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General features of chromosome substitutions in *Triticum aestivum* × *T. timopheevii* hybrids

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Summary. Based on a C-banded chromosome analysis of *Triticum aestivum* × *T. timopheevii* hybrid lines, we developed a classification of the A^t and G genome chromosomes that agrees with the standard genetic nomenclature of *T. aestivum* chromosomes. Transfer of genetic material from *T. timopheevii* to *T. aestivum* involved complete chromosomes, chromosome arms, or segments. Frequencies of chromosome substitution were highest for homoeologous group 2 and lowest for group 4. Moreover, B(G) substitutions were frequent compared to A(A^t). The pattern of chromosome substitutions and rearrangements were unequal and depended on the genotype of the parental *T. aestivum* cultivar.

Key words: *Triticum aestivum* × *T. timopheevii* hybrids – Chromosome substitution – Homoeology – Genetic nomenclature – C-banding

Introduction

Triticum timopheevii Zhuk. is a tetraploid wheat (genome formula A^tA^tGG) and occupies a unique position in the genus *Triticum*. Although *T. timopheevii* is morphologically similar to *T. durum* (AABB), it crosses poorly with this species and has distinctive biochemical and genetical traits, as well as karyotype structure (Bozzini and Giorgi 1969; Zurabishvili et al. 1978; Dorofejew and Migushova 1983; Konarev 1980; Hutchinson et al. 1982; Chen and Gill 1983; Tsunewaki and Ogihara 1983; Badaeva et al. 1986; Gill and Chen 1987; Kimber and Feldman 1987; Gill 1988; Shang et al. 1989). *T. timopheevii* possesses pest and disease resistance and, as a consequence, is considered to be a valuable donor of these properties. Involvement of *T. timopheevii* in breeding experiments is difficult because cytogenetic data are scarce. The majority of classifications of *T. timopheevii* chromosomes was developed based on cytologic data (Zurabishvili et al. 1978; Hutchinson et al. 1982; Chen and Gill 1983; Dvorak 1983; Badaeva et al. 1986; Shang et al. 1989), allowing for different chromosome numbering, especially in the A^t genome. Since the most reliable criterion of homoeology between the chromosomes is their ability to compensate for a *T. aestivum* chromosome in substitution lines, development of *T. timopheevii* chromosome nomenclature based on data from substitution lines appears to be necessary. Determination of the specificity of chromosomal substitutions and rearrangements in the hybrid karyotype would provide insight into the formation of allopolyploid genomes, and may be useful in breeding work and for understanding the phylogenetic relationships between various species as well as single chromosomes.

Materials and methods

We used 37 introgressive lines (F_7BC_1) derived from crosses of *T. timopheevii* ssp. *viticulosum* with three common wheat [*Triticum aestivum* (L.) em Thell.] cultivars without artificial selection: Saratovskaya 29 (cross combination ST), Novosibirskaya 67 (NS), and Pirotrix 28 (PX). Each line had a number of morphological traits or biochemical markers distinguishing it from the common wheat parental cultivar (Shkutina et al. 1988). The C-banding technique (Badaev et al. 1985) was used and ten plants for each of the 37 hybrid lines were analyzed.

Results and discussion

The chromosome composition of 35 hybrids was stable. The exceptional lines were 60-2 and 813-2. Among 813-2 plants, three karyotype variants were revealed: (1)

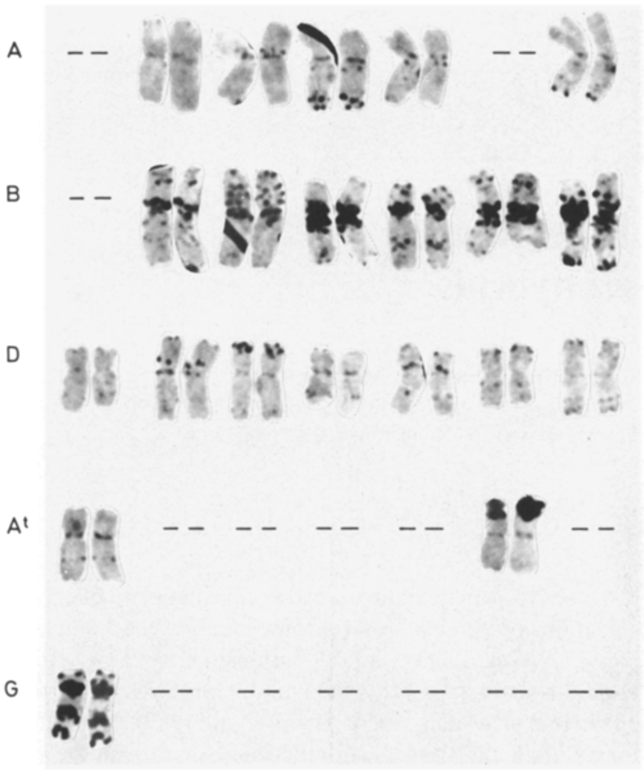

Fig. 1. C-banded karyotype of Pyrotrix 28 × *T. timopheevii* line (60-2) with $1A$ ($1A^t$), $1B$ ($1G$), $6A$ ($6A^t$) substitution

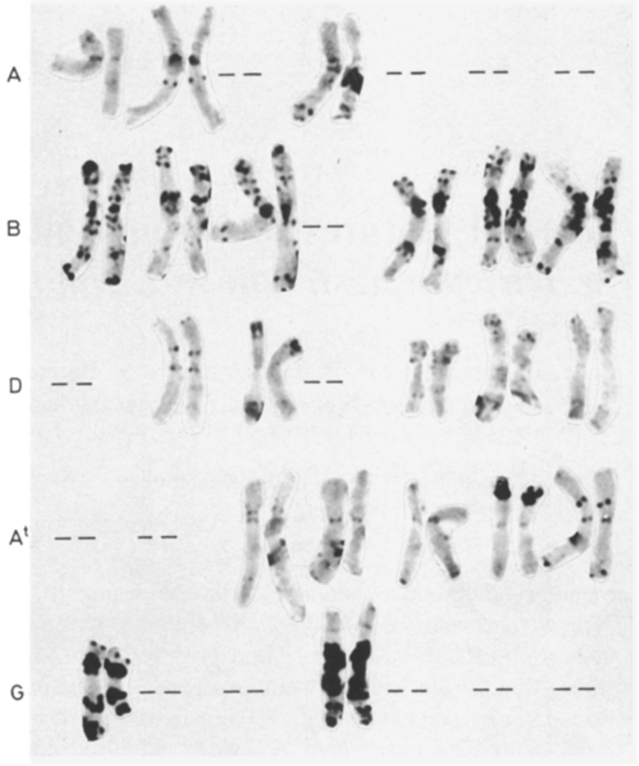

Fig 2. C-banded karyotype of Novosibirskaya 67 × *T. timopheevii* line (811-1) with $1D$ ($1G$), $3A$ ($3A^t$), $4B$ ($4G$), $4D$ ($4A^t$), $5A$ ($5A^t$), $6A$ ($6A^t$) substitution and a translocation of the $7A^t$S to the $7A$L

2B(*2G*) substitution; (2) double *2B*(*2G*) and *1D*(*1G*) substitution; (3) *2B*(*2G*) and substitution of one *1G* chromosome for *1D*. Some 60-2 plants differed in the presence or absence of a $7A^t$: $7A$L translocation. The karyotype of all lines studied included one to seven *T. timopheevii* chromosome pairs (Figs. 1–3, Table 1). From a comparison of hybrids obtained by different cross combinations, it was concluded that the genotype of the parental common wheat cultivar determined the level of introgression of alien genetic material. This conclusion confirms the influence of the wheat genetic background on the introgression process (Shkutina et al. 1988). The average substitution number per hybrid genome was estimated for hybrids as follows: 1.00 (ST): 1.71 (PX): 2.75 (NS). Furthermore, the parental common wheat genotype strongly affected the pattern of chromosome substitutions and rearrangements in hybrids. Thus, the highest number of chromosome substitutions was observed for homoeologous group 2 in ST cross lines, and for 3, 5, 6, and 7 in PX lines (Table 2). All types of chromosome substitutions, with predominance of groups 2, 5, 6, and 7, were noted in NS. Substitutions of the chromosomes of group 1 were revealed in all cross combinations, their frequencies being dependent on the common wheat genotype.

The process of karyotype formation is influenced by genotype as well as by environmental conditions (Badaev

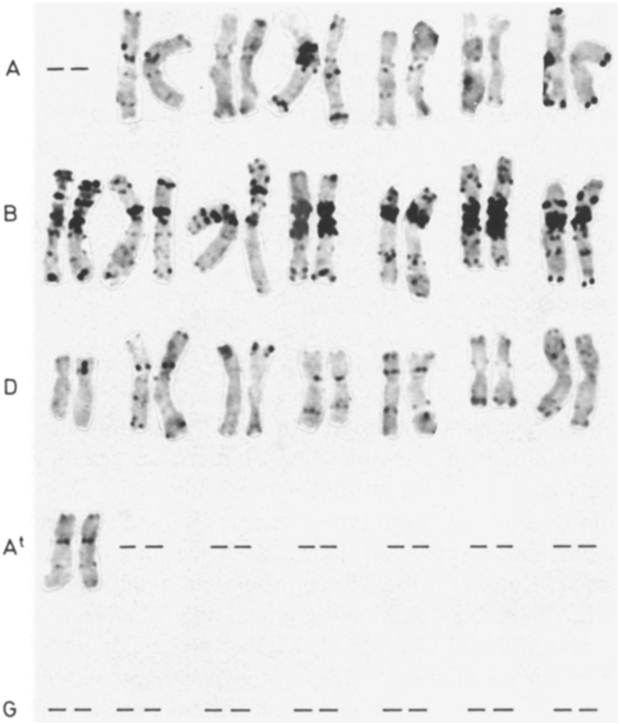

Fig. 3. C-banded karyotype of Saratovskaya 29 × *T. timopheevii* line 1319-4 with $1A$ ($1A^t$) substitution

Table 1. Types of chromosome substitutions in *T. aestivum* × *T. timopheevii* hybrids

Line	Homoeologous group/Genome																				
	1			2			3			4			5			6			7		
	A	B	D	A	B	D	A	B	D	A	B	D	A	B	D	A	B	D	A	B	D
Pyrotrix 28 × *T. timopheevii* (PX)																					
32-1	A^t	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	t^1	–	t^2
6	A^t	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	t^1	–	t^2
45-2	–	–	–	–	–	–	–	–	–	–	–	–	–	G^*	–	–	–	–	–	–	–
3	–	–	–	–	–	–	–	–	–	–	–	–	–	G^*	–	–	–	–	–	–	–
46-2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	G	–	–	–	–
6	–	–	–	–	–	–	t^3	–	–	–	–	–	–	–	–	–	–	–	–	–	–
60-2	A^t	G	–	–	–	–	–	–	–	–	–	–	–	–	–	A^t	–	–	t^1	–	–
61-1	–	–	–	–	–	–	–	G	–	–	–	–	–	G	–	–	–	–	A^t	–	–
62-3	–	–	–	–	–	–	–	G	–	–	–	–	–	G	–	–	–	–	A^t	–	–
63-2	–	–	–	–	–	–	–	G	–	–	–	–	–	G	–	–	–	–	A^t	–	–
64-1	–	–	–	–	–	–	–	G	–	–	–	–	–	G	–	–	–	–	A^t	–	–
81-1	–	–	–	–	–	–	–	–	–	–	t^4	–	–	t^5	–	–	G	–	–	–	–
3	–	–	–	–	–	–	–	–	–	–	t^4	–	–	t^5	–	–	G	–	–	–	–
124-3	–	–	–	–	–	–	–	G	–	–	–	–	–	t^5	–	–	G	–	A^t	–	–
4	–	–	–	–	–	–	–	G	–	–	–	–	–	t^5	–	–	G	–	A^t	–	–
131-2	–	–	t^6	–	–	–	–	t^9	–	–	–	–	–	–	–	–	–	–	–	–	–
164-2	–	–	–	–	G	–	–	–	–	–	–	–	–	–	–	–	–	–	t^1	–	–
Novosibirskaya 67 × *T. timopheevii* (NS)																					
731-1	–	–	–	A^t	–	–	–	t^7	–	–	–	–	–	G	–	–	G	–	–	–	–
3	–	–	–	A^t	–	–	–	t^7	–	–	–	–	–	G	–	–	G	–	–	–	–
735-1	–	–	–	A^t	G	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2	–	–	–	A^t	G	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
745-2	A^t	–	–	–	–	G	–	–	–	–	–	–	–	G	–	–	G	–	–	–	–
6	A^t	–	–	A^t	G	–	–	–	–	–	–	–	–	G	–	–	G	–	–	–	–
811-1	–	–	G	–	–	–	A^t	–	–	–	G	A^t	A^t	–	–	A^t	–	–	t^1	–	–
812-5	–	–	G	–	G	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
813-2	–	–	G	–	G	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
814-1	–	–	G	–	G	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
843-5	–	–	–	–	–	G	–	–	–	–	–	–	–	–	–	–	–	–	t^8	–	–
6	–	–	–	–	–	G	–	–	–	–	–	–	–	–	–	–	–	–	t^8	–	–
Saratovskaya 29 × *T. timopheevii* (ST)																					
1312-1	A^t	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
1313-3	–	–	–	A^t	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
1314-1	–	–	–	A^t	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
1315-4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	G
1316-8	–	–	–	–	G	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
1317-1	–	–	–	–	G	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
1318-8	–	–	–	–	G	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
1319-4	A^t	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Translocations: t^1–*7A*^{t} S:*7A*L; t^2–*7A*^{t} L:*7D*L; t^3–*3A*^{t} L: *3A*L; t^4–*4G*L telomeric C-band to *4B*L distal part; t^5–*5G*L telomeric C-band to *5B*L distal region; t^6–unidentified heterochromatic fragment to *1D*L; t^7–*3G*L:*3B*S; t^8–*7A*^{t} L:*7A*S; t^9–*3A*^{t} S:*3A*L. G^*–deletion of the *5G*S telomeric C-band

Table 2. Frequencies of different types of chromosomal substitutions in *T. aestivum* × *T. timopheevii* hybrids

Cross combination	Genome *T. timopheevii*	Homoeologous group/Genome of *T. aestivum*																				
		1			2			3			4			5			6			7		
		A	B	D	A	B	D	A	B	D	A	B	D	A	B	D	A	B	D	A	B	D
PX	A^t	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	6	–	–
	G	–	1	–	–	1	–	–	6	–	–	–	–	–	6	–	–	5	–	–	–	–
NS	A^t	2	–	–	5	–	–	1	–	–	–	–	1	1	–	–	1	–	–	–	–	–
	G	–	–	4	–	6	3	–	–	–	–	1	–	–	4	–	–	4	–	–	–	–
ST	A^t	2	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	G	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1

et al. 1990; Badaeva et al. 1990). Because all studied lines were developed under equal conditions, it was possible to estimate the influence of genotype on karyotype structure. Under other environmental conditions, the chromosomes may be ranked in a manner different from ours, e.g., as was described by Gill et al. (1988).

Substitutions were distributed among homoeologous groups in decreasing order: group 2 (22 substitutions), then groups 1 and 6 (12 variants each), group 5 (11 variants), groups 3 and 7 (7 variants each) and, lastly, group 4 (2 variants). This pattern was similar to data on the rate of wheat chromosomes stabilization during 4 × triticale karyotype formation (Lukaszewski et al. 1987a, b; Badaeva et al. 1989; Dubovets et al. 1989).

Two features of our results must be noted: (1) the relationship between substitution number per hybrid genome and the particular constitution of a substitution, and (2) the effect of the composition of some homoeologous groups on chromosome substitution types in other groups. Among 18 hybrid lines with a disomic substitution, 6 contained *2G*, 4 had *1A*^{t}, 3 had *6G*, whereas both *5G* and *2A*^{t} were each found in 2 lines and *7G* in 1 line. These *T. timopheevii* chromosomes alone or in combination with other chromosomes may substitute for a *T. aestivum* homoeologue, but do not ultimately determine the pattern of substitutions in other groups. However, *3B*(*3G*) was consistently associated with the *7A*(*7A*^{t}) substitution. The interrelationship of chromosome composition of homoeologous groups 3 and 7 has also been observed in the process of 4 × triticale karyotype formation (Dubovets et al. 1989).

The substitutions, as a rule, included chromosomes of the related genomes A and A^t, B and G, and may be explained by the fact that A-A^t and B-G genome chromosomes are less genetically divergent and pair at meiosis of F_1 interspecific hybrids (Gill and Chen 1987; Gill and Sears 1988). Exceptions were substitutions of *1G* and *7G* for D genome chromosomes and *2G*, which can substitute *2B* as well as *2D*. Gill and Chen (1987) concluded that *1G*, *3A*^{t}, *4A*^{t}, and *6A*^{t} chromosomes of *T. timopheevii* have been significantly modified during evolution. Chromosome *7B* of *T. turgidum* involves a cyclic translocation with *4A* and *5A* (Gill and Chen 1987; Naranjo et al. 1987). Consequently, *1B-1G* and *7B-7G* may be considered to be the most genetically divergent. Furthermore, selection pressure may favor chromosomes containing the NOR and, as a result, *1G* substitutes for *1D* but not *1B*.

Chromosome rearrangements were found in several lines (Tables 1 and 2; Figs. 4 and 5). Deletions of terminal C-bands were found in the long arm of chromosomes *1B* (four lines) and *5G* (two lines) in PX (Figs. 4a and b), and also in the *1B* satellite in lines 735-1 and 735-2 of NS (Fig. 4c). Translocations (T) involving chromosomes of different genomes occurred frequently in homoeologous

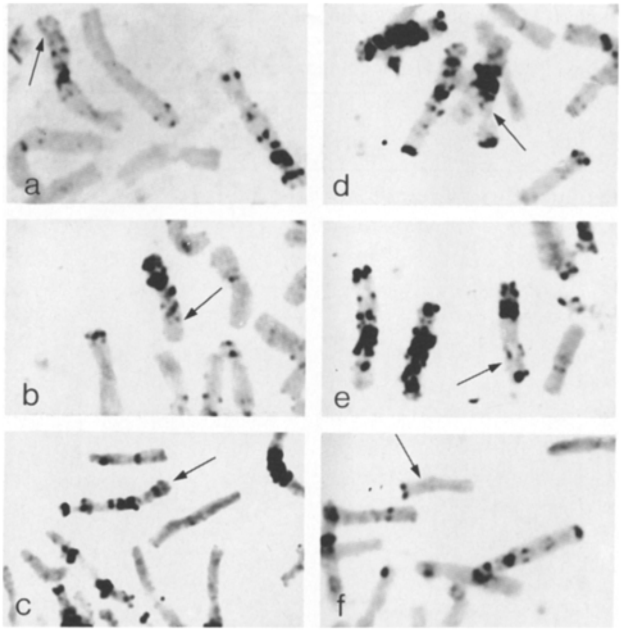

Fig. 4a–f. Chromosomal rearrangements identified by means of C-banding technique: **a** a deletion of the telomeric band of *1B*L (line 62-3); **b** a deletion of the telomeric C-band of *5G*L (line 45-3); **c** a deletion of the terminal band in a satellite of *1B* (line 735-1); **d** t^4, a translocation of the telomeric band of *4G*L to a distal region of *4B*L (line 81-1); **e** t^5, a translocation of the *5G*L telomeric C-band to a distal region of *5B*L (line 81-1); **f** t^6, a translocation of an unidentified fragment to the telomeric region of *1D*L (line 131-2)

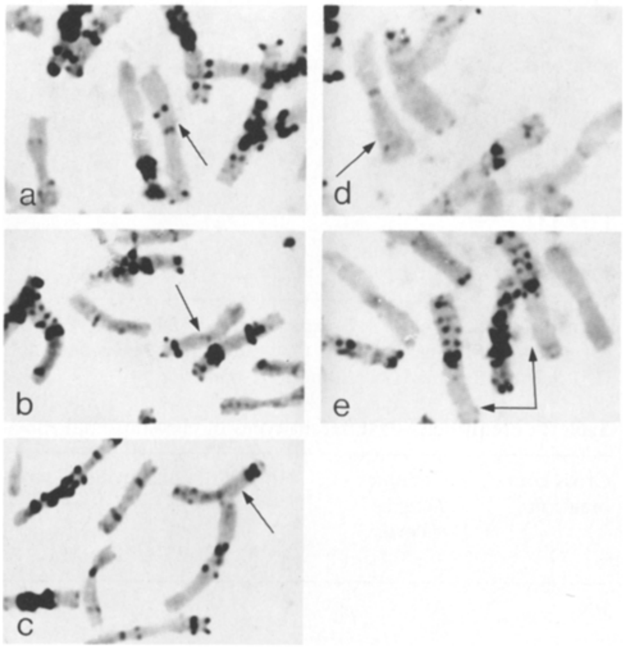

Fig. 5a–e. Translocations of centric-fusion type: **a** t^1, T *7A*^{t}S:*7A*L (line 811-1); **b** t^8, T *7A*^{t}L:*7A*S (line 843-6); **c** t^2, T *7A*^{t}L:*7D*L (line 32-1); **d** t^3, T *3A*L:*3A*^{t}L (line 46-6); **e** t^7, T *3B*S:*3G*L (line 731-1)

group 7, only occasionally in group 3. Chromosomes T *7A*L:$7A^t$S (Fig. 5a) were identified in the karyotype of five lines (four of PX and one of NS), T *7A*S:$7A^t$L (Fig. 5b) in two related lines (NS), and T *7D*L:$7A^t$L (Fig. 5c) in two other related lines (PX). Two related lines of NS contained a chromosome T *3B*S:*3G*L (Fig. 5e), and *3A*L was found to be translocated with $3A^t$L (Fig. 5d) in line 46-6 and with $3A^t$S in 131-2 (all of the PX). There were translocations of the terminal C-bands of G genome chromosomes to the distal regions of the homoeologous B genome chromosomes: one translocation involving *4G* (two PX-related lines, Fig. 4d), another involving *5G* (four PX-related lines, Fig. 4e). An unidentified translocation with the *1D* chromosome was found in the karyotype of PX line 131-2.

The number of detected rearrangements was 17 for PX, five for NS, and zero for ST. The data indicate that the number of chromosomal rearrangements is correlated with chromosome pairing. Thus, Shkutina et al. (1988) revealed the highest frequency of chiasma formation for PX, the lowest for ST, and intermediate between the two for NS. According to our observations, the number of *5B*(*5G*) substitutions was six for PX, four for NS, and null for ST (Tables 1 and 2); therefore, substitution *5B*(*5B*) influenced the level of disruption of meiosis and consequently the number of chromosome rearrangements.

Regarding the present data, it should be noted that: (1) G genome chromosomes (45 substitutions) rather than A^t genome chromosomes (27 substitutions) were substituted for *T. aestivum* homoeologues; and (2) intergenome translocations were infrequent compared to substitutions of whole chromosomes. The karyotype of all the studied hybrid lines comprised seven to eight chromosome pairs of B or B+G genomes. Chromosomes consistently present were *4A*, *7B*, *3D*, *5D*, and *6D*; those rarely substituted were *3A*, *5A*, *1B*, *4B*, *4D*, and *7D*. In most lines the number of NOR chromosomes was two: 1B+6B (26 lines), *1B*+*6G* (nine lines), $6A^t$+*6B* (one line), and in only one line the number of NORs was three, *1B*+*6B*+$6A^t$. All the A-A^t and B-G genome chromosomes with low frequencies of homoeologous substitution have been rearranged during the divergence of the two *Triticum* species. Consequently, the frequency of substitution may reflect the genetical distance of homoeologous chromosomes in related species.

The high frequency of certain types of substitutions was due, perhaps, to the better compensation ability of a particular substitution type. Thus, A/A^t genomes are genetically more diverse from the B/G genomes than from one another, and intragenomic (A^t/A and G/B) substitutions are more common than intergenomic substitutions (A^t/B or G/A). Also, following Naranjo et al. (1987) and Gill and Chen (1987), it may be suggested that chromosomes of homoeologous group 4 are the most divergent.

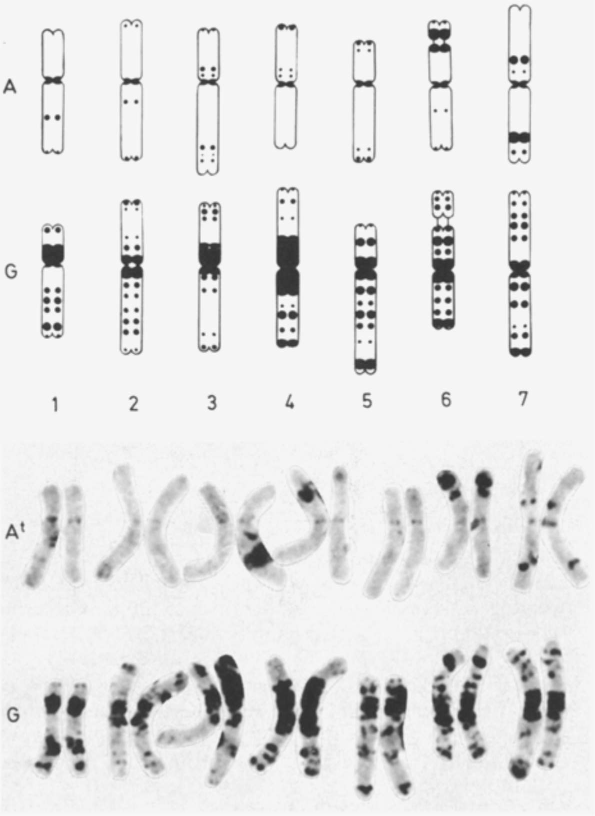

Fig. 6. Chromosomes of *T. timopheevii*. **a** the ideogram of C-banded chromosomes according to the standard genetic nomenclature. **b** C-banded karyotype of *T. timopheevii* ssp. *viticulosum*

Table 3. The list of genetic nomenclatures proposed for *T. timopheevii* chromosomes

Authors	Genome	Chromosome numbering						
Badaeva et al., present commun.	A^t	$1A^t$	$2A^t$	$3A^t$	$4A^t$	$5A^t$	$6A^t$	$7A^t$
	G	*1G*	*2G*	*3G*	*4G*	*5G*	*6G*	*7G*
Zurabishvili et al. 1978	A^t	14	6	7	10	12	13	4
	G	11	1	2	5	9	8	3
Hutchinson et al. 1982	A^t	f	d	a	e	b	g	c
	G	n	l	j	h	m	k	i
Dvorak 1983	A^t	$1A^t$	$3A^t$	$5A^t$	$7A^t$	$6A^t$	$4A^t$	$2A^t$
	G	$5B^t$	$3B^t$	$7B^t$	$4B^t$	$1B^t$	$6B^t$	$2B^t$
Chen and Gill 1983	A^t	$3A^t$	$5A^t$	$7A^t$	$6A^t$	$1A^t$	*4G*	$2A^t$
	G	*5G*	*1G*	*7G*	$4A^t$	*2G*	*6G*	*3G*
Badaeva et al., 1986	A^t	$5A^t$	$3A^t$	$2A^t$	$7A^t$	$1A^t$	$6A^t$	$4A^t$
	G	*5G*	*2G*	*7G*	*4G*	*1G*	*6G*	*3G*
Gill and Chen 1987	A^t	$1A^t$	$2A^t$	$5A^t$	$4A^t$	$3A^t$	$6A^t$	$7A^t$
	G	*5G*	*1G*	*7G*	*4G*	*2G*	*6G*	*3G*
Gill et al. 1988	A^t	–	–	$3A^t$	–	–	–	–
	G	*?G**	*2G*	–	*4G*	*5G*	*6G*	–
Shang et al. 1989	A^t	$4A^t$	$2A^t$	$5A^t$	$4B^t$	$1A^t$	$3A^t$	$7A^t$
	G	$5B^t$	$3B^t$	$2B^t$	$6A^t$	$1B^t$	$6B^t$	7B^t

* Unidentified chromosome of G genome

The data presented in this paper, in conjunction with the results of karyotype analysis of *T. aestivum* × *T. araraticum* hybrid lines (Badaeva et al. 1990), allowed us to establish homoeology between the A^t and G genome chromosomes of *T. timopheevii* and common wheat chromosomes (Fig. 6). Table 3 summarizes our nomenclature, as well as that of different authors, based on the result of substitution line analysis. This data may be used to create a unified genetic nomenclature of cereal chromosomes.

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