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New Cytoplasmic Male Sterility Sources in Common Wheat: Their Genetical and Breeding Considerations

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Summary. Nuclei from *Triticum aestivum* L. cultivars 'Penjamo 62' and 'Siete Cerros 66' were introduced into the cytoplasms of different species of *Aegilops* and some subspecies (varieties) of *T. dicoccoides* by backcrossing. The sterile alloplasmic lines obtained were compared with the normal cultivars used as the recurrent pollen parents. According to the cytoplasmic effect, these cytoplasms were subdivided into three main groups. The first group possesses C^u type cytoplasm, the second one possesses M type and the third group includes S, C and G type. Promising male sterile cytoplasms for hybrid wheat production were found in *Ae. mutica, Ae. triuncialis* and *T. dicoccoides* var. 'spontaneovillosum'. Based on these results and other information some conjectures were made concerning hybrid wheat breeding and phylogenetic differentiations of the cytoplasm.

Key words: *Aegilops* – *Triticum* – Hybrid wheat – Nucleo-cytoplasmic interaction

Introduction

With the discovery of *Triticum timopheevi*'s system for male sterility-fertility restoration (Wilson and Ross 1962; Schmidt et al. 1962) it was thought that hybrid wheat would be easily commercialized. However, the difficulties encountered with fertility restoration and such cytoplasmic side effects as shriveled kernels and low seed germination ability (Milohnic 1976) made further into finding new sources of male sterile cytoplasm very necessary.

In addition to the cytoplasms of *Aegilops caudata* (Kihara 1951), *Ae. ovata* (Fukasawa 1958) and the *T. timopheevi* complex (Wilson and Ross 1962; Nettevich and Fedorova 1966; Maan and Lucken 1967) there are several other cytoplasms of common wheat with sterilizing ability: these are the cytoplasms of *Ae. umbellulata* (Muramatsu 1965), *T. boeoticum* (Hori and Tsunewaki 1967), *Secale cereale, Ae. speltoides* and *T. dicoccoides* var. 'nudiglumis' (Maan and Lucken 1971a,b, 1972). During 1975-1976 there were several articles published reporting some new sources of male sterile cytoplasms (Maan 1975; Panayotov and Gotsov 1975, 1976; Popov et al. 1976; Tsunewaki et al. 1976). All the results in these articles are basically similar; the differences are probably due to the different geographical and genetical origins of the cytoplasm donors. Research into such a field will elucidate not only the phylogenetic relationship between the species in the subtribe *Triticinae*, but will provide possibilities to find new male sterility-fertility restoring systems. The present investigation is a part of our research work on nucleo-cytoplasmic interrelationships in *Triticinae* and is aimed mainly at elucidating the genetic characteristics of new sources of cytoplasmic male sterility and their values in hybrid wheat breeding. Since breeding value is determined by both sterilizing ability and influence on the growth and development of wheat plant, these two points were the main objects of the present investigation.

Materials and Methods

The following materials were used for producing alloplasmic lines of common wheat:

(a) Cytoplasm donors – The species used are listed in Table 1. They were used as the female parent in the initial cross prior to the subsequent backcrosses.

(b) Nucleus donors – Two spring cultivars of common wheat, *Triticum aestivum* L. (2n = 42, genome constitution AABBDD) were used; 'Penjamo 62' and 'Siete Cerros 66', both originally from Mexico. They were used as the recurrent male parent in the substitution backcrosses.

After four to seven substitution backcrosses, common wheat lines with cytoplasms of the species listed in Table 1 were confirmed to have 2n = 42 and 21 bivalents at the first meiotic metaphase.

In the first part of the present investigation, all these lines

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Table 1. Cytoplasm donors used in the present investigation

Species	2n	Genome (haploid)	Obtained from	Geographical origin
Aegilops caudata L. var. 'dichasians'	14	C	VIR[a], 647	(unknown)
Ae. heldreichii Holzm.	14	M	VIR, 641	(unknown)
Ae. comosa Sibth. et Sm.	14	M	VIR, 642	(unknown)
Ae. mutica Boiss.	14	Mt	VIR, 646	Palestine
Ae. aucheri Boiss.	14	S	VIR, 250	Palestine
Ae. longissima (Schw. et Muschl.) Eig	14	S^l	VIR, 202	Palestine
Ae. sharonensis Eig	14	S^l	VIR, 203	Palestine
Ae. ovata L.	28	M^oC^u [b]	Bulgaria	(unknown)
Ae. triuncialis L. var. 'typica'	28	CC^u [b]	Gatersleben, DDR	(unknown)
Ae. biuncialis Vis.	28	C^uM^b	VIR, 130	Azerbaijan, USSR
Ae. macrochaeta Rich.	28	C^uM^b	Bulgaria	(unknown)
Ae. columnaris Zhuk.	28	C^uM^c	VIR, 173	Azerbaijan, USSR
Ae. kotschyi Boiss.	28	S^vC^u [b]	VIR, 266	Azerbaijan, „
Ae. variabilis Eig	28	S^vC^u [b]	VIR, 644	(unknown)
Ae. cylindrica Host	28	DC^b	VIR, 24	Daghestan, USSR
Ae. ventricosa Tausch.	28	DM^v	VIR, 245	Uzbekistan, „
Ae. juvenalis (Thell.) Eig	42	DC^uM^j	VIR, 50	Turkmenistan, „
Ae. triaristata Willd. (6x)	42	$C^uM^tM^{t2}$	VIR, 73	Azerbaijan, „
Ae. recta (Zhuk.) Chen.	42	$C^uM^tM^{t2}$	VIR, 57	(unknown)
Ae. crassa Boiss. (6x)	42	DD^2M^{cr}	VIR, 256	Uzbekistan, USSR
Triticum dicoccoides (Aar.) Schweinf.				
var. 'pseudojordanicum' Jakubz.	28	AB	VIR, 41965	Israel
var. 'kotschyi' Jakubz.	28	AB	VIR, 5196	Israel
var. 'fulvovillosum' Perc.	28	AB	VIR, 5201	Israel
var. 'arabicum' Jakubz.	28	AB	VIR, 15901	Israel
var. 'spontaneonigrum' Flaksb.	28	AB	VIR, 17157	Syria
var. 'vavilovii' Jakubz.	28	AB	VIR, 17256	Israel
var. 'palestinicum' Vav.	28	AB	VIR, 26117	Israel
var. 'spontaneovillosum' Flaksm.	28	AB (GA^b)	VIR, 40120	Iraq
var. 'jordanicum' Vav.	28	AB	VIR, 42632	Iraq
var. 'namuricum' Jakubz.	28	AB	Gatersleben, DDR	(unknown)

[a] VIR means All Union Institute for Plant Industry, Leningrad, USSR
[b] The symbols are reversed according to cytoplasm donor

(2 nuclei × 30 cytoplasms = 60 lines) were grown in greenhouses during the Fall of 1976, and seed fertilities were surveyed under bagging (selfing) and after artificial pollination with normal pollen (crossing). Among the 30 cytoplasms tested 13 resulted in complete male sterility to either or both cultivars under investigation.

In the second part of the present investigation, all alloplasmic lines with the eleven cytoplasms which resulted in complete male sterility, except for *Ae. caudata* and *Ae. ovata* cytoplasms, were grown in greenhouses during the Spring of 1977 and the effects of these cytoplasms on the following characters of wheat cultivars were investigated: Heading date (counted from March 31), culm length, ear number, flag leaf length, ear length, number of spikelets per ear, occurrence of pistillody, seed set under bagging (selfing) and by hand- and openpollination. Hand pollination was made with normal pollen of the nucleus donors. Data were taken from more than 25 plants which were grown in a pair of rows, the distances between neighboring pairs, between two rows in the same pair, and between neighboring plants in the same row being 40, 20 and 10 cm, respectively. The recurrent pollen parents were used as the control. The *caudata* and *ovata* cytoplasms were excluded from the second part of the investigation, because their sterilizing effect and side effects on other plant characters were already reported by previous workers (Kihara 1951; Fukasawa 1959; Hori and Tsunewaki 1969).

Results

1 New Sources of Male Sterile Cytoplasms

Selfed and crossed seed fertilities of 60 alloplasmic lines of the common wheat cultivars are collectively shown in Table 2. Cytoplasms from *Ae. caudata, Ae. ovata, Ae. heldreichii, Ae. comosa, Ae. mutica, Ae. triuncialis, Ae. macrochaeta* and *T. dicoccoides* var. 'spontaneovillosum' caused complete male sterility in both cultivars, while the cytoplasms of *Ae. aucheri, Ae. biuncialis, Ae. columnaris, Ae. triaristata* and *Ae. recta* converted one of the two cultivars to a complete male sterile and the other to an

Table 2. Seed fertility of alloplasmic common wheat cultivars under selfing and artificial crossing with normal pollen[a]

Cytoplasm	Nucleus (cultivar)			
	Penjamo 62		Siete Cerros 66	
	Self	Cross	Self	Cross
caudata	0 %	32 %	0 %	47 %
heldreichii	0	57	0	57
comosa	0	20	0	54
mutica	0	36	0	40
aucheri	8	40	0	20
longissima	96	98	23	26
sharonensis	27	26	86	48
ovata	0	61	0	54
triuncialis	0	25	0	17
biuncialis	0	22	25	58
macrochaeta	0	30	15	67
columnaris	0	19	33	54
kotschyi	88	56	97	40
variabilis	83	48	68	64
cylindrica	71	33	88	78
ventricosa	75	60	87	29
juvenalis	75	63	61	46
triaristata (6x)	0	23	4	74
recta	0	44	19	40
crassa	58	81	46	36
T. dic-des 'pseudojordanicum'	96	83	96	58
'kotschyi'	98	83	97	56
'fulvoyillosum'	98	92	96	54
'arabicum'	98	60	97	57
'spontaneonigrum'	98	49	97	81
'vavilovii'	97	91	96	74
'palestinicum'	94	93	97	68
'spontaneovillosum'	0	75	0	74
'jordanicum'	97	82	97	45
'namuricum'	96	93	94	71

[a] The results were obtained in greenhouse during autumn-winter

almost sterile. The remaining 17 cytoplasms did not show any significant effect on the fertility of either cultivar.

The cytoplasms of *Ae. caudata, Ae. ovata, Ae. triuncialis, Ae. biuncialis, Ae. columnaris* and *Ae. triaristata* were already known to induce complete male sterility in some other common wheat cultivars (Kihara 1951; Fukasawa 1959; Tsunewaki et al. 1976). Induction of complete male sterility in common wheat by seven other cytoplasms, *Ae. heldreichii, Ae. comosa, Ae. mutica, Ae. aucheri, Ae. macrochaeta, Ae. recta* and *T. dicoccoides* var. 'spontaneovillosum', is first reported in this article.

2 *Effects of Eleven Male Sterile Cytoplasms on Various Wheat Characters*

From the 13 male sterile cytoplasms mentioned above, eleven, with the exceptions of the cytoplasms of *Ae. caudata* and *Ae. ovata*, were subjected to an investigation on their effects on various characters of common wheat. The results are summarized in Tablees 3 and 4.

From these results it became possible to classify the eleven cytoplasms into the following three main groups:

First group – This group, corresponding to the C^u plasma type of Tsunewaki et al. (1976), is comprised of the cytoplasms of *Ae. columnaris, Ae. biuncialis, Ae. macrochaeta, Ae. triaristata* (6x) and *Ae. recta* and exhibits a strong growth inhibiting effect on the wheat plant. These cytoplasms reduced culm length, ear length, spikelet number and flag leaf length to a greater extent in 'Penjamo 62' than in 'Siete Cerros 66' (Tables 3 and 4). Delay in heading and increase of ear number by these cytoplasms were of the same magnitude in both cultivars. The delay in heading and decrease of plant height, ear length, spikelet number and flag leaf length are different expressions of depressed growth vigor during the vegetative period that is in part due to chlorophyll variegation. The variegation was manifested as chlorotic stripes in leaves which developed best under fall-winter conditions. The tillering increased compared with the control, the increase being assumed to be a secondary effect of reduced fertility. These peculiarities were expressed with different degrees in different cultivars. This specific interaction was particularly remarkable on flag leaf length and ear length. Pollen fertility and seed fertilities after selfing, open pollination and artificial crossing with the normal pollen of the nucleus donors are collectively shown in Figure 1 with those of the nucleus donors as control. The interaction between the nucleus and the cytoplasm was typically expressed in seed set after selfing (Fig. 1) and in anther development. All alloplasmic lines with the 'Penjamo 62' nucleus, except for two lines with *Ae. recta* and *Ae. macrochaeta* cytoplasms, had strongly deformed anthers without any viable pollen grains; they also did not set any seeds after selfing. The lines with the 'Siete Cerros 66' nucleus on the other hand, showed high selfing fertility even under unfavorable growth conditions during the fall-winter season in the greenhouse. Under the same conditions 'Penjamo 62' with *Ae. recta* cytoplasm also showed some fertility.

Pollen fertilities of the alloplasmic lines of 'Siete Cerros 66' were also high, ranging from 34.2% with *Ae. recta* cytoplasm to 74.5% with *Ae. columnaris* cytoplasm. Sterile pollen grains which did not stain with acetocarmine were large in size but without sperm and vegetative nuclei. Although the percent stainable pollen was high in these lines, their selfed seed fertility was relatively low.

Seed set obtained after pollinating pollen grains of the recurrent parents was normal in all alloplasmic lines of this group. This shows no disturbances by these cytoplasms on female fertility. Seeds obtained were smaller than normal, though plumped, with high germination ability. Twins and pistillody were not observed.

Second group – To this group are classified the cytoplasms of *Ae. heldreichii, Ae. comosa* and *Ae. mutica*. This group is very special and rather variable. Alloplasmic lines of common wheat with these cytoplasms developed more weakly than normal ones, but the depression of growth was not so strong as that observed in the first group. In this connection, *Ae. heldreichii* cytoplasm can be said to be the intermediate between the two groups because it exerted stronger depression effects than the other two of this group.

The interactions of these three *Aegilops* cytoplasms with two common wheat nuclei are rather similar to each other for morphological characters. The data presented in Tables 3 and 4 show that these alloplasmic lines had longer ear and larger number of spikes but in the other characters they were equal or inferior to the recurrent parents. The action of these cytoplasms was very strong on anther development and due to this the stamens usually did not have filament and the anthers contained, in general, no viable pollen. The strongest among the three having this effect was the *Ae. heldreichii* cytoplasm, in which anthers did not develop at all. Anthers in two other cytoplasms were completely sterile. The female fertility estimated by artificial pollination was normal, stigmas developed well with flowers opening normally. Seeds obtained were also normal in appearance with high germination ability. Twins were not produced.

Table 3. Some agronomic characteristics of alloplasmic lines of *T. aestivum* cv. 'Penjamo 62' and their relative differences (in %) from the normal line

Cytoplasm	No. days to heading (after March 31)		Culm length (cm)		Ear length (cm)		No. spikelets/ spike		Flag leaf length (cm)		No. spikes/ plant	
	Average	Rel. diff.	Average	Rel. diff.	Average	Rel. diff.	Average	Rel. diff.	Average	Rel. diff.	Average	Rel. diff.
columnaris	23.1[a]	10	68.8[a]	−19	8.4[a]	−11	14.0[a]	−23	26.0	−10	7.6	12
biuncialis	24.4[a]	16	65.6[a]	−22	8.2[a]	−13	14.6[a]	−19	24.8[a]	−14	7.0	3
macrochaeta	23.7[a]	13	68.6[a]	−19	9.4	0	17.3	− 4	27.9	− 3	7.7	13
triaristata	24.5[a]	17	66.6[a]	−21	8.4[a]	−11	14.4[a]	−20	25.7[a]	−11	8.2	21
recta	20.1	− 4	74.6[a]	−12	9.5	1	16.9	− 7	27.8	− 4	9.0	32
heldreichii	22.0	5	67.9[a]	−20	9.7	3	16.3	−10	30.2	4	10.3[a]	51
comosa	22.6	8	71.0[a]	−16	10.8[a]	15	18.4	2	30.0	4	10.0	47
mutica	22.8	9	74.3[a]	−12	9.7	3	19.4	7	28.7	− 1	10.5[a]	54
aucheri	17.2[a]	−18	79.7	− 6	10.0	6	18.7	3	29.5	2	9.0	32
triuncialis	17.9[a]	−15	79.9	− 6	9.9	5	18.7	3	32.3[a]	12	10.7[a]	57
spontaneovillosum	21.7	3	84.0	− 1	11.0[a]	17	18.8	4	29.2	1	9.7[a]	43
Nucleus donor	21.0		84.6		9.4		18.1		28.9		6.8	

[a] Significantly different from the nucleus donor at the 5% level

Third group – In this group are included the cytoplasms of *Ae. aucheri, Ae. triuncialis* and *T. dicoccoides* var. 'spontaneovillosum'. Their nucleus substitution lines developed almost normally and some heterosis was even expressed in early growth stages. Eventually, this heterosis effect resulted in increased tiller number, ear length and number of spikelets per ear, but culm length slightly decreased.

The most specific in this group was the *Ae. triuncialis* cytoplasm, of which nucleus substitution lines had better growth till heading than control lines. Male sterility was very well expressed with 'Siete Cerros 66'; stigmas did not have filaments and anthers were flat with a few or no viable pollen. Pistillody occurred mainly in the top of the spike. Male sterility was not complete in 'Penjamo 62', showing 0.0-29.9% selfed seed fertility. Mean pollen fertility was 26.2% for this line. Apparently 'Penjamo 62' possesses some fertility restoring gene (s) for *Ae. triuncialis* cytoplasm. Despite of the pistillody female fertility was almost normal.

Ae. aucheri cytoplasm also sterilized completely the pollen of 'Siete Cerros 66'. Anthers developed well, extruding outside the floret during blooming. The line of 'Penjamo 62' with this cytoplasm had some selfed fertility under both summer and winter greenhouse conditions (seed set up to 14.7%). No pistillody was induced. All the lines showed low seed fertility after artificial pollination with normal pollen though stigmas appeared normal. The seed obtained were of normal size and of high germination ability, without producing any twins.

The third cytoplasm of this group, namely, *T. dicoccoides* var. 'spontaneovillosum', caused complete male

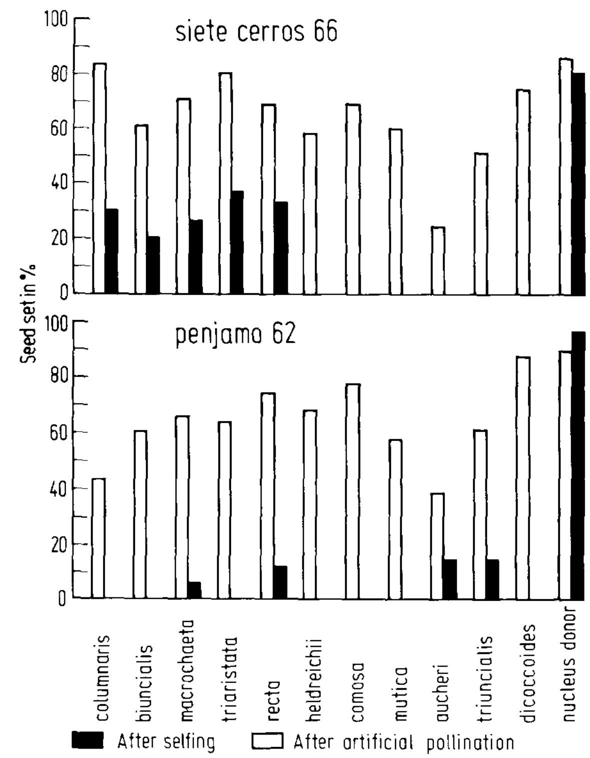

Fig. 1. Seed set of the alloplasmic lines of *T. aestivum* cv. 'Penjamo 62' and 'Siete Cerros 66'

sterility in all the lines without showing any significant side effects on vegetative characters or on development of female generative organs. Thus this cytoplasm appears to be of interest for hybrid wheat breeding. Anthers were usually formed but shriveled, and extruded out from the

Table 4. Some agronomic characteristics of alloplasmic lines of *T. eastivum* cv. 'Siete Cerros 66' and their relative differences (in %) from the normal line

Cytoplasm	No. days to heading (after March 31)		Culm length (cm)		Ear length (cm)		No. spikelets/ spike		Flag leaf length (cm)		No. spikes/ plant	
	Average	Rel. diff.	Average	Rel. diff.	Average	Rel. diff.	Average	Rel. diff.	Average	Rel. diff.	Average	Rel. diff.
columnaris	24.5[a]	26	82.0	– 4	9.2	5	20.5	– 4	31.4	1	7.7	– 5
biuncialis	22.2[a]	14	78.6[a]	– 8	9.6	9	20.4	– 4	33.7[a]	8	8.8	9
macrochaeta	22.0[a]	13	83.3	– 3	9.0	2	18.0[a]	–15	32.0	3	10.0	23
triaristata	23.2[a]	20	74.1[a]	–14	9.5	8	21.1	– 1	35.4[a]	13	9.0	11
recta	24.0[a]	24	76.1[a]	–11	9.5	9	21.4	0	31.6	1	9.2	14
heldreichii	23.5[a]	21	73.9[a]	–14	9.9	13	19.5	– 8	33.3	7	10.4[a]	28
comosa	20.7	7	73.4[a]	–14	10.0	14	20.1	– 6	31.4	1	9.7	20
mutica	22.0	13	79.1	– 8	9.6	9	20.7	– 3	31.0	– 1	9.5[a]	17
aucheri	21.0	8	76.0[a]	–11	10.0[a]	14	21.8	2	32.2	3	8.6	6
triuncialis	21.0	8	80.2	– 6	10.0	14	21.8	2	33.7[a]	8	8.9	10
spontaneovillosum	19.9	3	83.6	– 2	9.4	7	21.6	1	29.4	– 6	8.7	7
Nucleus donor	19.4		85.7		8.8		21.3		31.2		8.1	

[a] Significantly different from the nucleus donor at the 5% level

florets. The pollen fertility was 0 to 0.5% and complete sterility was observed after bagging. Seeds obtained were plump and of a normal size with high germination ability.

Discussion

The present results showed that in parallel with the effects on pollen sterility, the male sterile cytoplasms from eleven species exerted different degrees of effects on various wheat characters, i.e., greatly depressive to neutral on two common wheat cultivars, 'Penjamo 62' and 'Siete Cerros 66'. For better understanding of their physiological and developmental influence as well as their practical values, it is necessary to establish the genetical interrelationships of the cytoplasms among the species under study. According to Maan (1975), Mukai and Tsunewaki (1975) and Tsunewaki et al. (1976) *Ae. umbellulata* is the cytoplasm donor to *Ae. biuncialis, Ae. columnaris* and *Ae. triaristata*. Therefore, it is possible that this species has been the cytoplasm donor to all the species considered to belong to the first cytoplasm group. *Ae. umbellulata* can be easily pollinated by the other species because it is low in height and has florets to open blooming with the same flowering period as the M genome species.

Practical values of this group of the cytoplasms are questioned from the following facts: First, the restoration of male fertility against *Ae. unbellulata* cytoplasm requires two complementary genes (Tsunewaki 1974). Second, this and the related cytoplasms of the *umbellulata* group have strong depressive effects on wheat growth, as revealed by the present investigation and the works of Tsunewaki et al. (1976) as well. However, they can be used for the practical purpose by the following two ways: (a) Transfer of growth restoring genes into male sterile lines with these cytoplasms from their donors or from other sources. The present observations showed that some lines, for instance, 'Siete Cerros 66' with *Ae. biuncialis* cytoplasm grew vigorously. From such lines genes for normal growth can be transferred to other male sterile lines showing depressed growth. (b) Creation of fertility restorer lines, of which *Rf* genes also restore the growth. A similar mechanism to the latter was established for *T. boeoticum* cytoplasm by Maan and Lucken (1970). Some restorer lines we obtained for the cytoplasms of *Ae. columnaris, Ae. biuncialis, Ae. macrochaeta* and *Ae. recta* from their crosses to common wheat showed almost normal vigor with restored fertility (unpubl.).

A comparison of the genetic effects of the first cytoplasm group with those of other groups which also sterilize the pollen without depressing growth and development raises the question about a relationship between the genetic factors controlling male sterility and growth. Some alloplasmic lines showed rather frequently inhibited growth and almost normal fertility, while some others exhibited normal growth and complete male sterility. Among restorer lines which we produced, some showed high levels of both fertility and only partial growth restoration. These considerations lead to an assumption that cytoplasmic factors determining the male sterility and the growth are different from each other.

About the cytoplasms of the second group, it's difficult to determine the perspective of their use for hybrid wheat breeding, especially for *Ae. comosa* and *Ae. heldreichii* cytoplasms. In this relation the *Ae. comosa* cytoplasm seems to be better, because its influences on the growth are significantly less than those of *Ae. heldreichii* cytoplasm. According to such effects *Ae. heldreichii* cytoplasm is somewhat similar to the first group cytoplasms (*umbellulata* group), but its effect on the male fertility is completely different from them. This may mean that their cytoplasms are of different origin. Systematically *Ae. comosa* and *Ae. heldreichii* are very close with each other. Recently it was reported that the F_1 hybrid, *Ae. heldreichii* × *T. durum*, formed unreduced gametes at high frequency, and consequently became self fertile (Maan and Sasakuma 1977). We obtained similar fertile F_1 hybrids between *Ae. comosa* and *T. dicoccum*, resulting in spontaneous amphidiploids with $2n = 42$ (unpubl.). These results indicate the close genetic relation between the two species. On the other hand, the present investigation revealed clear cytoplasmic differences between them. Chennaveeraiah (1960) also found some differences in their chromosome structures. These facts suggest that some genetic differentiation has been taking place between the two species.

According to the inhibitory effects to wheat growth, *Ae. mutica* cytoplasm appears most interesting for hybrid wheat breeding among the three cytoplasms of this group, because it's side effects are very small and the male sterility induced is very stable.

The M genome-species group includes *Ae. heldreichii, Ae. comosa, Ae. mutica* and *Ae. uniaristata*. No success has been made so far to obtain the cytoplasm substitution line of common wheat with *Ae. uniaristata* cytoplasm. Thus, the inhibitory effects on wheat phenotypes of the cytoplasms of three M genome species are in the order of *Ae. heldreichii* > *Ae. comosa* > *Ae. mutica*.

As to the third cytoplasm group, *Ae. triuncialis* and *Ae. aucheri* cytoplasms can be definitely said to be neutral according to their influences on wheat characters. The decreased seed set after artificial pollination may be due to either or both unfavorable conditions during pollination and the presence of some female sterile genes derived from the cytoplasm donors. The latter's effect is more likely to be responsible because the zygotic sterility was reported by Endo and Tsunewaki (1975a) and Maan (1977) in the similar materials.

Concerning the origin of the cytoplasm of *Ae. triuncialis*, Kihara (1966) suggested it was from *Ae. caudata*, but, on the contrary, Endo and Tsunewaki (1975b) showed that the cytoplasm donor should have been *Ae. umbellulata*. A comparative study of the cytoplasms of three strains of *Ae. triuncialis*, which were independently introduced into common wheat by K. Tsunewaki, S.S. Maan and I. Panayotov, indicated that the cytoplasm introduced by the first author is similar to *Ae. umbellulata* cytoplasm, while the cytoplasm introduced by two other authors resemble that of *Ae. caudata* (Mukai et al. 1978), thus indicating the possible diphyletic origins of *Ae. triuncialis*. The present investigation revealed that *Ae. triuncialis* cytoplasm differed genetically from the cytoplasms of *umbellulata* group, further confirming the results of Mukai et al. (1978).

The genetic relation of *Ae. aucheri* cytoplasm to those of other Sitopsis species is not established yet. This species is generally treated as a variety of *Ae. speltoides*. Maan and Lucken (1971a) showed that *Ae. speltoides* cytoplasm is sterile for common wheat, but according to Suemoto (1973) and Tsunewaki et al. (1976) this cytoplasm is not sterile and is almost identical with 4× and 6× wheat cytoplasms. These cytoplasmic relationships among the species concerned are connected with the origin of B genome in polyploid wheats, of which still different opinions exist among the researchers. The difference between those reports is possibly due to genetical and geographical differentiation of the cytoplasm in *Ae. speltoides-Ae. aucheri* complex.

Such differentiation on chromosomal and cytoplasmic levels can be typically seen among the species of *Timopheevi* complex. Maan and Lucken (1972) found that the cytoplasm of *T. dicoccoides* var. 'nudiglumis' sterilizes the pollen of common wheat as *T. timopheevi* does. Tanaka and Ichikawa (1972) reported genetic differences among *T. araraticum* strains. In the present study ten varieties of *T. dicoccoides* were used, among which only one cytoplasm of var. 'spontaneovillosum' sterilized the common wheat. All other cytoplasms gave normal fertility and growth. Generally accepted genome formula to *T. dicoccoides* is AABB (Kihara 1924). However, according to Wagenaar (1966) and Maan (1973) some forms of this species of Iraq origin have the genome formula AAGG (or, if the genome of the cytoplasm donor should be written first, GGAA) and are closely related with *T. timopheevi*. Thus, it can be admitted that *T. dicoccoides* has originated in two different ways in different geographical areas. This assumption is supported by the finding that male sterility caused by *T. dicoccoides* var. 'spontaneovillosum' and var. 'nudiglumis' is similar to that induced by *T. timopheevi* cytoplasm.

For the realization of hybrid wheat, it is necessary to improve the present *T. timopheevi*'s sterility-fertility restoration system or to replace it with a new, more suitable system, because the present system requires a rather large number of fertility restoring genes for the complete restoration of male fertility with some deleterious, though not so obvious, side effects to agronomic characters of wheat. Basic studies on the genetic relationship of the cytoplasm between different species in the subtribe *Triticinae* will be the main step to break through this problem.

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