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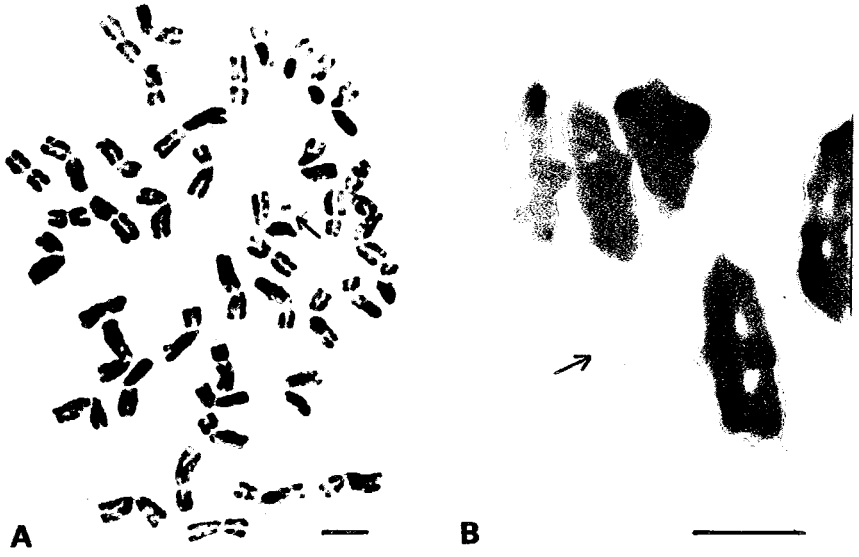
WHEAT INFORMATION SERVICE



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Wheat Information Service

Kihara Institute for Biological Research

Yokohama, Japan

Contents

Dr. Hitoshi KIHARA
(1893—1986)

It is our great sorrow that

Dr. Hitoshi KIHARA

Chairman of Wheat Information Service,
Members of Academy of Japan and other countries,
Emeritus Professor of Kyoto University,
Founder and Emeritus Director of Kihama Institute,
Former Director of National Institute of Genetics (Japan),
and, especially,
wheat geneticist

passed away on 27 July, 1986 at the age of 92.

It is needless to mention his great contributions to plant science, but just to state that we have to succeed heritage of wheat genetics from him for his memory and for the development of wheat study.

Masatake Tanaka

I. Research Notes

Identification of reciprocal translocation chromosome types in the emmer wheats. II. Thirty eight strains of *Triticum dicoccoides* Körn. with the fundamental chromosome structure.[1)]

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In the first paper of this series, Kawahara & Tanaka (1978) analyzed 22 strains of *Triticum dicoccoides* Körn. and found three chromosome types which differed by reciprocal translocations. This paper reports on the configurations of chromosome pairing in hybrids between strains of *T. dicoccoides* with the E_1 type chromosome structure.

The materials used were 38 strains of *T. dicoccoides* from Israel, Syria, Turkey, Iraq and Iran (Table 1). Two tester strains of the earlier repoer (Kawahara & Tanaka 1978), 108-3 and 108-5, were also used. Chromosome pairings were observed at first metaphase (MI) of the pollen mother cells with the aceto-carmine or aceto-orcein squash technique. In total, chromosome pairings of 70 hybrids were analyzed.

Table 2 shows the percentage of cells with multivalents in the F_1 hybrids. Results obtained by Kawahara & Tanaka (1978) are included in the table for comparison.

It is clear from Table 2 that most of the hybrids showed little or no multivalents at MI. This indicates the absence of a major reciprocal translocation between the two parental strains. In seven hybrid combinations, however, the frequency of multivalents (trivalents and quadrivalents) was rather high, *i.e.*, more than 30 percent. The combinations were 1921 x 108-2, 1978B x 108-3, 8541 x 108-3, 8737 x 108-3, 8816A x 108-2, 8941 x 108-2 and 8943 x 108-3. All of them were hybrids with 108-2 or 108-3. Since the average frequency of multivalents was not so high as that obtained in hybrids heterozygous for major translocations (Kawahara in preparation), these two strains were regarded to have one minor translocation as discussed below. Consequently, the chromosome structure of all the 38 strains listed in Table 1 were grouped into type E_1, 18 strains of which were newly identified in the present study.

As mentioned above, when 108-2 or 108-3 was used in the crosses, the frequency of multivalents was relatively high in the hybrids. On the other hand, when 108-5 was crossed to the common female parent as 108-2 or 108-3, the frequency of multivalents was low or they were not observed at all (Table 2). Among these three strains, no multivalent was observed in a hybrid 108-2 x 108-3 but in 108-5 x 108-3, a quadrivalent was observed at a very low frequency (1.6%). These observations would indicate that there is a minor translocation between 108-2 or 108-3 and several other strains including 108-5. Type E_1 was thus considered to be heterogeneous for

1) Adapted from a thesis submitted to the Kyoto University, Kyoto (Kawahara 1984).

minor translocations. An attempt was made to identify chromosome types differing with minor translocations. As shown in Table 2, no multivalent was found in the hybrids between 108-5 and 8541, 8736B, 8935, 8937B or 8943, but the frequency of multivalents varied greatly (0.0 – 36.4%) in the hybrids between 108-3 and these strains. That is, the frequency of quadrivalents produced by the estimated minor translocation varied greatly in different hybrid combinations. Therefore, for the sake of accuracy, each strain was classified into a subtype only when two or more hybrids were available.

Table 1. List of *T. dicoccoides* strains used

Strain No. (KU–)	Locality or source
108-1	unknown
108-2, 108-3	20 km NW of Sueida (Cheikh Meskine - Sueida), Syria
108-4, 108-5	Collection of MacKey, by Yamashita (1964)
110	Vavilov (1930), Suburbs of Tiberia, Palestine, Israel
198	Aaronsohn (1906), Mt. Canaan, Palestine, Israel
1921	155 km W of Mardin (Urfa - Mardin), Turkey
1947, 1948, 1951, 1953, 1955, 1959A, 1959B, 1972B, 1974, 1976B, 1978B, 1991	45 km SE of Maras (Maras - Gaziantep), Turkey
8536, 8539, 8541	20.3 km S from Sulaymaniyah to Qara Dagh, NE slope of Shakh i Baranan, Iraq
8736A, 8736B, 8737	SSW of Rowanduz, Iraq (alt. 850m)
8804, 8808, 8816A, 8816B, 8817	North slope of Jabal Sinjar, South of Kursi, Iraq
8821A, 8821C	15.3 km ENE from Dohuk to Amadiyah, Iraq (alt. 780m)
8935, 8937B	9.3 km SE from Ergani to Diyarbakir, Turkey (alt. 780m)
8941, 8942, 8943	58.8 km N from Kermanshah to Ravansar, Iran (alt. 1610m)

First, 108-5 and 108-3 were chosen as the standard E_{1a} and E_{1b} strain, respectively, based on the observations described above. Strains 8541, 8736B, 8935 and 8943 were classified into type E_{1a} because no multivalent was observed in hybrids with 108-5 but multivalents were observed at a low frequency in hybrids with 108-3. Also, 8536, 8736A, 8817 and 8821C were included into the E_{1a} type since no multivalent was observed in two or more hybrids with 108-5 or other E_{1a} strains mentioned above. No multivalent was formed in hybrids between the three strains, 1959B, 1976B and 1978B. This indicates the absence of a translocation between them. In the hybrid 1959B × 8536, no multivalent was formed but a quadrivalent was observed at a low frequency in hybrids between 1976B or 1978B and 108-3. Therefore, these three strains were also classified into type E_{1a}. Based on a similar rationale, 108-2 was included into E_{1b}. The average frequency of cells with multivalents in 11 hybrids between E_{1a} and E_{1b} was 16.3% (1.6 – 36.4%).

By the minor reciprocal translocation carried by 108-2 and 108-3, strains of *T. dicoccoides*

Table 2. Frequency of multivalents in F_1 hybrids between strains of *T. dicoccoides*

Cross combination	Type	No. of cells observed	Frequency of multivalents (%)
108-1 × 108-3*	E_1 × E_{1b}	50	1IV 4.0
108-2 × 108-3*	E_{1b} × E_{1b}	50	none
108-3 × 1978B	E_{1b} × E_{1a}	54	1IV 9.3, 1III 1.9
108-3 × 8808	E_{1b} × E_1	66	1IV 19.7
108-4 × 108-3	E_1 × E_{1b}	38	1IV 10.5, 1III 10.5
108-5 × 108-3*	E_{1a} × E_{1b}	64	1IV 1.6
110 × 108-3*	E_1 × E_{1b}	83	1IV 2.4
198 × 108-2	E_1 × E_{1b}	23	1IV 17.4
1921 × 108-2	E_1 × E_{1b}	33	1IV 54.5, 1III 9.1
1921 × 8817	E_1 × E_{1a}	33	1IV 9.1, 1III 3.0
1947 × 8935	E_1 × E_{1a}	33	none
1948 × 108-3	E_1 × E_{1b}	74	1IV 23.0
1948 × 1921	E_1 × E_1	33	1IV 3.0
1951 × 108-3	E_1 × E_{1b}	33	none
1953 × 8953	E_1 × E_{1a}	33	none
1955 × 1991	E_1 × E_1	33	none
1959A × 8937B	E_1 × E_1	33	1IV 3.0
1959B × 1921	E_{1a} × E_1	33	1IV21.2
1959B × 8536	E_{1a} × E_{1a}	33	none
1972B × 108-3	E_1 × E_{1b}	34	1IV 14.7, 1III 2.9
1974 × 1991	E_1 × E_1	33	none
1976B × 108-3	E_{1a} × E_{1b}	28	1IV 7.1
1976B × 1959B	E_{1a} × E_{1a}	33	none
1976B × 1978B	E_{1a} × E_{1a}	33	none
1978B × 108-3	E_{1a} × E_{1b}	50	1IV 28.0, 1III 2.0
1978B × 1959B	E_{1a} × E_{1a}	33	none
1991 × 108-3	E_1 × E_{1b}	34	1IV 5.9, 1III 2.9
8536 × 108-2*	E_{1a} × E_{1b}	58	1IV 10.3
8536 × 108-5	E_{1a} × E_{1a}	27	none
8536 × 8821C	E_{1a} × E_{1a}	34	1IV 2.9
8536 × 8943	E_{1a} × E_{1a}	25	none

Table 2. Frequency of multivalents in F1 hybrids between strains of *T. dicoccoides* (continued)

cross combination	Type	No. of cells observed	Frequency of multivalents (%)
8539 × 108-3*	E_1 × E_{1b}	50	1IV 2.0
8541 × 108-3	E_{1a} × E_{1b}	33	1IV 30.3, 1III 6.1
8541 × 108-5*	E_{1a} × E_{1a}	50	none
8736A × 108-5*	E_{1a} × E_{1a}	50	1IV 2.0
8736A × 8536	E_{1a} × E_{1a}	22	none
8736A × 8817	E_{1a} × E_{1a}	50	1IV 4.0
8736A × 8821C	E_{1a} × E_{1a}	50	1IV 2.0
8736A × 8943	E_{1a} × E_{1a}	37	none
8736B × 108-3*	E_{1a} × E_{1b}	50	1III 6.0
8736B × 108-5*	E_{1a} × E_{1a}	50	none
8737 × 108-3	E_1 × E_{1b}	25	1IV 40.0
8737 × 108-5	E_1 × E_{1b}	74	1IV 10.8, 1III 1.4
8804 × 108-3*	E_1 × E_{1b}	50	none
8816A × 108-2	E_1 × E_{1b}	28	1IV 21.4, 1III 10.7
8816B × 108-3*	E_1 × E_{1b}	50	1IV 4.0
8817 × 108-2	E_{1a} × E_{1b}	29	1IV 10.3
8817 × 108-5*	E_{1a} × E_{1a}	50	none
8817 × 8536	E_{1a} × E_{1a}	50	none
8817 × 8821C	E_{1a} × E_{1a}	50	none
8817 × 8935	E_{1a} × E_{1a}	23	none
8817 × 8943	E_{1a} × E_{1a}	50	none
8821A × 108-3*	E_1 × E_{1b}	50	1IV 6.0
8821C × 108-3	E_{1a} × E_{1b}	66	1IV 15.2
8821C × 8943	E_{1a} × E_{1a}	50	1IV 4.0
8935 × 108-3*	E_{1a} × E_{1b}	54	1IV 13.0, 1III 1.9
8935 × 108-5*	E_{1a} × E_{1a}	50	none
8935 × 8536.	E_{1a} × E_{1a}	50	none
8935 × 8736A	E_{1a} × E_{1a}	50	none
8935 × 8821C	E_{1a} × E_{1a}	50	none
8935 × 8943	E_{1a} × E_{1a}	50	none
8937B × 108-3*	E_1 × E_{1b}	50	none

Table 2. Frequency of multivalents in F_1 hybrids between strains of *T. dicoccoides* (continued)

Cross combination	Type	No. of cells observed	Frequency of multivalents (%)
8937B × 108-5*	E_1 × E_{1a}	50	none
8941 × 108-2	E_1 × E_{1b}	55	1IV 54.5, 1III 3.6
8941 × 108-5*	E_1 × E_{1a}	50	1IV 4.0
8942 × 108-2	E_1 × E_{1b}	24	1IV 20.8, 1III 4.2
8942 × 108-3	E_1 × E_{1b}	50	1IV 20.0, 1III 2.0
8943 × 108-3	E_{1a} × E_{1b}	33	1IV 30.3, 1III 6.1
8943 × 108-5*	E_{1a} × E_{1a}	50	none
8943 × 8536	E_{1a} × E_{1a}	50	none

* Data obtained by Kawahara and Tanaka (1978).

Table 3. Classification of the present materials into two subtypes by a minor reciprocal translocation (Kawahara 1984)

Subtype	Strain No.
E_{1a}	108-5, 1959B, 1976B, 1978B, 8536, 8541, 8736A, 8736B, 8817, 8821C, 8935, 8943
E_{1b}	108-2, 108-3
Unidentified	108-1, 108-4, 110, 198, 1921, 1947, 1948, 1951, 1953, 1955, 1959A, 1972B, 1974, 1991, 8539, 8737, 8804, 8808, 8816A, 8816B, 8821A, 8937B, 8941, 8942

were classified into the two subtypes, E_{1a} and E_{1b}, and an unidentified group (Table 3). Twelve of the 38 strains used in the present study belonged to type E_{1a} and two to E_{1b}. Of the two subtypes of E_1, E_{1b} was restricted to a single locality, Sueida in Syria, but E_{1a} was found in six localities in Turkey, Iraq and Iran.

The wide geographical distribution of E_{1a} strongly suggests that it is the fundamental chromosome structure of type E_1. Since type E_1 is believed to be the fundamental chromosome structure of *T. dicoccoides* (Kawahara and Tanaka 1981, 1983), E_{1a} may be the most fundamental and primitive chromosome structure of this species.

Acknowledgement

Thanks are due to Dr. M. Tanaka for his critical reading of the manuscript.

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Male fertility restoration against various alien cytoplasms. I. Comparison between the restoration abilities of three groups of lines

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Various sources of male sterility-inducing cytoplasms with origin from different *Triticum* and *Aegilops* species are available at present, but, nevertheless, the hybrid wheat breeding programmes on world-wide scale make use mainly of the cytoplasm of *T. timopheevi* (WILSON & ROSS 1962). By far, many authors had pointed out the complications that might arise from relying on a single source of male sterility. It is highly desirable then, to broaden the genetic basis of the male sterility-fertility restoration system in wheat by inclusion of other CMS-sources.

The results presented in this paper are part of a study on the phenotypic effects and male fertility-restoration systems of various alien cytoplasms.

Materials and Methods

Two common wheat cultivars, Aurora and Roussalka, were used as recurrent pollen parents for the production of the male sterile (MS) lines. The following *Triticum* and *Aegilops* species served as donors of the alien cytoplasms: *Aegilops triuncialis, Ae. mutica, Ae. comosa, Ae. speltoides* and *Triticum dicoccoides* var. *spontaneovillosum*. They exert neutral or slightly negative effect on the wheat phenotype (PANAYOTOV 1980) and as such, they might be included in hybrid wheat breeding as alternative sources of male sterility. The MS lines of Aurora and Roussalka with the cytoplasm of *T. timopheevi* were included in the experiment for comparison.

The alloplasmic lines were produced and maintained by one of the authors (Panayotov). At the beginning of the study they were in BC_4–BC_9 generation.

In an attempt to discover male fertility-restoring genes against the above mentioned cytoplasms we studied three groups of lines. First, we surveyed a group of 20 common wheat cultivars (or advanced true-bred lines). The other two groups consisted of restorers of male fertility, whose Rf-genes orginated from various *Triticum* and *Aegilops* species.

Crosses were made between the male sterile lines as female parents and the common wheat cultivars or the R-lines as pollen donors. The F_1 generation was grown either in the greenhouse or in the field (depending on the type of the R-line) and 2 to 3 spikes per plant were bagged before anthesis. The level of male fertility restoration was estimated as percentage of the seeds set in the 1st and 2nd florets of each spikelet.

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Table 1. Selfed seed fertilities (%) in F_1 hybrids between MS lines with different alien cytoplasms and the first group of fertility restorers

R-line		Cytoplasm					
Line No.	Rf-gene donor	*triunc.*	*mutica*	*comosa*	*dicoc.*	*spelt.*	*timoph*
R-1	*Aegilops macrochaeta*	2.4	0.0	0.0	4.6	1.0	2.1
R-5	*Aegilops triuncialis*	10.6	1.1	0.0	0.0	0.0	0.0
R-7	*Aegilops triaristata*	0.0	0.0	0.0	0.0	0.0	0.0
R-8	*Aegilops aucheri*	0.0	0.0	0.0	0.0	0.0	0.0
R-9	*Aegilops caudata*	28.4	0.0	0.0	0.0	0.0	0.0
R-11	*Aegilops biuncialis*	0.0	0.0	–	8.4	0.0	0.0
R-16	*Aegilops columnaris*	0.0	0.0	0.0	0.0	0.0	0.0
R-17	*Aegilops recta*	51.4	2.4	5.2	0.0	0.2	0.0
R-56	*Triticum dicoccoides* var. *spontaneovillosum*	6.6	55.2	0.0	8.8	0.9	5.9
R-68	*Triticum monococcum* var. *flavescens*	22.3	0.2	0.0	4.7	0.0	27.0

Table 2. Levels of male fertility restoration (%) in F_1 hybrids between MS lines of Aurora and Roussalka with different alien cytoplasms and R-17127, R-3206-143 and R-3169-5

MS-line	R-line			Average
	R-17127	R-3206-143	R-3169-5	
(*timoph*) – Aurora	90.8	63.3	–	77.0
(*timoph*) – Roussalka	76.8	79.3	73.9	76.6
(*dicoc*) – Aurora	69.2	31.8	–	50.5
(*dicoc*) – Roussalka	55.6	59.2	77.6	64.1
(*spelt*) – Aurora	51.4	21.8	–	36.6
(*spelt*) – Roussalka	–	73.0	–	–
(*triunc*) – Aurora	71.6	33.6	–	52.6
(*triunc*) – Roussalka	0.0	13.4	0.0	4.4
(*mutica*) – Aurora	0.0	–	–	0.0
(*mutica*) – Roussalka	0.0	0.7	0.1	0.3
(*comosa*) – Aurora	0.0	0.1	–	0.0
(*comosa*) – Roussalka	0.0	0.2	–	0.0

Note) The Rf-genes of all three R-lines originate from *T. timopheevi*.

Results and Discussion

The following 20 common wheat cultivars or advanced true-bred lines were tested for presence of fertility-restoring genes against various alien cytoplasms, namely, Zlatna dolina, Vratsa, Charodeika, Skitiya, Preslav, Jubilei, Kaloyan, Zenith, Pliska, Zlatoklas, Trakiya, Bezostaya 1, Kubrat, Kiten, 780-124, 19-16-98, 76-76, 609-144, 203-206 and 13 A-305. In the majority of the cases the F_1 hybrids between these cultivars and the MS lines with the cytoplasms of *Ae. triuncialis, Ae. mutica, Ae. comosa, Ae. speltoides, T. dicoccoides* var. *spontaneovillosum* and *T. timopheevi* were completely sterile; the low levels of selfed seed fertility (between 0.2 and 4.6%), observed in some of the hybrids were most probably due to failure in timely bagging. It is clear that the frequency of Rf-genes against the tested CMS-sources is very low, at least among the Bulgarian-bred common wheat cultivars and as such they should be regarded as maintainers of sterility.

The first group of fertility restorers tested in the present study comprised of the ten R-lines listed in Table 1. They were selected as fertile plants in the course of the backcross procedure used for the production of the alloplasmic lines and subsequently selfed to obtain the Rf-gene(s) in homozygous condition. The selfed seed fertilities of the F_1 hybrids between this group of restorers and the MS lines are also given in Table 1. It might be pointed out that, with two exceptions, these R-lines are ineffective or possess very weak male fertility-restoring genes against the cytoplasms of *Ae. triuncialis, Ae. mutica, Ae. comosa, Ae. speltoides, T. dicoccoides* var. *spontaneovillosum* and *T. timopheevi.* The lines R-17 and R-56 restored moderate levels of male fertility (51.4 and 55.2%, respectively) in their hybrids with male sterile wheat with *Ae. triuncialis* and *Ae. mutica* cytoplasms. Male fertility-restoring genes against the cytoplasm of *Ae. triuncialis* could be found in a number of diverse sources, e.g. not only in *Ae. recta* (R-17), but also in *Ae. caudata* (R-9) and *T. monococcum* (R-68), as well as in *Ae. triuncialis* (R-5) itself. The cytoplasm of *Ae. triuncialis,* available at the Institute for Wheat and Sunflower derives its origin from *Ae. caudata* (MUKAI *et al.* 1978) and it was assigned by Tsunewaki (1980) to the same plasma type (C) as its donor. It is quite natural then, that the species, donor of the sterile cytoplasm, harbors male fertility-restoring genes against that same cytoplasm.

The second group of R-lines consisted of R-17127, R-3206-143 and R-3169-5. They were produced by the breeding method, which is usually employed for the production of common wheat cultivars, but the whole procedure is carried out on the basis of *T. timopheevi* cytoplasm. As a consequence, these R-lines manifest high selfed seed fertility, short stem, strong disease resistance and very good grain quality.

The levels of male fertility-restoration in the F_1 hybrids between R-17127, R-3206-143 and R-3169-5 and the MS lines, included in the present investigation, are given in Table 2. Although the results differ between hybrids, it is clear that the R-lines show the highest efficiency against the cytoplasm of *T. timopheevi.* The level of male fertility restoration in the cross-combination MS (*timopheevi*)—Aurora × R-17127 (90.8%) is even higher than the selfed seed fertility of euplasmic Aurora. The other two R-lines are slightly less effective against the cytoplasm of *T. timopheevi,* when compared with R-17127.

A common feature of the R-lines, selected for the cytoplasm of *T. timopheevi,* is their ability

to restore male fertility against the cytoplasms of *Ae. speltoides* and *T. dicoccoides* var. *spontaneovillosum*. These three cytoplasms belong to the same plasma type (G) and our results are an evidence in proof of their common origin and the similarity of their male fertility restoration mechanisms.

Our data show that lines R-17127 and R-3206-143 restore male fertility against the cytoplasm of *Ae. triuncialis* in combination with the nucleus of Aurora but not with the nucleus of Roussalka. This means that the ability of one R-line to restore male fertility against some source of CMS should be understood in terms of the specific combination between alien cytoplasm, restorer genes and specific genetic background. Luhe *et al.* (1982) also showed that the common wheat cultivar Prof. Marchal, which carries Rf-genes for the cytoplasm of *T. timopheevi* can restore male fertility against the cytoplasm of *Ae. triuncialis*.

The data in Table 2 reveal that the restorers for the cytoplasm of *T. timopheevi* are not effective against the CMS, induced by the cytoplasms of *Ae. mutica* and *Ae. comosa*.

Conclusions

The comparison between the male fertility-restoration abilities of 3 groups of lines, i.e. true-bred cultivars, R-lines derived from fertile plants which were found in the course of the backcross procedure, and fertility restorers selected in the hybrid wheat breeding programme proved that the third group shows the highest efficiency. Our study revealed that effective restorer lines against the cytoplasm of *T. timopheevi* had already been produced in the Institute for Wheat and Sunflower, Bulgaria and they can be used as a basis for further improvement and breeding of R-lines against the cytoplasms of *T. dicoccoides* var. *spontaneovillosum* and *Ae. speltoides*.

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Allelic variation at the crossability loci in wheat (*Triticum aestivum*)

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The crossability of hexaploid wheat (*Triticum aestivum*) with rye (*Secale cereale*) has been shown to be controlled by three loci, designated Kr_1, Kr_2 (LEIN 1943) and Kr_3 (KROWLOW 1970), located on chromosomes 5B, 5A (RILEY & CHAPMAN 1967) and 5D (KROWLOW 1970) respectively. LEIN (1943) demonstrated that the dominant alleles at the Kr_1 and Kr_2 loci reduced crossability, with Kr_1 having a greater effect than Kr_2. A high positive correlation between the crossability of wheat with rye and *Hordeum bulbosum* has also been demonstrated (FALK & KASHA 1981; SITCH *et al.* 1985; SNAPE *et al.* 1979) and genetic studies involving comparisons of the crossability of the Chinese Spring (Hope) single chromosome substitution lines (SNAPE *et al.* 1979) and of recombinant lines for the Kr_1 locus, with rye and *H. bulbosum* (SITCH *et al.* 1985) confirm that the *Kr* loci control the crossability of wheat with both pollen parents.

An examination of the *H. bulbosum* and the rye crossability of the single chromosome substitution lines of the non-crossable varieties, Hope, Atlas 66 and Cheyenne into Chinese Spring, for all the homoeologous group 5 chromosomes by FALK & KASHA (1983) indicated that there may be multiple alleles for reduced crossability on chromosomes 5A and 5B. However, no evidence was found for variation at the Kr_3 locus on chromosome 5D of these varieties. The only significant evidence of a third crossability gene was obtained by FEDAK & JUI (1982), in pollinations of barley (*Hordeum vulgare*) cv. Betzes with the Chinese Spring (Hope) substitution lines.

This paper describes an investigation designed to ascertain whether there is any evidence of multiple allelism at the *Kr* loci of the non-crossable varieties Hope and Cappelle-Desprez and to determine whether different Kr_3 alleles exist in these varieties from that in Chinese Spring, from a study of the *H. bulbosum* crossability of the group 5 substitution lines of these varieties into Chinese Spring.

Materials and Methods

The single chromosome substitution lines of the group 5 homoeologous chromosomes of the varieties Hope and Cappelle Desprez into Chinese Spring were produced by Professor E. R. Sears, University of Missouri, Columbia, Missouri, U.S.A. and by Dr. C. N. Law and Mr. A. J. Worland, Plant Breeding Institute, Cambridge, England, respectively. SNAPE *et al.* (1979) demonstrated that these two donor varieties are non-crossable with tetraploid *H. bulbosum*. All *H. bulbosum* pollinations were made using the tetraploid *H. bulbosum* clone PB168, originally obtained from

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Dr. D. B. H. Sparrow, from the Turkey collection CPI 18968, entry number 73/3.

The chromosome 5D substitution lines were vernalized for two weeks, at 4°C with an 8-hour daylength, to promote flowering because both donor varieties possess winter alleles at the Vrn_3 locus on chromosome 5D controlling vernalization requirement (LAW *et al.* 1976). The *H. bulbosum* clones were vernalized under identical conditions for 8 weeks to promote flowering, and grown, together with the wheat genotypes, in an unheated glasshouse during the summer.

All crossing procedures were carried out as described by SITCH *et al.* (1985) on 12 spikes per genotype. The percent seed set was established for each spike individually and then averaged over contributing spikes. The statistical analysis was carried out using data transformed to angles.

Table 1. The mean *H. bullbosum* crossability of the Chinese Spring (Hope) and the Chinese Spring (Cappelle-Desprez) homoeologous group 5 single chromosome substitution lines and of Chinese Spring

	Variety		Chromosome Mean
	Hope	Cappelle-Desprez	
Chromosome 5A	15.3* (i)	6.6***	10.9
5B	2.5***	7.3*** (ii)	4.9
5D	29.9 NS	19.2 NS	24.5
Variety Mean	15.9	11.0	
Chinese Spring	23.0		

(i) Significant differences from Chinese Spring, as determined from transformed percentage data

(ii) Cappelle-Desprez contains the 5BS-7BS/5BL-7BL translocation and consequently this substitution line is for the 5BL-7BL chromosome.

Significance levels: NS = not significant, *= p=0.05 - 0.01, *** = p<0.001

Results

The table of means of Chinese Spring and the six substitution lines and the analysis of variance for seed setting ability are shown in Tables 1 and 2 respectively. The seven genotypes differed significantly in seed setting ability. The seed set obtained on the 5A and the 5B chromosome substitution lines of Hope and Cappelle-Desprez was significantly lower than that obtained on Chinese Spring. The crossability of the 5D substitution lines, however, was not significantly different from Chinese Spring. This implies either that Hope and Capelle-Desprez possess an allelle of small effect at the third crossability locus, Kr_3, on chromosome 5D or that, in these varieties, this locus is represented by an allele equivalent to that of Chinese Spring.

The variation in crossability of the six substitution lines was partitioned into the main effects of the three chromosomes, of the two varieties and the interaction between these two main effects, Table 2.

Table 2. The analysis of variance of *H. bulbosum* crossability (percent seed set, transformed to angles) of the Chinese Spring (Hope) and the Chinese Spring (Cappelle-Desprez) homoeologus group 5 single chromosome substitution lines

Item	df	MS	VR	
Between lines (including Chinese Spring)	6	1024.23	17.433	***
Between lines (excluding Chinese Spring)	5	1043.26	17.758	***
between chromosomes	2	2077.34	35.359	***
5B v remainder	1	2537.27	43.188	***
5A v 5D	1	1617.40	27.530	***
between varieties	1	147.01	2.502	NS
chromosome-variety interaction	2	457.30	7.784	***
5B v remainder	1	904.18	15.390	***
5A v 5D	1	10.43	0.177	NS
Within lines	77	58.75		

Significance levels: NS = not significant, *** $p < 0.001$

The overall crossability of chromosomes 5A, 5B and 5D differed significantly, the 5D chromosome substitution lines having the highest crossability and the 5B chromosome substitution lines the lowest. The variation between chromosomes was further partitioned to allow a comparison between chromosome 5B and the remaining chromosomes, and between chromosomes 5A and 5D. This indicated that a large proportion of the variation in the overall crossability was attributable to the severe reduction in percent seed set caused by Kr_1 on chromosome 5B. However, the allele Kr_2, on chromosome 5A, also contributed towards this variation since the overall crossability of the 5A substitution lines was significantly lower than that of the 5D substitution lines.

An overall comparison of the crossability of the substitution lines derived from Hope and from Cappelle-Desprez showed that the mean of the group 5 chromosome substitutions did not differ significantly. However, the significance of the interaction implies allelic variation between the homoeologous chromosomes of Hope and Cappelle-Desprez. A partitioning of this variation into a comparison between chromosome 5B and the remaining chromosomes, and between chromosomes 5A and 5D, revealed that the allelic variation between Hope and Cappelle-Desprez was attributable to allelic differences at both the Kr_1 and Kr_2 loci. The Kr_1 allele on chromosome 5B of Hope was significantly ($p < 0.05$) more potent than that of Cappelle-Desprez in suppressing crossability. In contrast, the Kr_2 allele from Hope was significantly ($p < 0.05$) less effective than that from Cappelle-Desprez.

Discussion

This investigation indicates that allelic variation probably exists at the Kr_1 and Kr_2 loci of the non-crossable varieties, Hope and Cappelle-Desprez. The similar study by FALK & KASHA (1983) using the group 5 chromosome substitution lines of Hope, Atlas 66 and Cheyenne into Chinese Spring also showed that the chromosomes carrying crossability genes differed in potency depending on the donor variety (FALK & KASHA 1983). Although other modifier genes on the substituted chromosome could have led to variation in the expression of the *Kr* genes, FALK & KASHA (1983) interpreted the results as possible evidence for the existence of a multiple allelic series at the *Kr* loci and this is also suggested by the data described here.

One method of overcoming the incompativility caused by the crossability genes is to back-cross the recessive crossability gene, Kr_1, from a crossable variety such as Chinese Spring, into the non-crossable variety (SNAPE & SIMPSON 1980). If this technique is to be used, it is important to ascertain the degree of allelic variation at the crossability loci of the recipient variety. In the case of Cappelle-Desprez, for example, the dominant alleles Kr_1 and Kr_2 are equally effective and consequently the substitution of Kr_1 of Chinese Spring into Cappelle-Desprez would make Cappelle-Desprez crossable, but only at a very low level.

From this study, the third *Kr* allele, Kr_3, of both Hope and Cappelle-Desprez appeared to be incapable of significantly reducing the crossability of Chinese Spring. In other studies, Chinese Spring (Hope 5D) showed a slight but again statistically non-significant reduction in seed setting ability, relative to Chinese Spring, in pollinations with rye (RILEY & CHAMPMAN 1967) and *H. bulbosum* (SNAPE *et al.* 1979).

The absolute values of the crossability of the substitution lines for Hope chromosomes 5A, 5B and 5D with *H. bulbosum* vary between the studies made by FALK & KASHA (1983), by SNAPE *et al.* (1979) and that described here. The highest seed set values were obtained by FALK & KASHA (1983) of 28, 4 and 50% for the three substitution lines respectively. The results obtained here were slightly lower; being 15.3, 2.5 and 29.9% seed set respectively. The lowest levels of seed set were obtained by SNAPE *et al.* (1979), of 4.9, 0.0 and 9.8%. These differences may reflect differences in the presence or absence of post-pollination applications of gibberellic acid (GA) or other environmental influences. In both the present investigation and in that of FALK & KASHA (1983) post-pollination GA applications were made one day after pollination and for three consecutive days after pollination respectively. The higher seed sets obtained by FALK & KASHA (1983) may reflect the greater number of GA applications. The lower seed sets obtained by SNAPE *et al.* (1979) may result from the lack of a post-pollination GA application, since previous investigations have shown that the application of GA has a stimulatory effect on pollen tube growth (LARTER & CHAUBEY 1965), the frequency of fertilization (SITCH & SNAPE 1986) and seed set (SITCH 1984).

Acknowledgements

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Location of gene(s) for branched spike character in a selection of bread wheat

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Branched spike character in *T. aestivum* has been reported by Sharman (1944), Tsitsin (1963), Swaminathan *et al.* (1966), Koric (1967, 1971, 1974 and 1978) and Singh and Joshi (1983). Recently cytological studies made by Singh and Joshi (1983) has revealed that branched spikes in bread wheat were trisomics ($2n = 43$). It was suggested that branching of spike in bread wheat (*T. aestivum*) may be the result of triplication of a particular gene(s) involved in spike formation.

In the present study an attempt was made to locate the gene(s) on specific chromosome in the branched material developed by Singh and Joshi (1983). For this purpose tetrasomic plants ($2n = 44$) with branched spikes (isolated by Singh and Joshi, 1983) were used as pollen parent and monosomic plants of var. Chinese Spring as female parents.

The F_1 hybrids of these crosses were analysed cytologically and $2n = 43$ (trisomic) $2n = 42$ (disomic) plants were identified in all the lines. Observations were made on the spike character on all the cytologically identified hybrid plants (Table - 1). It was observed that (disomic, $2n = 42$ as well as trisomic, $2n = 43$) all these F_1 hybrid plants produced first few spikes with branched character (with low expression) and rest of the spikes as normal except line 5A in which branched spikes were produced only by trisomic ($2n = 43$) plants while disomic ($2n = 42$) plants produced only normal (unbranched) spikes.

F_1 hybrids of monosomic 5A produced both types of plants, ie plants with branched spike and with unbranched spikes. Branched spikes were produced only by trisomic ($2n = 43$) plants where chromosome 5A was in three dosage while disomic ($2n = 42$) plants where 5A was present in two dosage produced only unbranched and spelta type of spikes. These observations clearly demonstrated that chromosome 5A may be involved in controlling the branched spike character in this selection of bread wheat. Occurrence of spelta spikes on disomic ($2n = 42$) plants also show that branched selection possesses *Q* locus in recessive form because it produces spelta spike in combination with Chinese Spring (where *Q* locus is present in dominant condition).

Low expressivity of branched character in the F_1 hybrids in present study could be the suppressive effect of *Q* locus (which is also located on chromosome 5A) which is present (although in hemizygous condition) in all these crosses except the F_1 disomic ($2n = 42$) hybrid plants. Similar suppressive effects were observed by Sharman (1944) in a F_1 hybrid of *T. vulgare* (normal) and *T. turgidum* (branched) and Swaminathan *et al.* (1966) in a F_1 hybrid of *T. aestivum* (var. Sonora 63) and branched mutant.

Present investigation and the findings of Sharman (1944) and Swaminathan *et al.* (1966) suggest that branched character can not be exploited in the presence of a gene (*Q* locus) which does not allow the full expression of branched character (even if *Q* is present in hemizygous condition). In the light of these observations it is suggested that the gene(s) for branched spike

Table 1. Chromosomal constitution and spike character of F1 hybrids of monosomic lines of var. Chinese Spring and branched wheat selection

F1 hybrids with	Chromosomal constitution	Spike character
1A	42	Partially branched
	41	" "
1B	42	" "
	41	" "
1D	42	" "
	41	" "
2A	42	" "
	41	" "
2B	42	" "
	41	" "
2D	42	" "
	41	" "
3A	42	" "
	41	" "
3B	42	" "
	41	" "
3D	42	" "
	41	" "
4A	42	" "
	41	" "
4B	42	" "
	41	" "
4D	42	" "
	41	" "
5A	42	" "
	41	Unbranched
5B	42	Partially branched
	41	" "
5D	42	" "
	41	" "
6A	42	" "
	41	" "
6B	42	" "
	41	" "
6D	42	" "
	41	" "
7A	42	" "
	41	" "
7B	42	" "
	41	" "
7D	42	" "
	41	" "

(located on chromosome 5A) present in the selection isolated by Singh and Joshi (1983) can serve as a useful source for transferring stable branched character in bread wheat provided the receipient variety carries *Q* locus in recessive form. Work towards this direction is in progress.

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Variation among EMS-Induced Wheat genotypes for chlorophyil content

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The artificial induction of mutations plays an important role in the study of the mechanism of heredity and evolution. Numerous experiments have contiributed to an increased knowledge of the fundamental concepts of genetics. Extensive research has also been reported on the inheritance and variation of chlorophyll contents among chlorophyll deficiency mutants for several crops including wheat (JENSEN 1957).

The present study was initiated to determine the variation of chlorophyll concentration among normal and EMS-induced populations of wheat genotypes. The improvement of genotypes with high chlorophyll content might result in the improvement of photosynthesis in wheat plant leading to the improvement of grain yield.

Material and Methods

Homogeneous seeds of five hexaploid wheat cultivars namely; Al-Samma, Arbian, Hinta Madina, Maaya and Yocorojo were treated with different doses of Ethyle Methane Sulphonate (EMS) with different durations in Rabi 1983 (Table 1). Treated seeds along with control were sown in pots in a complete randomized design in a greenhouse of the Department of Agronomy and Range Science, Gassim College of Agriculture, King Saud University, Saudi Arabia.

For Chlorophyll estimation leaf samples from second flag leaf of the main culm of all the genotypes from each treatment were collected just before flowering (80 days after sowing). Chlorophyll was extracted from 0.1 gm of freeze-dried leaf blades with 30 ml of 80% acetone. The plant extract was filtered through filter paper (Whatman No. 1) and made to 50 ml final volume. Absorbance was determined Spectrophotometrically at 645 and 663 mu (Bausch and Lomb Spectronic-2000) and total chlorophyll (mg chlorophyll/g dry weight) was calculated according to the equation of ARNON (1949).

The data was analysed statistically using the General Linear Models (GLM) procedures of SAS (HELWIG and COUNCIL, 1979). Duncan's Multiple Range Test was conducted to determine differences between means.

Results and Discussions

Visual differences for leaf color among EMS-induced M_1 populations and their parents are readily apparent. From Table 1, it may be inferred that total chlorophyll content of all the M_1 populations displayed general trend of increase over their parents (control) except variety Arabian where the character showed decrease at all doses and durations (except 0.4% and 0.6% at 9 and 7 hr respectively). It was further noted that there had been an absence of any linear decline. The

Table 1. Mean values for the chlorophyll content and ratios on dry weight basis of five hexaploid wheat genotypes at different EMS doses

Genotype/Origin	Visual green color	Chl a	Chl b	Total Chl	Chl a : b
		mg/gdw			
Al-Samma (Control)	Light	2.11	1.48	3.59	1.42
EMS 0.2% 3½ hr	Medium	2.80	2.93	5.73	0.96
EMS 0.2% 7 hr	Medium	3.00	3.05	6.05	0.98
EMS 0.2% 9 hr	Medium	2.58	2.70	5.28	0.96
EMS 0.4% 3½ hr	Medium	3.23	2.57	5.80	1.26
EMS 0.4% 7 hr	Dark	3.67	3.29	6.96	1.11
EMS 0.4% 9 hr	Light	2.45	2.27	4.72	1.08
EMS 0.6% 3½ hr	Light	1.97	1.81	3.78	1.08
EMS 0.6% 7 hr	Medium	3.00	2.63	5.63	1.14
EMS 0.6% 9 hr	Light	2.79	2.04	4.83	1.37
Arabian (Control)	Dark	4.04	2.93	6.97	1.38
EMS 0.2% 3½ hr	Light	1.53	1.63	3.16	0.94
EMS 0.2% 7 hr	Light	2.43	1.74	4.17	1.39
EMS 0.2% 9 hr	Medium	2.62	2.40	5.02	1.09
EMS 0.4% 3½ hr	Light	1.84	1.94	3.78	0.94
EMS 0.4% 7 hr	Medium	2.94	3.12	6.06	0.94
EMS 0.4% 9 hr	Dark	3.68	4.63	8.31	0.79
EMS 0.6% 3½ hr	Medium	3.13	2.36	5.49	1.32
EMS 0.6% 7 hr	Dark	4.27	3.34	7.61	1.27
EMS 0.6% 9 hr	Medium	3.00	2.72	5.72	1.10
Hinta Madina (Control)	Light	2.20	1.89	4.09	1.16
EMS 0.2% 3½ hr	Medium	2.58	3.02	5.61	0.85
EMS 0.2% 7 hr	Dark	3.09	5.06	8.15	0.61
EMS 0.2% 9 hr	Light	2.45	2.45	4.90	1.00
EMS 0.4% 3½ hr	Dark	4.35	4.35	8.70	0.99
EMS 0.4% 7 hr	Medium	3.25	2.30	5.55	1.41
EMS 0.4% 9 hr	Medium	3.55	2.30	5.85	1.54
EMS 0.6% 3½ hr	Dark	3.87	3.30	7.17	1.17
EMS 0.6% 7 hr	Medium	2.64	3.05	5.69	0.86
EMS 0.6% 9 hr	Dark	3.30	3.58	6.88	0.92
Maaya (Control)	Light	2.02	1.54	3.56	1.31
EMS 0.2% 3½ hr	Light	2.53	2.00	4.54	1.26
EMS 0.2% 7 hr	Light	2.35	2.35	4.70	1.00
EMS 0.2% 9 hr	Light	1.63	1.42	3.06	1.14
EMS 0.4% 3½ hr	Light	2.16	2.33	4.49	0.93
EMS 0.4% 7 hr	Medium	2.32	2.80	5.12	0.83
EMS 0.4% 9 hr	Light	2.24	1.84	4.08	1.21
EMS 0.6% 3½ hr	Light	1.90	2.35	4.25	0.80
EMS 0.6% 7 hr	Light	2.07	1.92	3.99	1.08
EMS 0.6% 9 hr	Dark	3.08	4.33	7.41	0.71
Yocorojo (Control)	Light	2.06	1.35	3.41	1.52
EMS 0.2% 3½ hr	Light	2.48	1.56	4.05	1.58
EMS 0.2% 7 hr	Light	2.13	1.24	3.37	1.72
EMS 0.2% 9 hr	Light	2.57	1.44	4.01	1.78
EMS 0.4% 3½ hr	Light	2.30	2.49	4.79	0.92
EMS 0.4% 7 hr	Light	2.29	1.42	3.71	1.61
EMS 0.4% 9 hr	Light	2.55	1.72	4.27	1.48
EMS 0.6% 3½ hr	Medium	2.17	3.22	5.39	0.67
EMS 0.6% 7 hr	Light	2.41	2.02	4.44	1.19
EMS 0.6% 9 hr	Medium	3.29	2.04	5.34	1.61

intensity of green coloration in the foliage differed among M_1 populations ranging from light green to dark green. The dark green populations were higher for total chlorophyll, chlorophyll a and chlorophyll b than the light green populations, while the medium color populations reacted in between them for chlorophyll characteristics. Similar results were reported by AASE (1971), JOHNSON & OHKI (1981) and LARIK *et al.* (1984) in barley and wheat respectively.

Chlorophyll concentrations of leaves may be of interest in breeding programs where the objective is to increase photosynthesis. Arabian (dark) and other cultivars (light) represented the extreme of the visual color classifications. When expressed on dry weight basis generally dark cultivars were approximately 50% higher in total chlorophyll content than the light cultivars. Differences among cultivars should allow for the improvement of the content of chlorophyll. Therefore, the visual differences between dark and light color of cultivars are apparently actual differences in chlorophyll concentrations. EMS 0.4% at 3½ hr duration in Hinta Madina displayed highest increase (8.70 mg/gdw) in total chlorophyll as compared to the rest of the treatments, which indicates the specific effect of this treatment in this particular genotype whereas, the same treatment does not showed similar effect in other genotypes. Most of the treated populations in variety Arabin displayed decrease in total chlorophyll content as compared to the parent. The highest reduction in total chlorophyll content was displayed by 0.2% at 3½ hr duration in this genotype. Chlorophyll deficiency is inherited character in these plants. The tillering capacity of the plants in these treatments was considerably high during the early growth stages but the percentage of productive tillers were quite low. Majority of the tillers produced from 30 to 60 days degenerated without flowering and fruiting. The chlorophyll deficiency may be one of the main reason for this, because the chlorophyll deficient genotypes are unable to meet the metabolic requirements of the plant which ultimately disturbs the whole physiology of a plant. However, the efficiency of the mutagen in not only dependent on dose alone but also on other variables such as presoaking time and p^H of the mutagen solution Results (Table 1) also indicate that positive changes in the alteration of chlorophyll synthesis in most of the M_1 populations has been brought by EMS and the simplest explanation is the accumulation and presence of more loci having dominant or partially dominant genes in these M_1 populations.

The ratio of chlorophyll a : b was higher for the light cultivars/M_1 populations than the dark cultivars/M_1 populations. In few M_1 populations chlorophyll b was higher than chlorophyll a, indicating that the EMS has affected photosystem I (PS I) in which chlorophyll a predominates on the contrary, PS II was accelerated by EMS in which chlorophyll b predominates. The light cultivars exhibited 29% higher ratio of chlorophyll a : b than the dark cultivars. JOHNSON & OHKI (1981) reported negative relationship between total chlorophyll and the ratio of chlorophyll a : b on dry weight basis and concluded that chlorophyll a was not increasing at the same rate as chlorophyll b.

Highly significant ($P \geqslant .01$) differences among varieties were detected for all the traits measured (Table 2), suggesting that varieties under study varied significantly from each other for these parameters. Although variation among varieties and treatments occurred for total chlorophyll, chlorophyll a, chlorophyll b and chlorophyll a : b, but the differences among treatments were not statistically significant. The breakdown of treatments into dose, duration and dose x duration also reveal non-significant effects suggesting that the doses at different durations were

Table 2. Analyses of variance on the effect of EMS treatments on the chlorophyll contents of five hexaploid wheat genotypes using the General Linear Models (GLM) procedures of Statistical Analysis (SAS)

Source	D.f.	Chl a	Chl b	Total Chl	Chl a:b
Varieties (V)	4	25.45**	43.84**	125.82**	4.48**
Treatments	9	13.53n.s	25.07n.s	67.17n.s	2.35n.s
Control	1	1.27n.s	11.67n.s	20.62n.s	1.23n.s
Dose	2	8.23n.s	5.93n.s	27.81n.s	0.16n.s
Duration	2	1.99n.s	0.47n.s	3.48n.s	0.77n.s
Dose x Duration	4	2.03n.s	7.00n.s	15.26n.s	0.18n.s
Varieties x Dose	8	14.60**	28.99**	47.95**	5.93**
Var. x Duration	8	17.18**	27.97**	72.62**	2.57**
Var. x Dose x Dura.	16	21.58**	54.45**	124.71**	3.61**
Error	176	0.38	0.25	0.58	0.15
$LSD_{(.01)}$** for varieties	=	0.055	0.046	0.071	0.037
$LSD_{(.01)}$** for varieties x Dose	=	0.032	0.026	0.041	0.021
$LSD_{(.01)}$** for Var. x Duration	=	0.032	0.026	0.041	0.021
$LSD_{(.01)}$** for Var. x Dose x Dura.	=	0.018	0.015	0.024	0.012
C.V. %	=	1.71	1.49	1.09	2.62

not effective in inducing significant genetic changes in the parameters studied. The interactions between varieties x dose, varieties x durations and varieties x dose x durations were highly significant indicating that varieties did not perform uniformly accross different doses and durations.

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Evaluation of dwarf mutants of bread wheat (*Triticum aestivum* L.)

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The search for shorter varieties has long been a pre-occupation of wheat breeders. Less and less height appears historically as an essential characteristics of the most productive varieties destined for farmers using more and more intensive cultivation. However, not all the dwarf varieties give equally higher yields and are no better than tall varieties (Jain *et al.* 1974). In the present investigation, the effect of further diminishing the height of semidwarf varieties on different yield components have been studied.

Material and Methods

Two dwarf mutants, one each of the varieties Sonalika and Arjun, owe their origin to 25 KR gamma rays (Co^{60}) treatment. Phenotypically stable mutants were evaluated in M_7 generation.

Homogeneous seeds of the mutants and respective control were sown in a plot of uniform fertility. Seeds were drilled in three rows, of six meter length with 22.5 cm inter-row spacing in a randomised block design with five replications.

Observations on ten plants per replication for the characters height, spike length, spikelets per spike, seeds per spike were recorded. Tiller number in a meter length and yield of a middle row was recorded. For thousand kernel weight, random sample of seed was considered. The data was analysed and phenotypic correlations worked out.

Results and Discussion

Analysis revealed that the dwarf mutants differed for all the characters except for tillering capacity. Spike length, spikelets per spike, seeds per spike, thousand kernel weight and tillers per unit area are reliable measure of yielding ability (Borojevic and Borojevic, 1972). As seen from Table-1, the dwarf mutant of Sonalika showed reduction in spike length, spikelets per spike, and seeds per spike. However, the mutant showed increase in kernel weight. The reduction in seed number per spike can be attributed to the reduction in the spikelength and number of spikelets per spike. There was no change in tillering capacity and yield of the mutant.

Dwarf mutant of Arjun showed decrease in spikelets per spike, kernel weight and yield, but no change in spike length, number of seeds per spike and tillering capacity.

It is known that the yield components seeds per spike, unit grain weight and number of tillers per unit area in wheat are negatively correlated (Sikka and Jain, 1958; Gandhi *et al.* 1964 Knott and Talukder, 1971). Thus, it was observed that the increase in kernel weight in case of

Table 1. Mean for seven characters in wheat

Culture	Plant height (cm)	Spike Length (cm)	Spkts/ spike	Seeds/ spike	1000 kernel wt. (gm)	Tillers/ m^2	Yield of a row (gm)
S-Dwarf mutant	85.66	10.47	14.82	38.50	55.40	125.60	792.40
S-Control	93.95	11.30	16.28	42.90	52.14	130.60	778.40
A-Dwarf mutant	71.10	9.96	15.62	48.32	33.78	138.60	627.40
A-control	85.22	10.29	18.80	47.16	36.84	128.20	760.40
C.D. @ 5%	7.63	0.36	0.43	3.73	1.46	–	17.66

S – Sonalika, A – Arjun

Table 2. Phenotypic correlation coefficients among all possible combination of five characters in control (upper diagonal) and dwarf mutant (lower diagonal) in two varieties of wheat

Characters correlated	Plant height	Spike Length	Spikelets/ spike	Seeds/ spike	Thousands kernel weight
			SONALIKA		
Plant height	–	.290*	.310*	.170	.090
Spike length	-.014	–	.700**	.570**	-.240
Spikelets/spike	-.189	.431**	–	.520**	.033
Seeds/spike	.043	.287*	.021	–	-.610**
Thousand kernel weight	-.215	-.048	.132	.045	–
			ARJUN		
Plant height	–	.084	-.144	.196	-.332
Spike length	.122	–	.250	.585**	-.029
Spikelets/spike	.089	.630**	–	.277**	.064
Seeds/spike	-.004	.610**	.423**	–	-.386
Thousand kernel weight	-.071	.101	.283*	.080	–

dwarf mutant of Sonalika has resulted in the decrease in number of seeds per spike. Since yield is the product of number of kernels per spike, kernel weight and number of tillers, all assume importance in efforts to attain new level of productivity in wheat. Any gain in a single yield component offset by decrease in one or both of the other components would produce no gain in the total yield. This is the reason why the dwarf mutant of Sonalika showed comparable yield to control. In case of dwarf mutant of Arjun the reduction in one of the important yield components kernel weight has resulted in the loss of yield. The observations are in agreement with the earlier findings that the mutants have generally reduced vitality (Gaul 1965; Siddiqui & Araih 1974).

Relation of height to spike length, spikelets per spike, number of seeds per spike and thousand kernel weight was studied (Table 2). Phenotypic correlations between plant height and these characters revealed that in case of Sonalika control, the height is positively correlated to spike length and spikelets per spike; spike length is positively correlated with spikelets per spike and seeds per spike. Spikelets per spike are positively correlated with seeds per spike but number of seeds per spike is negatively correlated with thousand kernel weight. In case of the dwarf mutant of Sonalika, spike length is positively correlated with spikelets per spike and seeds per spike. The most interesting fact is that in case of dwarf mutant, the negative correlation between seeds per spike and thousand kernel weight is weakened.

In case of Arjun control height is negatively correlated with thousand kernel weight and seeds per spike is positively correlated with spike length and spikelets per spike. The correlation between seeds per spike and thousand kernel weight is negative although not significant. In case of the dwarf mutant spike length is positively correlated with spikelets per spike and seeds per spike and spikelets per spike are positively correlated with seeds per spike and thousand kernel weight.

Thus, the results presented indicate that further reduction in plant height adversely affects the yield components in case of the variety Arjun. In case of the variety Sonalika further reduction in plant height has resulted in decrease in seeds per spike but increase in kernel weight. The dwarf mutant of Sonalika can be used as genetic stock in cross breeding with other varieties possessing high number of seeds per spike to combine these two characteristics.

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Studies on the physiology of dwarfism in wheat (*T. aestivum* L)
V. Effect of gibberellic acid.

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Genetic dwarfs of several plant species are reported to display increased or decreased response to applied GA_3, as compared to their tall counterparts (Proano & Greene 1968, Harada & Vergara 1971, Gale & Law 1973). On the other hand, there are reports particularly on wheat and rice, whereby dwarfs have failed to show any response to applied GA (Allan *et al.* 1959, Nagamatsu *et al.* 1964, Kumar *et al.* 1982). However, few reports are available on the metabolic aspects of such forms (Kumar *et al.* 1981, Kumar & Baijal 1985). In the present investigation, the authors report the effect of gibberellic acid induced α-amylase activity on endogenous sugar levels in a tall and three dwarf forms of wheat and their possible implication in the dwarfism.

Materials and Methods

Sterilized seeds of four wheat varieties viz., C-306 (tall), Sonalika (single dwarf), Kalyansona (double dwarf), Kalyansona (double dwarf) and Moti (triple dwarf) were soaked in test solutions [GA_3 - 00 (control), 0.1, 1.0, 10 and 25 mg/L] for 24 hours. The seedlings were grown according to previously described method (Kumar *et al.* 1982).

For α-amylase activity the samples were randomly collected and homogenised to a fine paste in a chilted mortar with 10 ml of citrate buffer (pH 5.0). The homogenised samples were centrifuged at 2500 r.p.m. for 15 minutes at 4°C. The supernatent was used for enzyme assay according to the method of Paleg (1960). The enzyme activity was expressed as mg starch digested $g^{-1}.h^{-1}$.

Reducing and total sugars were extracted from oven dried powdered samples in 80% ethanol. The extract was evaporated on a waterbath to let off the alcohol. Proteins were precipitated from this extract by adding equal volume of saturated neutral lead acetate. Excess lead from this was removed by adding saturated disodium phosphate. The extract was then made to a known volume.

The total sugars in the above solution were extracted by adding 3N HCl to 10 ml of it and hydrolysing at 110° in a water bath for 30 minutes. After cooling and neutralization, it was used for sugar assay. The assy was carried out according to the method of Nelson (1944) as modified by Somogyi (1952) and expressed as mg. g^{-1} dry wt.

Results and Discussion

The literature is well documented with the reports which indicate that GA_3 induces α-amylase

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Table 1. Effect of gibberellic acid on reducing sugar (R.S.) and total sugar (T.S.) content ($mg.g^{-1}$ dry wt) in seedlings of wheat

Variety	Gibberellic acid mg/L										Average	
	00		0.1		1.0		10		25			
	R.S	T.S	R.S.	T.S.	R.S.	T.S.	R.S.	T.S.	R.S.	T.S.	R.S.	T.S.
C-306	6.7	27.6	7.3	29.0	8.3	37.0	9.5	39.8	7.6	33.4	7.9	33.4
Sonalika	6.9	27.4	7.5	29.7	8.7	34.4	9.0	36.0	8.3	27.9	8.1	31.1
Kalyan sona	11.1	36.1	13.4	42.3	16.0	49.8	17.1	52.4	15.2	39.2	14.6	44.0
Moti	11.4	16.7	13.1	19.5	15.5	29.3	16.7	41.7	13.0	18.5	13.9	25.1
Average	9.0	27.0	10.3	30.1	12.1	37.6	13.1	42.5	11.0	29.8		

	Variety		GA_3		Var x GA_3	
	R.S.	T.S.	R.S.	T.S.	R.S.	T.S.
SE mt.	0.4	0.7	0.4	0.8	0.9	1.6
C.D.	1.1	2.0	1.2	2.3	N.S.	4.6

activity in cereal endosperm (Paleg 1960, Varner 1964) but there are hardly any showing the differential behaviour of tall and dwarf forms of plants for such a system. (Gale & Marshall 1975). The results of present investigation clearly reveal that not only the initial amylase activity was high in dwarf but they also showed greater increase due to GA treatment (Fig. 1). This is well reflected on its products i.e. reducing and total sugars in the four wheat varieties (Table 1). Infact changes in the α-amylase activity closely paralleled those in reducing sugars and total sugars (Fig. 2). Juliano & Varner (1969) also reported similar findings. It also lent credence to the contention

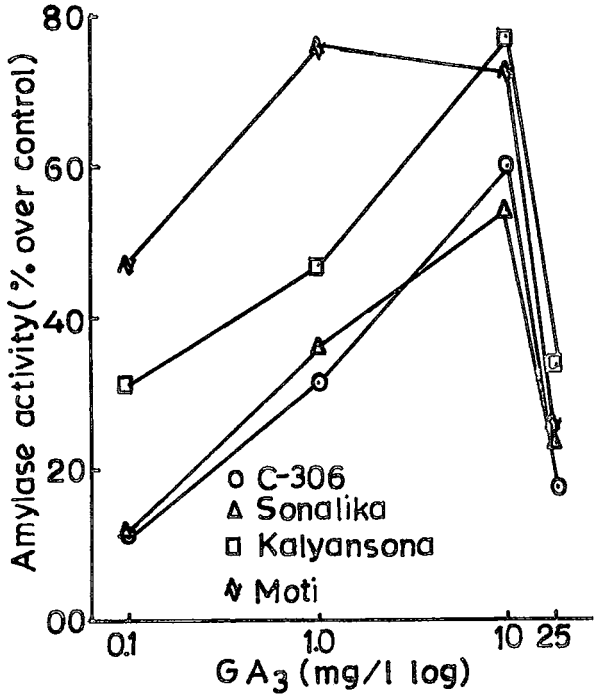

Fig. 1 Effect of gibberellic acid on the responsiveness of different wheat varieties to α-amylase activity

that GA induced α-amylase has considerable influence on the release of reducing sugar in *invivo* as well as *in vitro*. In the present investigation althought it was not attempted to but Paleg *et al.* (1962) and Filner & Varner (1967) confirmed that in wheat, GA induced amylase activity is due to *de novo* synthesis of the enzyme itself.

It may be interesting to note that all the three dwarfs showed GA induced amylase activity but one of them, the triple dwarf. Moti failed to respond in protease activity (Kumar *et al.* 1982). On the otherhand, Fick & Qualset (1973) and Gale and Marshall (1975) reported certain dwarf wheats which were GA insensitive in releasing α-amylase.

The reducing sugars and the total sugars increased with the age of seedlings (Table- 2) for the obvious reason that sugars are indispensible for meeting energy requirement through respiration. Rizvi and Sirohi (1974) have also reported this phenomenon in wheat. In this study a significant positive correlation (r = .81) was found between reducing sugars and respiration.

The varieties undertaken displayed different levels of amylase activity, reducing and total

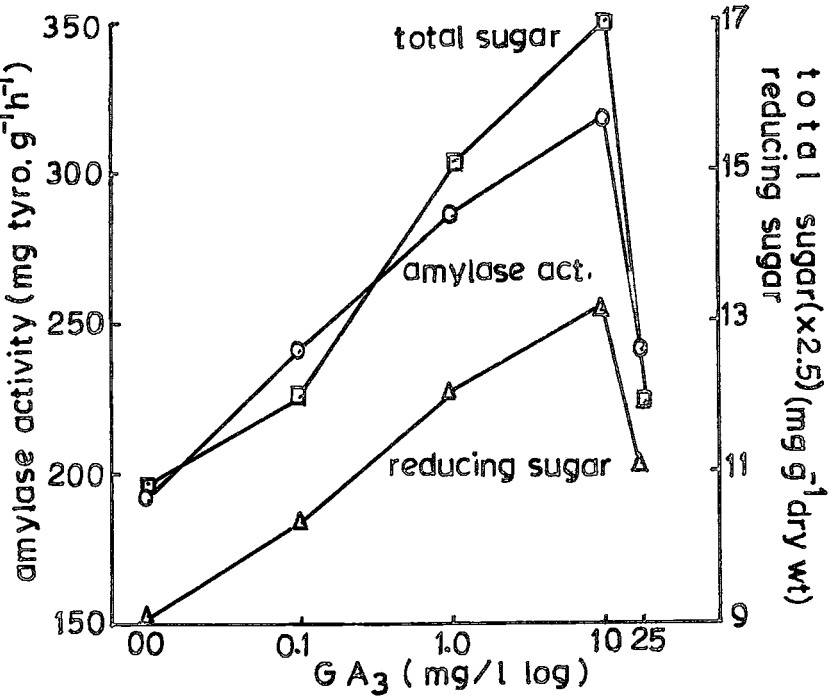

Fig. 2 Changes in α-amylase activity, reducing sugars and total sugars associated with gibberellic acid

sugars as a response to GA. This may primarily be due to the internal levels of these substances and secondly due to responsiveness of verieties to applied GA. The responsiveness depends on starch content, pH, calcium levels, protolyte activity, besides, endogenous hormone levels (Briggs 1968). Incidently, GA like substances were higher in dwarf varieties than the tall variety in our study (Kumar 1977) and so were the level of amylase activity and reducing sugars.

It may further be explicited (Fig. 3) that efficacy of different doses of GA_3 (% over 00 GA_3) at respective seedling age) was highest at 24 hours and lowest at 48 hours. Jones & Armstrong (1971) suggested that GA elicited α-amylase resulting in high levels of reducing sugars provides a means of further regulation by end product inhibitions. Such and product in this metabolic system, gives an osmotic effect which may act to dampen α-amylase activity. These sequences appear to have occurred during 24-48 hours in the present study.

Thus, whereas the importance of α-amylase in releasing sugars for meeting energy requirement for the manifestation of GA_3 induced growth ean not be disputed, it is difficult to explain a system in which GA induced amylase activity is observed but growth is unexpressed. Exactly that has happened with the triple dwarf Moti (Kumar *et al.* 1982). Radley (1970) also reported certain such semi-dwarf wheat genotypes. Nevertheless, the response of GA to certain metabolic systems but not to other (Kumar & Baijal 1984, 1985), clearly indicates that GA_3 operates at different sites of action, simultaneously but selectively regulating the physiology of dwarfism.

Table 2. Effect of gibberellic acid on reducing sugar (R.S.) and total sugar (T.S.) content (mg g^{-1} dry wt) at different seedling age in wheat

Variety	Seedling age (hrs)									
	00		24		48		72		96	
	R.S	T.S.	R.S.	T.S.	R.S.	T.S.	R.S.	T.S.	R.S.	T.S.
C-306	1.4	10.1	2.5	11.3	9.7	43.0	12.6	49.6	13.4	52.8
Sonalika	1.3	8.9	4.7	13.5	10.2	33.2	11.4	46.1	12.7	53.9
Sonalika	1.9	9.5	5.8	14.6	13.2	50.3	24.5	65.3	27.5	80.1
Moti	1.9	5.2	6.7	10.6	14.7	24.4	21.1	40.0	25.4	45.3
Average	1.6	8.4	4.9	12.5	11.9	37.7	17.4	50.3	19.7	58.0

	Seedling age		Var x age	
	R.S.	T.S.	R.S.	T.S.
SE mt.	0.4	0.8	0.9	1.6
C.D.	1.2	2.3	2.5	4.6

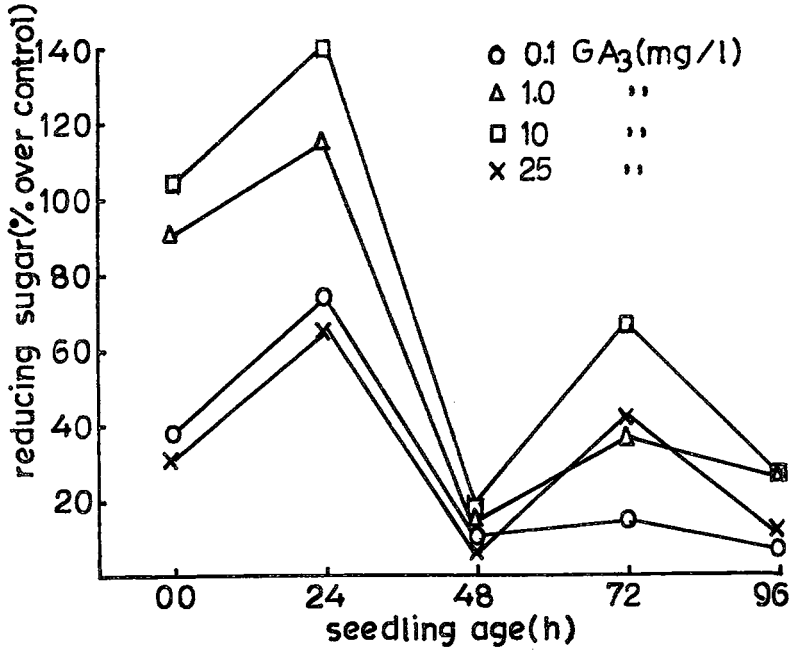

Fig. 3 Efficacy of gibberellic acid at different seedling age on the reducing sugars content.

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The authors than Dr. Mike D. Gale of Plant Breeding Institute. Cambridge, U.K. for his valuable suggestions and Principal, Agra College, Agra for providing facilities.

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II. Records

Abstructs presented in a symposium

Followings are the abstruct papers presented in Small Symposium on Genome Reorganization and Developmental Abnormality in Wheat held in August 2-3, 1987 at Mishima, Japan. The symposium was organized by Dr. K. Tsunewaki (Kyoto Univ.) under sponsership of National Institute of Genetics (Japan).

Gametocidal chromosomes in *Aegilops* species

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Endo & Tsunewaki (1975) and Maan (1975) independently found for the first time the peculiar phenomenon that an alien chromosome in common wheat could not be eliminated after many backcrosses with common wheat. Wheat plants with a monosome of this chromosome are partially fertile in male and female, while disomic plants for the same chromosome are fully fertile in both sexes. The alien chromosome addition or substitution plants produce two types of gametes, those with the alien chromosome and those without it. Cytological studies revealed that only the former gametes can function normally. Thus, the alien chromosome alone causes sterility in gametes lacking it, regardless of the plasmatype, and it is selectively retained in the offspring at the expense of the fertility of the plants bearing it. Endo (1978) called such alien chromosomes gametocidal chromosomes, and Miller (1983) named them Cuckoo' chromosomes, because of their selfish nature; once they are introduced into wheat, they can hardly be expelled even though they have harmful effects on the wheats that have them.

As shown in Table 1, gametocidal chromosomes have been transferred into common wheat from six *Aegilops* species. *Ae. caudata, Ae. triuncialis,* and *Ae. cylindrica* have the C genome in common, and the gametocidal chromosomes of the latter two species probably derived from their C genomes. Actually, the gametocidal chromosomes of *Ae. caudata* and *Ae triuncialis* pair well, and the addition plant having both of them show a normal fertility. The *Ae. cylindrica* chromosome, acrocentric like the *Ae. triuncialis* and *Ae. caudata* chromosomes is not found in *Ae. squarrosa,* the D genome donor to *Ae. cylindrica.* The *Ae. triuncialis* chromosome is successfully substituted for wheat homoeologous group 3 chromosomes (Endo 1978). *Ae. speltoides, Ae. sharonensis,* and *Ae. longissima* all have the S or modified S genome, and two or three gametocidal chromosomes have been extracted from each of them. Only a segment of the gametocidal *Ae.*

Table 1. *Aegilops* species from which gametocidal chromosomes were derived.

Species	Genome symbol	Reference
Ae. caudata	CC	Endo & Katayama 1978
Ae. triuncialis	CCC^uC^u	Endo & Tsunewaki 1975, Endo 1978
Synthetic *triuncialis*	CCC^uC^u	Endo & Tsunewaki 1975, Endo 1978
Ae. cylindrica	CCDD	Endo 1979
Ae. speltoides (two accessions)	SS	Tsujimoto & Tsunewaki 1984, Unpubl. data
Ae. sharonensis (three accessions)	S^1S^1	Maan 1975, Endo 1982, Miller *et al.* 1982
Ae. longissima (two accessions)	S^1S^1	Maan 1975, Endo 1985

speltoides chromosome was translocated to the distal end of the long arm of the 2B chromosome (unpubl. data).

The gametocidal actions of the *Ae. triuncialis*, *Ae. sharonensis*, and *Ae. longissima* chromosomes, belonging to homoeologous group 3, 2, and 4, respectively, were studied in double monosomic additions for each two of the chromosomes, and these three chromosomes were proved to have different gametocidal actions (Endo 1982). In the double monosomic additions for the *Ae. triuncialis* chromosome and the *Ae. sharonensis* or *Ae. longissima* chromosome, both gametocidal chromosomes are indispensable for the gametes to function normally; namely, the gametocidal action of the *Ae. triuncialis* chromosome can not be suppressed by the *Ae. sharonensis* or *Ae. longissima* chromosome and *vice versa.* In the double monosomic addition for the *Ae. sharonensis* and *Ae. longissima* chromosomes, only the *Ae. longissima* chromosome is needed for normal functioning of the gametes, which means that the *Ae. longissima* chromosome can suppress the gametocidal action of the *Ae. sharonensis* chromosome but the latter chromosome can not suppress the gametocidal action of the former one. Thus, there are at least three types of gametocidal chromosomes with respect to their gametocidal action and homoeology.

The gametocidal chromosomes isolated from different accessions of each of *Ae. sharonensis* and *Ae. longissima* were found to fall into two types, and those of the same homoeology, group 2 or group 4, from the different species have the same gametocidal action (Endo 1985).

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Genetic control of parthenogenesis in common wheat

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It has been known that the egg cell of *Triticum aestivum* strain Salmon with *Aegilops kotschyi* cytoplasm develops parthenogenetically at a high frequency due to an interaction between a 1BL-1RS translocation chromosome and an alien cytoplasm. In this study, mechanism controlling parthenogenesis of the egg cell was investigated embryologically and genetically using (*kotschyi*)-Salmon and its aneuploids.

Seven aneuploids of (*kotschyi*)-Salmon were produced in the backcrossed or selfed offspring from the cross, (*kotschyi*)-Salmon × ditelosomics 1BS of *T. aestivum* cv. Chinese Spring. The short arm of 1B chromosome of Chinese Spring (1BS) carries a fertility-restoring gene, *Rfv1*, for the *kotschyi* cytoplasm. Since these lines were backcrossed six times with Salmon's pollen, they are almost pure for the Salmon genetic background.

Embryological studies of (*kotschyi*)-Salmon revealed the following facts: (1) The egg cell starts haploid parthenogenesis before the fertilization and develops up to a globular embryo (20-50 cells). (2) The parthenogenetic embryos never develop any more in non-pollinated ovules. (3) When polar nuclei are fertilized by pollination, most haploid embryos develop normally owing to the formation of endosperm. (4) After the egg cell started development, one of synergids sometimes develops just like an egg cell. (5) When this synergid is fertilized, a diploid embryo is formed. The embryo sac contains the haplo-diplo twin embryos.

Frequencies of parthenogenetic embryo and haploid in (*kotschy*)-Salmon and its anueploids are shown in Table 1. From both embryological and genetical data, fate of the egg cells in four lines is summarized in Fig. 1. Di- and monosomics 1BL-1RS of (*kotschyi*)-Salmon formed parthenogenetic embryos in the half of ovules; the other half of egg cells died. In disomic 1BL-1RS, haploids were obtained at a frequency of 90.4% of germinated seeds. The single diploids could be derived from the diploid partners of n-2n twins, because the parthenogenetic haploid embryos were weak and died occasionally. Monosomics 1BL-1RS produced two kinds of haploid embryos. The haploid embryos lacking the 1BL-1RS translocation chromosome (2n=20) were very weak and often died during embryo development. When aneuploids of (*kotschyi*)-Salmon having one or more 1BS arms were backcrossed with Salmon's pollen, the diploid offspring always had the 1BS arm. Conversely, the 1BS arm was never transmitted to the haploid offspring. In alloplasmic aneuploids carrying two ro three 1BS arms, the egg cell lacking this arm was occasionally produced owing to desynapsis in meiosis, resulting in a parthenogenetic haploid embryo.

On the bases of the results, we can draw the following conclusions: (1) When the female sporophyte has the 1BL-1RS translocation chromosome, the egg cell without the 1BS arm develops parthenogenetically and forms haploid embryos. In the egg cell, the translocation chromosome is not necessary for induction of parthenogenesis. (2) On the other hand, the 1BS-carrying egg cell never develops parthenogenetically though it has the translocation chromosome

Table 1. Frequencies of parthenogenetically developed embryo and haploid in (*kotschyi*)-Salmon and its aneuploids

Line	Parthenogenetically developed embryo[2]		Haploid + n-2n twins[3]		Egg cell	
Chromosome constitution [1]	No. ovules examined	%	No. plants examined	%	Chromosome constitution[4]	Partheno-genesis
20″ + T″	80	56.3	125	90.4	20 + T	Do
20″ + T′	314	49.4	132	36.4	20	Do
					20 + T	Do
20″ + T″ + t′	228	32.0	154	59.3	20 + T	Do
					20 + T + t	No
20″ + T″ + t″	197	6.7	84	7.1	20 + T	Do
					20 + T + t	No
					20 + T + 2t	No
20″ + T″ + t‴	80	6.3	35	11.4	20 + T	Do
					20 + T + t	No
					20 + T + 2t	No
					20 + T + 3t	No
20″ + T′ + t′	265	64.5	69	37.3	20	Do
					20 + T	Do
					20 + t	No
					20 + T + t	No
20″ + T′ + t″	54	3.1	64	3.1	20	Do
					20 + T	Do
					20 + t	No
					20 + T + t	No
					20 + T + 2t	No
20″ + t″	32	0.0	43	0.0	20 + t	No

1) T and t indicate 1BL - 1RS translocation chromosome and 1BS arm, respectively.

2) In non-pollinated ovules.

3) In the backcrossed progenies.

4) Estimated from chromosome constitution of the backcrossed progenies.

coinsidently. Then, this egg cell takes part normally in the fertilization, resulting in diploid offspring. (3) Therefore, 1RS arm of the translocation chromosome carries a gene (*Ptg*) inducing haploid parthenogenesis sporophytically; 1BS arm carries a gene (*Spg*) suppressing haploid parthenogenesis gametophytically.

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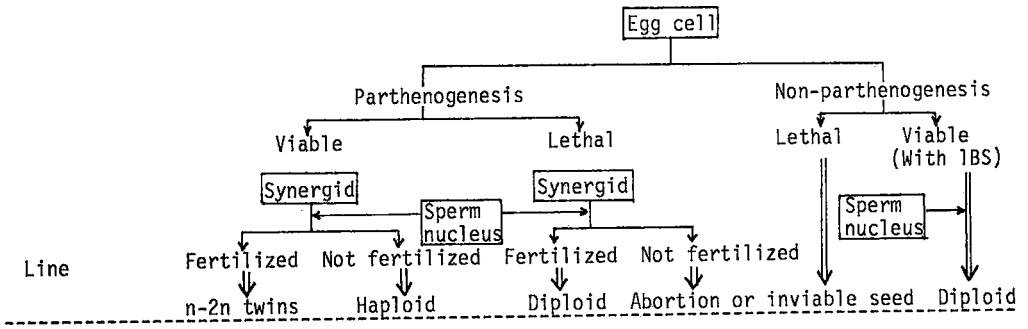

Line	n-2n twins	Haploid	Diploid	Abortion or inviable seed	Diploid
20" + T"	18	26	5	7	44	-
20" + T'	7	6	21	15	51	-
20" + T" + t'	12	17	1	2	49	19
20" + T' + t'	5	7	4	49	19	16

Fig. 1 Fate of the egg-apparatus of (*kotschyi*)-Salmon and its aneuploids. T and t indicate 1BL-1RS translocation chromosome and 1BS arm, respectively. Figures mean percent of total egg cells in each line.

Midget chromosome found in common wheat cv. Chinese Spring with rye cytoplasm

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In common wheat, *Triticum aestivum* cv. Chinese Spring (In abbreviation CS) ($2n = 6x = 42$) with *Secale cereale* cytoplasm, we found a diminute chromosome compared with wheat chromosomes and named it "midget chromosome". CS with *cereale* cytoplasm [(*cer*)-CS] was developed by means of the successive backcrosses of CS to the rye-wheat amphidiploid (T.Lelley personal communication) and has been maintained in our laboratory by the backcrosses of CS or self-pollination since 1974. The seeds of this line were kindly provided by Dr. T. Lelley, Göttingen University. We report here on the morphology, role, transmission and origin of this chromosome.

The midget chromosome was observed at both mitosis of root tip meristematic cell and meiosis of pollen mother cell (PMC) of (*cer*)-CS. At mitotic metaphase of root tip cells, the size of the midget chromosome was about half of the satellite region of wheat chromosomes 1B and 6B (Fig. 1A). At meiosis of PMC the midget chromosome synchronously behaved together with the normal wheat chromosomes and was attached by the spindle fibers (Fig. 1B). Judging from attaching position of the spindle fibers, the midget chromosome is telocentric or acrocentric. In (*cer*)-CS having two midget chromosomes, the midget chromosomes paired in 10 out of 35 cells observed.

In (*cer*)-CS, no plant without midget chromosome was obtained and the plants obtained had one or two midget chromosomes. (*cer*)-CS showed weaker plant vigor than the normal CS, i.e., CS with *aestivum* cytoplasm and without midget chromosome. The midget chromosome added to CS did not affect plant vigor. The effect of the midget chromosome on plant vigor of (*cer*)-CS was not apparent. Weak plant vigor of (*cer*)-CS may be induced by the *cereale* cytoplasm. Though there was no difference in pollen fertility between cytoplasms and among the number of the midget chromosomes, seed fertility of (*cer*)-CS was lower than that of CS without or with one midget chromosome (Table 1). Lower seed fertility of (*cer*)-CS seems to be the result of the partial female sterility caused by weaker plant vigor. The seeds of (*cer*)-CS segregated fully developed and shriveled ones. The percentage of the shriveled seeds of (*cer*)-CS with one midget chromosome was higher than that of (*cer*)-CS with two midget chromosomes (Table 1). No shriveled seed was produced in CS with one midget chromosome as in the normal CS. This indicates that an interaction effect between the midget chromosome and the *cereale* cytoplasm is critical on the seed development of (*cer*)-CS. Fully developed seeds of (*cer*)-CS germinated normally and had one or two midget chromosomes without exception, while shriveled seeds did not germinate and probably did not have the midget chromosome. By the aid of an embryo culture, however, it was possible to raise shoot from excised embryos. This shows that only the endosperm was degenerated in the shriveled seed.

In (*cer*)-CS with one midget chromosome, estimated transmission rate of the midget chromosome through female and male gametes was about 10% and 75%, respectively. The low trans-

mission rate through the female must be caused by elimination of the midget chromosome at meiosis of egg mother cell as in wheat monosomics. The high transmission through the male must be caused by the preferential fertilization of the pollen having midget chromosome. In CS with one midget chromosome, however, transmission rate was about 10% through both the gametes.

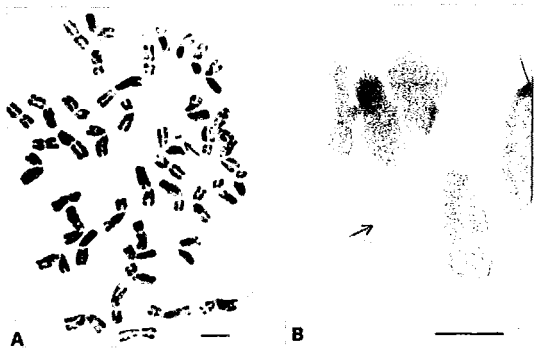

Fig. 1 Photomicrographs of midget chromosomes at mitosis(A) and meiosis(B) of Chinese Spring with *S. cereale* cytoplasm. Arrows indicate midget chromosomes. Bars indicate 5μm.

Table 1. Effects of cytoplasm and midget chromosome on pollen and seed fertility and percentage of shriveled seeds of Chinese Spring grown in the glasshouse

Cytoplasm	No. of midget chromo.	Pollen fertility		Seed fertility		% shriveled seeds	
		No. of plants examined	%	No. of plants examined	%	No. of seeds observed	%
S. cereale	2	2	96.2	6	79.9	422	4.3
	1	9	96.3	2	71.8	165	23.0
T. aestivum	1	5	97.5	4	92.0	889	0
	0	1	97.7	10	90.9	1966	0

The origin of the midget chromosome seems to be the rye chromosome of the initial amphidiploid, *Secalotricum*. In test crosses between (*cer*)-CS and Imperial rye disomic addition lines of CS, 79% of F_1 seeds between (*cer*)-CS and 1R disomic addition line fully developed. In all cross combinations involving other rye chromosome addition lines, more than 75% of F_1 seeds were shriveled. This indicates that chromosome 1R as well as the midget chromosome had the favorable effect on the endosperm development of (*cer*)-CS. Chromosome 1R had clear C-bands at the ends of both arms, while the midget chromosome had no band. These results indicate that the midget chromosome has to be derived from 1R by deleting the most part of both arms and retaining the centromere and the small region being responsible for the endosperm development.

Since the interaction effect between the midget chromosome and the *cereale* cytoplasm is critical on the endosperm development of common wheat with *cereale* cytoplasm, screening of plants having this chromosome is easy in common wheat with *cereale* cytoplasm. Therefore, this chromosome can be used for genetical and breeding research on such as the endosperm formation in wheat and rye.

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Difference in structural variability of genomes in *Triticum* and *Aegilops*

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In the tetraploid species of the genus *Triticum* and *Aegilops*, only two have the same genomes as their parental species. They are *Ae. triuncialis* with the C^uC^uCC genome and *Ae. cylindrica* with the CCDD genome (Kihara 1949). Other species have one genome homologous to that of a parental species but their second genome is closely related to but not identical with that of the other parental diploids. The latter genome is generally called a modified genome.

Zohary & Feldman (1962) proposed that modified genomes have evolved through introgression of chromosome or chromosomal segments between different genomes. In this process of genome modification, the common or pivotal genome, such as A in *Triticum* and C^u and D in *Aegilops*, play the role of a genetic buffer. However, an alternative and more simple explanation is that in *Triticum* and *Aegilops*, the genomes of several diploid species are stable in their chromosome structure but that those of other diploids are variable. In a tetraploid species, when the combination of genomes is one stable plus one variable genome, structural differentiation or segmental rearrangement would accumulate in the variable genome. Since one genome is stable and therefore acts as a genetic buffer, the chromosome structure of the second genome would change far more rapidly than that of the genomes of diploid species.

To verify this hypothesis, several studies have been carried out in tetraploid species of *Triticum* and *Aegilops*, by identifying the genomes on which breakpoints of spontaneous reciprocal translocations are located. The frequency of breakpoints would indicate the degree of structural variability of each of the two genomes. The data obtained so far are summarized below.

1. Emmer wheats with the AABB genome.

   Seven spontaneous reciprocal translocations were found. Of these, four were between the B genome chromosomes, two between the A and the B genome and one between the A genome chromosomes (Kawahara and Tanaka 1983, Kawahara 1984 and unpublished).

2. *T. araraticum* with the AAGG genome.

   Kawahara & Tanaka (1983) and Kawahara (1984) identified the translocations in *T. araraticum* and assumed the genomes involved in each translocation. Of 17 different translocations, 10 were between the G genome chromosomes, five were between the A and the G genome and two were between the A genome chromosomes.

3. *Ae. variabilis* and *Ae. kotschyi* with the $C^uC^uS^vS^v$ genome.

   Of seven translocations observed, three were between the S^v genome chromosomes, two were between the C^u and the S^v genome and one was between the C^u genome chromosomes. One breakpoint of the remaining one translocation is assumed to be on a S^v genome chromo-

some but the other is still unidentified (Kawahara unpublished).

In hexaploid dinkel wheats (AABBDD), many translocations were identified by using monosomic or other aneuploid series of *T. aestivum* cv. Chinese Spring (for a review, see Kawahara 1984). Chromosomes of the B genome are most frequently involved in translocations followed by those of the D genome and of the A genome. This tendency has become more apparent with the change of the designation of 4A to 4B according to Dvorák (1983).

Based on available data, the relative frequency of breakpoints on each genome was calculated as shown in Fig. 1. The number of breakpoints on modified genomes, B, G and S^v, is clearly about twice that on the pivotal ones, A and C^u, in tetraploid species. Similarly, breakpoints are located mainly on the B genome chromosomes in hexaploid dinkel wheats as mentioned above.

Therefore, it is concluded that genome rearrangement occurs more frequently in the modified genomes than in the pivotal ones, and that the modified genomes probably evolved through their high structural variability rather than through introgression between different genomes.

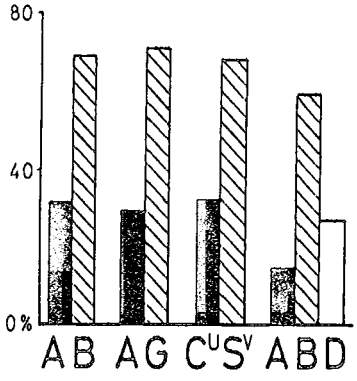

Fig. 1 Relative frequency of breakpoints on each genome in several species of *Triticum* and *Aegilops* (for details, see text).

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Chromosomal introgression and genomic reorganization by the interspecific hybridization in polyploid species of *Triticum* and *Aegilops*

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With respect to the origin of second modified genomes in tetraploid species of *Triticum* and *Aegilops*, Zohary & Feldman (1962) emphasized the introgressive hybridization or the introgression. In order to evaluate the introgression in tetraploid species, chromosomal and morphological analyses were carried out in the offsprings derived from some interspecific hybridizations (Furuta & Tanaka 1970, Furuta 1982, 1983).

In cytogenetically stable F_4 population derived from fertile F_1 hybrid between *Ae. triaristata* (C^uM^t genome) and *Ae. columnaris* (C^uM^c), in addition to both types, the restitution (*triaristata*) and the substitution (*columnaris*) types, the intermediate type occurred. Frequency of the restitution type is higher than those of two other types, however. Morphological hybrid swarm was also observed in the F_4 population.

Two other F_1 hybrids, between *Ae. triuncialis* (C^uC) and *Ae. columaris* and between *Ae. variabilis* (C^uSV) and *Ae. columnaris* differed from each other in the amount of chromosome pairing, but were sterile in common. The F_1 hybrids were backcrossed with each recurrent parent. B_1 plants with alien chromosome(s) from the non-recurrent parent were selected and B_1F_4 populations were obtained by selfing these B_1 plants at the following three generations. Among B_1F_4 populations, stable plants which form 14 bivalents in all or almost all PMC's at meiosis were analyzed as to chromosomal and morphological introgression. The chromosome constitution of B_1F_4 plants were tested by the observation of chromosome pairing in RF_1 plants derived from B_1F_4 plants crossed with the recurrent parent. The experimental results obtained are similar between these two hybrid combinations (Table 1). That is, about 70% plants in both B_1F_4 populations restituted to genome constitution of the recurrent parental type. Ten or 22% plants were substituted one non-homologous chromosome from the non-recurrent or pollen parents. One percent had two non-homologous substituted chromosomes. In several plants, translocation occurred in the previous generation or the translocated chromosome was introduced from the donor parent. Two or 12% of the plants tested were combination type of those mentioned above.

Chromosomal variations occurred in these two cross combinations are similar to intraspecific variation in natural populations of *Ae. triuncialis* (Furuta *et al.* 1984) and *Ae. variabilis* (Furuta 1981). Moreover, various morphological characters were introgressed from non-recurrent or pollen parents in both cross combinations.

Forth interspecific hybrids, between *Ae. columnaris* and *Ae. biuncialis* (C^uM^b) were backcrossed twice by *Ae. columnaris*, because B_1 plants backcrossed by *Ae. columnaris* were sterile owing to low chromosome pairing at meiosis. Of course, these B_2 populations were similar to the recurrent parent or *Ae. columnaris* in chromosome constitution and morphology. This points

Table 1. Comparison of chromosomal variation between two interspecific hybridization, cross combinations 2 (*Ae. triuncialis* and *Ae. columnaris*) and 3 (*Ae. variabilis* and *Ae. columnaris*)(Furuta, 1982)

Type of chromosomal variation	Number of RF_1 plants	
	Cross 2	Cross 3
Restitution to recurrent parent	69 (70)*	48 (70)
One non-homologous chromosome (segment) substitution	22 (22)	7 (10)
Two non-homologous chromosomes (segments) substitution	1 (1)	1 (1)
Translocation	5 (5)	5 (7)
Combination		
one chromosome substitution + translocation	1 (1)	8 (12)
two chromosomes substitution + translocation	1 (1)	
Total	99 (100)	69 (100)

* Percent in parenthesis.

out that this combination which is sterile in B_1 generation, produces less modification in cytological and morphological traits.

Since the substitution-type backcross pollinated by pollen parent needs about three more backcrosses for recovering of fertility, it is suggested that the restitution-type backcross produces more number of introgressed plants for morphology as well as chromosome constitution than the substitution-type backcross.

Hybrids between the synthesized tetraploids carrying one genome in common (S^bA and M^uA) released larger chromosome variation in their F_4 plants (Furuta and Tanaka unpublished). This is maybe due to the unestablished cytological stability in synthesized strains.

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Genome analysis of *Aegilops mutica* Boiss. based on the chromosome pairing in the hybrids with or without B-chromosomes

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Aegilops bicornis, Ae. longissima, Ae. sharonensis, Ae. speltoides, Ae. caudata, Ae. comosa, Ae. uniaristata, Ae. umbellulata and *Triticum boeoticum* were crossed by *Ae. mutica* with or without B-chromosomes(Bs), and A-chromosome pairing at MI of PMCs in the F_1 hybrid plants was observed to estimate the genome homology between *Ae. mutica* and these nine species. The mean chiasma frequencies per cell and their ranges in these F_1 hybrids are shown in Fig. 1. The F_1 hybrids without B-chromosomes(0B) from the crosses of *Ae. bicornis, Ae. longissima, Ae. sharonensis, Ae. speltoides, Ae. comosa* and *T. boeoticum* to *Ae. mutica* showed a very high frequency of A-chromosome pairing with a high chiasma frequency, while those from the crosses of *Ae. uniaristata, Ae. caudata* and *Ae. umbellulata* to *Ae. mutica* showed a lower frequency of A-chromosome pairing and/or a complicated configuration of A-chromosome pairing with a high frequency of multivalents. On the contrary, the F_1 hybrids with 2Bs from most cross combinations showed a very low frequency of A-chromosome pairing characteristically with no chiasma in their PMCs. In contrast, a high frequency of bivalents was found in the 2B hybrids from the cross of *Ae. speltoides* x *Ae. mutica.*

In addition to these results from chromosome pairing in F_1 hybrids, partially fertile 0B hybrid plants were obtained from the crosses of some strains of *Ae. speltoides* to *Ae. mutica* and their pollen fertility was up to 16.7%. From one of these fertile hybrids, six plump caryopses were obtained by open pollination. Three of them normally germinated, and two of the obtained seedlings had 14 chromosomes and the other had 15 chromosomes in their root tips. Therefore, the normal pollen grains in the partially fertile F_1 hybrids are reasonably assumed not to be unreduced gametes but to be normal gametes with seven chromosomes.

It is well-known that B-chromosomes of *Ae. mutica* remarkably suppress the pairing between homoeologous or partially homologous chromosomes but do not affect the pairing between fully homologous ones. Considering the present data and this fact, I conclude that the genome of *Ae. mutica* is most closely related to that of *Ae. speltoides.*

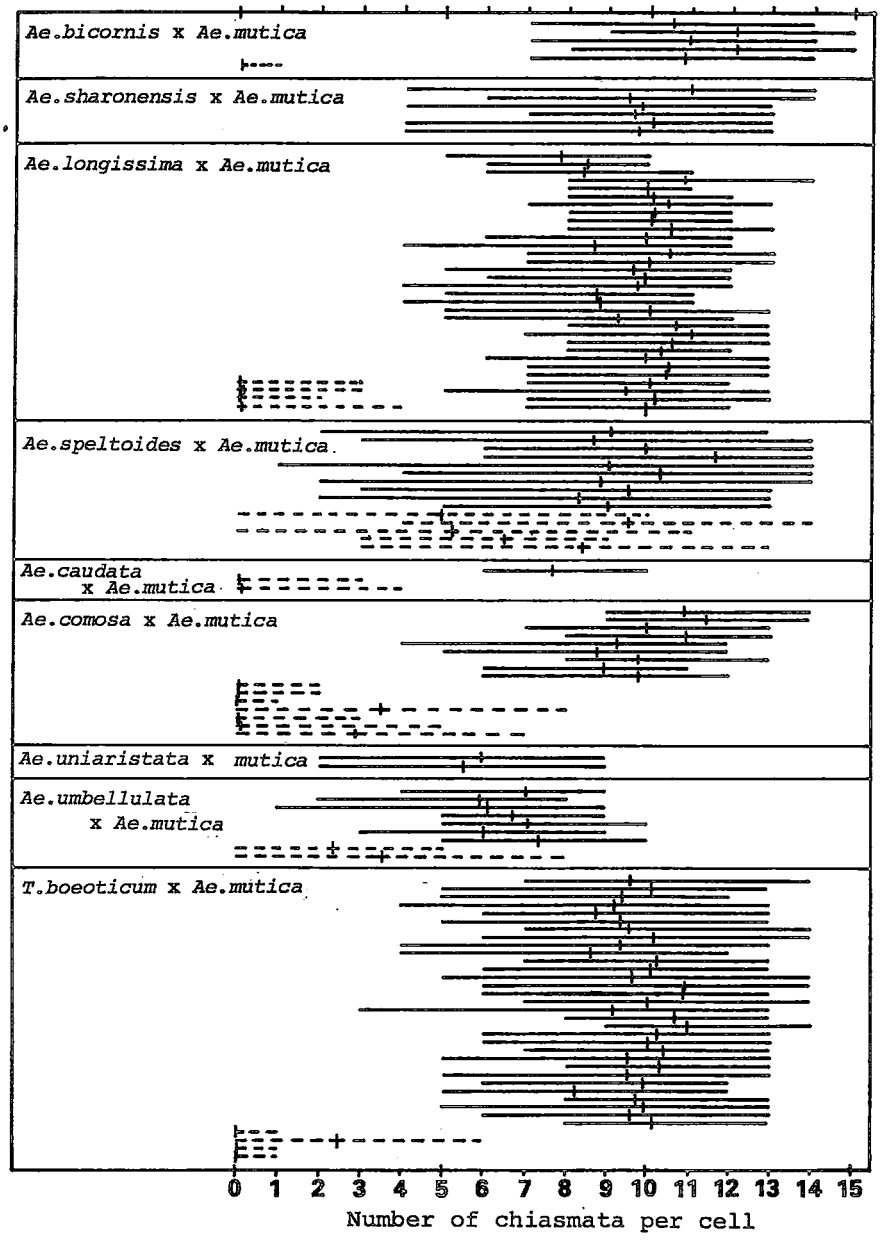

Fig. 1 Mean chiasma frequencies per cell and ranges of chiasmata per cell in the each F_1 hybrid plant between *Ae. mutica* and nine diploid *Aegilops* and *Triticum* species. Short vertical lines show the mean chiasma frequencies; solid and broken horizontal lines show the ranges of chiasmata per cell in the 0B and 2B hybrids respectively.

Hybrid dysgenesis in wheat: its determinants and utilization for wheat genetics and breeding

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Many abnormal phoenomena, e.g., gametic abortion, chromosome breakage, mutation, embryo and endosperm degeneration, and segregation distortion, appear in wheat lines carrying gametocidal genes of *Aegilops* or *Agropyron* species. This syndrome induced by the gametocidal genes is called "hybrid dysgenesis" (TSUJIMOTO & TSUNEWAKI 1985a). I report here the determinants of hybrid dysgenesis and its utilization for wheat genetics and breeding.

The gametocidal genes of two strains of *Ae. speltoides* were introduced into chromosome 2B of common wheat cultivar Chinese Spring (CS) (TSUJIMOTO & TSUNEWAKI 1984; TSUJIMOTO 1986a) and those of some other species are carried on their chromosomes which are added to CS genomes (Table 1). All genes except *Gc-Ag1* cause gametic abortion in both male and female sides when they exist in CS background in hetero- or hemizygous (monosomic addition) condition. *Gc-Ag1* causes abortion of female gametes only (KIBIRGE-SEBUNYA & KNOTT 1983). Many Japanese common wheat cultivars have a suppressor, *Igc1*, against the activity of *Gc-C*, thus, *Gc-C* does not cause gametic abortion in the background of such cultivars (TSUJIMOTO & TSUNEWAKI 1985b).

The gametocidal genes of Sitopsis species of *Aegilops*, i.e., *Gc1s*, *Gc1b* and *Gc-S*^{1}*1* cause hybrid dysgenesis in the progeny of CS carrying them, whereas *Gc-C* causes it, excpet gametic abortion, in cooperation with *Igc1* or a linked gene with it (TSUJIMOTO & TSUNEWAKI 1985b; TSUJIMOTO 1986b). Additionally, the actions of *Gc-C* is completely independent of those of Sitopsis gametocidal genes although Sitopsis gametocidal genes interact each other (TSUJIMOTO & TSUNEWAKI 1985c). Consequently, I propose to divide the hybrid dysgenesis in wheat into two types; one-gene system hybrid dysgenesis for the abnormalities caused by the Sitopsis gametocidal genes, and two-genes system for those by *Gc-C* and *Igc1*. No detailed studies have been made on the gametocidal genes of *Agropyron* species and *Gc-S*^{1}*2*.

Chromosome breakage and translocations caused by the two-genes system hybrid dysgenesis are useful to produce chromosome deletion or translocation lines effectively because production of genetically stable lines without gametocidal gene (*Gc-C*) is possible by the action of *Igc1*. Additionally, this system is available for alien gene transfer to wheat genomes without irradiation or skillful cytological technique.

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Table 1. Gametocidal genes and a suppressor in wheat and its relatives

Gametocidal gene[1)]	Chromosome location	Origin
Gc1a[2)]	2B	*Ae. speltoides* strain *aucheri*
Gc1b[3)]	2B	*Ae. speltoides*
(*Gc-S*^{1}*1*)	4S^1	*Ae. sharonensis*
"	"	*Ae. sharonensis*
"	"	*Ae. longissima*
(*Gc-S*^{1}*2*)	2S^1	*Ae. sharonensis*
"	"	*Ae. longissima*
(*Gc-C*)	3C	*Ae. triuncialis*
"	"	*Ae. caudata*
?	3C?	*Ae. cylindrica*
(*Gc-Ag1*)	7el2	*Ag. elongatum*
(*Gc-Ag2*)	?	*Ag. intermedium*
Igc1	3B	*T. aestivum* cv. Norin 26

1) Genes in parentheses are tentatively given.

2) Designated *Gc1* in TSUJIMOTO & TSUNEWAKI (1984, 1985a) and TSUJIMOTO (1986a).

3) Designated *Gc2* in TSUJIMOTO & TSUNEWAKI (1985a) and TSUJIMOTO (1986a)

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Genetic analysis of the compatible relationship between nuclear genes and cytoplasmic factors in wheats and their wild relatives

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It has been demonstrated previously that there are three types of tetraploid wheat nucleus, with regard to compatibility with the cytoplasm of *Aegilops squarrosa* (Ohtsuka 1983). Majority of Emmer wheats (AABB genomes, 9 strains of *Triticum dicoccoides*, 17 of *T. dicoccum*, 12 of *T. durum*, 3 of *T. turgidum*, 2 of *T. polonicum*, 2 of *T. aethiopicum*, 1 of *T. persicum=carthlicum*, 1 of *T. isphahanicum* and 1 of *T. orientale=turanicum*) were classified as AB type with no compatibility to *squarrosa* cytoplasm. All of Timopheevi wheats (AAGG genomes, 24 strains of *T. araraticum* and 9 of *T. timopheevi*), except one strain, were classified as AG type with complete compatibility to *squarrosa* cytoplasm. And, some species or strains of Emmer wheats (3 strains of *T. dicoccoides*, 9 of *T. persicum*, 4 of *T. palaeocolchicum=georgicum*, 4 of *T. pyramidale* and 2 of *T. orientale*) and one exceptional strain of Timopheevi wheat (1 of *T. araraticum*) were classified as AB' type with incomplete compatibility to squarrosa cytoplasm.

In Table 1, these three types of response of tetraploid wheat nuclus were summarized. The AB type nuclei were considered incompatible with *squarrosa* cytoplasm, because strict zygotic lethality of the cytoplasm-genomic constitution of (*squarrosa*)AABB and selective sterility of male gametes of (*squarrosa*)AB were manifested. And, the *1D* chromosome of *Ae. squarrosa* was indispensable for the compatible relation between the AB type AB genomes and *squarrosa* cytoplasm. On the other hand, AG type nuclei were considered complete compatible with *squarrosa* cytoplasm, because the normal plants with the genetic constitution of (*squarrosa*)-AAGG were obtained. When the (*squarrosa*) AABB+*1D* lines of AB type Emmer wheats were crossed with the AG type Timopheevi wheats (as male), all of the F_1 seed,including(*squarrosa*)-AABG+*1D* and (*squarrosa*)AABG, were viable and normal, and all of the F_1 seedlings, including 2n = 29 and 2n = 28, developed to the plants with normal growth (normal plant).

Different from the AB type and AG type nuclei, the AB' type nuclei were considered incomplete compatible with *squarrosa* cytoplasm. When the (*squarrosa*)AABB+*1D* lines of AB type Emmer wheats were crossed with the AB' type Emmer wheats (as male), all of the F_1 seed were viable, no abortive seed (zygotic lethal) appeared, but only the seed with *1D* chromosome were normal and the seed without *1D* chromosome were shriveled because of incomplete development of endosperm. And, in the F_1 seedlings, obvious segregation was also appeared. The F_1 seedlings with *1D* chromosome (2n = 29) grew to normal plants, but the F_1 seedlings without *1D* chromosome (2n = 28) turned to be midget plants with extreme reduction of plant vigour and with severe chlorophyll variegation under low temperature.

Gene analysis was conducted with regard to the difference in *squarrosa* cytoplasm compatibility between AB type and AB' type Emmer wheat species.

Table 1. Response types of tetraploid wheat nuclei to the cytoplasm of *Ae. squarrosa* appeared in seed morphology and seedling development of F_1 in the crosses to (*squarrosa*)AABB+*1D* lines of AB type Emmer wheats

Response type of male parent	Seed morphology			Seedling development	
	Viable		Abortive (zygotic lethal)	Normal plant	Midget plant (variegated)
	Normal	Shriveled			
AB type	(*sq*)AABB+*1D*	—	(*sq*)AABB	(*sq*)AABB+*1D* (2n = 29)	—
AB' type	(*sq*)AA'BB'+*1D*	(*sq*)AA'BB'	—	(*sq*)AA'BB'+*1D* (2n = 29)	(*sq*)AA'BB' (2n = 28)
AG type	(*sq*)AABG+*1D* (*sq*)AABG	—	—	(*sq*)AABG+*1D* (*sq*)AABG (2n = 29 & 28)	—

* In this table, the cytoplasm of *Ae. squarrosa* is represented as (*sq*).

** AB indicates the AB type AB genomes, and A'B' indicates the AB' type AB genomes.

Table 2. Genetic differentiation of nuclear genes for cytoplasmic factors among tetraploid wheats appeared in compatibility with the cytoplasm of *Ae. squarrosa*

Nuclear gene for cytoplasmic factor	Compatibility with *squarrosa* cytoplasm	Phenotypic expression with *squarrosa* cytoplasm
C_p gene (for plastid)		
C_p1 (AB type)	Incompatible	Zygotic lethal (abortion of endosperm = amyloplast) Gametic sterile in male (non development of starch grain = amyloplast)
C_p2 (AB' type)	Incompletely compatible	homo: Normal hetero with AB type: Shriveled seed (incomplete development of endosperm) Chlorophyll variegation under low temperature
C_p3 (AG type)	Completely compatible	Normal
C_v gene (for plant vigour)		
C_v1 (AB type)	Poorly compatible	(Extreme reduction of plant vigour)
C_v2 (AB' type)	Incompletely compatible	homo: Half reduction of plant vigour hetero with AB type: Extreme reduction of plant vigour
C_v3 (AG type)	Completely compatible	Normal

A segregation experiment was performed to examine B_1F_1 plants obtained from backcrosses of F_1 midget plants produced by crosses of (*squarrosa*)AABB+*1D* lines of AB type Emmer wheats x AB' type Emmer wheat species (as male). When the F_1 midget plants were backcrossed with AB type Emmer wheat species (as male), half of the B_1F_1 seed obtained were viable and the remaining half abortive. And, the viable B_1F_1 seed produced midget plants without an exception. On the other hand, when the F_1 midget plants were backcrossed with AB' type Emmer wheat species (as male), the B_1F_1 seed obtained were all viable, no abortive seed appearing. In the B_1F_1 lines produced from the B_1F_1 seed, four plant types, i.e. intermediate-I plant (without variegation, half reduction of plant vigour), weak plant (without variegation, extreme reduction of plant vigour), intermediate-II plant (with chlorophyll variegation, half reduction of plant vigour), and midget plant (with chlorophyll variegation, extreme reduction of plant vigour) were produced, in the ratio of 1:1:1:1.

The results suggest that AB' type AB genomes possess two kinds of nuclear genes controlling incomplete compatibility with *squarrosa* cytoplasm, which genes are inherited independently. One of the two alleles, which relates to the appearance of viable seed (shriveled because of incomplete development of endosperm) and the appearance of chlorophyll variegation, is regared as the nuclear gene controlling plastid development. The other, relating to plant vigour in B_1F_1 plants with *squarrosa* cytoplasm, is thus regarded as the nuclear gene controlling compatibility with the cytoplasmic factor relating to plant vigour (maybe mitochondrion).

When the two nuclear genes controlling compatibility with cytoplasmic factors are designated C_p (gene for plastid) and C_v (gene for plant vigour), segregation observed in the B_1F_1 plants can be explained as Table 2.

Genetic differentiation of these nuclear genes responsible to the compatibility with cytoplasmic factors were considered to be corresponding with the genetic differentiation of cytoplasmic factors among tetraploid wheats.

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III. Editoriral Remarks

Announcement for Future Issues

WIS No. 64 will be planned for publication in January, 1987, Manuscripts for this issue are most welcome and accepted any time, not later than December 31, 1986.

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The Managing Editor

Explanation of the figure on the cover

Midget chromosome appeared in alloplasmic *T. aestivum* cv Chinese Spring having cytoplasm of *Secale cereale.*
See the text article by Nakata *et al.* for detail.

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