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Structural chromosome differentiation between *Triticum timopheevii* and *T. turgidum* and *T. aestivum*

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Abstract. Chromosome pairing at metaphase-I was analyzed in F_1 hybrids among *T. turgidum* (AABB), *T. aestivum* (AABBDD), and *T. timopheevii* (A^tA^tGG) to study the chromosome structure of *T. timopheevii* relative to durum (*T. turgidum*) and bread (*T. aestivum*) wheats. Individual chromosomes and their arms were identified by means of C-banding. Homologous pairing between the A-genome chromosomes was similar in the three hybrid types AA^tBG, AA^tBGD, and AABBD. However, associations of B-G were less frequent than B-B. Homoeologous associations were also observed, especially in the AA^tBGD hybrids. *T. timopheevii* chromosomes $1A^t$, $2A^t$, $5A^t$, $7A^t$, 2G, 3G, 5G, and 6G do not differ structurally from their counterpart in the A and B genomes. Thus, these three polyploid species inherited translocation 5AL/4AL from the diploid A-genome donor. Chromosome rearrangements that occurred at the tetraploid level were different in *T. turgidum* and *T. timopheevii*. Translocation 4AL/7BS and a pericentric inversion of chromosome 4A originated only in the *T. turgidum* lineage. The two lines of *T. timophevii* studied carry four different translocations, $6A^tS/1GS$, 1GS/4GS, 4GS/$4A^tL$, and $4A^tL/3A^tL$, which most likely arose in that sequence. These structural differences support a diphyletic origin of polyploid wheats.

Key words Chromosome pairing · Translocations · *T. timopheevii* · *T. turgidum* · *T. aestivum* · Evolution

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Introduction

The polyploid wheats *Triticum turgidum* (genome AABB) and *T. aestivum* (genome AABBDD) comprise the emmer-dinkel group. *T. aestivum* originated from the hybridization of *T. turgidum* and *Aegilops tauschii*, which contributed the D genome (Kihara 1944; McFaden and Sears 1946). *T. timopheevii* (genome A^tA^tGG) and *T. zhukovskyi* (genome $A^mA^mA^tA^tGG$) comprise the timopheevi group. Hexaploid wheat *T. zhukovskyi* originated from the hybridization of *T. timopheevii* and *T. monococcum* (Upadya and Swaminathan 1963; Dvořák et al. 1993).

Early cytogenetic studies on the relationships between *T. timopheevii* and *T. turgidum* led to the conclusion that the A genome of both species was contributed by *T. monococcum* and that the B and G genomes were structurally different (Lilienfield and Kihara 1934; Kostoff 1937; Love 1941; Sachs 1953). From the variation of different repeated DNA sequences in polyploid wheats and related species, Dvořák et al. (1993) identified *T. urartu*, first reported as a donor of the B genome, as the A-genome donor of both of the tetraploid wheats *T. turgidum* and *T. timopheevii*. A controversial matter for many years was the source of the B and G genomes. *Ae. speltoides* is the most closely related extant diploid species based on molecular studies using nuclear DNA (Dvořák and Zhang 1990; Jiang and Gill 1994a; Badaeva et al. 1996; Sasanuma et al. 1996) chloroplast DNA (Ogihara and Tsunewaki 1988; Miyashita et al. 1994) and mitochondrial DNA (Terachi et al. 1990).

Chromosome pairing analysis using telocentrics in hybrids involving *T. aestivum* and *T. timopheevii* suggested that translocation differences between these species involved both the A and B or G genomes (Feldman 1966), which was confirmed later by means of C-banding (Hutchinson et al. 1982; Gill and Chen 1987). Structural chromosome modifications occurred in both

evolutionary lineages. C-banding analysis of homoeologous pairing allowed the identification of a double translocation between 5AL/4AL/7BS and a pericentric inversion of chromosome 4A in *T. turgidum* and *T. aestivum* (Naranjo et al. 1987; Naranjo 1990). The construction of genetic maps using molecular markers confirmed these structural changes and revealed the existence of a paracentric inversion in the long arm of chromosome 4A (Liu et al. 1992; Mickelson-Young et al. 1995, Devos et al. 1995). Another species-specific double translocation between 6A^{t}S/1GS/4GS was identified in *T. timopheevii* after sequential N-banding and genomic *in situ* hybridization of mitotic chromosomes (Jiang and Gill 1994b). C-banding karyotyping revealed that this ancestral chromosome structure has a very wide distribution among wild populations of *T. timopheevii* ssp. *araraticum* although further structural diversification occurred in different populations (Badaeva et al. 1994).

However, it is possible that additional evolutionary translocations not detected with those techniques, such as intragenomic translocations, may exist in *T. timopheevii*. In fact, translocation 5AL/4AL, which the emmer wheat inherited from *T. urartu* (Naranjo et al. 1987; Naranjo 1990; Devos et al. 1995) was also identified in *T. timopheevii* as deduced from the locations of ribosomal RNA gene loci (Jiang and Gill 1994a). On the other hand, the presence or absence of a pericentric inversion in chromosome 4A^t of *T. timopheevii* was not determined. Such an inversion appeared in *T. turgidum* at the early tetraploid stage (Naranjo 1990; Devos et al. 1995) and may be of interest when attempting to establish the phylogenetic relationships among polyploid wheats.

Meiotic pairing between chromosomes of common wheat and related species analyzed by C-banding is a useful tool by which to investigate the chromosome structure of different species relative to wheat (Naranjo and Fernández-Rueda 1991; Naranjo 1995; Maestra and Naranjo 1997, 1998). In order to determine in more detail structural differences that exist between the chromosomes of *T. timopheevii* and those of *T. turgidum* and *T. aestivum*, we studied chromosome pairing at metaphase-I in hybrids between these species.

Material and methods

Two accessions of *Triticum timopheevii* ssp. *timopheevii* (2n = 4x = 28, A^{t}A^{t}GG), accession CI14133 supplied by B. S. Gill, Kansas State University, Manhattan, USA, and a second one supplied by J. Orellana, Universidad Politécnica, Madrid, Spain, were crossed with *T. turgidum* (2n = 4x = 28, AABB) cv 'Cappelli' and *T. aestivum* (2n = 6x = 42, AABBDD) cv 'Chinese Spring', respectively. Pentaploid AABBD hybrids between 'Chinese Spring' and 'Cappelli' were also obtained. Two AABBD hybrids, three AA^{t}BG hybrids, and three AA^{t}BGD hybrids were used for this study. All of them 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 300 pollen mother cells (PMCs) (100 PMCs per plant) in both the AA^{t}BG and AA^{t}BGD hybrids and 200 PMCs in the AABBD hybrids were scored. Individual chromosomes, and their arms, were identified at the metaphase-I of the hybrids according to the C-banding pattern established for these species and previous studies of meiotic pairing (Gill and Kimber 1974; Gill and Chen 1987; Naranjo et al. 1987; Simeone et al. 1988; Gill et al. 1991).

Results

In pentaploid hybrids between *T. aestivum* and *T. turgidum*, associations at metaphase-I were almost completely restricted to homologous chromosomes. Chromosomes of the A and B genomes mainly formed ring bivalents, which demonstrated that they have the same structure in cvs 'Chinese Spring' and 'Cappelli'. The frequencies of association of the different chromosome arms are listed in Table 1. With the exception of 5AS, chromosome arms of the A genome were associated in more than 90% of the PMCs. Chromosome arms of the B genome showed on average a lower pairing frequency. Five arms, 1BS, 2BL, 5BS, 6BS, and 7BS, did not reach the level of 80%. Homoeologous associations A-D or B-D were found only in 3 PMCs (Table 3).

Homologous associations of the types A-A^t and B-G and their frequencies in the AA^{t}BG and AA^{t}BGD hybrids are given in Table 2. Examples of such associations are shown in Fig. 1. Homoeologous associations A-B or A^t-B and A-G or A^t-G in both types of hybrids, and A-D or A^t-D, B-D and G-D, in the AA^{t}BGD hybrids are summarized in Table 3. Homoeologous

Table 1 Frequency (%) of association at metaphase-I between homologous chromosome arms of *T. aestivum* and *T. turgidum* in interspecific hybrids

Chromosome arms	% PMCs	Chromosome arms	% PMCs
1AS	90.5	1BS	54.0
1AL	98.0	1BL	92.5
2AS	97.0	2BS	89.5
2AL	95.5	2BL	75.0
3AS	96.5	3BS	86.5
3AL	95.0	3BL	91.5
4AS	92.5	4BS	87.0
4AL	99.5	4BL	96.0
5AS	77.0	5BS	77.0
5AL	98.0	5BL	92.5
6AS	91.5	6BS	76.5
6AL	94.5	6BL	83.5
7AS[a]	93.8	7BS	77.5
7AL[a]	93.8	7BL	94.0

[a] The short and long arms could not be distinguished from one another. The mean pairing frequency of both arms was calculated

Table 2 Frequency (%) of the A-A^t and B-G associations at metaphase-I in *T. turgidum* × *T. timopheevii* (AA^{t}BG) and *T. aestivum* × *T. timopheevii* (AA^{t}BGD) hybrids

A-A^t associations	Type of hybrids		B-G associations	Type of hybrids	
	AA^{t}BG	AA^{t}BGD		AA^{t}BG	AA^{t}BGD
1AS-1A^{t}S	91.0	84.3	1BS-1GS	0.0	0.0
			1BS-6A^{t}S	58.7	69.0
1AL-1A^{t}L	97.0	88.0	1BL-1GL	43.0	23.7
2AS-2A^{t}S	92.3	88.7[a]	2BS-2GS	30.3	31.0
2AL-2A^{t}L	89.3	88.7[a]	2BL-2GL	63.0	75.0
3AS-3A^{t}S	94.7	95.3	3BS-3GS	49.7	24.3
3AL-3A^{t}L(I)	3.7	8.3	3BL-3GL	46.7	22.0
3AL-4A^{t}L(D)	70.3	64.3			
3AL-3A^{t}L-4A^{t}L	20.7	18.0			
3AL-3A^{t}L-4A^{t}L-4AL	2.0	4.3			
3AL-4A^{t}L-6AS	0.0	0.3			
4AS-4A^{t}S(D)	5.3	1.7	4BS-4GS(I)[b]	0.3	0.0
4AS-4A^{t}L(I)	0.0	1.3	4BS-1GS(D)[b]	3.3	4.0
4AL-4A^{t}S(I)	0.3	3.3			
4AL-4A^{t}L(I)	2.3	1.3	4BL-4GL	36.0	41.3
5AS-5A^{t}S	86.3	71.0	5BS-5GS	22.7	22.3
5AL-5A^{t}L	98.7	97.3	5BL-5GL	67.0	79.0
6AS-6A^{t}S(I)	1.0	0.3	6BS-6GS	42.0	28.7
6AS-6A^{t}S-1BS	0.3	1.0			
6AL-6A^{t}L	93.3	89.3	6BL-6GL	62.7	35.7
7AS-7A^{t}S	94.3	93.3	4AL-7GS	8.0	4.7
			7BS-7GS(I)[b]	0.3	0.0
			7BS-4GS	10.3	11.0
7AL-7A^{t}L	96.3	95.7	7BL-7GL	18.0	23.3

[a] The S and L arms of chromosomes 2A and 2A^t could not be identified in the AA^{t}BGD hybrids. The mean pairing frequency of both arms was calculated
[b] (I), Interstitial association; (D), very distal association

Table 3 Frequency (%) of homoeologous associations at metaphase-I in *T. turgidum* × *T. timopheevii* (AA^{t}BG), *T. aestivum* × *T. timopheevii* (AA^{t}BGD), and *T. aestivum* × *T. turgidum* (AABBD) hybrids

Pairing type	Individual associations	Pooled associations	Type of hybrids		
			AA^{t}BG	AA^{t}BGD	AABBD
A-B + A^t-B		All of them	3.7	1.7	0.0
A-G + A^t-G		All of them	6.3	4.3	
A-D + A^t-D	4AS-4DS			0.3	0.0
	4A^{t}S-4DS			4.7	
	4A^{t}L-3DL			1.3	
	6AS-6DS			8.7	0.0
	6AL-6DL			2.0	0.0
		Remaining		14.3	1.0
B-D		All of them		8.0	0.5
G-D	1GL-1DL			4.3	
	7GS-7DS			9.0	
		Remaining		11.3	

associations showed a much lower frequency than A-A^t or B-G associations. Eight chromosomes, chromosomes 1, 2, 5, and 7 from the A and A^t genomes and chromosomes 2, 3, 5, and 6 from the B and G genomes, do not differ structurally as deduced from exclusive homologous pairing between the short arms and the long arms in each chromosome pair. Likewise, the arm pairs 3AS-3A^{t}S, 6AL-6A^{t}L, 1BL-1GL, 4BL-4GL, and 7BL-7GL are homologous and have no apparent structural difference. The average frequency of A-A^t associations among the arms without structural modification was 93.3% in the AA^{t}BG hybrids and 89.2% in the AA^{t}BGD hybrids. These values are similar to that of 93.8% obtained for the same arms in the AABBD hybrids. However, the mean frequency of B-G pairing for chromosome arms without structural modifications, 43.7% in the AA^{t}BG hybrids and 36.9% in the AA^{t}BGD hybrids, was much lower than that of the 86.8% obtained for the corresponding B-B associations in the AABBD hybrids.

Chromosome arm 3AL paired interstitially with 3A^{t}L and distally with 4A^{t}L, which indicated that 3A^{t}L

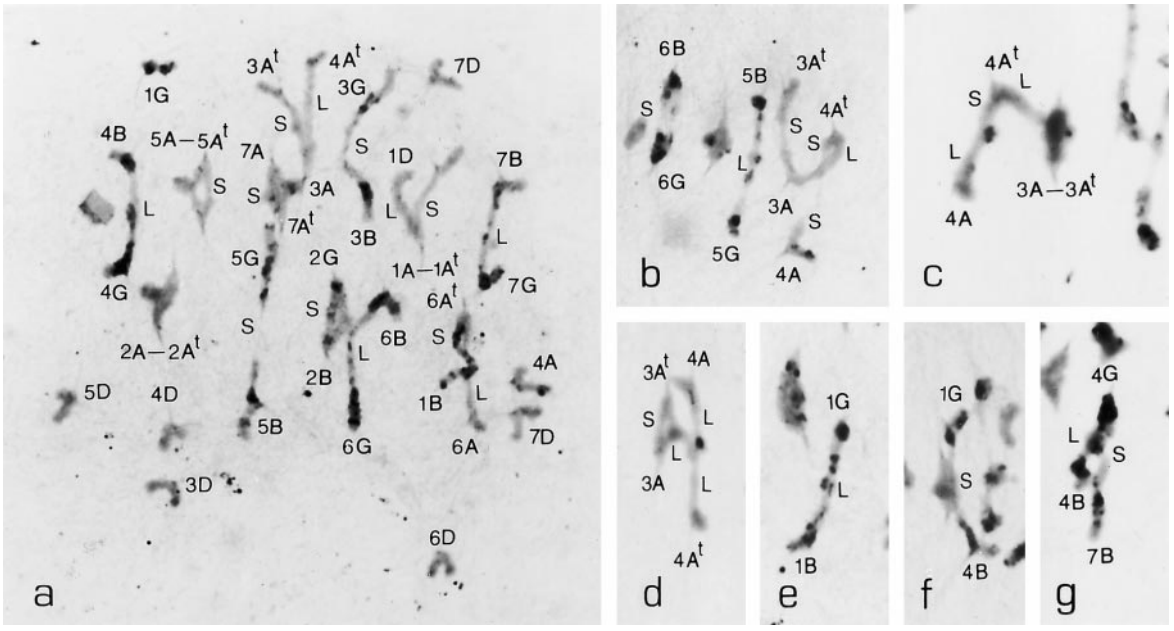

Fig. 1a–g Chromosome associations at metaphase-I in C-banded cells of AA^{t}BGD hybrids between *T. aestivum* and *T. timopheevii*. **a** Complete cell with three trivalents, nine bivalents, and eight univalents. All chromosomes and the arms being bound are indicated. Individual chromosomes of pairs 1A-1A^t, 2A-2A^t, and 5A-5A^t could not be distinguished from one another, neither could the arms S and L of chromosomes 2A and 2A^t. **b–g** Chromosome associations different from those of **a** are indicated. **b** A very distal association between 4AS-4A^{t}S and associations 6BS-6GS and 5BL-5GL, **c** intercalary association between 4AL and 4A^{t}S, **d** association of 4A^{t}L with 4AL and 3A^{t}L, **e** 1GL-1BL, **f** a very distal association between 1GS-4BS, **g** a very distal association between 4GS-7BS

and 4A^{t}L are translocated in *T. timopheevii*. Pairing between the arms of chromosomes 4A and 4A^t occurred at a low frequency and showed a heterogeneous pattern. This behavior indicated that these two chromosomes have a different structure. Chromosome 4A suffered several rearrangements during evolution and consists of different segments, which from the S telomere to the L telomere follow the sequence 4AS-4AL-centromere-4AS-5AL-4AL-7BS (Mickelson-Young et al. 1995; Devos et al. 1995). The 4A^{t}S arm paired distally with 4AS and intercalarily with 4AL. These associations reached frequencies of 5.3% and 3.3%, respectively. In the AA^{t}BGD hybrids, homoeologous associations 4AS-4DS and 4A^{t}S-4DS showed a frequency of 0.3% and 4.7%, respectively. All of these data suggest that while the structure of the short arm of chromosome 4A was modified by the pericentric inversion, the 4A^{t}S arm preserved the ancestral arrangement. Interstitial association 4A^{t}L-4AS involved proximal homologous segments with the standard and the inverted arrangement, respectively. Pairing between chromosomes 5A and 5A^t confirmed that *T. timopheevii* and *T. turgidum* inherited translocation 5AL/4AL from *T. urartu*. Thus, the 4A^{t}L arm is involved in different translocations with the arms 5A^{t}L and 3A^{t}L. Association between 4A^{t}L and 4AL had to occur in an intercalary region, which involves the subterminal 5AL-4AL segment of chromosome arm 4AL. This region is inverted in chromosome 4A, but its arrangement has not been established for the 4A^{t}L arm. The level of pairing, 5.6% = 4.3% + 1.3% in the AA^{t}BGD hybrids, observed in such a region suggests that 4A^{t}L may also contain genetic material from the 5A^{t}L arm.

Chromosome arm 6AS seldom paired. An interstitial association 6AS-6A^{t}S was observed in a few PMCs, and the distal part of 6AS was associated with 3AL and 4A^{t}L in another PMC. This behavior accounts for the frequency of 8.7% that homoeologous association 6AS-6DS reached in the AA^{t}BGD hybrids. The terminal heavily C-banded segment of 6A^{t}S paired with 1BS and, therefore, carries a translocated segment from 1GS. On the other hand, the 1GS arm was found to be distally associated with 4BS in 4% of the PMCs analyzed, which demonstrated that the distal part of 1GS corresponds to a translocated segment from 4GS. Chromosome arm 4GS associated interstially with 4BS in only 1 PMC of the AA^{t}BG hybrids. A terminal segment from 4GS paired with 7BS in 11% of the PMCs. Taking into account that 7BS carries a translocated segment from 5AL, a terminal segment of 4GS is derived from 5A^{t}L. The 7GS arm paired with 4AL, which carries a translocated segment from 7BS, and with 7DS in the AA^{t}BGD hybrids.

Discussion

Translocation 4AL/5AL took place before the polyploidization of wheat and was transmitted to both the

emmer and timopheevi wheats. In the emmer lineage, chromosome 4A suffered three more rearrangements, a pericentric inversion, translocation 4AL/7BS, and a paracentric inversion in the long arm. Neither translocation 4AL/7BS nor the pericentric inversion of chromosome 4A exists in *T. timopheevii* (Gill and Chen 1987; Jiang and Gill 1994a,b; present work). There is no information on the presence or absence in *T. timopheevii* of a paracentric inversion like that of 4AL from *T. turgidum* and *T. aestivum*.

Based on meiotic pairing between AB-genome telocentrics and *T. timopheevii* chromosomes Gill and Chen (1987) identified two translocations involving $6A^tS/1GS$ and $3A^tL/4A^tL$ in some lines of *T. timopheevii*. Jiang and Gill (1994b) investigated the chromosome structure of *T. timopheevii* using genomic *in situ* hybridization after identifying individual chromosomes with N-banding. They concluded that the arms $6A^tS$, 1GS, and 4GS are involved in two species-specific translocations and postulated the following sequence of interchanges. The arms $6A^tS$ and 1GS interchanged large distal segments in a first translocation. The modified 1GS arm and 4GS were involved in a second translocation. A small distal part of the transient 1GS, originally from $6A^tS$, and a tiny segment from 4GS were interchanged. Thus, 1GS would consist of a proximal part from the original 1GS arm, an intercalary large segment from $6A^tS$, and a distal short segment from 4GS. The $6A^tS$ would carry a large translocated segment from 1GS, and 4GS would carry a small translocated segment from $6A^tS$.

Our results confirm that genetic structure for chromosome arm $6A^tS$ and that 1GS carries a small distal translocated segment from 4GS. However, in the two accessions used here, the distal segment of 4GS was not derived from $6A^tS$ but from the ancestral 5AL segment that $4A^tL$ contained originally. Since these two accessions carry translocation $3A^tL/4A^tL$, 4GS was involved in an additional translocation with $4A^tL$ or $3A^tL$, which had to arise after translocation 4GS/1GS. The double translocation $4GS/4A^tL/3A^tL$ could occur in any of the three following sequences. (1) A distal segment of $4A^tL$ containing genetic material from 5AL and a tiny segment of 4GS, originally from $6A^tS$, were interchanged. Subsequently, a large distal segment from $3A^tL$ was translocated to $4A^tL$, while a very tiny segment, or no segment, from $4A^tL$ was translocated to $3A^tL$. (2) A first reciprocal translocation between $4A^tL$ and $3A^tL$ was followed by a translocation involving a distal segment of the transient $3A^tL$, with 5AL material, and a very small segment or no segment of 4GS. (3) An unequal translocation involving a large segment from $3A^tL$ and a very small segment, or no segment, from 4GS was followed by a reciprocal translocation between 4GS and $4A^tL$. The association $6AS\text{-}4A^tL\text{-}3AL$, which was found in only 1 PMC, could be a result of the existence of very small homologous segments in chromosome arms 6AS and $4A^tL$. Such arms may carry homologous segments in the case that the double translocation $4GS/4A^tL/3A^tL$ proceeded according to the first sequence mentioned above.

Five translocations account for the chromosome structure of the two accessions of *T. timopheevii* analyzed here. We postulate that these chromosome rearrangements occurred in the sequence shown in Fig. 2. Translocation 5AL/4AL was inherited from *T. urartu*

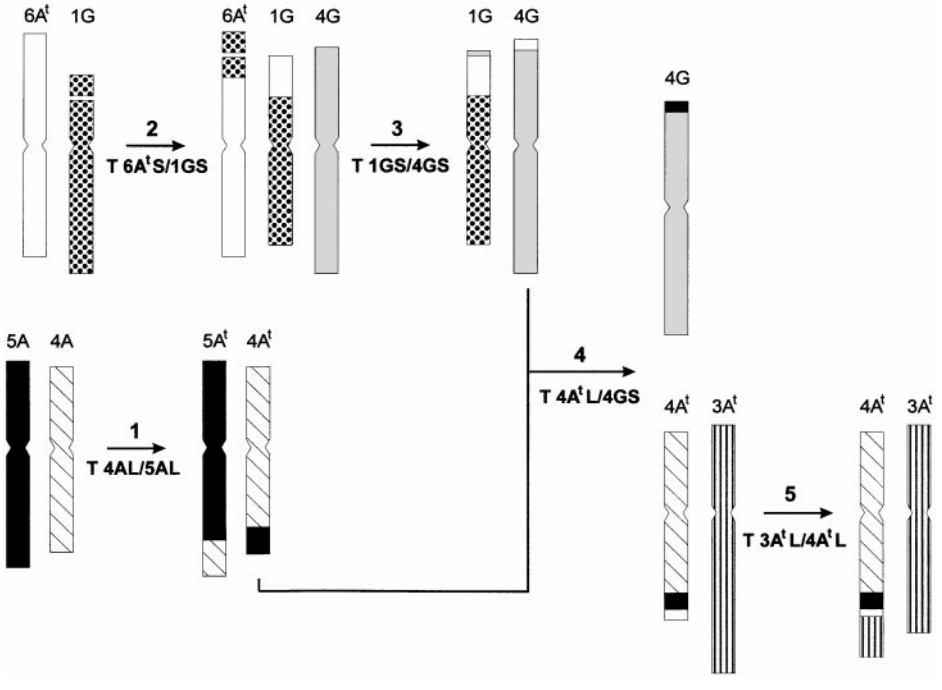

Fig. 2 A possible sequence, from *1* to *5*, of rearrangements for the origin of the five translocations detected in *T. timopheevii*. Translocation 4AL/5AL was inherited from *T. urartu*, and the remaining four translocations occurred at the tetraploid stage

and translocations $6A^tS/1BS$ and $1BS/4GS$ were fixed very early in the timopheevi lineage. The question arises whether the double translocation $4GS/4A^tL/3A^tL$ is also species-specific or originated only in some populations. Jiang and Gill (1994b) also studied the accession CI14133 used here. They reported no difference in the morphology and N-banding pattern of chromosome arm 4GS between this and five other accessions from *T. timopheevii* ssp. *timopheevii* and ssp. *araraticum*. The possibility exists that the six accessions carry the double translocation $4GS/4A^tL/3A^tL$.

Regardless of whether, the double translocation $4GS/4A^tL/3A^tL$ was species-specific or not, this structural rearrangement may be of additional interest. Translocation 4L/5L has been reported in a range of Triticeae species. In all of them, the breakpoints were mapped in similar positions (King et al. 1994; Devos et al. 1995; Zhang et al. 1998). A monophyletic origin of this translocation would explain such results. This hypothesis seems unlikely, however, since it is contradictory with the present view of taxonomy within the tribe. A recurrent generation of this translocation and its independent fixation in the donor species of the A genome of wheat and in rye was proposed by Naranjo et al. (1987) based on the degree of closeness between genomes measured from chromosome pairing. The 4AL arm is involved in two additional rearrangements, translocation 4AL/7BS in the emmer-dinkel wheats and translocation $4A^tL/4GS$ in *T. timopheevii*. The breakpoints were mapped in translocation 4AL/7BS (Devos et al. 1995) but not in translocation $4A^tL/4GS$. Obviously, the construction of restriction fragment length polymorphism (RFLP) maps in *T. timopheevii* would allow to test whether these two independent rearrangements of 4AL occurred in the same position. Zhang et al. (1998) reported examples of chromosomes that appeared to break at specific regions.

Two different hypotheses have been proposed on the origin of emmer and timopheevi wheats. One assumes that they had a monophyletic origin. Both lineages diverged at the tetraploid stage after a single hybridization event (Wagenaar 1961; Feldman 1966; Tanaka et al. 1978). The second hypothesis postulates a diphyletic origin. Emmer and timopheevi wheats arose after two independent hybridization events. The restriction endonuclease analyses of chloroplast (Ogihara and Tsunewaki 1988; Miyashita et al. 1994) mitochondrial (Terachi et al. 1990), and nuclear DNA (Mori et al. 1995) support this hypothesis and suggest that *T. turgidum* originated much earlier than *T. timopheevii*. Such a diphyletic origin was supported also by Jiang and Gill (1994a, b) in the light of the double translocation $6A^tS/1GS/4GS$ of timopheevi wheat. The absence of a pericentric inversion in chromosome $4A^t$ reported here reinforces this proposal.

With regards to the relationships between genomes, our results indicate that the degree of relatedness between the A and A^t genomes is similar to that between the A genomes of *T. turgidum* and *T. aestivum*, which is consistent with their common origin. Pairing between chromosomes of the B and G genomes reached a lower level than homologous A-A or B-B pairing in AABBD hybrids, but was much higher than any homoeologous pairing type. This result confirms that the B and G genomes are very closely related. Although the B and G genomes were most likely derived from *Ae. speltoides*, a diphyletic origin of AABB and A^tA^tGG tetraploids in space and time may account for the differences between B and G genomes compared to the B genomes of *T. turgidum* and *T. aestivum*.

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