DISTRIBUTION OF FERTILITY-RESTORING GENES IN HEXAPLOID WHEATS FOR *Ae. OVATA* AND *T. TIMOPHEEVI* CYTOPLASMS. I¹⁾

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Synopsis. Ninety-two varieties (or strains) of hexaploid wheat were tested as to fertility-restoration in two male-sterile cytoplasms derived from *Ae. ovata* and *T. timopheevi*. In total eight effective restorers were found, *i. e.*, P168, P170, P171, P173, P174, ABD-1 and ABE-16 for *Ae. ovata* cytoplasm and *T. spelta* var. *duhamelianum* for *T. timopheevi* cytoplasm. A few restorers were found among 6× cultivars, though none of them was very effective. All the restorers functioned only in either *Ae. ovata* or *T. timopheevi* cytoplasm.

After the discovery of male-sterility-inducing cytoplasms (KIYARA, 1951; FUKASAWA, 1959; WILSON and ROSS, 1961; MURAMATSU, 1965), some of those are used in the hybrid wheat breeding program. The possibility of breeding hybrid wheat became more distinct after the clarification of mechanism of fertility-restoration, as well as discovery of several effective fertility-restorers (SCHMIDT *et al.*, 1962; LIVERS, 1964; KIHARA and TSUNEWAKI, 1967). But the problem of restoration even still exists; the restorers at our hand are effective for certain varieties only, and there is also high degree of fluctuation in their effectiveness in different climatic zones. Therefore, there is a pressing need to investigate more number of restorers, preferably in 6× wheats to encounter these problems in fertility-restoration.

In the present experiment 92 varieties or strains of wheats of different localities and origins have been investigated as to whether they possess fertility-restoring genes for the cytoplasms of *Ae. ovata* and *T. timopheevi*. The results are reported here.

Materials and Methods

Several male-sterile lines of common wheat,

Triticum aestivum L. or *T. compactum* Host., which are listed in Table 1, were used as the tester for screening restorers to the cytoplasms of *Aegilops ovata* L. and *T. timopheevi* Zhuk. In total 92 varieties or strains of *T. aestivum* L., *T. compactum* Host., *T. sphaerococcum* Perc., *T. vavilovii* Jakubz., *T. spelta* L., and synthesized wheats listed in Table 2, were

Table 1. Male-sterile lines utilized as female parent for crosses to investigate fertility-restorers in 6× wheats

Cytoplasm	Strain	Pedigree
<i>Ae. ovata</i>	O-A	(<i>ovata</i>)-Norin 26 " × Norin 29 ³
	O-B	" × Norin 50 ³
	O-C	" × Idaed 59 ³
	O-D	" × Omaha ²
	O-E	" × Ottawa ²
<i>T. timopheevi</i>	T-A	(<i>timopheevi</i>)-Bison " × Kitakami Komugi ²
	T-B	" × Kokeshi Komugi ²
	T-C	" × Norin 29 ¹
	T-D	" × Norin 75 ¹
	T-E	" × Big Club 60 ²
	T-F	" × Lemhi 53 ²
	T-G	" × Wakeland ²

Superscript indicates the number of crosses using the indicated variety as the male parent.

Note: (*ovata*)-Norin 26 is a male-sterile line with *Ae. ovata* cytoplasm. (*timopheevi*)-Bison is, similarly, a male-sterile line of Bison with *T. timopheevi* cytoplasm. These lines were kindly provided by Dr. H. FUKASAWA and Dr. J. W. SCHMIDT, respectively.

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Table 2. Seed fertilities of F₁ hybrids between hexaploid wheat varieties (or strains) and cytoplasmically male-sterile lines having *Ae. ovata* or *T. timopheevi* cytoplasm

Species and variety	Strain or cultivar	Country	<i>ovata</i> cytoplasm		<i>timopheevi</i> cytoplasm		Species and variety	Strain or cultivar	Country	<i>ovata</i> cytoplasm		<i>timopheevi</i> cytoplasm	
			Tester strain	F ₁ 's seed fert. (%)	Tester strain	F ₁ 's seed fert. (%)				Tester strain	F ₁ 's seed fert. (%)	Tester strain	F ₁ 's seed fert. (%)
<i>T. aestivum erythrospermum</i>							<i>T. aestivum</i>	BMUK No. 3762	Egypt	O-A	0.0	T-A	0.0
"	P 168	Japan	"	93.3	"	0.0	"	3763	"	"	0.0	"	0.0
"	P 169	"	"	0.1	"	0.0	"	3764	"	"	0.0	"	0.0
"	P 170	"	"	67.5	"	0.0	"	3765	"	"	0.0	"	0.0
"	P 171	"	"	50.0	"	0.0	"	3766	"	"	0.0	T-C	0.0
"	P 172	"	"	0.0	"	0.0	"	3767	"	"	0.0	"	0.0
"	P 173	"	"	44.0	"	0.0	"	3769	"	"	0.0	"	0.7
"	P 174	"	"	76.0	"	0.0	"	3770	"	"	0.0	"	3.4
"	Chinese Spring	"	"		"	0.0	"	3772	"	"	0.0	"	0.0
"	No. 44	China	O-A	0.0	T-A	0.0	"	3773	"	"	0.0	"	0.0
<i>T. compactum</i>							"	3774	"	"	0.0	"	0.0
<i>T. spelta duhamelianum</i>							"	3775	"	"	0.0	"	0.0
<i>T. vavilovii vaneum</i>							"	3776	"	"	0.0	"	0.0
<i>T. sphaerococcum</i>							"	3777	Jordan	"	0.0	"	0.0
"	Canada Pak	Canada	O-C	0.0	T-D	0.0	"	3779	Syria	O-C	0.0	T-D	0.0
"	"	Pakistan	O-A	0.0	T-A	0.0	"	3780	"	O-A	0.0	T-C	0.0
"	"	"	"	0.0	"	0.0	"	3781	Turkey	"	0.0	"	0.0
"	"	"	"	0.0	"	0.0	"	3782	"	"	0.0	"	0.0
<i>T. aestivum</i>							"	3783	"	"	0.0	"	0.0
"	BMUK No. 3751	Egypt	"	0.0	"	0.0	"	3784	"	"	0.0	"	0.0
"	3752	"	"	0.0	"	0.0	"	3785	"	"	0.0	"	0.0
"	3753	"	"	0.0	"	0.0	"	3786	"	"	0.0	"	0.0
"	3754	"	"	0.0	"	0.0	"	3788	"	"	0.0	"	0.0
"	3755	"	"	0.0	"	0.0	"	3789	"	O-C	0.0	T-D	0.0
"	3756	"	"	0.0	"	0.0	"	3790	"	O-A	0.0	T-C	0.0
"	3757	"	"	0.0	"	0.0	"	3791	"	O-C	0.0	T-D	0.0
"	3758	"	"	0.0	"	0.0	"	3793	"	O-A	0.0	T-C	0.0
"	3759	"	"	0.0	"	0.0	"	3795	"	O-C	0.0	T-D	0.0
"	3760	"	"	0.0	"	0.0	"	3796	"	O-A	0.0	T-C	0.0
"	3761	"	"	0.0	"	0.0	"						

Species and variety	Strain or cultivar	Country	ovata cytoplasm		Strain	timopheevi cytoplasm		Tester F ₁ 's seed strain fert. (%)	ovata cytoplasm		timopheevi cytoplasm	
			Tester F ₁ 's seed strain fert. (%)	F ₁ 's seed fert. (%)		Tester F ₁ 's seed strain fert. (%)	F ₁ 's seed fert. (%)		Tester F ₁ 's seed strain fert. (%)	F ₁ 's seed fert. (%)		
<i>T. aestivum</i>	BMUK No. 3799	Turkey	C-O	0.0	T-D	0.0	Synthesized hexaploid wheat					
"	3801	"	"	0.0	"	12.6	ABD-1 (<i>T. dicoccoides spont.</i> × <i>Ae. squarrosa typica</i> No. 2)	O-D	53.6	T-F	0.0	
"	3802	"	"	0.0	"	0.0	ABD-9 (<i>T. dicoccoides spont.</i> × <i>Ae. squarrosa strangulata</i>)	O-E	0.0	"	0.0	
"	3804	"	"	0.0	"	0.0	ABD-11 (<i>T. carthlicum</i> × <i>Ae. squarrosa strangulata</i>)	"	0.0	"	0.0	
"	3805	"	"	0.0	"	0.0	ABD-13 (<i>T. dicoccum</i> Vernal × <i>Ae. squarrosa strangulata</i>)	"	?	"	0.0	
"	3811	"	"	0.0	"	0.0	ABD-14 (<i>T. durum</i> Gulab × <i>Ae. squarrosa strangulata</i>)	"	0.0	"	0.0	
"	3814	"	"	0.0	"	0.0	ABD-16 (<i>T. durum</i> Gulab × <i>Ae. squarrosa meyeri</i>)	O-D	76.8	"	0.0	
"	3822	"	O-B	0.0	T-B	0.0	ABD-22 (<i>T. carthlicum</i> × <i>Ae. squarrosa meyeri</i>)	"	?	"	0.0	
"	3826	"	"	0.0	"	0.0	ABD-23 (<i>T. orientale</i> × <i>Ae. squarrosa strangulata</i>)	O-E	0.0	T-G	0.0	
"	3827	"	"	0.0	"	0.0	ABD-Vernal (<i>T. dicoccum</i> Vernal × <i>Ae. squarrosa typica</i>)	"	0.0	"	0.0	
"	3830	"	"	2.2	"	0.0	ABD-Golden Ball (<i>T. durum</i> Golden Ball × <i>Ae. squarrosa typica</i>)	"	9.2	"	0.0	
"	3834	"	"	0.0	"	0.0	ABD-Carleton (<i>T. durum</i> Carleton × <i>Ae. squarrosa typica</i>)	"	0.0	"	3.0	
"	3839	"	"	0.0	"	0.0	ABD-Pentad (<i>T. durum</i> Pentad × <i>Ae. squarrosa typica</i>)	"	0.0	"	—	
"	3841	"	"	0.3	"	0.0						
"	3842	"	"	0.0	"	0.0						
"	3844	"	O-E	0.0	T-E	0.0						
"	3845	"	O-B	1.5	T-B	0.0						
"	3848	"	"	0.0	"	0.0						
"	3852	"	"	0.0	"	0.0						
"	3853	"	O-E	0.0	T-E	0.0						
"	3854	"	"	0.0	T-B	0.0						
"	3855	"	"	0.0	T-E	0.0						
"	3860	"	"	0.0	"	0.0						
"	3862	"	"	0.0	"	0.0						

? Seed fertility could not be estimated as all the F₁ plants were dwarf and did not head.

— Seed fertility unknown.

Note: Identification of species and varieties for the collections of BMUK (The Botanical Mission of the University of Kyoto to the Eastern Mediterranean Countries) was made by Dr. M. TANAKA, Kyoto University.

crossed as pollen parent to the testers. F_1 seeds obtained from those crosses were sown in sterilized soil, and the seedlings grown were transferred to the field. At the time of head emergence, three spikes from each of two plants in each F_1 progeny were covered with paraffin paper bags before anthesis to prevent cross-pollination. At the time of maturity the bagged spikes were harvested and the seed fertility was estimated from the seeds set in the first and second florets of each spike. When some seed fertility was found in the F_1 hybrid, the pollen parent was assumed to carry a dominant gene (or genes) for fertility-restoration.

Results and Discussion

Fertility-restorers for *Ae. ovata* cytoplasm.

Selfed seed fertility of F_1 hybrids between male-sterile wheat and various pollen parents is given in Table 2. Out of 73 *T. aestivum* varieties or strains tested for *Ae. ovata* cytoplasm, only nine strains, namely, P168 (93.3%), P169 (0.1%), P170 (67.5%), P171 (50.0%), P173 (44.0%), P174 (76.0%), BMUK nos. 3830 (2.2%), 3841 (0.3%), and 3845 (1.5%) restored male fertility in various degrees as shown in parenthesis. Out of these, P168, P169, P170, P171, P173 and P174 are 6 $\times$ derivatives from the cross between *Ae. caudata* and *T. aestivum* var. *erythrosperrum*. P168 and P174 are known to carry a pair of a *caudata* chromosome C-sat-2, besides 20 pairs of wheat chromosomes (KIHARA, 1959). These lines are so-called chromosome substitution lines of *T. aestivum* var. *erythrosperrum*, whose chromosome 1D is replaced by C-sat-2 (MURAMATSU, 1959). All these derivative strains except P169 seem to have received restoring gene(s) from *Ae. caudata*, as *T. aestivum* var. *erythrosperrum* with *Ae. ovata* cytoplasm is completely male sterile. In these strains, there is a strong correlation between fertility-restoration and black ear character (Fig. 1), as all the strains with black (P168, P170, P171 and P174) or brown (P173) spikes showed high degrees of fertility-restoration, and the strains having yellow spikes (P169 and P172) were sterile.

None of the other species, *i. e.*, *T. compactum*, *T. spelta*, *T. sphaerococcum* and *T. vilovii*, was found to possess dominant restor-

Fig. 1 Spike color of 6 $\times$ derivative strains which were produced for the cross, *Ae. caudata* $\times$ *T. aestivum* var. *erythrosperrum* by KIHARA (1959).

From left to right, *T. aestivum* var. *erythrosperrum* (indicated as T. v. e.) P168, P169, P170, P171, P172, P173, P174 and *Ae. caudata*.

ing genes, since all the F_1 hybrids were completely sterile. WILSON and ROSS (1961) in search of restoring genes screened 124 varieties and found only a few varieties that partially restored fertility. It is in good conformity with the present results, indicating the slim hope for the discovery of effective restorers to *Ae. ovata* cytoplasm in cultivated 6 $\times$ varieties.

Among the synthesized wheats, the seed fertilities of ABD-13 and ABD-22 could not be estimated as all the F_1 plants remained dwarf throughout the growing season and did not head. ABD-1, ABD-16 and ABD-Golden Ball restored the fertility up to 53.6%, 76.8% and 9.2% respectively, in the F_1 s. Though ABD-1 and ABD-9 have the same emmer parent, only the former restored fertility. Therefore, the restoring gene(s) of ABD-1 is assumed to have been derived from *Ae. squarrosa typica* No. 2. Similarly, ABD-14 and ABD-16 have the same emmer parent, and only the later had restoring gene(s). In this line, too, the gene(s) seems to have been derived from *Ae. squarrosa* parent.

Fertility-restorers for *T. timopheevi* cytoplasm.

Out of 73 *T. aestivum* varieties or strains tested for *T. timopheevi* cytoplasm, only three, namely, BMUK nos. 3769 and 3770 of Egyptian origin and BMUK no. 3801 from Turkey were found to possess very weak restoring

gene(s), because their F_1 hybrids restored some fertility (0.7, 3.4 and 12.6% respectively). All the rest gave completely male-sterile F_1 hybrids (Table 2). In the other $6\times$ species, only *T. spelta* var. *duhamelianum* was found to carry restoring gene and exhibited very high seed fertility (98.5%) in the F_1 , confirming the earlier report of KIHARA and TSUNEWAKI (1967). Previously LIVERS (1964) reported the absence of the restoring gene in common wheat varieties, Aztec, CI 13285 and CI 13546 and induction of partial fertility by six varieties, Blackhawk, Cheyenne, Gage, Itana, Lancer and Relief. ZEVEN (1967) screened 274 cultivars of *T. aestivum*, one of *T. compactum* and one of *T. macha*; and found only a few weak restorers. The facts suggest that the effective restorer to *T. timopheevi* cytoplasm is rare among $6\times$ cultivars.

Among the 12 synthesized wheat strains tested, only ABD-Carleton was found to carry some weak restoring gene(s). KIHARA and TSUNEWAKI (1967) reported that *T. dicoccoides spontaneonigrum*, *T. carthlicum* and many others carry some restoring genes to *T. timopheevi* cytoplasm. On the other hand, ABD-1 and other synthesized wheats did not behave as a restorer. MAAN and LUCKEN (1968) showed that *T. aestivum* Chinese Spring with *T. timopheevi* cytoplasm became completely male sterile while its mono-7D restores some fertility. All these facts indicate that *D* genome in common wheat as well as in *Ae. squarrosa* carries some inhibitor to fertility-restoration.

It is interesting to note that none of 92 varieties or strains of $6\times$ wheats tested for *Ae. ovata* and *T. timopheevi* cytoplasm was found to carry restoring genes in common for these cytoplasm. The restorers, which induced partial or complete fertility in *Ae. ovata* cytoplasm, did not function in *T. timopheevi* cytoplasm and, similarly, the strains, which induced complete or partial fertility in *T. timopheevi* cytoplasm, did not show any sign of fertility-restoration in *Ae. ovata* cytoplasm. The interaction between restorer and male-sterile cytoplasm is undoubtedly very specific as already pointed out by KIHARA and TSUNEWAKI (1967).

Summary

Ninety-two varieties (or strains) of $6\times$ wheat were tested as to restoration in two male-sterile cytoplasm derived from *Ae. ovata* and *T. timopheevi*. In total eight effective restorers were found, i. e., P168, P170, P171, P173, P174, ABD-1 and ABD-16 for *Ae. ovata* cytoplasm and *T. spelta* var. *duhamelianum* for *T. timopheevi* cytoplasm. Restoring gene(s) of P168, P170, P171, P173, and P174 were assumed to have been derived from *Ae. caudata*, while that of ABD-1 and ABD-16 from *Ae. squarrosa*. In general, *D* genome has an effect to suppress fertility-restoration in *T. timopheevi* cytoplasm. A few restorers were also found among $6\times$ cultivars, but none of them was very effective. All the restorers functioned only in either *Ae. ovata* or *T. timopheevi* cytoplasm.

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Ae. ovata および *T. timopheevi* 細胞質に対する 稔性回復遺伝子の 6 倍性コムギにおける分布 I

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雑種コムギの育成に必要な稔性回復遺伝子を探求するため、6 倍性コムギ 92 品種(系統)の *Ae. ovata* および *T. timopheevi* 細胞質に対する稔性回復作用を調査した。その結果、*Ae. ovata* 細胞質に対しては P168, P170, P171, P173, P174, ABD-1 および ABD-16 の 7 系統が、*T. timopheevi* 細胞質に対しては *T. spelta* var. *duhamelianum* が効果的な優性稔性回復遺伝子をもって

いることを発見ないし再確認した。これらの品種(系統)以外に数品種が弱い稔性回復遺伝子をもっていた。P168, P170, P171, P173 および P174 の稔性回復遺伝子は *Ae. caudata* から、ABD-1 および ABD-16 のものは *Ae. squarrosa* から由来したものと思われる。*Ae. ovata* と *T. timopheevi* の両細胞質に共通に作用する稔性回復因子系統はひとつもなかった。