Orellana J (1994) Metaphase-I bound-arm frequency and genome anlysis in wheat-*Aegilops* hybrids. 3. Similar relationships between the B genome of wheat and the S or S^1 genomes of *Ae. speltoides*, *Ae. longissima* and *Ae. sharonensis*. Theor Appl Genet 88:1043–1049

Friebe B, Tuleen N, Jian J, Gill BS (1993) Standard karyotype of *Triticum longissimum* and its cytogenetic relationship with *T. aestivum*. Genome 36:731–742

Giráldez R, Cermeño MC, Orellana J (1979) Comparison of C-banding pattern in the chromosomes of inbred lines and open-pollinated varieties of rye Secale cereale L. Z Pflanzenzuecht 83:40–48

Hutchinson J, Miller TE, Reader SM (1983) C-banding at meiosis as a means of assessing chromosome affinities in the Triticeae. Can J Genet Cytol 25:319–323

Islam AKMR, Shepherd KW (1991) Alien genetic variation in wheat improvement. In: Gupta PK, Tsuchiya T (eds) Chromosome engineering in plants: genetics, breeding, evolution. Elsevier, Amsterdam, pp 291–312

Islam AKMR, Shepherd KW (1992) Production of wheat-barley recombinant chromosomes through induced homoeologus pairing. 1. Isolation of recombinants involving barley arms 3HL and 6HL. Theor Appl Genet 83:489–494

Jaujar PP, Riera-Lizarazu O, Dewey WG, Gill BS, Crane CF, Benett JH (1991) Chromosome pairing relationships among the A, B, and D genomes of bread wheat. Theor Appl Genet 82:441–449

Kerby K, Kuspira J (1987) The phylogeny of the polyploid wheats *Triticum aestivum* (bread wheat) and *Triticum turgidum* (macaroni wheat). Genome 29:722–737

Kimber G (1983) Genome analysis in the genus Triticum. In: Sakamoto S (ed) Proc 6th Int Wheat Genet Symp, Kyoto University, Kyoto, pp 23–28

Kimber G, Alonso LC (1981) The analysis of meiosis in hybrids. III. Tetraploid hybrids. Can J Genet Cytol 23:235–254

Mello-Sampayo T (1971) Genetic regulation of meiotic chromosome pairing by chromosome 3D of *Triticum aestivum*. Nature New Biol 230:22–23

Naranjo T (1990) Chromosome structure of durum wheat. Theor Appl Genet 79:397–400

Naranjo T (1992) The use of homoeologous pairing in the identification of homoeologous relationships in the Triticeae. Hereditas 116:219–223

Naranjo T (1994) The homoeologous relationships of the arms of wheat chromosomes 2A and 2D to chromosome 2B and their effect on homoeolgous pairing. Chromosome Research 2:275–279

Naranjo T (1995) Chromosome structure of *Triticum longissimum* relative to wheat. Theor Appl Genet 91:105–109

Naranjo T, Fernández-Rueda P (1991) Homoeology of rye chromosome arms to wheat. Theor Appl Genet 82:577–586

Naranjo T, Roca A, Goicoechea PG, Giráldez R (1987) Arm homoeology of wheat and rye chromosomes. Genome 29:873–882

Naranjo T, Roca A, Goicoechea PG, Giráldez R (1988a) Chromosome structure of common wheat: genome reassignment of chromosomes 4A and 4B. In: Miller TE, Koebner RMD (eds) Proc 7th Int Wheat Genet Symp, Bath Press, Bath, UK, pp 115–120

Naranjo T, Roca A, Goicoechea PG, Giráldez R (1988b) Chromosome pairing in hybrids of *ph1b* mutant wheat with rye. Genome 30:639–646

Riley R, Chapman V (1958) Genetic control of the cytologically diploid behaviour of hexaploid wheat. Nature 182:713–715

Rogowsky PM, Guidet FLY, Langridge P, Shepherd KW, Koebner RMD (1991) Isolation and characterization of wheat-rye recombinants involving chromosome arm 1DS of wheat. Theor Appl Genet 82:537–544

Sears ER (1977) An induced mutant with homoeologus pairing in wheat. Can J Genet Cytol 19:585–593

Sears ER (1982) A wheat mutation conditioning an intermediate level of homoeologous chromosome pairing. Can J Genet Cytol 24: 715–719

Sears ER (1984) Mutations in wheat that raise the level of meiotic chromosome pairing. In: Gustafson JP (ed) Proc 16th Stadler Genet Symp, Columbia, Mo. Plenum Press, New York, pp 295–300

Sears ER, Okamoto M (1958) Intergenomic chromosome relationships in hexaploid wheat. Proc 10th Int Congr Genet 2:258–259

Upadhya MD, Swaminathan MS (1967) Mechanisms regulating chromosome pairing in *Triticum*. Biol Zentrabbl 86 (suppl): 239–255

Wall AM, Riley R, Chapman V (1971a) Wheat mutants permitting homoeologous chromosome pairing. Genet Res 18:311–328

Wall AM, Riley R, Gale MD (1971b) The position of a locus on chromosome 5B of *Triticum aestivum* affecting homoeologous pairing. Genet Res 18:329–339