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The origin and the differentiation of the B and G genomes of the tetraploid wheats.[1)]

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The tetraploid wheats are divided into the Emmer and the Timopheevi group based on their morphological and cytogenetical characteristics. The genomic constitution of the Emmer group is AABB but that of the Timopheevi group is AAGG (Lilienfeld and Kihara, 1934). It is the widely accepted theory that A genome parent of both groups of the tetraploid wheats is *Triticum boeoticum* Boiss. (AA). Regarding to the other genomes (B and G), a number of workers suggested *Aegilops speltoides* Tausch. (SS) as the donor of the B genome to the Emmer (Jenkins, 1929; Pathak, 1940; Sarker and Stebbins, 1956; Riley *et al.*, 1958), though there was not decisive evidences that the S genome is homologous to the B genome. On the other hand, some workers suggested that *Ae. speltoides* is the donor of the G genome to *T. timopheevi* Zhuk. (Shands and Kimber, 1973). Also, Tanaka and Ishii (1973) suggested that both groups have undergone a tremendous degree of chromosomal as well as morphological differentiation during the speciation process, probably from a single ancestor.

The present paper describes the detailed study on the origin and evolution of the tetraploid wheats.

Examination of cytogenetical relationships between the Emmer and the Timopheevi group.

The two wild tetraploid wheats, *T. dicoccoides* Körn. and *T. araraticum* Jakubz. are generally accepted as the ancestral species of the Emmer and the Timopheevi group of the tetraploid wheats, respectively. Using several samples of *T. dicoccoides* and *T. araraticum* from a mixed stand near Amadiyah, Iraq, Tanaka and Kawahara (1976) and Tanaka *et al.* (1978) observed chromosome pairings in interspecific F_1 hybrids. They found that almost all the chromosomes of the two species can pair with each other at meiosis. To examine cytogenetical relationships of these samples to other strains of the tetraploid wheats, several experiments were carried out.

Materials used in the present study were 11 strains of *T. dicoccoides*, 11 of *T. araraticum* and one of *T. timopheevi* (Table 1). They include two *dicoccoides* and four *araraticum* strains from Amadiyah. Reciprocal translocation chromosome type of each of two *araraticum* strains, 8718A and 8827, and one *timopheevi* strain, 107–1, was already reported by Kawahara and Tanaka (1977). The type of 10 *dicoccoides* strains except for 8821C was also detected by Kawahara and Tanaka (1978). For cytological observations, aceto-carmine squash method was used.

Table 2 shows chromosome pairings in hybrids of nine *dicoccoides* strains including 8821A and 8821C. These two strains showed high chromosome pairings in hybrids with *araraticum* strains from the same locality (Tanaka and Kawahara, 1976). When 8821A and 8821C were crossed to 107–1 of *T. timopheevi*, their hybrids also showed high chromosome pairings. In a

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Table 1. Strains of the tetraploid wheats used in the present study

Stock No. (KU-)[1]	Species[2]	Locality or source
107–1	t	Zhukovsky (1931)
108–3	d	20 km NW of Sueida (Cheikh Meakine-Sueida), Syria (BMUK)[3]
108–5	d	Collection of Mac Key
8539	d	NE slope of Shakh i Baranan, Iraq (BEM)[4]
8541	d	// //
8718A	a	17.9 km W from Shaqlawa to Arbil, NE slope of Pirman Dagh, Iraq (alt. 880 m) (BEM)
8736B	d	SSW of Rowanduz, Iraq (BEM)
8804	d	North slope of Jabal Sinjar, South of Kursi, Iraq (BEM)
8816B	d	// //
8819	a	15.3 km ENE from Dohuk to Amadiyah, Iraq (alt. 780 m) (BEM)
8821A	d	// //
8821B	a	// //
8821C	d	// //
8822	a	// //
8827	a	// //
8873	a	4.4 km NW from Amadiyah, Mazorka Gorge, Iraq (alt. 1120 m) (BEM)
8882	a	13.4 km W from Amadiyah to Bamarni, Iraq (alt. 940 m) (BEM)
8912	a	26.3 km NE from Mardin to Midyat, Turkey (alt. 960 m) (BEM)
8924	a	17.3 km E from Silvan to Bitlis, Turkey (alt. 660 m) (BEM)
8928	a	// //
8937B	d	9.3 km SE from Ergani to Diyarbakir, Turkey (alt. 780 m) (BEM)
8941	d	58.8 km N from Kermanshah to Ravansar, Iran (alt. 1610 m) (BEM)
8948	a	15.1 km NW from Karand to Quasri Shirin, Iran (alt. 1540 m) (BEM)

1) Stock No. of the Plant Germ-plasm Institute, Faculty of Agriculture, Kyoto University.
2) d=*T. dicoccoides* a=*T. araraticum* t=*T. timopheevi.*
3) the Botanical Mission of the University of Kyoto, 1959.
4) the Botanical Expedition of Kyoto University to the Northern Highlands of Mesopotamia, 1970.

hybrid 8821A×107–1, the most common chromosome configuration was $1_I+12_{II}+1_{III}$ (24%) and 24 per cent of the PMCs formed no univalents. Higher pairings were observed in a hybrid 8821C×107–1, in which $11_{II}+2_{III}$ were most frequent (24%) and 32 per cent of the cells had no univalents. The average univalent chromosome number of hybrids 8821A×107–1 and 8821C ×107–1 were 1.86 and 1.56, respectively. Comparing to these two, the other seven *dicoccoides* strains gave more univalents at meiosis in hybrids with 107–1. The average number of univalents in these seven hybrids ranged from 4.20 to 8.77. All hybrids of *T. dicoccoides* with *timopheevi* 107–1 set no seeds when bagged.

The average chromosome pairings in F_1 hybrids between eight strains of *T. araraticum* and *dicoccoides* 108–5 from Palestine are shown in Table 3. Similar to the hybrids *dicoccoides* ×*timopheevi* 107–1 mentioned above, degree of chromosome pairing in crosses *araraticum*× *dicoccoides* 108–5 varied from hybrid to hybrid. These eight hybrids showed variation in univalent chromosome number from 3.38 to 8.02. But number of the bivalents varied little; 8.64–9.73. Among these eight hybrids, smaller amount of univalents at meiosis was observed

Table 2. Chromosome pairings of F_1 hybrids between 9 *dicoccoides* strains and tester strains; *timopheevi* 107–1 and *dicoccoides* 108–3

Cross combination	No. of cells observed	Chromosome pairing*				
		I	II	III	IV	V
8599 ×107–1	50	6.34 (1–11)	9.40 (7–12)	0.90 (0–2)	0.04 (0–1)	—
8541 ×107–1	50	4.66 (1–11)	10.08 (6–13)	1.06 (0–3)	—	—
8736B ×107–1	50	4.20 (1–9)	10.18 (7–13)	0.98 (0–2)	0.10 (0–2)	0.02 (0–1)
8804 ×107–1	50	5.42 (1–9)	9.88 (7–13)	0.88 (0–2)	0.02 (0–1)	0.02 (0–1)
8816B ×107–1	50	5.28 (1–11)	9.56 (7–12)	1.04 (0–2)	0.12 (0–1)	—
8821A ×107–1	50	1.86 (0–5)	10.84 (8–12)	1.18 (0–2)	0.18 (0–1)	0.04 (0–1)
8821C ×107–1	50	1.56 (0–6)	11.36 (7–14)	1.04 (0–3)	0.10 (0–1)	0.04 (0–1)
8937B ×107–1	26	8.77 (4–14)	9.15 (6–11)	0.31 (0–2)	—	—
8941 ×107–1	50	7.22 (3–14)	9.28 (6–12)	0.74 (0–2)	—	—
8821C ×108–3**	50	0.02	13.76	0.02	0.10	—

* Values indicate means and ranges (in parentheses).
** Average chromosome pairing was calculated from unpublished raw data obtained by Tanaka and Ishii (1973).

in hybrids with 8924 (4.14_I) and 8928 (3.38_I). These two strains were collected from the same locality in Turkey (Table 1). The three *araraticum* strains from Amadiyah did not show high pairing in hybrids with 108–5 as compaired to those with *dicoccoides* strains from the same locality.

To examine reciprocal translocation chromosome type of each *araraticum* strains used, 11 *araraticum* strains and one tester strain, *timopheevi* 107–1, were intercrossed. Table 4 shows the average chromosome pairings of the F_1 hybrids. Almost all the PMCs of 12 F_1 hbyrids showed normal meiosis with 14 bivalents. But a cell with a tetravelent was observed in the following two hybrids, 8827×8928 and 8882×107–1. These data indicate the absence of major structural differentiation in chromosomes among the strains of the Timopheevi wheats used in the present study.

The data presented in this section clearly show that the amount of chromosome pairing in the hybrids between the Emmer and the Timopheevi wheats is affected by the genetic factors contained in both species. As is shown in Table 2, variation in genetic system affecting the degree of chromosome pairing is observed in *T. dicoccoides*. Also, *T. araraticum* might have factor(s) that control pairing (Table 3). The present observation suggests that the genetic system in *T. dicoccoides* is the major factor that is responsible for the high pairing in hybrids *dicoccoides*×*timopheevi* (Table 2) and *dicoccoides*×*araraticum* (Tanaka and Kawahara, 1976). A number of workers have observed intraspecific variation of genetic systems influencing the degree of chromosome pairing in interspecific hybrids. Dover and Riley (1972) reported four classes of

Table 3. Chromosome pairings of F_1 hybrids between *T. araraticum* and *T. dicoccoides* 108-5

Cross combination	No. of cells observed	Chromosome pairing			
		I	II	III	IV
8819 ×108-5	50	5.88 (1-12)	9.16 (6-12)	1.16 (0-3)	0.08 (0-1)
8821B ×108-5	50	7.06 (1-11)	8.94 (5-12)	0.90 (0-3)	0.12 (0-1)
8827 ×108-5	50	5.48 (1-10)	9.08 (6-12)	1.24 (0-3)	0.16 (0-1)
8873 ×108-5	50	7.88 (3-14)	8.78 (5-11)	0.80 (0-3)	0.04 (0-1)
8882 ×108-5	50	6.62 (1-14)	8.90 (7-12)	1.06 (0-3)	0.10 (0-1)
8912 ×108-5	50	8.02 (3-14)	8.64 (5-11)	0.82 (0-2)	0.06 (0-1)
8924 ×108-5	50	4.14 (0-10)	9.54 (7-12)	1.46 (0-4)	0.10 (0-1)
8928 ×108-5	37	3.38 (0-8)	9.73 (7-13)	1.32 (0-4)	0.30 (0-1)

pairing in hybrids of *Ae. mutica* Boiss. Dvorak (1972) and Kimber and Athwal (1972) recognized three classes in *Ae. speltoides*. Variations were also observed among several cultivars of *T. aestivum* L. (Driscoll and Quinn, 1970). Wagenaar (1961) reported great variation of chromosome pairing in hybrids of many samples of the Emmer wheats with *T. timopheevi*. He observed continuous variation in the average number of univalents ranging from 2.97 to 12.06 per cell.

Table 4. Chromosome pairings of F_1 hybrids among strains of the Timopheevi wheats

Cross combination	No. of cells observed	Chromosome pairing			
		I	II	III	IV
8819 ×8827	39	—	14.00	—	—
8821B × 107-1	30	0.20	13.90	—	—
8821B ×8948	50	—	14.00	—	—
8822 ×8827	33	—	14.00	—	—
8827 ×8928	50	0.08	13.92	—	0.02
8873 × 107-1*	50	—	14.00	—	—
8882 × 107-1*	50	0.40	13.76	—	0.02
8912 × 107-1*	50	0.08	13.96	—	—
8924 ×8912	50	0.28	13.86	—	—
8928 × 107-1	50	—	14.00	—	—
8948 × 107-1*	50	—	14.00	—	—
8948 ×8718A	37	—	14.00	—	—

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

Further, it may be suggested from the present data that the factor(s) affecting pairing in the hybrids of the tetraploid wheats is genic. For, differences in chromosome pairing were not due to the differences in the structure of chromosomes of each strains used. All the *dicoccoides* strains employed in the crosses with *timopheevi* 107–1 have "wild" type chromosome structure of *T. dicoccoides* (Table 2, Kawahara and Tanaka, 1978) Similary, eight *araraticum* strains crossed to *dicoccoides* 108–5 have chromosomes of the B type of the Timopheevi wheats (Table 4, Kawahara and Tanaka, 1977). This type was shown to be "wild" among the Timopheevi group (Tanaka *et al.*, 1978). Genes affecting pairing carried by the tetraploid wheats are possibly of similar nature to various genes reported in *T. aestivum* L. cultivar Chinese Spring (for the review, see Sears, 1976).

These observations would indicate abundant genetic variation of each species in Southeastern Turkey, Northern Iraq and Western Iran.

Backcross experiments in hybrids between *T. dicoccoides* and *T. araraticum*.

In this section, results of backcross experiments are presented to show close proximity in genetic constitution between the Emmer and the Timopheevi group of the tetraploid wheats.

Strains used were 8821B (*T. araraticum*) and 8821C (*T. dicoccoides*) from Amadiyah, Iraq (Table 1). These two strains were crossed to each other and the reciprocal F_1 plants were pollinated by *dicoccoides* 8821C. In total, seven B_1 plants were obtained. A hybrid 8821C × 8821B produced five backcross progenies; three plants with 28 chromosomes, one with 27 and one with 29. Of these, one plant with 29 chromosomes was self-fertile. While, a hybrid 8821B × 8821C gave two progenies; both with 2n=28 chromosomes and one plant set seeds. Chromo-

Table 5. Chromosome pairing and fertility in F_1 and B_1 hybrids between *T. araraticum* 8821B and *T. dicoccoides* 8821C*

Cross combination	Chromosome number	No. of cells observed	Chromosome pairing					Fertility (%)	
			I	II	III	IV	V	pollen	seed
8821C × 8821B	28	41	2.46 (0-7)	10.37 (8-12)	1.27 (0-4)	0.22 (0-2)	0.02 (0-1)	1.4	—
F_1 × 8821C	28	50	2.18 (0-7)	11.02 (9-13)	1.26 (0-0)	—	—	40.8	0.0
〃	28	33	1.21 (0-4)	10.64 (8-14)	1.64 (0-2)	0.15 (0-1)	—	27.0	0.0
〃	28	33	1.06 (1-3)	11.97 (11-12)	1.00 (1)	—	—	32.2	0.0
〃	29	50	1.96 (0-5)	10.94 (9-14)	1.64 (0-3)	0.06 (0-1)	—	35.0	1.1
〃	27	50	1.36 (1-3)	12.82 (12-13)	—	—	—	—	—
8821B × 8821C	28	35	2.37 (0-7)	10.91 (8-13)	1.11 (0-2)	0.11 (0-1)	—	5.9	—
F_1 × 8821C	28	35	2.14 (0-5)	10.49 (8-13)	0.60 (0-2)	0.77 (0-2)	—	56.6	2.2
〃	28	33	1.27 (0-2)	13.36 (13-14)	—	—	—	82.3	0.0

* Including data obtained by Tanaka *et al.* (1978).

some pairings and fertilities of F_1 and B_1 hybrids are summarized in Table 5. All B_1 plants showed normal vigor except for that with 27 chromosomes, which was a dwarf plant with only a few tillers.

The present data clearly show that the seed setting in B_1 plants does not necessarily require high chromosome pairing at meiosis. The fertile B_1 plant in nucleus restoration line had a chromosome in excess ($2n=29$) and the most common chromosome configuration was $1_I+11_{II}+2_{III}$ (36%). Two plants were obtained in substitution line. One showed good pairing; of 33 PMCs examined, 12 were 14_{II} and 21 were 2_I+13_{II}. In spite of high pollen fertility (82.3%), this plant did not produce any seed on the three bagged spikes. The other formed polyvalents and more univalents at meiosis but was fertile.

The occurrence of fertile B_1 plants strongly suggests high compensation ability between the B and G genomes.

The artificial amphidiploid SSAA from the hybrid between *Ae. speltoides* and *T. boeoticum*.

In 1966, the senior author has obtained the amphidiploid SSAA from the cross between *Ae. speltoides* and *T. boeoticum*. The average chromosome pairing and seed fertility of the SSAA with 28 chromosomes at F_4, F_8 and F_{12} generations are summarized in Table 6. As shown in this table, the chromosome pairing of the amphidiploid SSAA was very low at the F_4 and F_8 generations with a large number of univalents indicating cytogenetically unstable. The PMCs with 14 bivalents could not entirely be found. However, at the F_{12} generation after synthesis, rather high chromosome pairing was observed. It formed more polyvalents but less univalents than the earlier generations. This shows the possibility of occurrence of some chromosomal and/or genic changes in this unstable amphidiploid at the recent generations.

The F_1 hybrids of synthesized SSAA at earlier generations crossed with the Emmer or the Timopheevi wheats were highly sterile (Tanaka unpublished). In 1976, crosses between SSAA at the F_{11} generation and *T. dicoccum* Schübl. or *T. araraticum* were made and two F_1 hybrid combinations were examined cytologically (Table 7). These hybrids showed rather high chromosome pairings with a few univalents. Furthermore, one hybrid plant produced two viable seeds though seed fertility of the bagged spikes was very low (0.21%). Two F_2 hybrid plants obtained were also examined cytologically (Table 7). Among them, one plant with 28 chromosomes showed higher chromosome pairing than F_1 plants and seed fertility of the bagged spikes increased to some extent.

From these observations, the occurrence of genetic changes that were tending toward higher chromosome pairings in hybrids of the Emmer wheats is supposed during the progression of generations in the synthesized SSAA. All F_1 plants set no seeds in the hybrid between SSAA (F_{11}) and *T. araraticum*. However, the similar occurrence of the genetic constitution which will be closer to the Timopheevi wheats might be expected during the advance of generations in the synthesized SSAA.

Distribution of the wild tetraploid wheats.

The distribution area of the wild tetraploid wheats, *T. dicoccoides* and *T. araraticum*, is divided into three geographical regions: Palestine and Southern Syria; Southeastern Turkey,

Table 6. Chromosome pairings and seed fertilities of the amphidiploid SSAA having 28 chromosomes

Generation (year)	No. of plants examined	Chromosome pairings							Seed fertility (%)
		I	II	III	IV	V-VIII			
F_4 (1969)	3	10.01	8.64	0.20	0.03		—		8.5
F_8 (1973)	4	13.98	6.58	0.18	0.08		—		7.8
F_{12} (1977)	1	4.58 (0–13)	8.88 (3–13)	0.67 (0–4)	1.04 (0–4)	0.05_{VI} (0–3)	0.02_{VII} (0–1)	0.02_{VIII} (0–1)	11.7

Table 7. Chromosome pairings and seed fertilities of the F_1 and F_2 hybrids SSAA × *T. dicoccum* and SSAA × *T. araraticum*

Cross combination (Chromosome No.)	No. of cells observed	Chromosome pairing						Seed fertility (%)
		I	II	III	IV	V	VI	
SSAA (F_{11}) × *T. dicoccum*	60	4.44 (1–10)	6.64 (3–12)	1.60 (0–4)	1.27 (0–4)	0.08 (0–2)	—	0.21
F_2 (2n=28)	50	2.98 (0–7)	6.96 (4–10)	1.14 (0–3)	1.60 (0–5)	0.16 (0–1)	0.08 (0–1)	4.1
F_2 (2n=30)	20	2.95 (0–5)	8.15 (5–13)	1.30 (0–3)	1.20 (0–4)	0.35 (0–2)	0.05 (0–1)	0.0
SSAA (F_{11}) × *T. araraticum*	30	2.30 (0–5)	7.03 (3–10)	1.87 (0–4)	1.23 (0–3)	0.10 (0–1)	0.10 (0–1)	0.0

Northern Iraq and Wastern Iran (the Zagros Mountains) and the Transcaucasus. The wild tetraploid wheats collected from Palestine and Southern Syria are exclusively of the Emmer group; *T. dicoccoides*. While those from the Transcaucasus are *T. araraticum*. Both wild species are found in the Zagros Mountains.

In 1970, the Botanical Expedition of Kyoto University to the Northern Highlands of Mesopotamia (BEM) collected a great many samples of wild tetraploid wheats. Using these samples, cytogenetical studies on the speciation of the wild tetraploids were carried out (Tanaka and Ishii, 1973). They found that the wild tetraploid wheats in this area consisted of two species (Fig. 1). *T. araraticum* was distributed widely and abundantly at 31 localities in nine regions but *T. dicoccoides* was found sporadically at a single locality in each of seven different regions. Both species were found sympatrically at four localities, Sulaymaniyah, Rowanduz and Amadiyah in Iraq and Silvan in Turkey. At three localities, Sinjar in Iraq, Ergani in Turkey and Ravansir in Iran, only the Emmer type was found. Further, they observed that the wild tetraploid wheats occured almost always intermixed with its putative progenitors, *T. boeoticum* and *Ae. speltoides*. These two wild diploid species were distributed widely and abundantly in the Zagros Mountains.

Recently, the Kyoto University Scientific Exploration to the Eastern Turkey (KUET, 1976) found a massive stand of the wild tetraploids near Maras, Turkey (Tanaka, 1978). At this locality, both species of the wild tetraploid wheats grew and *T. dicoccoides* were also as abundant as *T. araraticum*.

Thus, distribution of the two wild tetraploid wheats clearly overlaps in Southeastern Turkey, Northern Iraq and Western Iran, the distribution center of the wild tetraploid species.

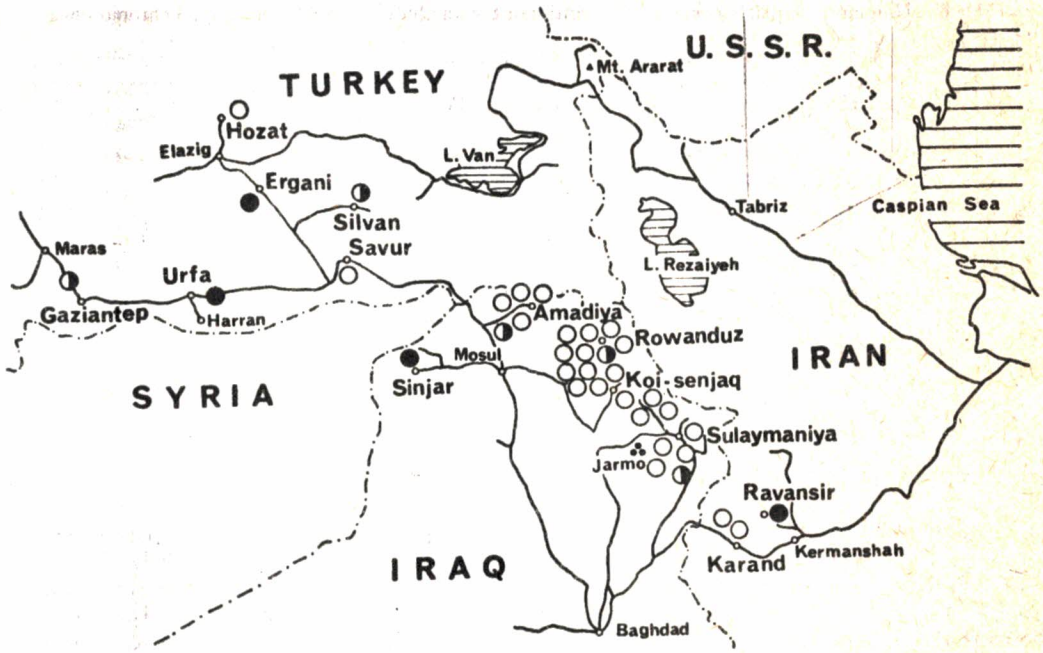

Fig. 1. Distribution of the Emmer and Timopheevi types of the BEM and the KUET collections.
●=Emmer, ○=Timopheevi, ◑=Mixed

Morphological and physiological observations.

Morphological differences between Palestinian *dicoccoides* and Transcaucasian ***araraticum*** are clearly recognized in several characteristics; shape of upper margin of empty glume, ear size etc. On the contrary, among the samples from the Zagros Mountains, little morphological differences were observed between the two species but wide and continuous variation was found in each species. However, the leaf surface of *T. dicoccoides* was exclusively glabrous, while that of *T. araraticum* was pubescent (Tanaka and Ishii, 1973). Accordingly, glabrous vs. pubescent in leaf hariness is the specific feature between *T. dicoccoides* and *T. araraticum* (Tanaka and Sakamoto, 1979). Using the samples collected from four mixed stands of *T. dicoccoides* and *T. araraticum*, Tanaka and Sakamoto (1979) found independent pattern in the frequency of variations between the two species. From these observations, they concluded that there is not a possibility of introgressive hybridization between the two species in the present time.

As demonstrated by Tanaka and Sakamoto (1979) and by Saito and Ishida (1979), almost all the morphological and physiological variations in the wild tetraploid wheats, especially in *T. araraticum*, concentrate in the Sulaymaniyah, Rowanduz and Amadiyah regions. These regions are the center of diversity of the wild tetraploid wheats.

The origin and the differentiation of the B and G genomes of the tetraploid wheats.

After the donation of AAGG genome to *T. timopheevi* (Lilienfeld and Kihara, 1934), some workers paid attention to the partial homology between the B and the G genome (Kostoff, 1937). But in the presence of the pairing control gene, high chromosome pairing does not necessarily

mean the homology between the two genomes. As is shown in the previous section, hybrids between the Emmer and the Timopheevi group are highly sterile even when chromosome pairings are extremely good. This strong genetic isolation mechanism must be properly evaluated. However, it seems also true that the B and G genomes are more closely related to each other than any other genome of a diploid species of the genus *Triticum* and *Aegilpos*. It may be confirmed by the present finding of fertile B_1 plants from the cross between *T. dicoccoides* and *T. araraticum*. Morphological resemblance between the two wild tetraploid wheats would also support this (Dagan and Zohary, 1970; Tanaka and Ishii, 1973). Synaptic evidence is also available. As observed by Feldman (1966), the chromosomes of the B genome of *T. aestivum* cv. Chinese Spring pair to some extent with corresponding chromosomes of *T. timopheevi* under the genetical background of a hybrid *T. aestivum* × *T. timopheevi-Ae. squarrosa* amphidiploid. In this hybrid, chromosome pairing seems to show the homology of the two genomes because of many factors supressing homoeologous pairing (Sears, 1976). Thus, it seems unnecessary to postulate that the two second genomes (B and G) of the tetraploid wheats were originated from different progenitors.

The general acceptance of *Ae. speltoides* as the B genome donor was based on several kinds of evidences: Morphological evidences provided by Sarker and Stebbins (1956), karyotypic and geographical evidence gathered by Riley *et al.* (1958) and evidence from the amount of nuclear DNA given by Rees (1963). On the other hand, cytoplasmic evidence was shown to suggest *Ae. speltoides* as the G genome donor to the Timopheevi group (Maan, 1973; Suemoto, 1973). From the observation of two isoenzymes, Jaaska (1974) considered *T. boeoticum* and *Ae. speltoides* as the most probable genome donors of the tetraploid wheats. In accepting *Ae. speltoides* as the ancestral species that contributed the second genome of the tetraploid wheats, one of the obstacles has been the sterility in hybrids of *Ae. speltoides-T. boeoticum* amphidiploid with the Emmer or the Timopheevi wheats. However, the data presented in this paper clearly show that the amphidiploid SSAA has ability to produce fertile hybrids with, at least, the Emmer wheats. Riley *et al.* (1958) concluded that the amphidiploid *T. monococcum-Ae. speltoides* was relatively true breeding in spite of low fertility. But the present data points the possibility of the occurence of genetical rearrangements during the advance of generations in synthesized SSAA.

Many workers have observed the differentiation in chromosome structure at the tetraploid level. Some species and strains in the Emmer wheats differ from the other by one or two translocations (Nishikawa, 1962). Three types in chromosome structure are known in wild *T. dicoccoides* (Kawahara and Tanaka, 1978). Tanaka *et al.* (1978) reported seven translocation chromosome types in the Timopheevi wheats. Also, Riley et al. (1967) found several reciprocal translocations among the varieties of *T. aestivum*. This shows that rearrangements in chromosome structure has occured at the hexaploid level even in the presence of strong diplodising mechanisms.

Therefore it is highly probable that the differentiation in chromosome structure occured in the raw amphidiploid SSAA and that the Emmer and the Timopheevi wheats were derived from this common ancestor.

General Conclusion

Since 1972, it was our conviction that the structural differentiation of chromosomes must have played an important role in the evolutionary courses of the tetraploid wheats, which originated from probably a single ancestor (Tanaka and Ichikawa, 1972).

As the results of our cytological, morphological, physiological and geographical investigations, we could add strong evidences supporting this theory. From the data presented in this paper, it was concluded that the origin and the differentiation of the Emmer and the Timopheevi group of the tetraploid wheats underwent the following process:

1) Tetraploid wheat derived from an amphidiploid (SSAA) between *Aegilops speltoides* and *Triticum boeoticum*.

2) Disruptive differentiation occured in natural amphidiploid SSAA in the Zagros Mountains gave rise to the two wild tetraploid species, *T. araraticum* belonging to the Timopheevi group and *T. dicoccoides* belonging to the Emmer group (Fig. 2).

Aegilops speltoides (SS)
Triticum boeoticum (AA)
→ SSAA →
T. araraticum (AAGG)
T. dicoccoides (AABB)

Fig. 2. A representation of evolutionary pathways of the tetraploid wheats.

Literature Cited

Dagan, J. and D. Zohary, 1970 Wild tetraploid wheat from West Iran cytogenetically identical with Israeli *T. dicoccoides*. Wheat Inform. Serv. **31**: 15–17.

Dover, G. A. and R. Riley, 1973 Prevention of pairing of homoeologous meiotic chromosomes by an activity of supernumerary chromosomes of *Aegilops*. Nature **240**: 159–161.

Driscoll, C. J. and C. J. Quinn, 1970 Genetic variation in *Triticum* affecting the level of chromosome pairing in intergeneric hybrids. Can. J. Genet. Cytol. **12**: 278–282.

Dvorak, J., 1972 Genetic variation in *Aegilops speltoides* affecting homeologous pairing in wheat. Can. J. Genet. Cytol. **14**: 371–380.

Feldman, M., 1966 Identification of unpaired chromosomes in F_1 hybrids involving *Triticum aestivum* and *T. timopheevi*. Can. J. Genet. Cytol. **8**: 144–151.

Jaaska, V., 1974 The origin of tetraploid wheats on the basis of electropholetic studies of enzymes. Esti NSV TA Toimetised, Bioloogia **23**: 201–220.

Jenkins, J. A., 1929 Chromosome homologies in wheat and *Aegilops*. Amer. J. Bot. **16**: 238–245.

Kawahara, T. and M. Tanaka, 1977 Six chromosome types in *Triticum araraticum* Jakubz. differing with reciprocal translocations. Japan. J. Genet. **52**: 261–267.

Kawahara, T. and M. Tanaka, 1978 Identification of reciprocal translocation chromosome types in the emmer wheats, I. *Triticum dicoccoides* Körn. Wheat Inform. Serv. **45**: 29–31.

Kimber, G. and R. S. Athwal, 1972 A reassessment of the course of evolution of wheat. Proc. Nat. Acad. Sci. U.S.A. **69**: 912–915.

Kostoff, D., 1937 Chromosome behaviour in *Triticum* hybrids and allied genera. I. Interspecific hybrids with *Triticum timopheevi*. Proc. Indian Acad. Sci. **5**: 23–36.

Lilienfeld, F. and H. Kihara, 1934 Genomanalyse bei *Triticum* und *Aegilops*. V. *Triticum timopheevi* Zhuk. Cytologia **6**: 87–122.

Maan, S. S., 1973 Cytoplasmic and cytogenetic relationships among tetraploid *Triticum* species. Euphytica **22**: 287–300.

Nishikawa, K., 1962 Reciprocal translocation in Emmer wheat. Mational Insti. Genet. Japan, Annual Report **13**: 50–51.

Pathak, G. N., 1940 Studies on the cytology of cereals. J. Genet. **39**: 437–467.

Rees, H., 1963 Deoxyribonucleic acid and the ancestry of wheat. Nature **198**: 108–109.
Riley, R., J. Unrau and V. Chapamn, 1958 Evidence on the origin of the B genome of wheat. J. Hered **49**: 90–98.
Riley, R., H. Coucoli and V. Chapman, 1967 Chromosomal interchanges and the phylogeny of wheat. Heredity **22**: 283–247.
Saito, H. and N. Ishida, 1979 Speciation of wild tetraploid wheats concerning susceptibility to leaf rust. (in press)
Sarker, P. and G. L. Stebbins, 1956 Morphological evidence concerning the origin of the B-genome in wheat. Amer. J. Bot. **43**: 297–304.
Sears, E. R., 1976 Genetic control of chromosome pairing in wheat. Ann. Rev. Genet. **10**: 31–51.
Shands, H. and G. Kimber, 1973 Reallocation of the genomes of *Triticum timopheevi* Zhuk. Proc. 4th. Intern. Wheat Genetic Symp.: 101–108.
Sumeoto, H., 1973 The origin of the cytoplasm of tetraploid wheat. Proc. 4th Intern. Wheat Genetics Symp.: 109–113.
Tanaka, M. 1978 A preliminary report of the Kyoto University Scientific Exploration to the Eastern Turkey, 1976. Peport of Plant Germ-plasm Inst. Kyoto Univ. No. 3
Tanaka, M. and S. Ichikawa, 1972 Cytogenetical relationships of two types of *Triticum araraticum* Jakubz. to other tetraploid wheat species. Japan. J. Genet. **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 T. Kawahara, 1976 Wild tetraploid wheats from Northern Iraq cytogenetically closely related to each other. Wheat Inform. Serv. **43**: 3–4.
Tanaka, M., T. Kawahara and J. Sano, 1978 The evolution of wild tetraploid wheats. Proc. 5th Intern. Wheat Genet. Symp. (in press)
Tanaka, M. and S. Sakamoto, 1979 Morphological and physiological studies in wild tetraploid wheats collecced from the Zagros Mountains. (in press)
Wagenaar, E. B., 1961 Studies on the genome constitution of *Triticum timopheevi* Zhuk. I. Evidence for genetic control of meiotic irregularities in tetraploid hybrids. Can. J. Genet. Cytol. **3**: 47–60.