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CYTOGENETICAL EVIDENCE ON THE SPECIATION OF WILD TETRAPLOID WHEATS COLLECTED IN IRAQ, TURKEY, AND IRAN[1]

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SUMMARY

A great many samples of wild tetraploid wheats were collected from 38 localities of Northern Iraq, Southeastern Turkey, and Western Iran by our recent botanical expedition (BEM). From their morphological characteristics and collection sites they were divided into 489 strains. Among them, 95 strains covering almost all localities were crossed with testers of the Emmer group and the Timopheevi group, and the F_1 hybrids were examined cytogenetically. Sixteen strains fell into an Emmer group and 79 into a distinctly different Timopheevi group.

Mixed stands of these two types were found in four localities in Iraq and Turkey, while three localities in Iraq, Turkey, and Iran were purely of the Emmer type.

Morphological differences between the Emmer type and the Timopheevi type were not clear; however, the leaf surface of the former was exclusively glabrous, while that of the latter was pubescent.

It was concluded that structural differentiation of the chromosomes must have played an important role in the speciation of the wild tetraploid wheats, which probably originated from a single ancestor.

INTRODUCTION

The phylogenetic relationships between the Emmer group and the Timopheevi group of tetraploid wheats have been studied by many workers from various viewpoints.

The distribution area of the wild tetraploid wheats is divided into three geographical regions: Palestine and Southern Syria; Southeastern Turkey, Northern Iraq, and Western Iran (or the eastern part of the Fertile Crescent); and Transcaucasus. It is well known that the wild tetraploid wheats collected from Palestine and Transcaucasus are exclusively of the Emmer group and the Timopheevi group, respectively; namely, *Triticum dicoccoides* Körn. and *T. araraticum* Jakubz. On the other hand, both wild species have been found in Northern Iraq (WAGENAAR, 1966), in Southeastern Turkey (RAO and SMITH, 1968), and

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in Western Iran (DAGAN and ZOHARY, 1970). However, only a few limited materials collected from those regions have been used so far. It is necessary, therefore, to examine more materials for the complete understanding of the variation and speciation of the wild tetraploid wheats in those areas.

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 those samples, cytogenetical studies on the speciation of the wild tetraploids were carried out. The present report comprises the results obtained from the F_1 hybrids between the BEM collections and tester strains of the Emmer group and the Timopheevi group.

MATERIALS AND METHODS

From 38 localities in Northern Iraq, Southeastern Turkey, and Western Iran the samples collected of wild tetraploid wheats were divided into 489 strains based on their morphological characteristics and collection sites. Ninety-five strains, selected randomly from 34 localities, were crossed with the following four tester strains: two Emmer testers, *T. dicoccoides* Körn. var. *kotschyanum* Schulz, strain nos. 108-3 and 108-5, both collected from Palestine; and two Timopheevi testers, a strain of *T. timopheevi* Zhuk. var. *typicum* Zhuk., 107-1, from Georgia, and a strain of *T. araraticum* Jakubz. var. *thumaniani* Jakubz., 196-1, from Armenia. The 95 strains of the BEM collections used in this experiment came from 11 regions, five in Iraq, four in Turkey, and two in Iran, as shown in Table 1.

Table 1. Number of crossed strains from 11 regions of Northern Iraq, Southeastern Turkey and Western Iran

Regions	No. of localities	No. of strains crossed with: 1 Emmer & 1 Timoph. tester	Both Emmer testers	Both Timoph. testers
IRAQ				
Sulaymaniya	8	12	15	1
Koi-Senjaq	3	6	3	-
Rowanduz	10	15	9	2
Amadiya	5	5	6	1
Sinjar	1	2	2	-
TURKEY				
Savur	1	1	1	-
Silvan	1	1	2	1
Ergani	1	1	-	-
Hozat	1	2	-	1
IRAN				
Karand	2	2	1	-
Ravansir	1	1	2	-
Total	34	48	41	6

For cytological observations the anthers were fixed in Farmer's solution (3 ethanol : 1 acetic acid) and stored in a refrigerator. Chromosome pairing was

observed at MI of PMCs using the aceto-carmine squash technique. The amount of chromosome association in the F_1 hybrid was expressed in two ways: (1) the average number of chromosomes associated--*i.e.*, 28 less the average number of univalents (Figs. 1 and 2); and (2) the range and average of chromosome pairing (Table 2). Pollen fertility was examined by the aceto-carmine staining method, and seed fertility was determined in the first and second florets of bagged spikes.

RESULTS

Hybrids with the Emmer Testers

The average number of chromosomes associated in 89 F_1 hybrids between 89 strains and the Emmer testers (Fig. 1A and B) showed no definite differences between crosses with 108-3 and 108-5. The F_1 hybrids were divided into two groups, I and II, according to the amount of chromosome association (Table 2). Out of 89 F_1 hybrids,

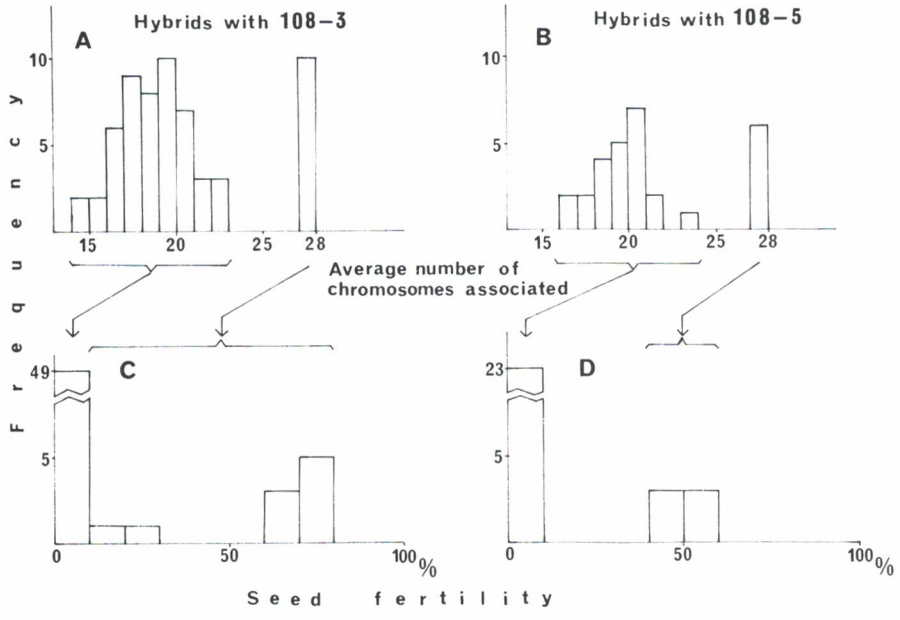

Figure 1. Frequency distributions of chromosome pairing and seed fertility of the F_1 hybrids from crosses with the Emmer testers

16 belonged to group I and had no univalents at MI, while 73 belonged to group II and showed varying numbers of univalents (2 to 13). Almost all hybrids in group I had normal meiosis except for one which showed multivalent formation. On the other hand, the chromosome association of group II was highly irregular, with many univalents and multivalents, and quite variable.

The group-I hybrids were seed-fertile or semi-fertile (Fig. 1C and D), varying widely in spite of the relatively small variations in pollen fertility, which ranged from 73.1 to 94.9 per cent. On the contrary, the group-II hybrids showed complete pollen and seed sterility.

Judging from the chromosome association and fertility of the hybrids with the Emmer testers, the 16 parental strains of the group-I hybrids are considered to belong to the Emmer group, and the 73 strains of the group-II hybrids to the Timopheevi group.

Hybrids with the Timopheevi Testers

From the average number of chromosomes associated in 54 F_1 hybrids between 54 strains of the BEM collections and the Timopheevi testers, 107-1 and 196-1 (Fig. 2A and B), the F_1 hybrids were also

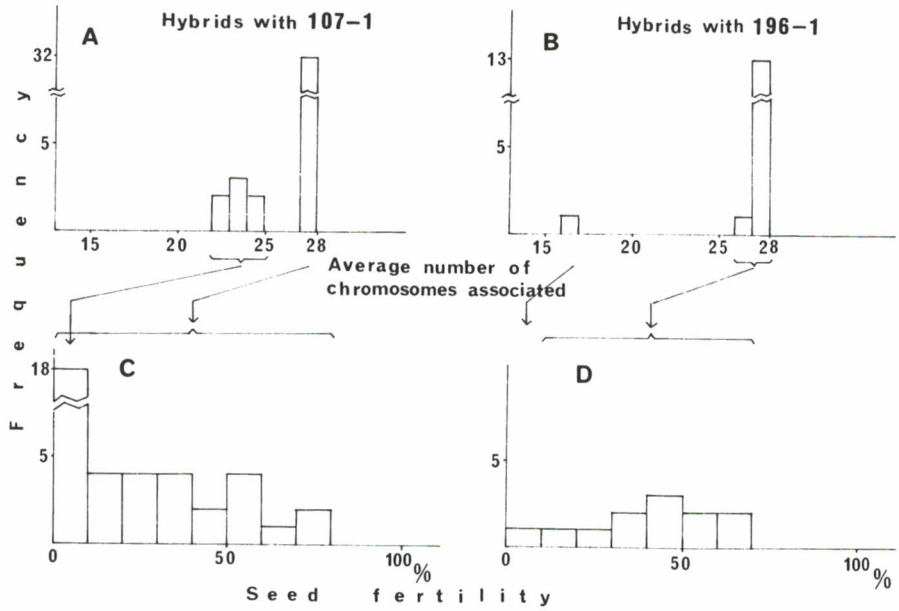

Figure 2. Frequency distributions of the F_1 hybrids with the Timopheevi testers

divided into two groups, III and IV, according to the amount of chromosome association. Among them, 46 F_1 hybrids belonged to group III and had no univalents or almost none, while eight were included in the other group, IV, which had many univalents at MI. Chromosome association in the F_1 hybrids crossed with 107-1 were somewhat different from those with 196-1 (Table 2). Thirty-two F_1 hybrids of group III crossed with 107-1 had a tendency to have a lower frequency of multivalent formation than 14 hybrids of the same group whose tester parent was 196-1. The frequent formation of multivalents at MI of those hybrids suggests that they may be heterozygous for one to three chromosome interchanges.

A variation from completely seed-sterile to almost fertile was observed among the group-III hybrids with the 107-1 tester (Fig. 2C, D), and from semi-sterile to almost fertile among the same group crossed with the 196-1 tester. The latter hybrids had a tendency to show a relatively higher fertility than the former, without regard to the higher frequency of multivalent formation at MI. Judging from these results, the 46 parental strains of the group-III hybrids are

considered cytogenetically to belong to the Timopheevi group, while the 8 strains of the group-IV hybrids should be placed in the Emmer group.

Table 2. Average and range (in parentheses) of chromosome pairing and fertility of the F_1 hybrids between the BEM collections and the testers of the Emmer group and the Timopheevi group

Testers	Hybrid groups	No. of hybrids	Chromosome pairing I	II	III	IV	Fertility pollen	seed
Emmer								
108-3	I	10	0.27 (0.02-0.76)	13.75 (13.52-13.98)	0.02 (0.00-0.04)	0.05 (0.00-0.14)	84.9 (73.1-94.9)	60.6 (16.5-77.9)
	II[1]	50	9.34 (5.06-13.66)	7.61 (4.94-9.56)	0.99 (0.54-1.58)	0.12 (0.00-0.62)	2.0 (0.0-6.1)	0.0 (0.0-0.0)
108-5	I	6	0.08 (0.00-0.16)	13.57 (12.06-14.00)	0.00 (0.00-0.02)	0.19 (0.00-0.94)	82.90 (75.9-92.9)	49.8 (42.1-56.9)
	II[2]	23	8.40 (4.68-11.47)	8.00 (6.88-9.40)	1.04 (0.72-1.38)	0.11 (0.00-0.44)	2.5 (0.0-9.0)	0.0 (0.0-0.0)
Timoph.								
107-1	III	32	0.10 (0.00-0.94)	13.55 (11.08-14.00)	0.01 (0.00-0.14)	0.20 (0.00-1.33)	37.1 (14.7-76.2)	26.9 (0.0-77.3)
	IV[3]	7	4.62 (3.02-5.60)	9.50 (9.10-10.12)	1.19 (0.84-1.62)	0.20 (0.08-0.48)	1.3 (0.0-5.4)	0.0 (0.0-0.0)
196-1	III[4]	14	0.47 (0.16-1.36)	11.52 (9.66-13.04)	0.18 (0.02-0.46)	0.81 (0.22-2.02)	65.1 (37.6-80.4)	44.0 (18.0-65.3)
	IV	1	11.62	6.78	0.86	0.06	0.0	0.0

[1]Rare quinquevalents (0.00-0.06) and sexivalents (0.00-0.02) not listed
[2]0.01V (0.00-0.04) omitted
[3]0.00VI (0.00-0.02) omitted
[4]0.00V (0.00-0.02) and 0.12VI (0.00-0.74) omitted

Considering the chromosome association and fertility of the F_1 hybrids between the BEM collections and the Emmer and Timopheevi testers, it was concluded that of the 95 strains examined

cytogenetically, 16 belong to the Emmer group and 79 to the Timopheevi group. No strains were found which had the same kind of chromosome association (either good or irregular) when hybridized with the Emmer testers as when crossed with the Timopheevi testers.

Morphological differences between the strains of the Emmer type and those of the Timopheevi type were not clear; however, the leaf surface of the former was exclusively glabrous while that of the latter was pubescent.

DISCUSSION

The eastern part of the Fertile Crescent was regarded from older findings to be the most important area which could provide interesting materials with respect to the origin, speciation, and domestication of tetraploid wheats (WAGENAAR, 1966; and others). In the present studies it was clearly shown that the wild tetraploid wheats of the BEM collections consisted of two distinct types: an Emmer type, cytogenetically identical with Palestinian *T. dicoccoides*, and a Timopheevi type, identical with Armenian *T. araraticum* or Georgian *T. timopheevi*. This finding was mainly based on observations of chromosome association and fertility of F_1 hybrids between the present collections and testers of the Emmer- and Timopheevi-groups.

The Emmer type was found sporadically in a single locality in each of seven different regions (Fig. 3), while the Timopheevi type

Figure 3. Distribution of the Emmer and Timopheevi types of the BEM collections
● = Emmer; ▲ = Timopheevi; ◑ = Mixed

was collected at 31 localities of nine regions and was distributed widely. Both types were found sympatrically at four localities, Sulaymaniya, Rowanduz, and Amadiya in Iraq, and Silvan in Turkey.

At three localities, Sinjar in Iraq, Eregani in Turkey, and Ravansir in Iran, only the Emmer type was found.

Massive stands of the Timopheevi type were found frequently in the deciduous oak forests spreading on the foothills of the Zagros Mountains (Fig. 3). This type occurred almost always with its putative progenitors, *Triticum boeoticum* Boiss. and *Aegilops speltoides* Tausch, while the Emmer type was found sporadically, always with *T. boeoticum*, but rather infrequently with *Ae. speltoides*.

Very small variations in univalent formation were observed in the F_1 hybrids between strains of the Emmer type and the Emmer testers as well as the Timopheevi testers (groups I and IV in Table 2). This seems to indicate low structural differentiation among the strains of the Emmer type. On the contrary, the hybrids involving strains of the Timopheevi type showed an extensive variation in univalent as well as multivalent formation (group II and the lower half of group III in Table 2). The data clearly indicate high chromosomal differentiation among the strains of the Timopheevi type in the present collections. This view is also supported by the wide variation of seed fertility observed (18.0-65.3%) among the F_1 hybrids between the Timopheevi type and the 196-1 tester. However, an exceptional case was the F_1 hybrids between the Timopheevi type and *T. timopheevi* 107-1, as shown in the upper half of group III in Table 2. In this case, no extensive variations of chromosome association were observed, in spite of wide variation in the seed fertility (0.0-77.3%) of the hybrids. This might be attributable to the specific but unknown cytological factors found in the *T. timopheevi* strain 107-1, as also observed by TANAKA and ICHIKAWA (1972).

It was concluded that the wild tetraploid wheats distributed widely from Palestine to Armenia through the eastern part of the Fertile Crescent have displayed a tremendous degree of chromosomal as well as morphological differentiation during the speciation process which occurred in this area, probably from a single ancestor which might have grown in the Zagros Mountains, a diversity center of the wild tetraploid wheats.

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