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The cytoplasm of tetraploid wheats[1)]

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Triticum turgidum having einkorn cytoplasm shows complete male sterility, abnormal growth and severe variegation in seedlings, while *T. turgidum* having *Aegilops speltoides* cytoplasm shows moderately high male fertility and normal growth. In addition, *T. timopheevi* having *speltoides* cytoplasm are completely normal in their fertility and growth habit, but that having einkorn cytoplasm shows abnormal growth and male sterility.

It seems like that the cytoplasm of tetraploid wheats have been derived from their second genome ancestor (BB or GG) not but AA ancestor. Furthermore, the cytoplasm of *Ae. speltoides* seems to be more closely related to the cytoplasm of *T. timopheevi* than that of emmer wheats (Suemoto 1968, 1973).

Table 1. Materials used for production of substitution lines

A. Cytoplasm donor

species	Genome symbol	Stock No.[1)]	
Ae. speltoides	S	KU-5725C[2)]	Cytoplasm donor of emmer substitution lines
〃		KU-5725E[2)]	Cytoplasm donor of *timopheevi* substitution lines
S^bS^bAA[3)]			
Ae. longissima	S^l	KU-4-1	
Ae. sharonensis	S^l	KU-5-1	
Ae. caudata	C	KU-6	
Ae. heldreichii	M	KU-18-1	
Ae. comosa	〃	KU-17-1	
T. boeoticum	A	KU-101-1	

B. Genome parents

species	Genome	Stock No.	Code No. in present investigation
T. dicoccoides kotschyanum	AB	KU-108-3	E_1
〃 *spontaneo-nigrum*	〃	KU-109	E_2
T. dicoccum liguliforme	〃	KU-111	E_3
T. durum reichenbachii	〃	KU-125	E_4
T. turgidum nigrobarbatum	〃	KU-147	E_5
T. araraticum	AG	KU-196-1	T_1
T. timopheevi	〃	KU-107-2	T_2

1) Genetic stock No. in Germ-plasm Institute, Fac. of Agriculture, Kyoto University.
2) Collection of Botanical Mission of the University of Kyoto to the Eastern Mediterranean Countries.
3) Induced by Dr. Sears from the cross *Ae. bicornis* (♀) × einkorn (♂).

1) Contributions from the Laboratory of Genetics, Biological Institute, Kyoto University, No. 424.

In the present paper, the responses of emmer and *timopheevi* genomes to the cytoplasms of seven *Aegilops* and one einkorn species are compared.

Materials and Methods

The materials used are shown in Table 1A and B, with their stock number in Kyoto University. The number of backcross generations and average bivalent in substitution lines used are summarized in Table 2.

Cytoplasmic relationships were estimated by the effects of adding an alien cytoplasm to a genome. These effects are expressed in the variegation in seedlings, abnormal delay in maturity, the degree of pollen and selfed seed fertility, and the manner of the changes in pollen fertility accompanied with increase in the number of bivalents (Fig. 2).

Table 2. Number of backcross generations and their average bivalents in substitution lines

Cytoplasm	Genome	Emmer wheats					*Timopheevi* G.	
		E_1	E_2	E_3	E_4	E_5	T_1	T_2
Ae. speltoides	B. C. Gen.	10	10	9	8	13	8	11
	Av. bivalents	13.9^{M}	14.0^{M}	13.9	13.9	14.0	14.0	14.0
Ae. bicornis	B. C. Gen.	7	6	6	7	10	6	6
	Ave. bivalents	14.0	14.0	14.0	14.0	14.0	14.0	14.0
Ae. longissima	B. C. Gen.	6	6	2	5	11	4	3
	Ave. bivalents	14.0	14.0	14.0^{M}	13.9	14.0	14.0	13.6^{M}
Ae. sharonensis	B. C. Gen.	6	4	4	3	11		5
	Ave. bivalents	13.9	13.9	14.0	13.9	14.0		14.0
Ae. caudata	B. C. Gen.		4	2	3	3		
	Ave. bivalents		14.0	13.8	—	—		
Ae. heldreichii	B. C. Gen.	3	6	5	6	7		
	Ave. bivalents	14.0	14.0	14.0	14.0	14.0		
Ae. comosa	B. C. Gen.	3	3	5	2	7		1
	Ave. bivalents	14.0	14.0	14.0	14.0	13.8		9.0
T. boeoticum	B. C. Gen.	3	9	3		12		5
	Ave. bivalents	14.0	14.0	14.0		14.0		14.0

M: multivalent.

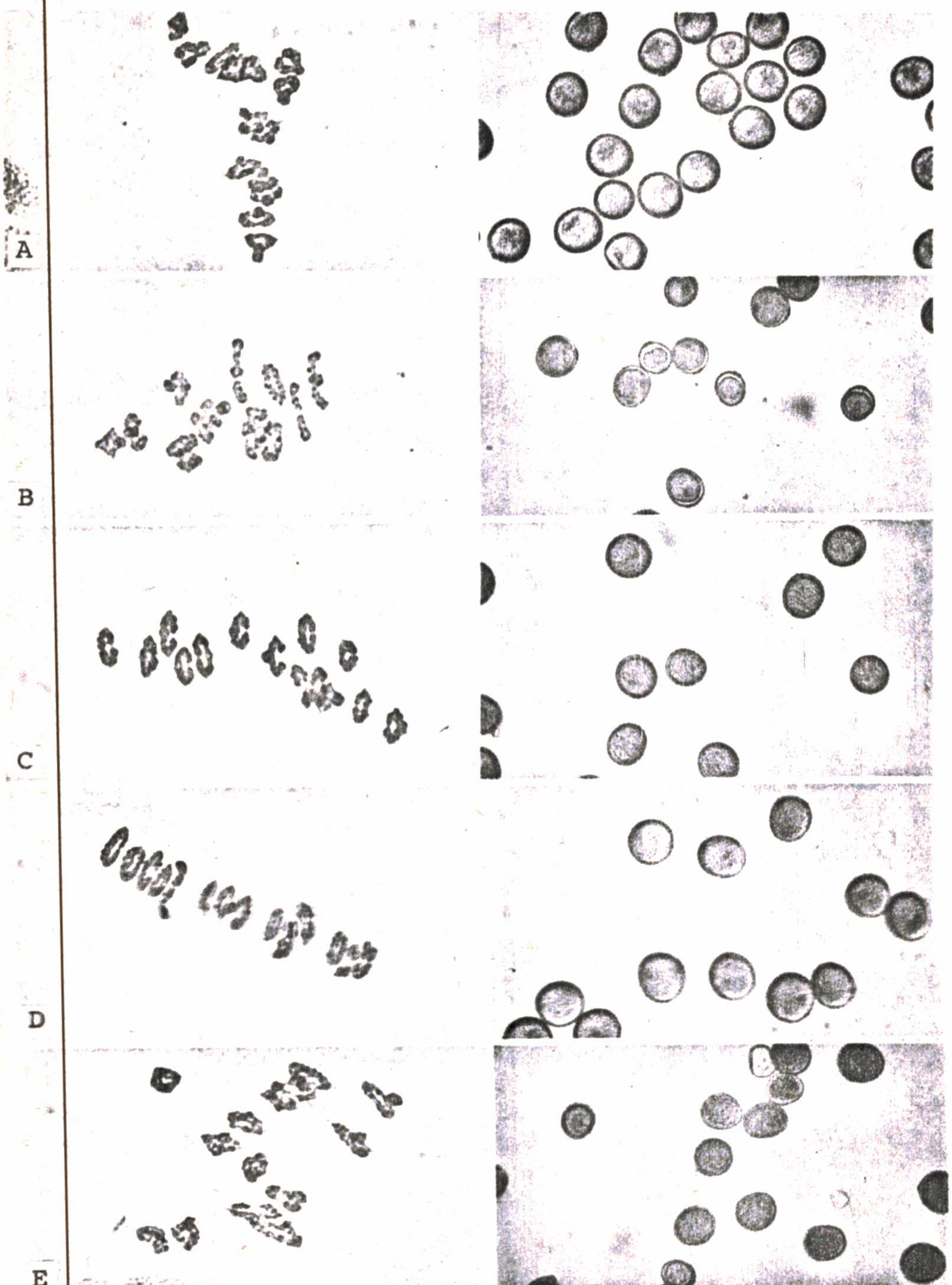

Fig. 1. Chromosome pairing and pollen fertility.
A: *T. turgidum* (control), B: (*Ae. speltoides*)-*turgidum*, C: (*Ae. bicornis*)-*turgidum*, D: (*Ae. longissima*)-*turgidum*, E: (*Ae. sharonensis*)-*turgidum*. left: chromosome pairing, right: pollen.

Results and Conclusions

The effects of eight cytoplasms to wheat genomes are summarized in Table 3. As seen Table 3, these cytoplasms can be divided roughly into two groups from their effects to wheat genomes, namely, Sitopsis cytoplasm group and other four cytoplasms group. Wheat genomes having Sitopsis cytoplasms show considerable normal growth and fertility, while those having other four cytoplasms show complete male sterility, variegation and delay in maturity, except *T. dicoccum liguliforme* genome (including 4 combinations). From these results, it is considered that Sitopsis cytoplasms, as a whole, are related to the cytoplasm of tetraploid wheats.

Figure 1 shows the pollen fertility and chromosome pairing in these cytoplasmic substitution lines. *T. turgidum* having *speltoides* cytoplasm shows fourteen bivalents in chromosome pairing but does not show considerable high pollen fertility (Fig. 1B). On the other hand, *T. turgidum* having *bicornis*, *longissima* and *sharonensis* cytoplasm show fourteen bivalents and considerable

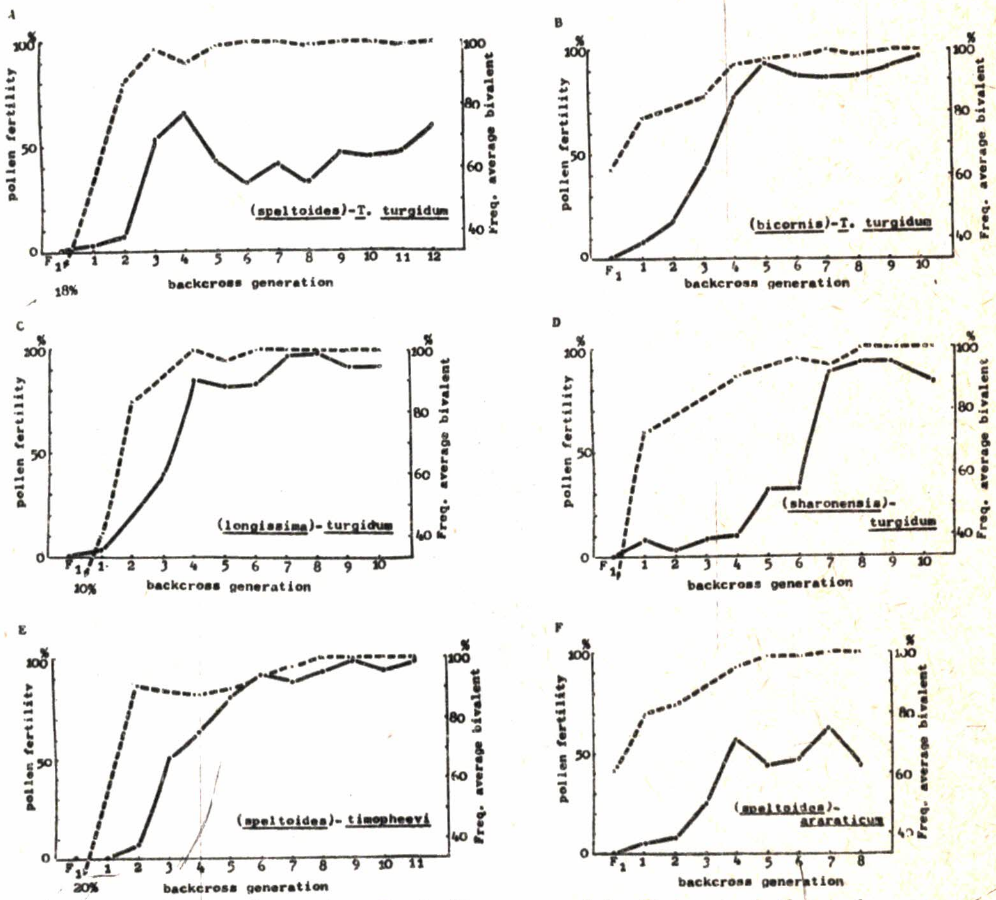

Fig. 2. The changes in pollen fertility accompanied with increase in the number of bivalents.
Solid line: pollen fertility, broken line: freq. average bivalent number.

Table 3. Reaction of alien cytoplasm to wheat genomes

Cytoplasm	Genomes	Emmer wheats					*Timopheevi* G.	
		E1 1)	E2	E3	E4	E5	T1	T2
speltoides	seedling variegation							
bicornis	seedling variegation				○	○		
longissima	seedling variegation				○	○		
sharonensis	seedling variegation				○	○	—	
caudata	seedling variegation	—			○	○		—
heldreichii	seedling variegation				○	○	○	○
comosa	seedling variegation				○	○		
boeoticum	seedling variegation	○			—	○	—	

○: seedling variegation

Cytoplasm	Genomes	E1	E2	E3	E4	E5	T1	T2
speltoides	delay in maturity	○				○		
bicornis	delay in maturity							
longissima	delay in maturity	○				○		○
sharonensis	delay in maturity	○				○	—	○
caudata	delay in maturity	—	—	—	—	—	—	—
heldreichii	delay in maturity	○		○		○	—	—
comosa	delay in maturity	○				○		
boeoticum	delay in maturity	○			—	○	—	○

○: delay in maturity

Cytoplasm	Genomes	E1	E2	E3	E4	E5	T1	T2
speltoides	pollen fertility	+ 2)	+	++ 2)	++ 2)	+	+	++
bicornis	pollen fertility	++	++	++	++	++	++	++
longissima	pollen fertility	++	++	++	++ 2)	++	++	—
sharonensis	pollen fertility	+ 2)	+ 2)	++	+ 2)	++	—	++
caudata	pollen fertility	—	—	—	—	—	—	—
heldreichii	pollen fertility	—	—	—	— 2)	—	—	—
comosa	pollen fertility	—	—	++	— 2)	— 2)	—	—
boeoticum	pollen fertility	—	—	+	—	—	—	—

Cytoplasm	Genomes	E1	E2	E3	E4	E5	T1	T2
speltoides	selfed seed fertility	± 2)	±	+	±	±	—	++
bicornis	selfed seed fertility	++	++	++	++	++	++	++
longissima	selfed seed fertility	++	++	++	+ 2)	++	++	
sharonensis	selfed seed fertility	— 2)	± 2)	++	— 2)	++		++
caudata	selfed seed fertility	—	—	—	—	—	—	—
heldreichii	selfed seed fertility	—	—	—	— 2)	—	—	—
comosa	selfed seed fertility	—	—	+	— 2)	— 2)	—	—
boeoticum	selfed seed fertility	—	—	+	—	—	—	—

++: fertility 60–100% +: 30–60% ±: 10–30% —: 0%

1) Code No., see Table 1B.
2) Average bivalent is lower than 14_{II}.

high pollen fertilities (Fig. 1C, D and E, respectively).

Table 4 summarized the relationships between chromosome pairing and fertility in these substitution lines. The pollen and seed fertility in ***turgidum*** and ***araraticum*** having ***speltoides*** cytoplasm is lower than in those having ***bicornis***, ***longissima*** and ***sharonensis*** cytoplasm. While, ***timopheevi*** having ***speltoides*** cytoplasm shows fourteen bivalents and high fertility.

Furthermore, in *T.* ***turgidum*** having ***speltoides*** cytoplasm the increase of the pollen fertility is not accompanied by an increase in the number of average bivalents as seen Fig. 2A. In the cytoplasm line of *Ae. bicornis*, ***longissima*** and ***sharonensis***, the increase of the pollen fertility is accompanied by an increase of the number of average bivalents (Fig. 2B, C, D, respectively). Emmer wheats having ***speltoides*** cytoplasm, however, show complete normal growth and do not show any variegation in seedlings. While those having ***bicornis***, ***longissima*** and ***sharonensis*** cytoplasm show severe variegation in seedlings.

On the other hand, *T.* ***timopheevi*** having ***speltoides*** cytoplasm shows completely normal growth and fertility (Table 3 and 4). And in this line, the restoration of pollen fertility is accompanied by an increase in the number of average bivalents (Fig. 2E). From these observations it seems that the cytoplasm of ***timopheevi*** closely related to ***speltoides*** cytoplasm. However, the manner of the response of *T.* ***araraticum*** genomes to the ***speltoides*** cytoplasm does not resembles that of *T.* ***timopheevi*** but resembles that of ***trugidum*** (Table 4 and Fig. 2F).

We have another evidence that *T.* ***araraticum*** cytoplasm is closely related to that of *T.* ***timopheevi***. We have two substitution lines started from the reciprocal cross between ***timopheevi*** and ***araraticum***. The B_5-plants in both lines show same degree of fertility in the pollen and selfed seed (85% or more) and complete normal growth. Indeed, substitution lines of emmer wheats and *T.* ***araraticum*** started from ***Ae. speltoides*** 5725C (Table 1), while substitution lines of ***timopheevi*** started from ***speltoides*** 5725E. ***Ae. speltoides*** 5725C and 5725E were collected from same population in Ankara, Turkey, but they are separated each other by their morphological characters by Dr. M. Tanaka in Kyoto University. So, it seems like that the difference between (***speltoides***)-***timopheevi*** and (***speltoides***)-***araraticum*** due to differentiation in ***Ae. speltoides***.

Table 4. The number of average bivalent and fertility in Sitopsis substitution line

Substitution line	B. C. gen.	No. ave. bivalent	Fertility	
			pollen	seed (free)
(*speltoides* 5725C)-***turgidum***	13	14.0	56.7	25.9
(*bicornis*)- 〃	10	14.0	94.2	100.0
(*longissima*)- 〃	11	14.0	96.3	98.4
(*sharonensis*)- 〃		14.0	91.4	95.2
(*speltoides* 5725E)-***timopheevi***	12	14.0	96.6	97.7
(*bicornis*)- 〃	7	14.0	97.1	95.0
(*sharonensis*)- 〃	6	14.0	94.1	91.3
(*longissima*)-***araraticum***	5	14.0	88.7	96.7
(*speltoides* 5725C)-***araraticum***	9	14.0	46.0	5.6

General Conclusions

From all the above considerations, it is concluded that the cytoplasm of *T. timopheevi* has been derived from *Ae. speltoides*, and the cytoplasm of *T. araraticum* has been also derived from the same donor. Furthermore, the cytoplasms in Sitopsis seem to be closely related to the cytoplasms of emmer wheats, as a whole. It is difficult to conclude which of the species in Sitopsis has contributed the cytoplasm to emmer wheats. We can say, however, it is most plausible that the cytoplasm of *Ae. speltoides* has contributed the cytoplasm to emmer wheats.

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