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Molecular cytogenetic evidence for a high level of chromosome pairing among different genomes in *Triticum aestivum* – *Thinopyrum intermedium* hybrids

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Abstract Intergeneric hybrids (ABDJJ^{s}S genomes) were made between *Triticum aestivum* cv. Chinese Spring (CS) and *Thinopyrum intermedium*. Genomic *in situ* hybridization (GISH) using genomic DNA probes from *Pseudoroegneria libanotica* (Hackel) D.R. Dewey (genome S, 2*n* = 14) was used to study chromosome pairing among J, J^s, S and wheat ABD genomes in the hybrids. It was shown that in the hexaploid (ABDJJ^{s}S) hybrids, high pairing occurred among wheat chromosomes and among *Thinopyrum* chromosomes. A closer relationship was observed among the three genomes of *Th. intermedium* than among the three genomes of *T. aestivum*. It was further discerned that S genome chromosomes paired with J- and J^s-genome chromosomes at a high frequency. The frequency of heterologous pairing between S and J or S and J^s chromosomes was higher than those between J and J^s chromosomes, indicating that the S-genome was more closely related with these two genomes. Our results provided direct molecular cytogenetic evidence for the hypothesis that S-genome chromosomes are genetically similar to the J-genome chromosomes and, therefore, genetic exchange between these genomes is possible. The discovery of a close relationship among S, J and J^s genomes provides valuable markers for molecular cytogenetic analyses using S-genomic DNA probes in monitoring the transfer of useful traits from *Thinopyrum* species into wheat.

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Introduction

Intermediate wheatgrass, *Thinopyrum intermedium* (Host) Barkworth & D.R. Dewey [syn. *Agropyron intermedium* (Host) Beauv. and *Elytrigia intermedia* (Host) Nevski] (2*n* = 6*x* = 42) is an important source of genetic variation for wheat improvement. *Th. intermedium* has been extensively used since the 1930s because of its resistance to a number of pests and diseases of wheat as well as its stress tolerance and high crossability with various *Triticum* species (Dewey 1984). Many desirable genes have been characterized and transferred from this wild grass species into wheat, which has led to the development of several useful wheat germplasm lines and cultivars with new resistance genes for stem rust and leaf rust (Cauderon 1966; Cauderon et al. 1973; Dvorak 1985; Whelan and Hart 1988; Xin et al. 1988; Banks et al. 1993; McIntosh et al. 1998; Mujeeb-Kazi 1994; Sharma et al. 1995; Friebe et al. 1996).

The genomic composition of *Th. intermedium* has been reported to be an auto-allohexaploid with the genomic formula J^{e}J^{e}J^{e}J^{e}SS (Liu and Wang 1993) or JJJ^{s}J^{s}SS (Chen et al. 1998a). According to these studies, the S genome chromosomes in *Th. intermedium* are closely related to those of *Pseudoroegneria libanotica* (Hackel) D.R. Dewey, and the J and J^s genomes are more or less closely related to the genome of *Th. bessarabicum* (Savul. & Rayss) A. Love and/or *Th. elongatum* (Host) D. Dewey (Chen et al. 1998a,b).

Cytogenetic studies on intergeneric hybrids between wheat and *Th. intermedium* and between *Thinopyrum* species have shown that the J, J^s and S genomes present in *Th. intermedium* are related (Liu and Wang 1993; Chen et al. 1998a, b). Close relationships between J-genome chromosomes with the wheat ABD genomes has also been documented (Dvorak 1981; Jauhar 1995;

Zhang et al. 1996; Chen et al. 1998a). Although some information is available on chromosome pairing among *Thinopyrum* and wheat chromosomes in hybrids (Dvorak 1985; Cai and Jones 1997), the pairing frequency among J-, J^s- and S-genome chromosomes is virtually unknown. Apparently, this is because of the difficulty in distinguishing these chromosomes in the hybrids using conventional chromosome techniques or the genomic *in situ* hybridization (GISH) technique using *Thinopyrum* genomic DNA probes (Liu and Wang 1989, 1993; Cai and Jones 1997). The question still remains as to how close is the relationship among the S, J and J^s genomes.

The objective of the study reported here was to employ GISH using S-genomic DNA as a probe to distinguish the S, J and J^s genomes from wheat ABD genomes in wheat-*Th. intermedium* hybrids and to analyze their chromosome pairing behavior in the wheat background.

Materials and methods

The hexaploid *Thinopyrum intermedium* accessions PI547333 and PI578696 were kindly provided by Dr. George Fedak and were used as male parents in crosses with the *Triticum aestivum* cv. Chinese Spring (CS). Interspecific hybrid seeds were obtained by conventional crossing techniques, and embryo rescue was used to avoid delays caused by seed dormancy. The F_1 hybrid plants were grown under greenhouse conditions at 21°C and a 16-h (light) photoperiod.

Preparation of mitotic and meiotic slides

Root tips for chromosome preparation were collected from the plants and pre-treated in ice water for 24 h, then fixed in 1:3 acetic acid-ethanol. After fixation for 1 day at 4°C, the roots were stained in 0.1% acetocarmine for 20 min and squashed in 45% acetic acid. Cover glasses were removed after freezing the slides at –80°C. Then the chromosomes on the slide were fixed again in 45% acetic acid for 8 min, air-dried and stored at –80°C. To analyze chromosome pairing in the hybrids of *Th. intermedium* with *T. aestivum*, we fixed the anthers at metaphase I (MI) of meiosis from hybrid plants in 1:3 acetic acid–ethanol for 2–3 weeks at 4°C. Slides were prepared according to the procedure of Chen et al. (1996).

Preparation of genomic DNA and GISH procedure

GISH was used for the analysis of mitotic and meiotic chromosomes at MI in pollen mother cells (PMCs) of the hybrid plants. Total genomic DNA was extracted from *Pseudoroegneria libanotica* and labelled with biotin-11-dUTP via nick translation. The genomic DNA probe was mixed in a 1:40 ratio with non-labelled block genomic wheat DNA. Details of the procedures used for DNA isolation and probe labelling, GISH and the detection of hybridization sites have been described previously by Chen et al. (1995, 1996).

Results

Wheat × *Th. intermedium* hybridization and chromosome composition of the hybrids

Hybrids between wheat and *Th. intermedium* were not difficult to obtain. The *Th. intermedium* species showed high cross-compatibility with wheat. Seed set of the crosses ranged from 30.2 to 62.5%, and five to ten F_1 plants from each combination were obtained. Chromosome counts were carried out on ten plants. Root-tip metaphase spreads showed that six hybrid plants had a chromosome number of $2n$=42, while the other four had $2n$=41.

A genomic DNA probe of *Ps. libanotica*, in the presence of wheat DNA as a block, was used to hybridize with mitotic chromosomes in the hybrid lines. In this case, the S-genome chromosomes showed green hybridization signals along their entire length, J^s-genome chromosome showed yellow centromere signals and J chromosomes showed dispersed and weak signals on whole chromosomes with a special yellow signal on the highly repeated telomeric regions. The wheat chromosomes, on the other hand, were red because of the propidium iodide (PI) that was used for the counterstaining (Fig. 1a). Hence, GISH using S-genomic DNA as a probe allowed us to discriminate the S-, J^s- and J-genome chromosomes from wheat chromosomes in wheat × *Th. intermedium* hybrids.

Analysis of the wheat × *Th. intermedium* hybrids using GISH revealed that wheat chromosomes ranged in number from 20 to 21 and that there were 21 *Th. intermedium* chromosomes (corresponding to hybrids with 41 or 42 chromosomes). In F_1 hybrid plants with 2n=41 chromosomes, seven chromosomes fluoresced bright yellow along all or most of their length, indicating that they belonged to the S-genome chromosomes of *Th. intermedium*. Five chromosomes displayed strong centromeric signals, so belonged to the J^s genome, while the other nine alien chromosomes showed fluorescent signals typical of the J genome. The remaining 21 chromosomes in the hybrid plant were completely blocked by ABD genome DNA and fluoresced dark red with the PI counterstain and hence belonged to wheat chromosomes (Fig. 1b). These results indicated that the hybrids of wheat -*Th. intermedium* carried the ABDJJ^{s}S genomes.

Chromosome pairing in the wheat × *Th. intermedium* hybrids

Chromosome pairing patterns in wheat × *Th. intermedium* hybrids were analyzed at MI of meiosis in PMCs by GISH using total S genomic DNA as the probe. However, the S-, J^s- and J-genome chromosomes at the meiotic stage did not always show the strong, clear GISH signals that they did at the mitotic stage in these hybrids. In the present study, a total of 60 PMC cells were examined, but only 20 PMCs had clear S-, J^s- and J-genome GISH signals (Table 1; Fig. 1c,d). The mean chromosome association for the 20 MI cells was 23.6 I + 7.6II +0.6III + 0.05 IV (Table 1), which was slightly different from the average configuration of 22.6 I + 8.5 II +0.8 III +0.04 IV reported by Cai and Jones (1997). Out of a total of 152 bivalents observed, 33.6% (51 II) were involved in wheat-wheat chromosome pairing (defined as W-W pairing), and 61.8% occurred among *Th. intermedium* chro-

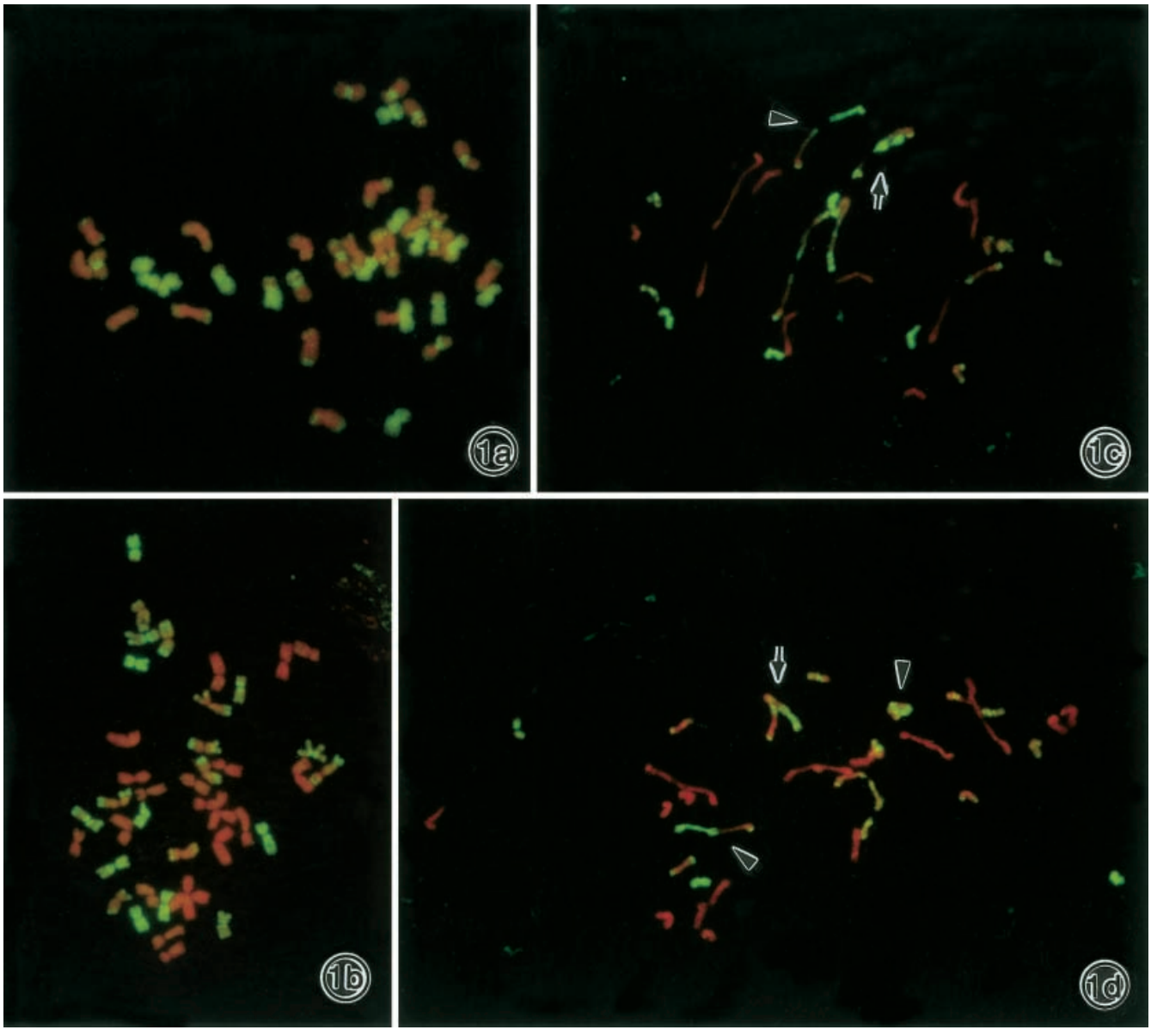

Fig. 1a,b GISH on somatic metaphase cells from root tips of *Th. intermedium* (**a**) and F_1 hybrid of wheat x *Thinopyrum intermedium* (**b**). Sites of probe hybridization fluoresce *yellow* or *greenish yellow* with FITC, while non-hybridized sites fluoresce *red* with the propidium iodide counterstain. The S genome was completely labelled along the entire chromosome length. The J^s genome was labelled only in the centromere areas, while the J-genome chromosomes showed dispersed weak fluorescence, except for terminal regions in some chromosomes where strong *yellow* fluorescence was observed; wheat chromosomes showed red fluorescence over all of their length. **a** Mitotic chromosomes of *Th. intermedium* probed with the S genome of *Ps. libanotica* and blocked with E-genomic DNA of *Th. elongatum* shows 14 S-genome chromosomes, 10 J^s-genome chromosomes, 18 J-genome chromosomes.**b** Mitotic chromosomes of F_1 hybrid of wheat × *Th. intermedium* probed with the S genome of *Ps. libanotica* and blocked with ABD genomic DNA of wheat shows 7 S-genome chromosomes, 5 J^s-genome chromosomes, 9 J-genome chromosomes and 20 wheat chromosomes. **c** Meiotic chromosomes of F_1 hybrid of wheat × *Th. intermedium* probed with the S genome of *Ps. libanotica* and blocked with the ABD genomic DNA of wheat shows S genome chromosomes (*yellow-green*) pairing with J- and J^s-genome chromosomes to form a bivalent (*arrowhead*) and a trivalent (*arrow*). **d** Meiotic chromosomes of F_1 hybrid of wheat × *Th. intermedium* probed with the S genome of *Ps. libanotica* and blocked with the ABD genomic DNA of wheat shows S genome chromosomes (*yellow-green*) pairing with J- and J^s-genome chromosomes to form bivalents (*arrowheads*) and a trivalent (*arrow*)

mosomes (defined as T-T pairing) (Table 1). The pairing between wheat and *Th. intermedium* chromosomes (defined as W-T) was very low, with a mean pairing frequency of 4.6%, and all of these bivalents occurred between wheat and J or J^s chromosomes. No S-genome chromosomes were involved in W-T pairing. Close observation on the *Th. intermedium* S-, J- and J^s-chromosome pairing configurations in the hybrids showed that the S-genome chromosomes not only paired with S chromosomes, but also with J or J^s chromosomes at high fre-

Table 1 Chromosome pairing of F_1 hybrids (ABDSJ^{s}J) of wheat × *Thinopyrum intermedium* at metaphase I of meiosis

		Chromosome configuration					
		I[a]	II ring	II rod	II total	III	IV
Total no.		472	22	130	152	12	1
Mean		23.6	1.1	6.5	7.6	0.6	0.05
Chromosome pairing							
W[b]		276 (58.4)[c]					
T[d]		196 (41.5)					
	J	82 (17.4)					
	J^s	40 (8.5)					
	S	74 (15.6)					
W-W			10 (45.5)	41 (31.5)	51 (33.6)		
T-T			12 (54.5)	82 (63.1)	94 (61.8)		
	J-J		0	20	20		
	J-J^s		4	6	10		
	J^s-J^s		2	6	8		
	Subtotal of J and J^s pairing		6	32	38 (40.4% of 94 T-T II)		
	S-J		0	30	30		
	S-J^s		4	18	22		
	Subtotal of S-J & S-J^s pairing		4	48	52 (55.3% of 94 T-T II)		
	S-S		2	2	4		
W-T				7 (5.3)	7 (4.6)		
	W-J			5 (3.8)	5 (3.2)		
	W-J^s			2 (1.5)	2 (1.3)		
	W-S			0	0		
W-W-W						4 (33.3)	
J-J-J^s						3 (25.0)	
J-J-S						3 (25.0)	
J-J^s-S						2 (16.6)	
J-J-J^s-S							1 (100)

[a] I, Univalent; II, bivalent; III, trivalent; IV, quadrivalent
[b] W, Wheat chromosome
[c] T, *Th. intermedium* chromosome
[d] Figures represent the number of chromosome configurations observed, and those in parenthesis are the percentages

quencies (Fig. 1c) and that J and J^s chromosomes paired with each other. The heterologous S-J or S-J^s pairing included rod and ring bivalents, and rod S-J-J^s or rod S-J-J trivalents also occurred frequently (Fig. 1c,d). Out of a total of 94 T-T pairing bivalents, the pairing frequency (55.3%) between S and J or J^s was higher than that observed between the J and J^s genomes (40.4%) (Table 1). The frequency of trivalents between S and J or J^s was also higher than that found among J and J^s. Out of 23.6 univalents observed, the number of unpaired chromosomes from the J, J^s and S genomes was lower than that from the wheat chromosomes (Table 1).

Discussion

GISH has proven to be a useful technique to differentiate genetically close genomes and assess genomic relationships in polyploid alien species and in different wheat-alien hybrid lines (Schwarzacher et al. 1989; Xu et al. 1994; Chen et al. 1995). This technique has also been used to distinguish alien chromosomes from wheat chromosomes and wheat-alien translocated chromosomes in a wheat background (Heslop-Harrison 1991; Jiang et al. 1993; Chen et al. 1998b; Ahmad et al. 2000). In the present study, GISH using S-genomic DNA as a probe provides a powerful tool in differentiating chromosomes from the three genomes of *Th. intermedium* because heterologous and homoeologous pairing could be clearly distinguished with the S-genomic DNA probe (Chen et al. 1998 a,b). This allowed a precise study of the chromosome composition and chromosome pairing among *Thinopyrum* chromosomes and their relationships with wheat chromosomes in a wheat genetic background. Through this approach, the genomic composition of the wheat-*Th. intermedium* hybrids was clearly identified in the mitotic stage and shown to consist of 20 wheat chromosomes derived from wheat ABD genomes and 21 chromosomes from the J, J^s and S genomes of *Th. intermedium*. GISH analysis of the S-, J^s- and J-genome chromosomes at meiosis metaphase I stage is still technically difficult. However, meiotic chromosomes from the J, J^s and S genomes were successfully distinguished from the meiotic wheat chromosomes in the PMCs of these hybrids (Fig. 1b), which allowed observation of chromosome pairing in these hybrids and the accurate identification of chromosomes derived from different *Th. intermedium* genomes.

Chromosome pairing analysis has been critical to genome analyses of allopolyploids and the determination of the genomic relationships between species. Some of the early work involved in studies on genomic relationships among S and J or J^s genomes was based on conventional chromosome and molecular analyses as well as on GISH using *Thinopyrum* DNA probes (Liu and Wang 1989, 1993; Pienaar 1990; Hsiao et al. 1995; Jauhar

1995; Cai and Jones 1997). However, heterologous pairing and homoeologous pairing in wheat-*Thinopyrum* hybrids could not be differentiated due to the limitations of conventional chromosome techniques and the *Thinopyrum* DNA probes used (Jauhar 1995; Cai and Jones 1997). In most cases, the intergenomic pairing (S and J or J^s) could be deduced only when there were more than seven bivalents or the presence of trivalents. Liu and Wang (1989) observed high frequencies of chromosome pairing among the three genomes in triploid J^bJ^eS hybrids of *Th. bessarabicum* × *Th. caespitosum* (C. Koch) R.R.-C. Wang. In the analysis of the hybrids with J^bJ^eS genomes, homoeologous pairing between the two closest genomes, J^b and J^e, has been taken for granted (Wang 1992; Liu and Wang 1993). However, GISH analysis results from the present study showed that the percentage of T-T pairing bivalents was about 61.8% (94 II) of the 152 bivalents observed in hybrids of wheat × *Th. intermedium*. In the 94 T-T bivalents observed, the percentage of heterogeneous pairing (55.3%) between S-J and S-J^s chromosomes was greater than the frequency of chromosome pairing between J-J^s and J-J (40.4%) (Table 1). The higher frequency of bivalent formation between *Th. intermedium* S and J or J^s chromosomes than that of bivalents formed by J and J^s chromosomes indicates that the high pairing resulted from the higher heterologous pairing among the three genomes of *Th. intermedium* rather than homologous pairing between the J and J^s genomes of *Th. intermedium*. The earlier conclusion that the S and J (including J and J^s) genomes are very closely related was drawn from molecular and cytogenetic studies (Wang 1992; Hsiao et al. 1995). In fact, Liu and Wang (1993) also observed that $J^bJ^eJ^e$ S and $J^eJ^eJ^eS$ hybrids have a very similar chromosome pairing pattern to that observed in the J^eJ^eSS hybrids, which strongly indicates that the S genome has as close a relationship with the J genome as the J genome has with the J^s genome. The present study established direct evidence using GISH of chromosome pairing between J and S or J^s and S genomes.

GISH patterns on meiotic chromosomes at MI in the hybrid of wheat × *Th. intermedium* also indicated the relationship between wheat and *Thinopyrum* chromosomes. Chromosome pairing in the hybrid mainly occurred among wheat chromosomes and among *Th. intermedium* chromosomes, and the mean pairing frequencies of W-W and T-T were 40% and 54%, respectively. The frequency of chromosome pairing among *Th. intermedium* J-, J^s- and S genome chromosomes was higher than that among wheat ABD chromosomes, suggesting that the three genomes of *Th. intermedium* are more closely related to each other than for the three genomes of typical allohexaploid *T. aestivum* (Jauhar et al. 1991). Cai and Jones (1997) also observed that the relationship among the three genomes of *Th. intermedium* was closer than it was to the three genomes of *T. aestivum*. Therefore, *Th. intermedium* should be designated as an allohexaploid. Pairing between wheat and *Th. intermedium* chromosomes was very rare and only occurred with J or J^s chromosomes (Table 1). No S-genome chromosomes were observed to pair with wheat chromosomes. This demonstrated that the relationships between *T. aestivum* genomes and *Th. intermedium* J and J^s genomes are much closer than the relationships between *T. aestivum* and the S genome. This is one reason we can use the S-genomic DNA probe more efficiently and confidently to distinguish J, J^s and S chromosomes from wheat chromosomes in wheat-*Thinopyrum* hybrids as compared to using the J or J^s genomic DNA probes.

Our results demonstrate that GISH using a S-genome DNA probe offers a reliable means to increase precision in discriminating the identity of chromosomes involved in pairing. This observation may significantly improve our understanding of genomic relationships within the Triticeae. This is especially valuable when the genomes of parents belong to *Thinopyrum* species. Great possibilities exist for extending the analysis of chromosomes, genomes and phylogenies using this technique, especially for the analysis of complex polyploids and their hybrids with wheat. Knowledge of the relationships between the S, J and J^s genomes is also helpful to our understanding of the inheritance of beneficial characters and for planning more efficient strategies for transferring target gene(s) from *Th. intermedium* to wheat. This understanding is likely to increase the precision and confidence with which plant breeders can use these alien genetic resources for forage and cereal breeding.

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