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Spontaneous translocations in *Triticum araraticum* Jakubz.

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Summary
Spontaneous reciprocal translocations were identified in *Triticum araraticum* Jakubz. by crossing experiments. Seventy-nine strains had the standard chromosome arrangements without translocation. Twenty-one strains were classified into 14 chromosome types based on these translocations but 35 strains remained unidentified. Furthermore, karyotypes were analyzed by C-banding on 17 strains representing all the chromosome types. Of 18 translocations, 12 were between G-genome chromosomes, five were between the G- and A^t-genome and one was between A^t-genome chromosomes. Within the G genome, 4G and 6G had higher frequencies of their involvement in translocations than the others. The present study revealed the wide structural variation of chromosomes and the high frequency of breakpoints on the G genome in *T. araraticum*.

Key words: *Triticum araraticum*, reciprocal translocation, translocation breakpoint, C-banding

Introduction

Triticum araraticum Jakubz. is a wild tetraploid wheat belonging to the Timopheevi group with A^tA^tGG genome (2n=4x=28). It grows in Eastern Turkey, Northern Iraq, Western Iran and in Transcaucasus, Armenia, Azerbaijan and Nachichevan. It differs cytogenetically from another wild tetraploid wheat, *T. dicoccoides* Körn. with AABB genome. Hybrids of the two species can be easily obtained but they are completely male sterile due to abnormal meiosis. *T. araraticum* is highly polymorphic in morphological characters, resistance to disease and DNA amounts (Tanaka and Sakamoto 1979, Saito and Ishida 1979, Nishikawa et al. 1979, 1988). Thus, it has a high potential as a gene resource for breeding of cultivated wheats.

Analysis of chromosome pairing at meiosis of intraspecific hybrids, as well as karyotype analysis by C-banding, showed that chromosomal rearrangements played an important role in the formation of intraspecific diversity of *T. araraticum* (Kawahara and Tanaka 1977, 1983, Badaeva et al. 1990). Badaeva et al. (1994) observed karyotypes of 185 accessions by C-banding and described chromosomal divergence in this species. However, several translocations reported earlier could not be detected by C-banding alone due to an insufficient number of marker bands on the A^t genome chromosomes. To clarify the whole pattern of chromosomal rearrangements we synthesized the data obtained from chromosome pairing and C-banding.

Materials and methods

A total of 135 strains of *T. araraticum*, 47 from Turkey, 67 from Iraq, 4 from Iran and 17 from Armenia were used (for strain No., see Table 1). All the materials were maintained by controlled selfing at the Plant Germplasm Institute, Faculty of Agriculture, Kyoto University. Detailed passport data of the materials are listed in the Catalogue of the Institute (Tanaka 1983). These strains were intercrossed and chromosome pairing patterns of the hybrids were observed at first meiotic metaphase (MI) by the acetic-orcein squash method. Seventeen strains were further analyzed by C-banding; chromosome preparation and C-banding technique were described earlier (Badaeva et al. 1994).

Table 1. Chromosome types due to spontaneous translocations in different strains of *Triticum araraticum* Jakubz.

Chromosome type	Strain No. (KU-)*
T_1	196-2, 1901, 1902, 1903, 1904, 1905, 1906, 1914, 1923, 1924, 1925, 1926A, 1927, 1928, 1929, 1931, 1932, 1933, 1934, 1935, 1936, 1937, 1939, 1960, 1963, 1964, 1965, 1969, 1978A, 8456, 8469, 8478, 8491, 8528A, 8529, 8543, 8551, 8561, 8593, 8597, 8616, 8673, 8697, 8700, 8707, 8709, 8711, 8712, 8718A, 8724, 8731, 8735, 8742, 8761, 8770, 8779, 8797, 8799B, 8802, 8819, 8821B, 8822, 8827, 8831, 8873, 8880, 8882, 8884, 8890, 8907, 8912, 8913, 8924, 8926, 8928, 8933, 8940, 8947, 8948
T_2	196-1
T_3	1907A, 1908A, 1909A, 1909B
T_4	8567, 8572, 8732
T_5	8674
T_6	8714A, 8719
T_7	8824A, 8824B
T_8	8784
T_9	1909C
T_{10}	1911
T_{11}	8460
T_{12}	8715
T_{13}	8725
T_{14}	8866
T_{15}	8713
unidentified	1907B, 1908B, 1938, 1943, 1946, 1950, 1958, 1962, 1966, 1967, 1972A, 1979A, 1980A, 1981A, 1982, 1983, 1985, 1986, 1987, 1988, 1990, 8497, 8500, 8514, 8521, 8544, 8601, 8662, 8668, 8720, 8729, 8733, 8734, 8944, 8945

* Strain no. of the Plant Germ-plasm Institute, Kyoto University.

Results and discussion

Reciprocal translocations in T. araraticum and their geographical distribution.
Based on the analysis of chromosome pairing at first meiotic metaphase of intraspecific hybrids (detailed data not shown), strains were grouped into 15 chromosome types as listed in Table 1. Seventy-nine strains were grouped into T_1 type and meiosis was normal with 14 bivalents in hybrids within this type. This was regarded as standard chromosome structure because the majority (58.5%) of the strains examined belonged to this group. Types T_2 to T_7 differ from T_1 by one translocation, T_8 to T_{14} differ from T_1 by two and T_{15} had three translocations relative to T_1 (Table 2). Thirty-five strains were tentatively classified as unidentified. They have one or two translocations relative to T_1 but the chromosome type was not determined due to the lack of several cross combinations with other chromosome types.

Table 3 summarizes the geographical distribution of each chromosome type. T_1 is found in all the regions where this species was sampled, while the derived types were mostly restricted in a single locality. Types T_2, T_3, T_9 and T_{10} were found in Armenia. The remaining ten types were found in Iraq. Two types, T_4 and T_6, were not restricted to a single site. 8567 and 8572 of T_4 were found in Sulaymaniyah, Iraq, and the third strain, 8732 was collected in Rowanduz, Iraq. The two strains of T_6, 8714A and 8719, were collected at two sites in Rowanduz, Iraq. Apparently, strains with certain structural rearrangements have a wider geographical distribution as also reported by Badaeva et al. (1994). This further suggests that derived types other than T_4. and T_6 also are found in two or more localities if more strains of *T. araraticum* are examined.

Table 2. Multivalents observed among 15 chromosome types of *T. araraticum*

	T_1	T_2	T_3	T_4	T_5	T_6	T_7	T_8	T_9	T_{10}	T_{11}	T_{12}	T_{13}	T_{14}
T_2	IV													
T_3	IV	VI												
T_4	IV	2 IV	2 IV											
T_5	IV	NO[a]	VI	VI										
T_6	IV	2 IV	2 IV	VI	2 IV									
T_7	IV	2 IV	VI	VI	NO	VI								
T_8	VI	IV+VI	VIII	VI	VIII	VIII	IV							
T_9	2 IV	IV+VI	NO	2 IV	VIII	IV+VI	VIII	VI						
T_{10}	2 IV	3 IV	3 IV	IV+VI	IV+VI	3 IV	NO	IV+VIII	2 IV+VI					
T_{11}	2 IV	3 IV	IV+VI	VIII	IV+VI	IV+VI	NO	VI	X	2 IV+VI				
T_{12}	IV	3 IV	3 IV	NO	IV+VI	2 IV	NO	X	IV+VIII	NO	NO			
T_{13}	2 IV	3 IV	3 IV	3 IV	3 IV	3 IV	3 IV	2 IV+VI	4 IV	2 IV+VI	4 IV	2 IV+VI		
T_{14}	2 IV	IV+VI	3 IV	IV+VI	IV+VI	IV+VI	3 IV	IV+VIII	2 IV+VI	2 IV+VI	2 IV+VI	2 VI	2 IV+VI	
T_{15}	IV+VI	2 VI	2IV+VI	X	2 VI	VI +VI	IV+VIII	XII	IV+X	NO	VI+VIII	VIII	2 IV+VIII	VIII

[a] NO indicates not observed.

Table 3. Geographical distribution of chromosome types in *T. araraticum*

Country /Region	No. of strains	Chromosome type														
		T_1	T_2	T_3	T_4	T_5	T_6	T_7	T_8	T_9	T_{10}	T_{11}	T_{12}	T_{13}	T_{14}	T_{15}	unidentified
Armenia	17	8	1	4	0	0	0	0	0	1	1	0	0	0	0	0	2
Turkey																	
Hozat	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Silvan	20	19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Mardin-Midyat	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Maras-Gaziantep	24	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	18
Iraq																	
Amadiyah	14	11	0	0	0	0	0	2	0	0	0	0	0	0	1	0	0
Rowanduz	22	11	0	0	1	0	2	0	1	0	0	0	1	1	0	1	4
Koi Sanjaq	6	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sulaymaniyah	25	13	0	0	2	1	0	0	0	0	0	1	0	0	0	0	8
Iran	4	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Total	135	79	1	4	3	1	2	2	1	1	1	1	1	1	1	1	35

Identification of chromosomes involved in translocations.
Chromosomes involved in each translocation were estimated from the occurrence of multivalents among 15 translocation types. Chromosomes involved in the translocation between T_1 and T_2 were numbered as 1 and 2. Chromosomes of other translocations were numbered successively based on the presence or absence of common chromosomes involved in translocations as summarized in Table 4. For example, T_2 and T_3 have one translocation relative to T_1, and forms a sexivalent in hybrids between them (Table 2). Thus translocations of these two types share a pair of chromosomes in common. This shared pair of chromosomes was arbitrarily assumed as 1 and the translocation of T_3 assigned as 1 and 3. In some cases, two or more translocations occurred independently on the same chromosome pair. T_4 have 4-5 translocation and T_8 have two translocations, 3-4 and 4-5. If these two types share a common 4-5 translocation, a quadrivalent will be observed at MI in the hybrid T_4 x T_8. However, since a sexivalent was found we concluded that the 4-5 translocation carried by the two types had a different origin.

Table 4. Chromosome classification of translocations in *T. araraticum*

Chromosome type	Origin	No. of translocations	Chromosome classification[a]	
			pairing data	pairing and banding data
T_1	Iran, Iraq Turkey, Armenia	0	Standard type	Standard type
T_2	Armenia	1	1-2	1G-5G (1GS:5GL+5GS:1GL)[b]
T_3	Armenia	1	1-3	1G-2G (1GS:2GL+2GS:1GL)
T_4	Iraq	1	4-5a	4G-6Ga (4GS:6GL+6GS:4GL)
T_5	Iraq	1	1-5	1G-4G (1GS:4GL+4GS:1GL)
T_6	Iraq	1	4-6a	6G-7Ga (6GS:7GL+7GS:6GL)
T_7	Iraq	1	3-4	2G-6G (2GS:6GL+6GS:2GL)
T_8	Iraq	2	3-4.4-5b	2G-6G. 4G-6Gb (2GS:6GL+4GS:6GS+2GL:4GL)
T_9	Armenia	2	1-3, 4-5b	1G-2G, 4G-6Gb (1GS:2GL+2GS:1GL, 4GS:6GS+4GL:6GL)
T_{10}	Armenia	2	5-8, 9-10	$2A^t$-4G, A^t_1-3G ($2A^tS$:4GS+$2A^tL$:4GL, -)
T_{11}	Iraq	2	3-4, 5-11	A^t_2-4G, 2G-6G (- , 2GS:6GL+6GS:2GL)
T_{12}	Iraq	2	4-6b, 5-x (x=8 or 9)	3G-4G, 6G-7Gb (3GS:4GS+3GL:4GL, -)
T_{13}	Iraq	2	7-x, 12-13	A^t_3-A^t_4, $5A^t$-3G (- , 3GS:$5A^tL$+$5A^tS$:3GL)
T_{14}	Iraq	2	2-5, 6-7	$5A^t$-7G, 4G-5Ga ($5A^tS$:7GS+$5A^tL$:7GL, 5GL-4GS:4GL)
T_{15}	Iraq	3	2-5, 4-6b.4-x	3G-6G.6G-7Gb, 4G-5Gb (3GS:6GS+3GL:6GL, - , 4GS:5GS+4GL:5GL)

a Correspondence of chromosomes are as follows; 1=1G 2=5G 3=2G, 4=6G, 5=4G, 6=7G, 7=$5A^t$, 8=$2A^t$, 9=x=3G, 10=A^t_1, 11=A^t_2, 12=A^t_3 and 13=A^t_4.
b Structures of the translocation are indicated in parentheses. Dash indicates arm combination could not be detected by banding.

Karyotypes of 17 strains representing 15 chromosome types were further analyzed by C-banding. Chromosomes were identified according to the genetic nomenclature (Badaeva et al. 1991, Gill et al. 1991). By combining two types of data, pairing and banding, it was possible to identify chromosomes involved in these translocations completely (Table 4). However, only two chromosomes, $2A^t$ and $5A^t$, were identified genetically in the A genome because others lacked marker bands. Then, the remaining four A^t chromosomes were tentatively numbered from A^t_1 to A^t_4.

Pattern of chromosomal rearrangements in T. araraticum.
Since the chromosomes involved in spontaneous translocations have all been identified, we can determine the patterns of chromosomal rearrangements in *T. araraticum.* Eighteen different translocations were identified from the chromosome pairing of intraspecific hybrids and C-banding. Therefore these translocations are assumed to represent a random sample of entire structural rearrangements. The 4G chromosome was included in 8 translocations, 6G in 6 followed by 3G (4), 1G, 5G and 7G (3). 2G and $5A^t$ were involved in two different translocations and $2A^t$, A^t_1, A^t_2, A^t_3 and A^t_4 in one translocation, respectively. Differences in the number of breakpoints on each chromosome would reflect structural variability of respective chromosomes. Apparently, chromosomes of the G genome are more frequently included in translocations (29 breakpoints), while the A^t-genome chromosomes are included in 7 translocations. The present findings confirm those reported earlier (Badaeva et al. 1994) demonstrating the difference in variability among chromosomes and between the two genomes, A^t and G. Thus the G-genome chromosomes are three to four times more variable than the A^t-genome chromosomes. This may be caused by the higher amount of heterochromatin which increases the probability of chromosome breaks and consequently the frequencies of chromosomal aberrations as was suggested by Badaeva et al. (1994).

Furthermore, such a high variability of the G-genome chromosome has great implications in the evolutionary process of this species. Two second genomes of tetraploid wheats, B and G, are assumed to have originated from some species of the section Sitopsis of genus *Aegilops,* most likely from *Ae. speltoides* (Sarker and Stebbins 1956, Shands and Kimber 1973, Tanaka et al. 1978, Tsunewaki 1989, Dvorak and Zhang 1990). In the initial stage of tetraploid formation, raw amphidiploid AASS would have formed various progenies with a wide range of chromosomal rearrangements, in which rearrangements including the S genome chromosomes occurred more frequently. From this wide array of recombinants, better adapted types would be selected. The degree of chromosomal rearrangements was so high in S genome that we could not detect high homoeology between the S and G genomes. Stable A-genome chromosomes would serve as a genetic buffer in this chromosome repattering stage and we can easily detect high homoeology between the A genome of diploid wheat and A^t genome. During this process of chromosome repatterning, species-specific translocations of $6A^t$-lG-4G (Jiang and Gill 1994) would have been fixed. Thus the G genome chromosomes played a major role in the polyploid formation and adaptation process in T. *araraticum.*

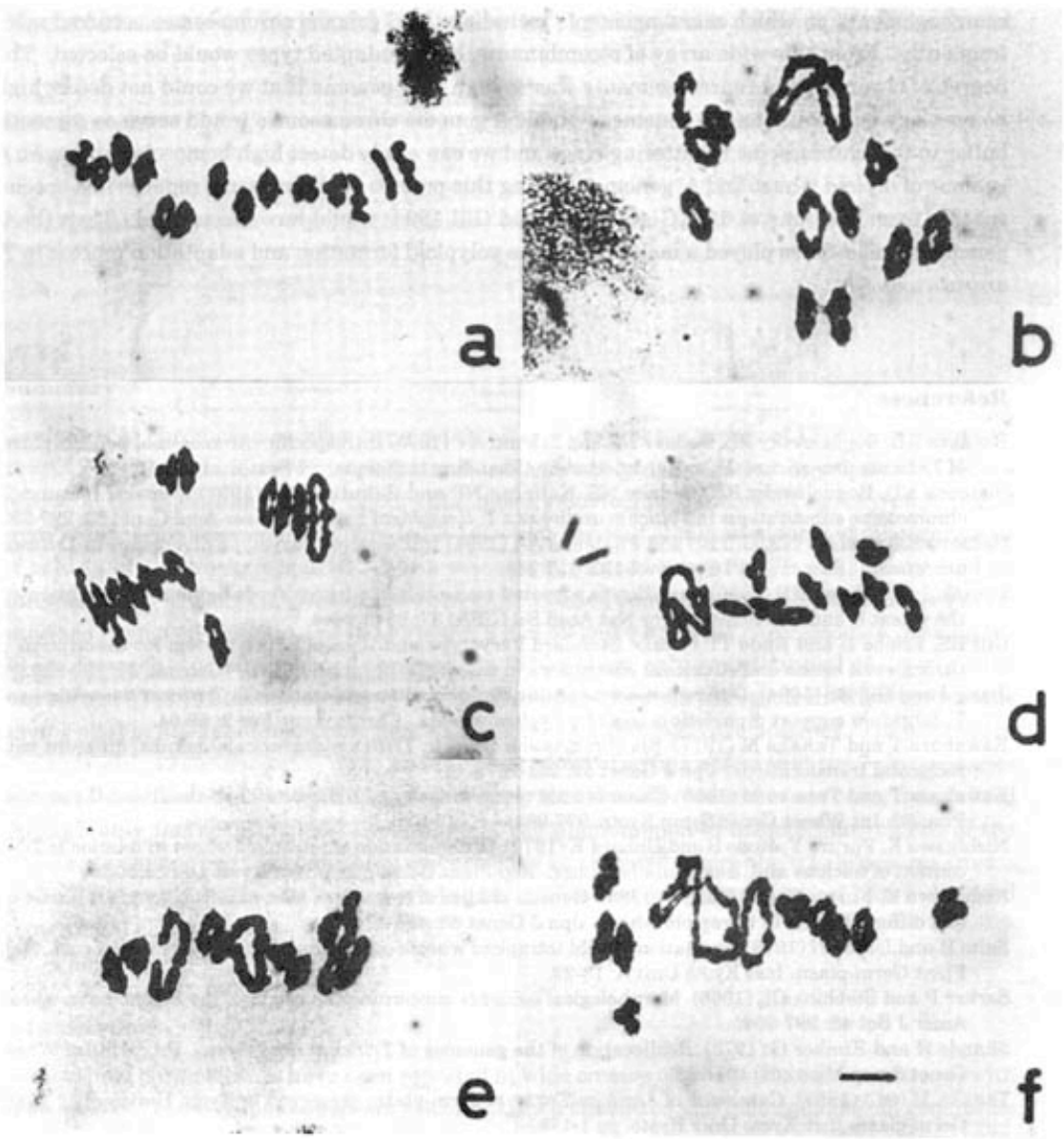

Fig. 1. Chromosome pairing at MI in hybrids among chromosome types in *T. ararticum* (bar=10μm), a: 14II in 8731 x 107-1(*T. timopheevi*) (T_1 x T_1), b:11II + 1VI in 8824A x 8719(T_7 x T_8), c: 10II + 2 IV in 8572 x 196-1 (T_4 x T_2), d: 10 II + 1 VIII in 1908A x 8784 (T_3 x T_8), e: 7 II + 2 IV + 1 VI in 8866 x 8725 (T_{14} x T_{13}), f: 9 II + 1 X in 8732 x 8713 (T_4 x T_{15})

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