SIX CHROMOSOME TYPES IN *TRITICUM ARARATICUM* JAKUBZ. DIFFERING WITH RECIPROCAL TRANSLOCATIONS¹⁾

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Tetraploid wheats are divided into the Emmer and the Timopheevi group based on their morphological and cytogenetical characteristics. *Triticum araraticum* is a wild species belonging to the Timopheevi group and is distributed in the Transcaucasus, the southern U.S.S.R., and in the eastern part of the Fertile Crescent; which comprises southeastern Turkey, Northern Iraq and Western Iran.

The chromosome structures of species in the Emmer group are relatively homogeneous and their hybrids usually form 14 bivalents at metaphase I. However, *T. araraticum* is known to have various degree of structural differentiation in chromosome involving several interchanges (Svetozarova 1939; Wagenaar 1966; Tanaka and Ichikawa 1968, 1972).

Recently, Tanaka and Ishii (1975) analyzed interchanges in *T. timopheevi* Zhuk., a cultivated species in the Timopheevi group, and in *T. araraticum* from the Transcaucasus and reported three chromosome types differing with reciprocal translocations.

The present study deals with chromosomal interchanges in *T. araraticum* from southeastern Turkey and Northern Iraq and reports cytogenetical relationships among the strains of *T. araraticum* and *T. timopheevi*.

MATERIALS AND METHODS

The following eight strains of *T. araraticum* were used:

Strain No.	Collection Site
8714A	19.1 km W from Shaqlawa to Arbil, SW slope of Pirman Dag, Iraq (alt. 880 m).
8718A and 8719	17.9 km W from Shaqlawa to Arbil, NE slope of Pirman Dag, Iraq (alt. 880 m).
8732	7.1 km NE from Shaqlawa to Rowanduz, Iraq (alt. 680 m).
8784	4.8 km NNE from Shaqlawa to Rowanduz, Iraq.
8797	Shaqlawa, Iraq.
8827	15.3 km ENE from Dohuk to Amadiyah, Iraq (alt. 780 m).
8940	39.9 km N from Elazig to Hozat, Turkey (alt. 1,000 m).

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All were collected by the Botanical Expedition of Kyoto University to the Northern Highlands of Mesopotamia in 1970. Three strains, *timopheevi* 107-1 and *araraticum* 196-1 and 1908A from the Transcaucasus, were used as testers. The cytogenetical behavior of these tester strains was described by Tanaka and Ichikawa (1972) and by Tanaka and Ishii (1975).

For cytological observations, young anthers were fixed in Farmer's solution and the aceto-carmine squash method was used. Seed fertility was calculated from seed setting on three bagged spikes.

RESULTS

The chromosome pairings and seed fertilities of the F_1 hybrids between eight strains of *T. araraticum* and three tester strains, 107-1, 196-1 and 1908A, are shown in Table 1.

Meiosis was normal in hybrids between three of the *araraticum* strains, 8718A, 8827 and 8940, and *timopheevi* 107-1. In spite of the good chromosome pairings at MI, their seed fertilities were not constant, ranging from almost sterile (2.5%) or semi-fertile (24.6%) to fully fertile (83.0%). One hybrid, 8797 $\times$ 107-1, showed almost normal meiosis. Eighty two per cent of the PMCs formed 14 bivalents at MI. A tetravalent was observed in 80 per cent of the PMCs of hybrid 8940 $\times$ 196-1. But cells with a trivalent and a tetravalent or with two tetravalents were observed occasionally. The F_1 hybrid between 8714A and 196-1 showed a high frequency of tetravalent formation at MI; 30 per cent of the cells produced three tetravalents per cell and 42 per cent formed two per cell. The average number of tetravalents in this hybrid was 2.02 per cell. In hybrid 8732 $\times$ 1908A, 2_{IV}+10_{II} were observed in 77 per cent of the PMCs which

Table 1. Chromosome pairings and seed fertilities of F_1 hybrids between eight strains of *T. araraticum* and three tester strains; 107-1, 196-1 and 1908A

Cross combination	No. of PMCs observed	Chromosome pairings					Seed fertility (%)
		I	II	III	IV	V-VI	
8714A $\times$ 196-1*	50	0.24	9.66	0.12	2.02	—	27.8
8718A $\times$ 107-1*	50	—	14.00	—	—	—	24.6
8719 $\times$ 107-1*	50	0.08	12.24	—	0.86	—	31.8
8732 $\times$ 107-1*	50	—	12.04	—	0.98	—	8.4
8732 $\times$ 1908A	56	0.09	10.32	0.09	1.75	—	44.7
8784 $\times$ 107-1	50	0.04	11.42	0.76	0.26	0.30 _{VI}	4.7
8784 $\times$ 196-1*	50	0.32	10.48	0.34	0.50	0.02 _V 0.60 _{VI}	30.0
8797 $\times$ 107-1	38	0.18	13.66	0.03	0.11	—	—
8827 $\times$ 107-1*	50	—	14.00	—	—	—	2.5
8940 $\times$ 107-1	57	0.04	13.98	—	—	—	83.0
8940 $\times$ 196-1*	50	0.42	11.80	0.26	0.80	—	—

* Average chromosome pairing was calculated from unpublished raw data obtained by Tanaka and Ishii (1973).

Table 2. Chromosome pairings and seed fertilities of F₁ hybrids of eight strains of *T. araraticum*

Cross combination	No. of PMCs observed	Chromosome pairings					Seed fertility (%)
		I	II	III	IV	V-X	
8714A × 8827	38	0.05	12.08	—	0.95	—	40.1
8714A × 8784	24	—	10.63	0.08	0.21	0.38 _{VI} 0.38 _{VIII} 0.04 _X	54.2
8718A × 8714A	23	—	12.00	—	1.00	—	76.9
8719 × 8714A	50	—	14.00	—	—	—	82.9
8719 × 8784	38	0.11	11.08	0.11	0.16	0.45 _{VI} 0.26 _{VIII}	54.6
8719 × 8940	29	0.14	12.24	0.07	0.79	—	—
8732 × 8714A	40	—	11.05	0.05	0.05	0.93 _{VI}	35.0
8784 × 8718A	50	—	11.04	—	0.08	0.96 _{VI}	40.9
8784 × 8732	50	0.04	10.98	0.04	—	0.98 _{VI}	27.4
8784 × 8827	50	0.04	11.06	—	0.08	0.92 _{VI}	39.7
8797 × 8784	43	—	11.72	—	0.42	0.44 _{VI} 0.02 _X	43.7

showed a high frequency of tetravalent formation. Hybrids 8784×107-1 and 8784×196-1 formed a hexavalent at MI. In the former combination, 30 per cent of the cells had a hexavalent per cell, 36 per cent formed two trivalents and 26 per cent produced a tetravalent. Since it is apparent that higher associations tend to break down into smaller configurations, it is possible that two trivalents or a tetravalent could arise from the breakdown of a hexavalent. In 8784×196-1, the most common chromosome configuration was 1_{VI}+11_{II} (34%), next was 1_{VI}+1_{IV}+9_{II} (16%), then 1_{IV}+12_{II} (10%). A tetravalent and two trivalents or a tetravalent and a trivalent were observed in a few cells. It is also likely that a hexavalent and a tetravalent were formed initially in the cells, but that these could only be maintained under favorable cellular circumstances.

The chromosome pairings and seed fertilities of the F₁ hybrids of eight strains of *T. araraticum* are shown in Table 2.

Of eleven hybrid combinations, only 8719×8714A showed normal meiosis with 14 bivalents and it was fully fertile. Three hybrids, 8714A×8827, 8718A×8714A and 8719×8940, involving 8714A or 8719 showed almost identical meiotic behavior forming a tetravalent per cell. The three parents, 8718A, 8827 and 8940, involved in these three combinations produced 14 bivalents at MI in the hybrids with *timopheevi* 107-1. Of the 24 PMCs observed in hybrid 8714A×8784, nine cells were 1_{VIII}+10_{II} and nine other cells were 1_{VI}+11_{II}. Moreover, an association of ten chromosomes was observed in a cell. In hybrid 8719×8784, of the 38 cells examined, 16 were 1_{IV}+11_{II} and ten cells were 1_{VIII}+10_{II}. Hexavalent formation (one per cell) was observed in almost all the PMCs of the following four hybrids; 8732×8714A, 8784×8718A, 8784×8732 and 8784×8827. In a hybrid of 8784 with 8797, which formed a tetravalent in several of its PMCs when crossed with 107-1, cells having a hexavalent or a tetravalent were common (67%). A few cells with both a hexavalent and a tetravalent and one cell with an association of ten chromosomes were also observed.

DISCUSSION

Tanaka and Ishii (1975) examined chromosomal interchanges among Transcaucasian *T. timopheevi* and *T. araraticum* and found three chromosome types with regard to reciprocal translocation. In the present study, these chromosome types are designated as the A, B and C types. Using this terminology, the *T. araraticum* 196-1, *T. timopheevi* 107-1 and the *T. araraticum* 1908A in the present study can be called A, B and C type testers, respectively.

The present data indicate no major chromosome differentiation between the four *araraticum* strains, 8718A, 8797, 8827 and 8940, and *timopheevi* 107-1. These strains may be regarded to belong to the B type though some minor structural differentiation in the chromosomes of 8797 is suggested from a few polyvalent formations in 8797 × 107-1 (Table 1).

The chromosome structures of the remaining four strains of *T. araraticum* collected from Northern Iraq are rather complicated. Strains 8714A and 8719 showed normal meiosis with 14 bivalents when they were intercrossed, indicating close similarities in their chromosomal structures. This was also confirmed by the meiotic behavior of their hybrids with 8784. A comparison of the chromosome pairings of these two hybrids suggests some minor structural differentiation in the chromosomes of strain 8714A due to the presence of an association of ten chromosomes. Both 8714A and 8719 form a tetravalent per cell at MI in hybrids with B type strains (Tables 1 and 2). A hybrid of 8714A with A type (196-1) produced two or three tetravalents (Table 1). Thus, 8714A and 8719 have chromosome structures which differ from the A, B and C types and therefore were designated the D type. One interchange exists between the B and D types. According to Tanaka and Ishii (1975), one interchange was observed between the A and B types, therefore two interchanges are expected between the A and D types. The formation of three tetravalents in hybrid 8714A × 196-1 is perhaps due to minor structural differentiation in the chromosomes of 8714A as mentioned above.

A similar analysis was made of the chromosome structures of strains 8732 and 8784. Since strain 8732 formed a tetravalent per cell in a hybrid with 107-1 of the B type and two tetravalents in a hybrid with 1908A of the C type (Table 1), its chromosome type was named the E type. It produced a hexavalent at MI in a hybrid with 8714A of the D type (Table 2). Strain 8784, which had a hexavalent at MI when crossed with a B type tester, was named the F type. It also produced a hexavalent in a hybrid with the E type (Table 2). An octavalent was observed in the PMCs of hybrids between the D and F types. As above, one interchange was observed between the A and B types and two interchanges involving one common pair of chromosome was observed between the B and F types. If these interchanges are located on different pairs of chromosome, a tetravalent and a hexavalent should occur in the PMCs of a hybrid A × F type. The meiotic behavior of hybrid 8784 × 196-1 seems to support this as shown in Table 1. Expected polyvalent formations among six chromosome types found in the present study are shown in Fig. 1. Strain numbers belonging to each types are summarized in Table 3.

Fig. 1. Expected polyvalent formations among six chromosome types in the Timopheevi group of tetraploid wheats. Data obtained by Tanaka and Ishii (1975) were included.

Table 3. Six chromosome types found in strains of *T. araraticum**

Type	Strain No.
A	196-1
B	196-2, 1901, 1902, 1903, 1904, 1905, 1906, 8718A, 8797, 8827, 8940
C	1908A
D	8714A, 8719
E	8732
F	8784

* Including data obtained by Tanaka and Ishii (1975).

Wagenaar (1966) suggested that chromosome differentiation in the Timopheevi wheats is restricted to the northern regions of the distribution area (the Transcaucasus and northeastern tip of Turkey). Similarly, Ishii (unpublished) considered that the translocations found in several strains of *T. araraticum* occurred secondarily in the Transcaucasus. But the present data show that chromosome differentiation in *T. araraticum* is also abundant in the center of its distribution area. Strains of *T. araraticum* of types B, D, E and F were all collected from Shaqlawa and its adjacent area in Northern Iraq. Type B (8718A) and type D (8719) were found to occur sympatrically

on the slope of Pirman Dag, Iraq. Two samples from the northern tip of Iraq (Amadiyah) and Turkey (Hozat) were of B type. Though the number of strains examined is rather small at present, it is evident that chromosome differentiation in *T. araraticum* is not limited to the Transcaucasus. It is also found on the slopes of the Zagros mountains where wild tetraploid wheats form a massive stand (Tanaka and Ishii 1973). There is the possibility of discovering more than the six different chromosome types presented in this study, if wider collections of *T. araraticum* from various areas of its distribution are examined.

In contrast, no chromosome differentiation has been reported in *T. timopheevi*. In the Transcaucasus where this tetraploid is endemic, most *araraticum* and all the *timopheevi* strains have chromosome of the B type. This provides evidence to support the widely accepted theory that cultivated *T. timopheevi* was produced from the wild *T. araraticum* in the Transcaucasus. It seems probable that wild plants having chromosomes of the B type, which is the most prevalent type in this region, might have been brought into cultivation. This is further confirmed by the present finding of an *araraticum* strain that produces fertile hybrids when crossed with *T. timopheevi*.

For a long time, *T. araraticum* has been thought to give sterile (Svetozarova 1939; Sachs 1953; Wagenaar 1966) or at best semi-fertile hybrids (Tanaka and Ichikawa 1968, 1972; Tanaka and Ishii 1975), when crossed with *T. timopheevi*. However, in the present study, a hybrid between a strain of *T. araraticum* (8940) collected from south-eastern Turkey and *T. timopheevi* 107-1 was fully fertile. This clearly indicates that reproductive barriers between the two species of the Timopheevi group are incomplete. The wide range of seed fertility seen in hybrids between the B type *araraticum* and *timopheevi* 107-1 may be partly due to the difference in cryptic structural hybridity in the chromosomes as suggested by Sachs (1953). In 13 hybrids of *T. araraticum*, a high correlation was observed between the number of bivalents and seed fertility ($r=0.784$). A reduction in seed fertility in hybrids of the *araraticum* strains seems to be caused largely by meiotic irregularities such as polyvalent formations.

SUMMARY

The chromosome structures of eight strains of *T. araraticum* collected in south-eastern Turkey and Northern Iraq were analyzed by hybridization with three chromosome type tester strains; the A type of *araraticum* 196-1, the B type of *timopheevi* 107-1 and the C type of *araraticum* 1908A. Concurrently, the chromosome pairings of hybrids of eight *araraticum* strains were observed.

Results of the present experiment clearly show that of the eight strains studied, four were the B type. The remaining four strains were classified into three chromosome types different from the A, B and C types. These were designated the D, E and F types. A tetravalent was formed in the PMCs of hybrids between the B and D types and between the B and E types. A hexavalent was observed in hybrids between the D and E types, between the E and F types and between the B and F types. Two tetravalents were recognized in hybrids between the A and D types and between

the C and E types. A hybrid between the D and F types showed an octavalent formation at meiosis. Both a tetravalent and a hexavalent were observed in a hybrid between the A and F types.

Reduced seed fertility in hybrids of the strains of *T. araraticum* seems to be caused by meiotic irregularities such as polyvalent formations. The seed fertilities of hybrids between the B type strains of *T. araraticum* and *T. timopheevi* varied from almost sterile to fully fertile. An *araraticum* strain collected near Hozat, Turkey, was found to be fully fertile when crossed with *T. timopheevi*. This provides evidence for the theory that *T. araraticum* is the ancestral species of cultivated *T. timopheevi*.

This study has clearly shown that chromosome differentiation in *T. araraticum* is more abundant in Northern Iraq than in Transcaucasus. This would indicate that the Timopheevi group of tetraploid wheats first originated in the eastern part of the Fertile Crescent and that later its distribution area was extended northward to the Transcaucasus.

LITERATURE CITED

- Sachs, L., 1953 Chromosome behaviour in hybrids with *Triticum timopheevi*. *Heredity* 7: 49-58.
- Svetozarova, V. V., 1939 Second genome of *Triticum timopheevi* Zhuk. *Comp. Rend Acad. Sci., U.S.S.R.* 23: 473-477.
- Tanaka, M., and S. Ichikawa, 1968 Cytogenetic examinations of *Triticum araraticum* Jakubz., a wild-type tetraploid wheat species. *Genetics* 60: 229.
- Tanaka, M., and S. Ichikawa, 1972 Cytogenetical relationships of two types of *Triticum araraticum* Jakubz. to other tetraploid wheat species. *Japan. J. Genetics* 47: 103-114.
- Tanaka, M., and H. Ishii, 1973 Cytogenetical evidence on the speciation of wild tetraploid wheats collected in Iraq, Turkey and Iran. *Proc. 4th Intern. Wheat Genetics Symp.* 115-121.
- Tanaka, M., and H. Ishii, 1975 Hybrid sterility and chromosomal interchanges found in the Timopheevi group of tetraploid wheat. *Japan. J. Genetics* 50: 141-149.
- Wagenaar, E. B., 1966 Studies on the genome constitution of *Triticum timopheevi* Zhuk., II. The timopheevi complex and its origin. *Evolution* 20: 150-164.