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THE ORIGIN OF THE CYTOPLASM OF TETRAPLOID WHEATS [1]

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Until recently, the role of the cytoplasm in the evolution of wheats was mostly left out of consideration, except for KIHARA's (1951, 1968) pioneering studies. In 1968, I reported that *Triticum turgidum* having einkorn cytoplasm shows complete male sterility, abnormal growth and variegation in seedlings, while *T. turgidum* with *Aegilops speltoides* cytoplasm shows moderately high pollen fertility and normal growth. In addition, I concluded that the cytoplasm of emmer wheat has been derived from its BB ancestor.

In the present paper, the responses of emmer genomes to the cytoplasm of four *Aegilops* species in the Sitopsis section are compared, and the origin of the cytoplasm of emmer, *timopheevi*, and common wheats is discussed.

MATERIALS AND METHODS

Substitution lines used are shown in Table 1.

Cytoplasmic relationships were estimated by the effects of adding an alien cytoplasm to a genome. Those effects are expressed in the variegation in seedlings, the abnormality of growth and the degree of pollen fertility.

RESULTS AND CONCLUSIONS

Origin of the Cytoplasm of Emmer Wheats

The effects of four cytoplasms of Sitopsis species on the genomes of emmer wheats are shown in Table 2. *T. turgidum* having *Ae. bicornis* cytoplasm and *T. turgidum* having *Ae. longissima* cytoplasm show high pollen fertility and normal growth but severe seedling variegation. Pollen fertility of *T. turgidum* having *Ae. speltoides* cytoplasm is lower than that of *(bicornis)-T. turgidum* and *(longissima)-T. turgidum*, but variegation is not observed in their seedlings. *T. turdigum* having *sharonensis* cytoplasm shows considerable pollen fertility, but it also shows severe weakness, variegation and delayed growth.

Figure 1 shows the changes in pollen fertility and in the number of bivalents in the course of successive backcrosses in the substitution lines. In *(speltoides)-T. turgidum*, the decrease of pollen fertility is accompanied by an increase in the number of bivalents. (Figure 1a).

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Table 1. Materials used for determination of cytoplasmic effects

Substitution lines	B.C. gen.	Procedure of substitution
(Ae. spelt.)-T. turgidum	B_8	*(Ae. speltoides* x *T. turdigum nigrobarbatum)* F_1 x *T. turdigum nigrobarbatum*[6]
(Ae. spelt.)-T. durum	B_3	(")B_4 x *T. durum reichenbachii*[4]
(Ae. spelt.)-T. dicoccum	B_4	(")B_3 x *T. dicoccum liguliforme*[5]
(Ae. spelt.)-T. d'oides kot.	B_5	(")B_2 x T. dicoccoides *kotschyanum*[6]
(Ae. spelt.)-T. d'coides spont.	B_5	(")B_2 x *T. dicoccoides spontaneonigrum*[6]
(Ae. spelt.)-T. araraticum	B_4	(")B_2 x *T. araraticum*[5]
(Ae. spelt.)-T. vulgare eryth.	B_5	(")B_2 x *T. vulgare erythrospermum*[6]
(Ae. spelt.)-T. spelta duh.	B_4	(")B_3 x *T. spelta duhamelianum*[5]
(Ae. spelt.)-T. timopheevi	B_7	*(Ae. speltoides* x *T. timopheevi)*F_1 x *T. timopheevi*[7]
(Ae. bic.)-T. turgidum	B_5	(S^bS^bAA* x *T. dicoccum* R.26)F_1 x *T. turdigum nigrobarbatum*[6]
(Ae. long.)-T. turgidum	B_6	*(Ae. longissima* x *T. turgidum nigrobarbatum)*F_1 x *T. turgidum nigrobarbatum*[6]
(Ae. shar.)-T. turgidum	B_6	*(Ae. sharonensis* x *T. turgidum nigrobarbatum)*F_1 x *T. turgidum nigrobarbatum*[6]

*Induced by Dr. Sears from the cross *Ae. bicornis*(♀) x einkorn(♂).

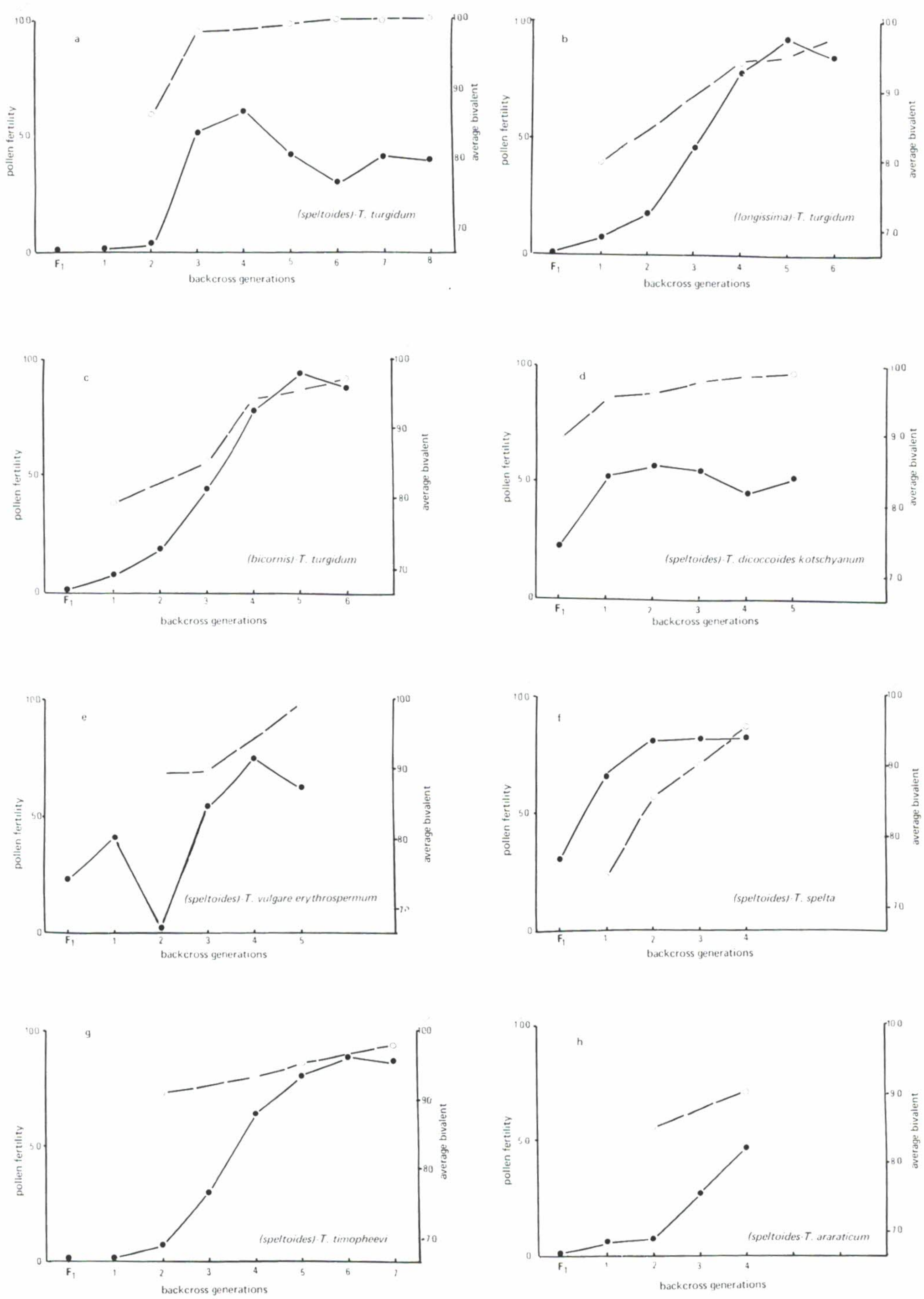

Figure 1. Changes in pollen fertility and in the number of bivalents in the course of successive backcrosses.

Solid line = pollen fertility.

Broken line = average bivalent frequency.

On the other hand, in *(longissima)-T. turgidum*, chromosome pairing does not reach 14 bivalents (Figure 1b). But a high degree of pollen fertility is observed in this line, so it seems that high pollen fertility is due to a chromosome segment from the cytoplasmic parent. Since *(bicornis)-T. turgidum* started from an F_1 hybrid

Table 2. Reaction of alien cytoplasm to 4x and 6x wheat genomes

Substitution lines	Ave. no. bivalents	Seedling variegation	Weak, delayed growth	Pollen fertility
(spelt.)-T. turgidum	14	No	No	33.8 ± 4.9%
(bic.)-T. turgidum	13.8	Yes	No	88.4 ± 5.0%
(long.)-T. turgidum	13.85	Yes	No	77.4 ± 5.4%
(shar.)-T. turgidum	-	Yes	Yes	30.4%
(spelt.)-T. durum	14	No	No	44.4%
(spelt.)-T. dicoccum	13.8	No	No	60.5%
(spelt.)-T. dicocc. kot.	13.8	No	No	51.8 ± 1.4%
(spelt.)-T. dicocc. spont.	13.5	No	No	53.3 ± 6.9%
(spelt.)-T. vulgare eryth.	21	No	No	61.4 ± 14.7%
(spelt.)-T. spelta duh.	20.6	No	No	82.6 ± 6.5%
(spelt.)-T. timopheevi	13.9	No	No	84.5 ± 5.0%
(spelt.)-T. araraticum	13.5	No	No	47.1 ± 0.4%

between S^bS^bAA and *T. dicoccum* R26 (Table 1), it seems that a chromosome or chromosome segment from the *T. dicoccum* genome remains in this line and also that high pollen fertility is caused by heterosis (Figure 1c). Therefore, the pollen fertility in these lines may drop as backcrossing progresses, as in the substitution lines with *Ae. speltoides* cytoplasm.

The response of *speltoides* cytoplasm to the genomes of other emmers is shown in Table 2 and Figure 2d. The pollen fertility in these lines is higher than that of *(speltoides)-T. turdigum*. This high pollen fertility seems to be caused by heterosis.

From these results, it is difficult to discuss which of the species of Sitopsis has contributed the cytoplasm to emmer wheats. We can say, however, that the cytoplasm of Sitopsis species is related to emmer cytoplasm.

Origin of the Cytoplasm of Common Wheats

Common wheats having *Ae. speltoides* cytoplasm show normal growth and fairly high pollen fertility (Table 2). In these lines, however, the number of backcross generations was not sufficient (Figure 1e, f). We must wait until at least B_7 or B_8 has been reached. At present, we can say the cytoplasm of common wheats seems to be related to the cytoplasm of *Ae. speltoides*.

Origin of the Cytoplasm of the *timopheevi* group

T. timopheevi having *speltoides* cytoplasm shows completely normal growth, dehiscent anthers and a high degree of pollen fertility (Table 2). Furthermore, the restoration of pollen fertility is accompanied by an increase in the number of bivalents throughout successive backcross generations (Figure 1g). From these results, the cytoplasm of *T. timopheevi* seems to be closely related to the cytoplasm of *Ae. speltoides*.

The manner of response of *Ae. speltoides* cytoplasm to the *T. araraticum* genome resembles that of *T. timopheevi* (Table 2 and Figure 1h). Though the number of backcross generations is not sufficient in the line of *T. araraticum*, it seems that *T. araraticum* cytoplasm is related to *Ae. speltoides* cytoplasm and also to *T. timopheevi* cytoplasm. We have other evidence which supports this assumption. We have two nucleus-substitution lines started from F_1 hybrids between *T. timopheevi* and *T. araraticum*. The B_1 plants in these lines show considerable pollen fertility (ca. 13%). TANAKA and ICHIKAWA (1968) found that *T. timopheevi* and *T. araraticum* are genomically very similar.

GENERAL CONCLUSION

From all the above considerations, the cytoplasm of *Ae. speltoides* seems to be more closely related to the cytoplasm of *T. timopheevi* than to the cytoplasm of emmer and common wheats and seems to be slightly different from emmer cytoplasm. Furthermore, we can say it is most plausible that the GG ancestor of the *T. timopheevi* group has been derived from *Ae. speltoides* or, if not, from its relatives.

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