Role of Cytoplasm-Specific Introgression in the Evolution of the Polyploid Wheats

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Evolution

Role of cytoplasm-specific introgression in the evolution of the polyploid wheats

(metaphase I pairing/chromosome banding/speciation/*Triticum turgidum*/*Triticum timopheevii*)

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ABSTRACT **Studies of N-banded mitotic and meiotic karyotypes of *Triticum turgidum* L. ($2n = 28$; AABB) and *Triticum timopheevii* Zhuk. ($2n = 28$; AAGG) and hybrids between them, along with observations of meiotic pairing between telocentrics of the AB-genome chromosomes and their respective homologues and homeologues in *T. timopheevii*, showed that chromosome 4 (m4) of *Triticum monococcum* L. is present (as $4A^t$) in *T. timopheevii* but is lacking in *T. turgidum*. Neither 4A nor 4B pairs with $4A^t$, but 4A pairs with 4G and, for this reason and because of its banding pattern, must be considered a B-genome chromosome. *T. timopheevii* chromosomes $4A^t$ and $3A^t$ are involved in a reciprocal translocation, and $2A^t$, 1G, 2G, and 5G are also involved in translocations. Chromosome arm 4BL occasionally pairs with 7G. The satellites are on the short arms of chromosomes $6A^t$ and 6G of *T. timopheevii* and 1B and 6B of *T. turgidum*. It is suggested that (*i*) *T. timopheevii* orginated as an allotetraploid of *Aegilops speltoides* Tausch/*T. monococcum* and (*ii*) *T. turgidum* was derived from *T. timopheevii* by introgressive hybridization with an unknown diploid species, which contributed its distinctive cytoplasm, chromosome 4B or a substantial portion of it, and additional chromosome segments. Rapid fixation of 4B in *T. turgidum* was ensured by cytoplasm-specific transmission.**

Cultivated common wheat (*Triticum aestivum* L., $2n = 42$, genome formula AABBDD) originated as an allohexaploid hybrid of cultivated emmer (*Triticum turgidum* L., AABB) and wild *Aegilops squarrosa* L. (DD). Cultivated *T. turgidum* var. *durum* is a domesticated form of wild emmer, *T. turgidum* var. *dicoccoides* Körn., often accorded specific rank as *T. dicoccoides*. Similarly, another tetraploid, *Triticum timopheevii* Zhuk. (AAGG), is a domesticated form of the wild var. *araraticum*, frequently designated simply as *T. araraticum*. The origin and phylogeny of the two wild tetraploids remains controversial. They occur sympatrically in southern Turkey, northern Iraq, and western Iran, and in this area of their distribution they tend to introgress with each other. However, distinct forms of *T. dicoccoides* occur exclusively in the southern part of the Fertile Crescent, and *T. araraticum* is found only in Transcaucasia (1).

Both tetraploids received their A genome from the wild diploid *Triticum monococcum* L. var. *boeoticum* Bois. Their B and G genomes have greater genetic affinity for each other than does either of them for the genome of any other putative progenitor, including the diploids *Aegilops speltoides* Tausch, *A. longissima* Schweinf. and Muschli, *A. sharonensis* Eig, *A. bicornis* (Forsk.) Jaub. and Sp., and *A. searsii* Feld. and Kisl. The presence of the *Ph1* gene inhibiting the pairing of homeologous (related) meiotic chromosomes in the tetraploid *Triticum* species and their interspecific hybrids indicates that *T. dicoccoides* may have evolved from *T. araraticum* or vice versa. Five possibilities for genome differentiation that may explain the reduced meiotic pairing between the B- and G-genome chromosomes have been proposed: complementary gene action (2), chromosomal differentiation due to introgressive hybridization (3), differentiation resulting from mutation and chromosomal rearrangements (4), differential heterochromatinization of chromosomes (5), and rapid divergence of the DNA sequences (6). Only the second of these hypotheses is compatible with the evidence of cytoplasmic differences between the AB- and AG-genome species. None of them accounts for the higher meiotic pairing in the *T. timopheevii* × *T. monococcum* F_1 than in *T. turgidum* × *T. monococcum* (e.g., see ref. 7).

T. monococcum var. *boeoticum* (wild diploid wheat) is cytoplasmically different from *T. dicoccoides* and *T. araraticum*, indicating that neither tetraploid arose as an amphiploid in which *T. boeoticum* was the female parent. Cytoplasmic evidence suggests that *A. speltoides* was the donor the cytoplasm of *T. araraticum* (8, 9). Similarly, the cytoplasm of the B genome of *T. dicoccoides* is similar to that of *A. longissima* (e.g., see ref. 9).

Maan (10) suggested that the AB genomes of the wild emmer may have been derived from the AG genomes of a progenitor of *T. araraticum* by introgressive hybridization involving a third diploid species, which was the source of cytoplasm and certain cytoplasm-specific nuclear genes of *T. dicoccoides*. This paper provides cytogenetic evidence supporting this hypothesis.

MATERIALS AND METHODS

The accessions of wild emmer *T. dicoccoides* (TA54 from Israel, TA71 from Lebanon, TA84 from Turkey, TA1058 from Syria), *T. timopheevii* (TA103), and *T. araraticum* (TA1 from the USSR, TA5 from Iran, TA6 from Turkey, TA39 from Iraq) analyzed for karyotype and chromosome pairing are maintained by the Wheat Genetics Resource Center, Kansas State University (Manhattan, KS). The *T. turgidum* var. *durum* cv. Langdon euploid and double-ditelosomics used in pairing analysis were kindly supplied by L. R. Joppa (USDA-ARS, North Dakota State University, Fargo, ND). In each of these 13 lines, a particular chromosome was represented by two pairs of telosomes. A *T. turgidum* line having chromosome m4 of *T. monococcum* substituted for 4B was also obtained from L. R. Joppa.

Somatic chromosome preparations were made from root tips of seedling plants and were stained by an established technique (11). The same technique was used for staining microsporocytes of the various species and hybrids analyzed at meiosis.

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Abbreviations: DMT, double monotelosomic; PMC, pollen mother cell.

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RESULTS

Although it was not possible to identify every chromosome solely by its morphology, particularly at meiosis, this proved not to be necessary. There was no difficulty in distinguishing the lightly banded chromosomes of the emmer A genome (including 4B instead of 4A) and those of the *T. timopheevii* A genome (here designated A^t) from the much more heavily banded chromosomes of the B genome (including 4A instead of 4B) and the G genome. How often each A- and B-genome chromosome paired in a rod bivalent, ring bivalent, trivalent, or quadrivalent was determined from studies of the double-ditelosomic emmer wheat × *T. timopheevii* hybrids, in which each arm of a particular A- or B-genome chromosome was represented by an easily recognizable telosome. For the A genome, whose rate of pairing was high, it could safely be concluded that, with rare exceptions involving heavily banded chromosomes, the pairing was homologous, involving 1A with $1A^t$, etc. For the B-genome chromosomes, pairing was less frequent but clearly involved primarily the heavily banded G-genome chromosomes. This pairing, although not regular enough to be classed as strictly homologous, was much more frequent than that between A- and B-genome homeologues and almost certainly involved same-numbered B and G chromosomes except as noted. We refer to the B/G pairing as strongly homeologous.

Somatic karyotypes of the *T. turgidum* (Fig. 1*a*) and *T. dicoccoides* accessions all contained seven lightly N-banded chromosomes (1A, 2A, 3A, 5A, 6A, 7A, and the anomalous chromosome 4B). All accessions showed seven highly banded chromosomes (1B, 2B, 3B, 5B, 6B, 7B, and 4A). Somatic karyotypes of the *T. timopheevii* (Fig. 1*b*) and *T. araraticum* accessions also showed seven lightly banded and seven highly banded chromosomes. The lightly banded seven, which are similar to the A-genome chromosomes (except 4B) of emmer wheats, were identified as the A^t genome. Chromosome $7A^t$ showed banding more like 4B of emmer wheats than 7A, but nevertheless paired with 7A in hybrids (see Fig. 3*f*). *T. timopheevii* has no chromosome like 4B in banding pattern. Whereas in emmer wheats the satellited chromosomes are 1B and 6B, in *T. timopheevii* wheats they are $6A^t$ and 6G.

The G-genome chromosomes of *T. timopheevii* wheats, which tended to be somewhat more heavily banded than those of the B-genome of emmer wheats (including 4A), were shown by the pairing data to be strongly homeologous to the corresponding B-genome chromosomes. Some of the differences found in banding patterns between B- and G-genome chromosomes appear to be due to the numerous chromosome translocations that were revealed by the pairing analysis.

In F_1 hybrids of *T. turgidum* with *T. timopheevii* and *T. araraticum*, the pairing of A with A^t chromosomes (both lightly banded) can be distinguished from that of B with G (heavily banded). In a nucleus with maximum pairing (Fig. 2), the A and A^t chromosomes were paired as 1 I(4B) + 3 II ring + 2 II rod + 1 III [$(4A^t\text{-}3A^t)/3A/(3A^t\text{-}4A^t)$]. Relative to genome A of *T. turgidum*, the group 3 ($3A^t$) and group 4 ($4A^t$) chromosomes of *T. timopheevii* must be reciprocally translocated ($3A^t\text{-}4A^t$ + $4A\text{-}3A^t$), for they both paired with 3A to form a trivalent (in 75% of sporocytes). The group 4 chromosome of genome A, chromosome 4B, did not pair with either of the two translocated $4A^t$ chromosomes, and thus a quadrivalent involving them was never found. (A rare pairing of 4BS with a $4A^t$ arm in a trivalent was observed, however.)

The lightly banded chromosome 4B was typically unpaired (Fig. 2). The highly banded B and G chromosomes (including 4A) paired maximally as 2 I + 1 II ring + 4 II rod. (In Fig. 2, chromosome 6B is represented by two telosomes, converting 6B/6G bivalents into 6BS/6G/6BL trivalents.)

The total average chromosome pairing observed in 29 chromosome F_1 hybrids of *T. turgidum* double ditelosomics with *T. timopheevii* was 7.8 I + 3.4 II ring + 5.5 II rod + 0.97 III + 0.03 IV per cell. Excluding heteromorphic (banded/unbanded) and quadrivalent pairing, A/A^t pairing was 1.8 I (4B in 90% of the cells) + 2.9 II ring + 1.9 II rod (including $6A/6A^t$ in 90% of the cells) + 0.75 III [$(4A^t\text{-}3A^t)/3A/(3A^t\text{-}4A^t)$]. The B and G chromosomes paired as 6.0 I + 0.5 II ring + 3.5 II rod + 0.12 III. (Univalents are overrepresented in these data, compared to values from ordinary *T. turgidum* × *T. timopheevii* hybrids. Having one chromosome represented by two telosomes increases the number of univalents, primarily by converting one univalent to two, and one rod bivalent to one bivalent and one univalent.)

Specific homologies of individual *T. timopheevii* chromosomes were determined from their pairing frequency with the *T. turgidum* double monotelosomes (DMT; Fig. 3, Table 1). DMT 1A, 2A, and 7A were paired as t1t III with unbanded A^t chromosomes in 55–70% of the pollen mother cells (PMCs; Fig. 3 *a*, *b*, and *f*), and as t1 II in 25–30%. DMT2A paired as 2 t1 II with two banded chromosomes in one PMC, indicating a minor translocation of $2A^t$ with an unknown chromosome. For DMT5A, the only five cells scored showed t1 II + t I pairing; however, in hybrids with *T. araraticum* TA1, t1t III pairing was observed in 30% of PMCs (Fig. 3*d*). DMT6A showed pairing of its long arm with a satellited $6A^t$ chromosome, leaving its short arm unpaired in 100% of the cells (Fig. 3*e*). DMT3A was not available for analysis; however, as mentioned before and as determined from its N-banding pattern, 3A paired in a trivalent with the translocated $3A^t\text{-}4A^t$ chromosomes in 90% of PMCs (Fig. 2). The 4B telosomes

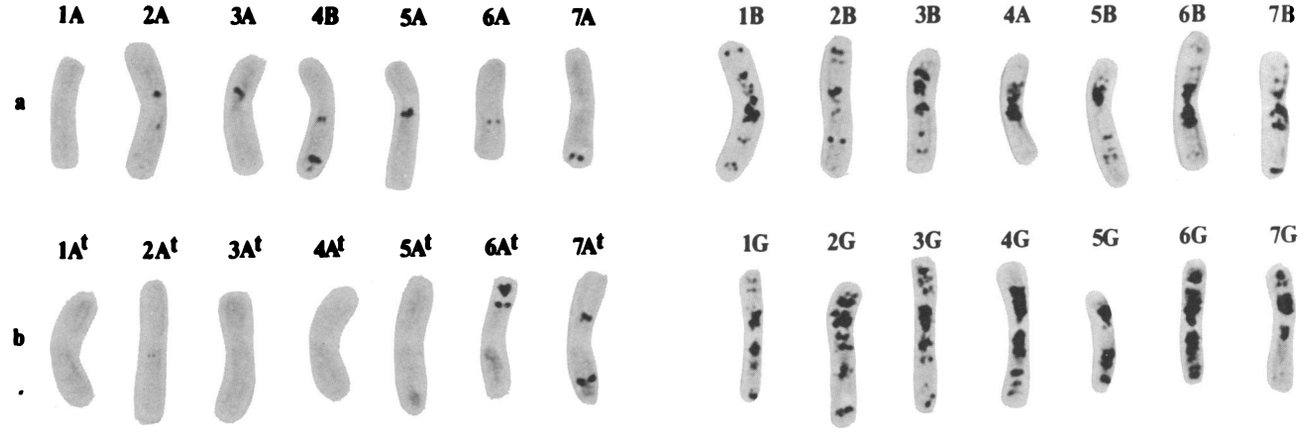

FIG. 1. Somatic metaphase N-banded chromosomes. (*a*) *T. turgidum* var. *durum* cv. Langdon. (*b*) *T. timopheevii* (TA103).

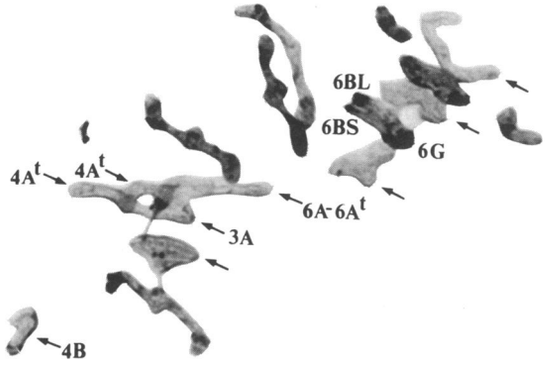

FIG. 2. N-banded meiotic-metaphase PMC of F_1 hybrid *T. turgidum* double-ditelosomic 6B × *T. timopheevii* (TA103). Arrows indicate lightly banded (A-A^t and 4B) chromosomes paired as 1 I (4B) + 3 II (ring) + 2 II (rod) + 1 III [(4A^t-3A^t)/3A/(3A^t-4A^t)]. The highly banded B-G chromosomes are paired as 2 I + 1 II (ring) + 4 II (rod) + 1 III (6B ditelos - 6G).

were univalent in 85% of PMCs; in the remaining 15%, 4BL paired with either 7G alone (Fig. 3*c*) or in a trivalent association with 7G and 7B (Fig. 3*r*). In a hybrid of DDT4B × *T. araraticum* TA1, 4BS was observed in a rare pairing with 3A/3A^t-4A^t.

T. turgidum DMT 2B, 3B, 4A, and 6B showed t1t III pairing with G-genome chromosomes in only 5–25% of PMCs (Fig. 3 *i*, *k*, and *o*). DMT5B was observed in a t1t III in hybrids with *T. araraticum* (Fig. 3*m*). The B-genome (including 4A) DMTs, mostly their long-arm telosomes, showed t1 pairs in 15–75% of PMCs (Fig. 3 *g*, *h*, *j*, *l*, *n*, and *p*). Heteromorphic associations included pairing of telo 1BS with the set arm of 6A^t (Fig. 3*g*), and 1B, 2B, and 5B telos with nonhomologous banded and unbanded chromosomes (Fig. 3 *h*, *j*, and *n*; Table 1).

Among several other examples of heteromorphic pairing was one rare PMC in which 7GS was paired with 4A^t-3A^t, 3A, and 3A^t-4A^t In a quadrivalent (Fig. 3*q*). Trivalents 4B/7G/7B and 1B/6A^t/6A occurred (Fig. 3 *r* and *s*), as well as heteromorphic multivalents involving unidentified banded (B or G) and unbanded (A or A^t) chromosomes resulting from translocations (Fig. 3 *t* and *u*). It appears that in addition to 3A^t and 4A^t, chromosomes 2A^t, 1G, 2G, and 5G are involved in translocations.

In hybrids of *T. timopheevii* with a *T. turgidum* that had m4 of *T. monococcum* substituted for 4B, 4A^t paired with m4 in 50% of the PMCs (PMCs scored = 30), whereas in *T. timopheevii* × *T. turgidum* hybrids 4A^t paired with 4B in only 3% of PMCs (PMCs scored = 240). In the former hybrids, quadrivalent association presumably involving m4/(4A^t-3A^t)/3A/(3A^t-4A^t) was observed in 23.3% of PMCs (Fig. 4).

DISCUSSION

The karyotypic and chromosome pairing data show that *T. monococcum* contributed seven pairs of chromosomes to *T. timopheevii* but only six pairs to *T. turgidum*. Chromosome 4B of *T. turgidum* paired only rarely with 4A^t of *T. timopheevii*. Similarly, 4A^t of *T. timopheevii* did not pair with any of *T. turgidum* chromosomes but paired with the m4 chromosome of *T. monococcum*. However, m4 and 4A^t paired only in 50% of the PMCs and a ring quadrivalent of m4 with 3A and 3A^t/4A^t was never observed; thus, pairing of chromosomes m4 and 4A^t should be considered as near-homologous. Therefore, the *T. timopheevii* complex, although containing genomes considerably modified from the putative allopolyploid, may still be considered to contain, more or less, seven A-genome chromosomes derived from *T.*

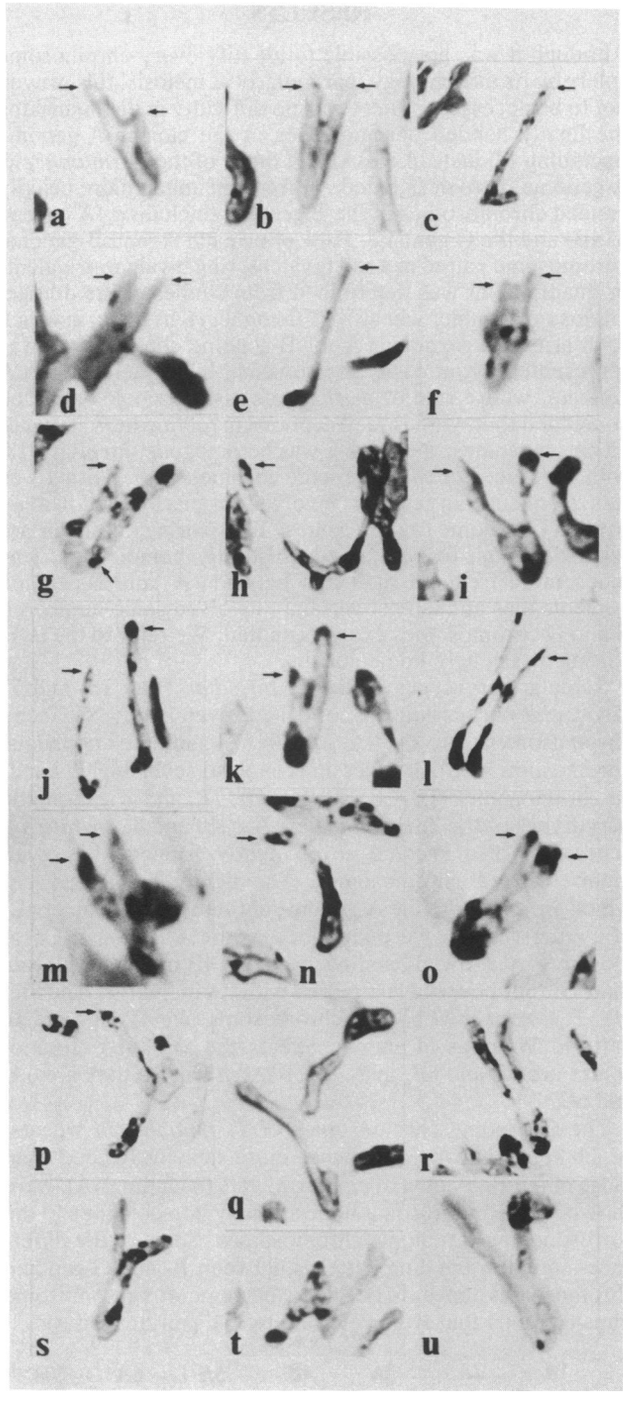

FIG. 3. Bivalent (t1 II), trivalent (t1t III), and multivalent pairing in hybrids of different double ditelosomics of *T. turgidum* with *T. timopheevii* (*a*, *b*, *e*, *g*, *i*, *j*, *n–s*, and *u*) and *T. araraticum* TA1 (*c*, *d*, *f*, *h*, *k–m*, and *t*). Telosomic chromosomes are indicated by arrows. (*a*) t1t III showing 1AS and 1AL paired with chromosome 1A^t. (*b*) t1t III, DMT2A-2A^t. (*c*) t1 II, 4BL-7G. (*d*) t1t III, DMT5A-5A^t. (*e*) t1 II, 6AL-6A^t. (*f*) t1t III, DMT7A-7A^t. (*g*) t1 II (1BS-6A^t) on left + t1 II (1BL-1G). (*h*) t3 IV showing 1BL paired with 3 banded chromosomes. (*i*) t1t III, DMT2B-2G. (*j*) t1 II (2BL-2G) on left + t1 II(2BS-G chromosome). (*k*) t1t III, DMT3B-3G. (*l*) t1 II, 4AL-4G. (*m*) t1t III, DMT5B-5G. (*n*) t1 II, 5BS-unidentified G chromosome. (*o*) t1t III, DMT6B-6G. (*p*) t1 II, 7BL-7G. (*q*) 7G (banded)/(4A^t-3A^t)/3A/(3A^t-4A^t) quadrivalent. (*r*) 7B (left)-7G (center)-4B (right) III. (*s*) 6A (left)-6A^t (center)-1B (right) III. (*t*) Two unidentified G-genome chromosomes paired with two unidentified A-genome chromosomes. (*u*) III showing 2A (center) paired with an unidentified A genome chromosome (left) and a G genome chromosome (right).

Table 1. Pairing of double monotelosomes of *T. turgidum* chromosomes in hybrids with *T. timopheevii*

Chromosome	Number of cells with indicated behavior of telosomes: Neither paired	One or both paired as A/A^t or B/G: t1+t	t1t	t2+t	Other pairing
1A	2	5	13	0	
2A	1	5	11	1	1(t1+t2) 1[(t1+t)/G]
4B	17	0	0	0	2[tL/(7G+tS)] 1[tL/7G/(7B+tS)]
5A	0	5	0	0	
6A	0	20	0	0	
7A	0	6	14	0	
1B	15	3	0	1	1[tL/(1G+tS)/6A^t]
2B	9	5	1	3	1(t3+t) 1[t/(A^t+t)]
3B	7	6	5	1	1[t/(A^t+t)]
4A	8	11	1	0	
5B	5	14	0	0	1[t/(2A^t+t)]
6B	6	11	3	0	
7B	3	15	0	1	1(t2+t1)

t, t1, t2, t3 = one telosome paired with 0, 1, 2, or 3 chromosomes in a univalent, bivalent, trivalent, or quadrivalent. t/G = telosome paired with a G-genome chromosome. t/A^t = telosome paired with an A^t-genome chromosome. Cells per entry = 20, except 5 for 5A.

monococcum and seven G-genome chromosomes derived from a second species, possibly *A. speltoides*.

Diverse *T. turgidum* accessions reveal the universal occurrence of chromosome 4B in this species. In *T. aestivum* × *T. timopheevii* hybrids, 4BL has been shown to pair with a *T. timopheevii* chromosome in 10–20% of PMCs (6, 12). From these data, it has been assumed that a chromosome similar to 4B is present in *timopheevii* wheats. Recent data indicate that 4A is a B-genome chromosome (13). Dvořák (13) considered 4B to be a modified A-genome chromosome, but we find that 4B pairs occasionally with 7G, rarely with 4A^t, and not with any other A^t-genome chromosome. It appears probable that in *T. turgidum* neither 4A nor 4B was derived from 4A (m4) of *T. monococcum*, which is contrary to Wazuddin and Driscoll's (14) assumption, or that m4 became more drastically modified than heretofore suspected.

These observations suggest that *T. araraticum* antedated *T. turgidum* and that *T. turgidum* was derived from *T. araraticum* by hybridization with a third species, which donated its distinctive cytoplasm and most or all of chromosome pair 4B. Thus, chromosome 4B should show specificity to the cytoplasm of the diploid species that contributed the cytoplasm and 4B to *T. turgidum*. Cytoplasm-specific nuclear introgression and exclusive transmission of gametes controlled by alien cytoplasm is well documented in the wheat group (15, 16). This provides a mechanism for the fixation of an alien chromosome in one generation.

FIG. 4. N-banded meiotic-metaphase PMC of F_1 hybrid *T. turgidum* nullisomic-4B disomic-m4 × *T. araraticum* (TA1). Lightly banded A-A^t chromosomes paired as 5 II + 1 IV [m4/(4A^t-3A^t)/3A/(3A^t-4A^t)].

Chromosomes with close genetic affinities to 4B have been reported in the *Sitopsis* section of *Aegilops* (15–18). Also, there are reports of homeologous group 4 chromosomes in *A. longissima* and *A. sharonensis* that show exclusive cytoplasm-specific transmission in wheat (15, 16).

There is further evidence that chromosome 4B of *T. turgidum* may carry cytoplasm-specific female and male fertility genes. Mochizuki (19) failed to isolate a 4B monosomic in *T. turgidum*, indicating the presence of a sporophytic sterility gene on this chromosome. Also, *T. turgidum* plants having *T. monococcum* chromosome m4 substituted for 4B were male sterile (20). Introgression into *T. araraticum* of chromosome 4B, of a different cytoplasm, and of cytoplasm-specific 4B nuclear sporophytic fertility genes from a diploid species may have led to the origin of a new species, *T. dicoccoides*, that spread into the southern part of the Fertile Crescent.

Besides the introgressed chromosome 4B, there may be other alien chromosome segments that differentiate the chromosomes of the two tetraploid *Triticum* species complexes. *T. turgidum* telosomes 6AS, 1BS, 4AS, and 7BS were rarely paired with any *timopheevii* chromosomes. Similar results were previously reported for these arms (6, 12). It may be surmised that homeologous chromosome segments were introgressed from the species that contributed chromosome 4B and cytoplasm to *T. turgidum* and perhaps from one or more other species. This cytoplasmic and nuclear introgression may also have triggered hybrid dysgenic elements (21) that led to structural alterations, including multiple chromosomal translocations and the differentiation of the A, A^t, B, and G genomes of the two evolutionarily successful tetraploids. These observations also suggest the futility of searching for a single diploid donor of the B genome (22).

With respect to chromosome structural changes, it should be pointed out that 4B has undergone an inversion (6) and also a translocation with a group 7 chromosome, as judged from its pairing with chromosome 7G and observed 4BL-7AS pairing in *T. turgidum* × *A. speltoides* hybrids (unpublished data). The suggested partial homology between arms 7AS and 4BL is also supported by the location of a peroxidase locus on these arms and not 7BS (which was presumably translocated to 4B) (23). This means 7BS is also structurally modified, and this may explain the lack of pairing between 7BS and 7G chromosomes. Similarly, the reduced pairing of 6AS with 6A^{t}S could be partly accounted for by the presence of a 1GS satellite arm translocation to the 6A^t chromosome, since a satellited 1G chromosome has been reported in one accession of *T. araraticum* (6). If major structural changes can lead to drastically reduced pairing, the possibility cannot be ruled out that presence of an inversion and a translocation in chromosome 4B may explain its lack of pairing ability, and hence the origin of 4B from several putative donors including *T. monococcum* cannot be totally ruled out.

Our model of genome evolution does not support a strict pivotal genome process (3), because the supposedly pivotal A genome of each tetraploid species was modified to some extent, although not as much as B and G, and also because the pivotal genome hypothesis does not recognize the critical role of species-specific cytoplasmic and nuclear genes in genome differentiation of polyploid species complexes (24). Similarly, our evidence does not lend support to a primary role in genome evolution of the other mechanisms alluded to earlier in the Introduction (4–6).

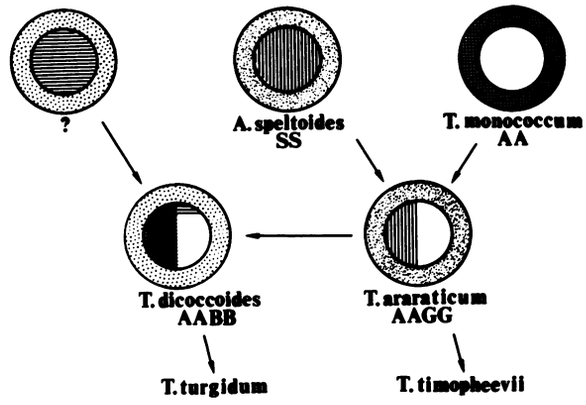

FIG. 5. Proposed phylogeny of tetraploid *Triticum* species. Specific cytoplasmic (outer circle) and nuclear (inner circle) genome contributions of various species are indicated. The genome designated GG in *T. araraticum* is assumed to have been derived from the S genome of *A. speltoides*. In *T. dicoccoides*, chromosome 4B (cross lines) from an unknown species (?) is believed to have been substituted for chromosome $4A^t$ of *T. araraticum*. Additional homeologous chromosome transfers from the same unknown species presumably modified the G genome to give rise to the B genome of *T. turgidum*.

We suggest that the phylogeny of the two tetraploid wheat species traces back to three diploids (Fig. 5). First, *T. araraticum* originated from *A. speltoides* (which also contributed its cytoplasm) and *T. monococcum* (8, 9). *T. araraticum*, by introgressive hybridization with an unknown diploid species, then gave rise to *T. dicoccoides*. The cytoplasm and at least a large part of chromosome 4B of *T. dicoccoides* were derived from this unknown species. As an alternative to this scenario for the origin of the two tetraploids, we cannot presently rule out the production of two different *Aegilops/T. monococcum* amphiploids, with subsequent hybridization and joint introgression between them.

It is probable that the cytoplasm and chromosome 4B of *T. turgidum* were derived from an *Aegilops* species belonging to the *Sitopsis* section. There is conflicting evidence concerning cytoplasmic homology of *A. longissima* with *T. turgidum* (9, 25). The various species that have been suggested as the source of the B genome, with the exception of *A. longissima*, have been ruled out as cytoplasmic donors. It seems that the cytoplasmic donor should also account for the origin of chromosome 4B.

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