M. Feldman

Proc. 4th Internat. Wheat Genetics Symposium
Missouri Agr. Exp. Sta., Columbia, Mo. 1973
pp. 101-108

REALLOCATION OF THE GENOMES OF *TRITICUM TIMOPHEEVII* ZHUK.

HENRY SHANDS[1] AND GORDON KIMBER

Department of Agronomy
Curtis Hall
University of Missouri
Columbia, Missouri

SUMMARY

A high level of homologous pairing in hybrids of Triticum timopheevii with Triticum speltoides and a corresponding lack of homology in Triticum durum x T. speltoides hybrids were found. This demonstrates that T. speltoides should be considered the donor of the second genome of T. timopheevii and the genomic formula should be AASS. A slight excess of bivalent pairing in T. timopheevii x T. durum crosses is attributed to translocations.

Evidence presented by KIMBER and ATHWAL (1972) that *Triticum speltoides (Aegilops speltoides)* can no longer be considered the donor of the B-genome of common wheat (*T. aestivum* L.) has opened the way for reassessing the course of evolution of this and related species. That one of the diploid wheats contributed the A-genome to the various tetraploid and hexaploid wheats and that *T. tauschii (A. squarrosa)* contributed the D-genome to the hexaploid wheats is still accepted.

The tetraploid *T. timopheevii* Zhuk. was described by LILIENFIELD and KIHARA (1934) to have the genomic constitution AG due to structural differences of the second genome from that of B. KOSTOFF (1937) assigned the formula $A\beta$ due to the partial homology of the second genome to that of B. LOVE (1941) and SACHS (1953) indicated the homologies of the genomes to be similar enough to have been derived by structural differentiation, while SEARS (1948) felt the two were of different origins. WAGENAAR (1961) believed a genetically controlled system in *T. timopheevii* induced asynapsis in F_1 hybrids, concluded this to be more important than the structural differences, and further concluded (1966) the species probably arose from *T. dicoccoides*. FELDMAN (1966) presented data suggesting hybrids of *T. timopheevii* and *T. turgidum* or *T. aestivum* had poor meiotic pairing due to chromosomal differences and concluded that B^t, the second genome, could have differentiated from B as a result of exchanges of homoeologous chromosomal segments with other genomes. He suggested that *T. turgidum* could have evolved from *T. timopheevii*, or the reverse, or that both evolved from a common progenitor, with B and B^t as new genomic combinations.

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[1] DEKALB AgResearch, Inc., 1211 Cumberland Ave., W. Lafayette, Indiana. Contribution from the Missouri Agricultural Experiment Station. Journal Series No. 6726.

MAAN and LUCKEN (1971) found that the male-sterile plants of *T. speltoides* crossed with *T. durum* and *T. aestivum* closely resemble those bearing the cytoplasm of the *timopheevii*-complex in similar crosses. On the basis of this cytoplasmic evidence, they suggested that *T. speltoides* may have contributed the G-genome and cytoplasm to the *timopheevii*-complex. These workers further showed (1972) that fertility-restorer lines bearing *T. timopheevii* restoration factors would restore fertility in F_1 hybrids with A-lines having either the *speltoides* or *timopheevii*-complex cytoplasms.

Table 1. Designation and source of materials used in crosses.

Designation	Item	Source
G1064	*T. speltoides* (low pairing)	U. of California-Riverside
G1316	*T. speltoides* (low pairing)	U. of California-Riverside
G366	*T. speltoides* (intermediate pairing)	U. of California-Riverside
G1039	*T. speltoides* (high pairing)	U. of California-Riverside
G576[1]	*T. durum* Desf. var *provenciale* Al.	U. of California-Riverside
G839	*T. durum* Desf. var *aestivum f. acme*	U. of California-Riverside
CI13771	*T. durum* cult. Stewart 63	USDA - Beltsville
L81076	*T. durum* breeding selection	DEKALB AgResearch, Inc.
G383	*T. timopheevii*	U. of California-Riverside
G384	*T. timopheevii*	U. of California-Riverside
G986	*T. zhukovskyi*	U. of California-Riverside
CI12933	*T. aestivum* cult. Itana	DEKALB AgResearch, Inc.

[1] Equals 2m of Wagenaar (*loc. cit.*)

KIMBER and ATHWAL (*loc. cit.*) have described a range of variation in *T. speltoides* and divided it into low-, intermediate-, and high-pairing groups, based on meiotic associations. Their results, showing lack of homology between *T. speltoides* chromosomes and those of the B-genome of *T. aestivum*, were substantiated by LARSEN and KIMBER (1973), who found no differences in chromosome pairing and chiasma frequency between the diploids and the induced autotetraploids of the low- and high-pairing lines of *T. speltoides*. This suggested that the genes in *speltoides* affecting chromosome pairing in hybrids did not interfere with the pairing of homologous chromosomes. Thus, homologous pairing is not affected by the genetic system of *T. speltoides*, but in intermediate- and high-pairing lines, homoeologous pairing is allowed.

The study reported in this paper was designed to reassess the relationship, if any, between the *T. speltoides* genome and genomes of *T. timopheevii* (and *T. zhukovskyi*). In controlled crosses of low, intermediate-, and high-pairing *speltoides* to *T. timopheevii* and *T. durum*, pairing relationships should indicate the homology between the S, G and B genomes.

Table 2. Mean and range of chromosome pairing in F_1 hybrids of *T. durum* and *T. speltoides*

Cross number	Cross	No. of cells	I[1]	II rod	II ring	III	IV
72-31	G839 x G1064 (LP)[2]	20	20.20 17-21	0.40 0-2	-	-	-
72-44	G576 x G366 (IP)	20	12.10 8-15	2.70 1-5	1.45 0-4	0.20 0-2	–
72-202	G839 x G1039 (HP)	20[3]	8.80 6-14	3.50 2-6	0.40 0-2	1.40 0-3	0.10 0-1

[1] I = univalent, II = bivalent, III = trivalent, IV = quadrivalent.

[2] LP = low-pairing, IP = intermediate-pairing, and HP = high-pairing forms of *T. speltoides*.

[3] 10 cells from each of 2 plants of this cross combined.

Table 3. Mean and range of chromosome pairing in F_1 hybrids of *T. timopheevii* and *T. speltoides*

Cross number	Cross	No. of cells	I	II rod	II ring	III	IV	Other
72-17	G383 x G1064 (LP)	60[1]	7.20 2-13	3.15 0-6	1.72 0-4	1.55 0-4	0.17 0-1	-
72-30	G383 x G1316 (LP)	60[2]	7.25 3-12	3.53 1-7	1.39 0-3	1.07 0-4	0.27 0-2	0.05 0-1
72-47	G384 x G1316 (LP)	10	7.20 5-11	3.30 2-4	1.80 0-3	1.20 0-2	-	-
	Average (LP)	130	7.22 2-13	3.34 0-7	1.57 0-4	1.30 0-4	0.20 0-2	0.02 0-1
72-46	G384 x G366 (IP)	20	6.70 4-11	3.70 2-6	1.40 0-3	1.30 0-3	0.05 0-1	-
72-48	G384 x G366 (IP)	20	5.40 2-8	3.20 1-7	0.95 0-3	2.10 0-4	0.25 0-1	-
	Average (IP)	40	6.05 2-11	3.45 1-7	1.18 0-3	1.70 0-4	0.15 0-1	-
72-199	G384 x G1039 (HP)	30	3.77 1-7	2.87 0-6	1.30 0-4	2.70 0-6	0.20 0-1	-

[1] 10, 10, and 40 cells from 3 plants of this cross combined.

[2] 10, 20, and 30 cells from 3 plants of this cross combined.

MATERIALS

The materials used came from a variety of different sources, as shown in Table 1. The lines of *T. speltoides* were the same as used by KIMBER and ATHWAL (*loc. cit.*).

RESULTS

T. durum x *T. speltoides*

Results of crosses to *T. durum* with low-, intermediate-, and high-pairing lines of *T. speltoides* are given in Table 2. The almost complete lack of pairing (20.20 univalents) in the low-pairing *speltoides* hybrid (Fig. 1) establishes that there is no homology between the B (or A) and S genomes, substantiating, at the tetraploid level, the data of KIMBER and ATHWAL (*loc. cit.*). The intermediate- and high-pairing *speltoides* showed increased homoeologous pairing (Fig. 2) in the F_1 hybrids with *durum*, indicating that the pairing factor(s) observed at the hexaploid level are also functioning at the tetraploid level.

T. timopheevii x *T. speltoides*

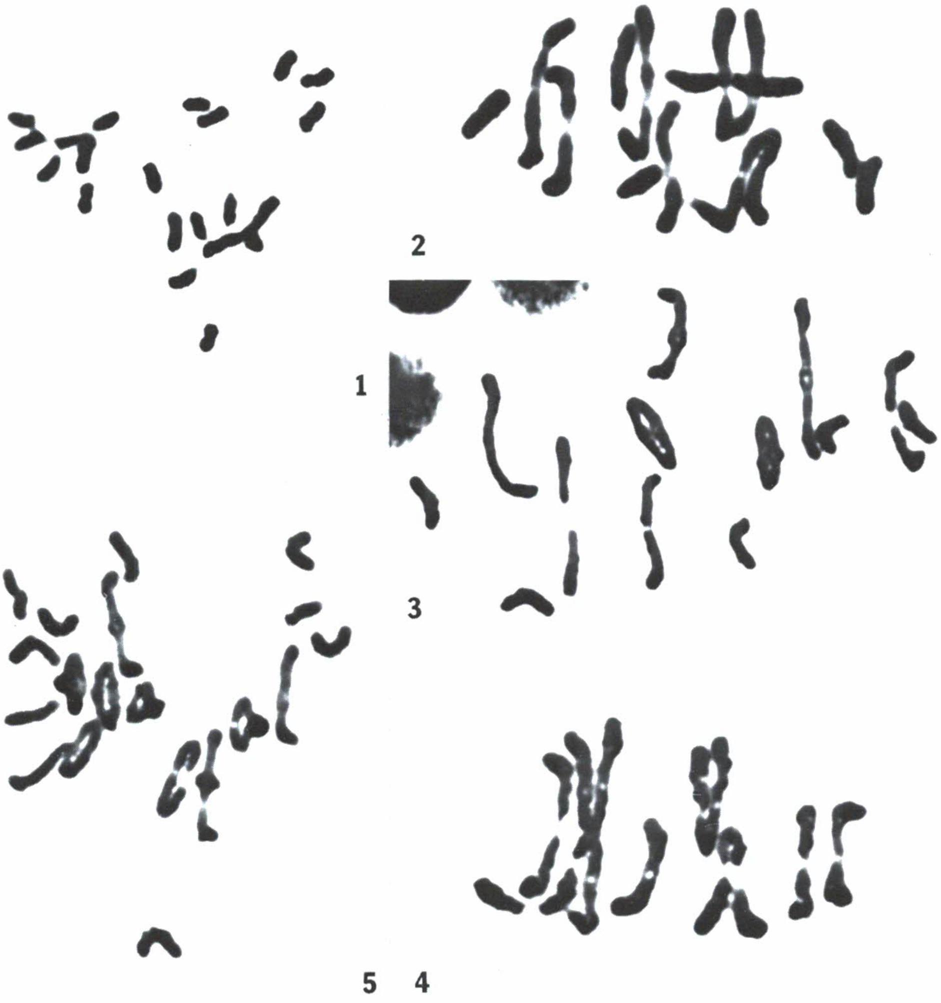
Lines of *T. timopheevii* were crossed with low-, intermediate-, and high-pairing *speltoides* (Table 3). Homologous chromosome pairing in the low-pairing *speltoides* cross was the equivalent of 6.89 bivalents per cell (Fig. 3), essentially that of the whole genome. Intermediate- and high-pairing *speltoides* again permitted homoeologous pairing, and increased frequencies of multivalents were obtained (Fig. 4).

T. timopheevii x *T. durum*

Bivalent associations in the *timopheevii* by *durum* hybrids averaged in excess of the expected seven bivalents per cell (Table 4). The excess may be attributed to pairing between chromosomes of the G and B genomes and/or the presence of translocations. However, a very low number of multivalents (0.55) was found (Fig. 5).

T. zhukovskyi x *T. aestivum*

Multivalent associations, presumably of the thrice-represented A genome, complicated the analysis of this cross (Table 4). These data are presented to show that the number of bivalent associations is similar to the number found in the *timopheevii* x *durum* cross but not necessarily for the same reason. Further study is being conducted on this and other crosses involving *T. zhukovskyi*.



Figures 1 to 5. Meiosis in various hybrids, X1150. (1) Cross 72-31, *Triticum durum* (G839) x (LP) *T. speltoides* (G1064), with 21 univalents. (2) Cross 72-202, *Triticum durum* (G839) x (HP) *T. speltoides* (G1039), with 6 univalents, 3 rod bivalents and 3 trivalents. (3) Cross 72-30, *Triticum timopheevii* (G383) x (LP) *T. speltoides* (G1316), with 5 univalents, 6 rod and 2 ring bivalents. (4) Cross 72-199, *Triticum timopheevii* (G384) x (HP) *T. speltoides* (G1039), with 1 univalent, 4 rod bivalents and 4 trivalents. (5) Cross 72-S6, *Triticum timopheevii* (G383) x *T. durum* (L81076), with 9 univalents, 3 rod and 5 ring bivalents and 1 trivalent.

Table 4. Mean and range of chromosome pairing in F_1 hybrids of *T. timopheevii* x *T. durum* and *T. zhukovskyi* x *T. aestivum*

Cross number	Cross	No. of cells	I[1]	II rod	II ring	III	IV	V	VI
			T. timopheevii x *T. durum*						
72-S5	G383 x CI 13771	40[2]	7.55 2-12	5.95 3-10	3.83 1-5	0.20 0-2	0.08 0-1	-	-
72-S6	G383 x L81076	35[3]	8.46 2-14	5.31 3-9	3.17 1-6	0.86 0-2	-	-	-
	Average	75	7.97 2-14	5.65 3-10	3.52 1-6	0.51 0-2	0.04 0-1		
			T. zhukovskyi x *T. aestivum*						
72-S8	G986 x CI 12933	15	11.27 7-20	5.53 3-10	3.47 1-7	3.13 1-6	0.40 0-2	0.07 0-1	0.07 0-1

[1] I=univalent, II=bivalent, III=trivalent, etc.

[2] 20 cells from each of 2 plants of this cross combined.

[3] 15 and 20 cells from 2 plants of this cross combined.

DISCUSSION

The lack of homology between the B and S genomes is clearly displayed in the cross of *T. durum* x low-pairing *speltoides*. Homoeologous pairing increases in crosses involving intermediate- and high-pairing lines of *speltoides*. This further corroborates the data of KIMBER and ATHWAL (*loc. cit.*), who found the parallel situation in crosses with *T. aestivum* and concluded that *T. speltoides* cannot be considered the donor of the B genome of polyploid wheats.

The crosses of *T. timopheevii* and low-pairing *speltoides*, on the other hand, show a high degree of homology between the G and S genomes. Corresponding increases in homoeology are displayed in the crosses involving *timopheevii* and intermediate- and high-pairing *speltoides*. These nuclear data are taken to demonstrate conclusively that there is a genome in common between these two species. Cytoplasmic observations by MAAN and LUCKEN (1971, *loc. cit.*) complement this conclusion. Therefore, if *T. speltoides* is the donor of the other genome to *timopheevii*, the genomic constitution of *T. timopheevii* must be AASS.

In the *timopheevii* x *durum* crosses, the chromosome pairing was in excess of the seven bivalents per cell expected. This increase can be considered to be principally due to translocations.

The results of the crosses involving *T. zhukovskyi* and *T. aestivum* are similar to those of UPADHYA and SWAMINATHAN (1965). Further studies are being conducted to clarify pairing relationships of *T. zhukovskyi* genomes with the G, S and B genomes.

ACKNOWLEDGEMENTS

The authors wish to acknowledge the technical assistance of Mr. Percy Sallee and to express thanks to Dr. E. R. Sears for his critical discussion of the work.

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