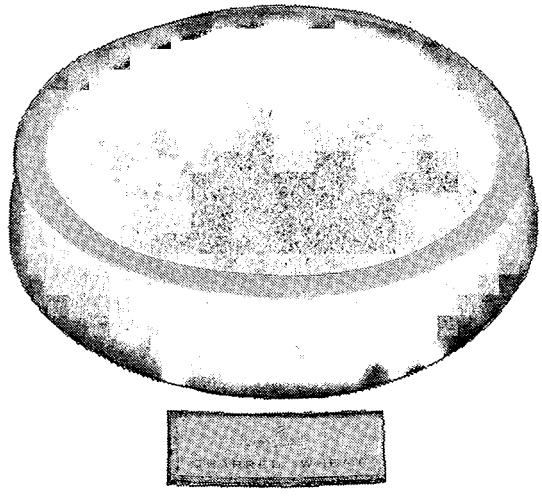
WHEAT INFORMATION SERVICE



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I. Research Notes

Origin and dispersion of wheats with special reference to peripheral diversity (a preliminary report)[1)]

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Introduction

During the Technical Meeting on Plant Exploration and Introduction held by F.A.O. in 1961, I tried to say that VAVILOV's theory had become outdated as the leading philosophy for exploration, and some other new theory should be sought, but my opinion did not seem to draw much attention. Later, however, ZOHARY (1970) stated in his article in "Genetic Resources in Plants – their Exploration and Conservation (edited by FRANKEL and BENNETT, 1970) that "Vavilovian concept of centers of origin should be discarded or at least greatly revised", and HARLAN (1978) concluded in his speech at the Plenary Session of the XIV International Genetic Congress on N.I. VAVILOV Heritage in Modern Genetics, that "Additional collecting, biosystematic analyses, and archeological work have added much to our knowledge. On the other hand, the world of VAVILOV has all but vanished; old centers of diversity have disappeared under the impact of modern agriculture."

World Centers of the Most Important Cultivated Plants

VAVILOV (1951) stated that "in modern times, the distribution of plant species on the earth is not uniform. There are a number of regions which possess exceptionally large numbers of varieties. Southeastern China, Indo-China, the Malay Archipelago, southwestern Asia, tropical Africa, the Cape regions, Abyssinia, Central America, South America, southern Mexico, countries along the shores of the Mediterranean, and the Near East possess extraordinary concentrations of plant varieties". In summarizing the works of numerous expeditions, VAVILOV located eight independent centers of origin of the world's

1) A full-paper of this article will be published in Seiken Ziho, Report from the Kihara Institute for Biological Research, Nos. 27, 28, December, 1978.

most important cultivvated plants. In VAVILOV's concept, the centers of diversity are referred to as centers of origin.

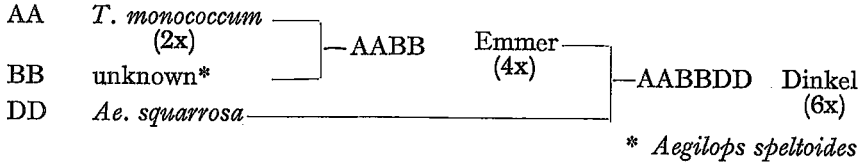
SCHIEMANN gave the comparable gene centers (Genzentren) after ROEMER and TROLL (1937) and her own (1931) in her article "Gedanken zur Genzentrentheorie VAVILOVS (1939).

In VAVILOV (1951), there may arise a few questions: (1) Why does the same genus (or species) occur in more than one or even several centers of origin, although polyphyletic origins for certain cultivated plants are not postulated by him? (2) How are we to interpret various expressions, for instance, "secondary centers of origin", "secondary center", "one of the centers of origin", "basic center", "one of the centers", and "a center", given for certain species? To quote ZOHARY (1970) again, "in many cases VAVILOV found centers of diversity for given crops very far away from the areas in which their wild relatives occur. A conspicuous case is the Ethiopian center. Here, wheats, barleys, peas, flax and lentils occur in an extraordinarily rich collection of varieties. Tetraploid wheats, for instance, manifested here according to Vavilov their widest variation. But significantly for all of these crops, they have not a single wild relative in Ethiopia. They therefore could not have possibly been domesticated there." I visited Ethiopia in 1964 and 1968, and I agree with ZOHARY's interpretation. YAMASHITA *et al.* (1969) stated "any species of *Aegilops, Secale* and *Agropyron*, related to wheats, were not found, therefore *durum* wheats rich in variation is presumed not to be originated in Ethiopia or Abyssinian highland. They must have been introduced in ancient times and have yielded diverse variations there."

HARLAN proposed *diffuse origins* in his earlier papers (HARLAN, 1956, 1961, 1966): "Cultivated plants did not enter into domestication as the full blown crops we know today. They started as something much less impressive and more or less equivalent to their wild progenitors. Since, in some cases, we do not know the wild progenitors, we have only a general idea of what the earliest domesticates were like. We do have good evidence, in a number of instances, that the crops picked up additional germ plasm as they spread out of their nuclear areas of origination and came into contact with wild relatives." and "In wheat, we know that the heredity of *Aegilops squarrosa* was added to tetraploid wheat some time after domestication" (HARLAN, 1970).

Origin of Wheats

The genealogical relationships of the wheats have been established by KIHARA (1944) based on genome as well as morphological analyses, as follows:



* *Aegilops speltoides*?

In 1959, we were favored with an opportunity to visit the Agricultural Museum in Cairo, and to examine carbonated samples of disarticulated spikelets of wheat excavated from one of the oldest pyramids of Egypt estimated to be as old as about 7,000 years. They were identified by us to be *T. dicoccum* (4x). From the excavated material from Jarmo visited by BEM[2] it has been also suggested that the origin of the 4x wheats can date back more than 7,000 years before the present.

In the Mohenjodaro excavates of Indus civilization, wheat grains, estimated to be as old as 5,000 years before the present, were found. I saw them in the museum on my visit in 1950 (ref. figure on cover i). They are probably *T. sphaerococcum* (6x).

If we assume that the 6x wheats originated from the 4x wheats under cultivation, then they originated at a later time, a time when the 4x wheats had a wide distribution. Since cytogenetically the 6x wheats seem to have a single origin - from 4x wheats × *Aegilops squarrosa* - we might conclude that they had a single geographical point of origin not necessarily the same as the point of origin of the 4x wheats.

KIHARA (1975) stated: "As for the place of origination, we think Azerbaijan and its adjacent region might be the candidates. — We think that the present day 6x wheats may have been arisen in ancient farmers field as the hybrids between cultivated emmer and *Ae. squarrosa* and they were preserved.", and further," The problem is the time of cultivation of wheat. This cannot be estimated biologically at present. However, archaeological excavations in Iraq and Afghanistan yielded carbonated grains of hexaploid wheat. So at least 6,000 to 8,000 years ago wheat was cultivated in this area. So we might be justified in estimating the time of origination as roughly 8 to 10 thousand years ago."

In general, the place of origin of the alloploid crops is to be found where the ancestral species occurred, but it is difficult or almost impossible to point out precisely where the diploid ancestors were domesticated. HARLAN (1970) suggested that ,"the general locale for wheat and barley domestication seems to be in or near the oak woodland belts in an arc through the hilly country surrounding the Syrian-Mesopotamian plains. The arc stretches from Kuzestan in Iran through the Western Zagros, the Tauros of Turkey and down the Antilebanon to the Southern Jordan highlands near the Dead Sea rift." We in 1970, observed the same geobotanical situations where, in many places, wild diploid wheat, *Aegilops speltoides* and wild tetraploid wheat occurred in association.

Dispersion of Wheats

From the presumed place of origin, cultivated wheats dispersed west- and east-wards. The west-bound dispersion took two pathways, one through the European continent and the other along the Mediterranean Sea. The former brought forth the differentiation of the varieties of 6x wheats, and the latter the differentiation of 4x wheats.

"In *Italy* the greatest interest attaches to the hybridization work of the Institute headed by the eminent breeder STRAMPELLI, who created a number of excellent varieties which today are widely cultivated, not only in Italy but also in neighboring countries. Particularly outstanding is his variety Ardito. From Italy this variety has centered in Argentina,

Chile, and France, and today occupies millions of hectares. Its one serious defect is its shattering. Its pedigree includes an English wheat of the squarehead type and an Italian local form of the Rieti type, while a decisive role in Ardito's formation was played by the Japanese variety Akagomughi, which has an oriental appearance, is low growing, with bright yellow color, and shatters easily, a characteristic of Japanese wheats. The role of Japanese varieties is an outstanding feature of recent Italian breeding." (VAVILOV, 1951).

In the East, *T. compactum* (6x) had differentiated in the Hindukush areas and *T. sphaerococcum* (6x) in the Indus areas in the early stage, as stated before. KIHARA, YAMASHITA and TANAKA (1965) described 50 varieties of *T. vulgare*, one of *T. compactum*, five of *T. durum* and one of *T. turgidum* in the materials collected by KUSE.

For further dispersion, KIHARA and LILIENFELD (1949) stated "(1) From the description of various Chinese classics it seems to be quite sure that wheat ws already introduced and cultivated in the period of Chou (1100 B.C.). However, there is no archaeological evidence. Above all there arises a question whether or not the ancient wheat in China was tetraploid. If the origin of *T. vulgare* were very recent, ancient Chinese wheat and its presumable descendants in Korea and Japan cannot have been hexaploid common wheats. Both historical records and deposits of ancient Korea show that wheat cultivation was very common in the middle of the third century. Carbonized wheat grains excavated from a military granary in Fuyo, Chusei-Nando, are, according to my collaborator Mr. NAKAO, perhaps the seeds of *T. compactum* or *T. vulgare*. There is no indication that the grains are those of a tetraploid wheat. The relics are believed to be from the middle part of the seventh century. I had no opportunity to see Japanese wheat grains found as deposits. But the native wheat varieties, which are believed to be cultivated since ancient times, are hexaploid. (2) There arises a suspicion that the once cultivated tetraploid wheat has been substituted by the present hexaploid one. In the Far East, however, there is no proof that Emmer or any other 4x-wheats were cultivated, as there is no 4x wheat left either in Korea or in Japan. *T. durum* and *T. turgidum*, which are sporadically cultivated in Mongolia and China, are believed to have been introduced in very recent times (HOSONO, 1935 and HIRAYOSHI, 1940).

From these considerations we may conclude that Chinese, Korean and Japanese varieties, used in ancient times, seem to be hexaploid."

It is interesting to refer to HOSONO (1935) who studied systematically his collections of wheats from various localities in China. He found a considerable diversity of varieties of wheats. The majority of the materials were 6x wheats, *T. vulgare* and *compactum*, and only 1 sample was proved to be *T. turgidum*.

Concerning the introduction of wheats to China, HOSONO (1935) stated that "geht hervor dass Hopei, Shantung und Yuennan die meisten Varietaeten beherbergen. — Die reichste Provinz an Varietaeten ist fraglos Yuennan: unter 20 *vulgare*-Proben stellten 10 verschie dene Varietaeten dar. Auch die in Indien endemische *bengalense*-Varietaet wurde nur in dieser Provinz gefunden. Daraus kann man schliessen, dass der heute nicht mehr wichtige Burma-Yuennan-Hand-elsweg bei der Verbreitung der Weizen in Suedchina eine gewisse

Rolle gespielt haben muss." It is also noteworthy that "Aus folgenden Gruenden ist es aber sehr wahrscheinlich, dass die im Norden gefundenen Weizen durch den Nordweg eingefuehrt wurden. 1. In Kansu kommt die in Mittelasien endemische vulgare-Varietaet *turcomanicum* vor. 2. Die benachbarte Mongolei, die sehr spaerlich bevolkert ist und nur geringe Weizenproduktion aufweist, ist reicher an Varietaeten als ganz China (VAVILOV, 1923)" "Wahrscheinlich sind die Weizen aus dem Ursprungszentrum nach China nicht ueber die seit dem Mittelalter gebrauchten Handelswege, sondern in vorhistorischer Zeit auf dem Wege der Voelkerwanderungen gekommen."

Their dispersion in the remote ages would have taken place slowly from man to man through communications between remote villages. The dispersion was so slow that it was not until the 7th century that the first samples of wheat grains reached Japan from China. It may be presumed that there were already cultivations of wheats in the Tang era in China.

Among many improved modern cultivated varieties of wheat, "*Norin 10*", a Japanese dwarf wheat variety, has become well known for its dwarfness as the breeding material for Mexican semidwarfs. Its pedigree is as follows, after INAZUKA (1971): *Norin* 10 was obtained from an artificial cross of *Turkey red* as mother and *Fultz-Daruma* as father. According to the old records, *Fultz* and *Turkey red* were introduced from the U.S.A., *Fultz* around 1892 and Turkey red later. *Fultz-Daruma* was a line from a cross of *Daruma* as female and *Glassy Fultz* as male. *Daruma* is believed to have been a representative variety of the Kanto district, known as *Shiro-Daruma*, while *Glassy-Fultz* is believed to have been a glassy derivative from *Fultz* with mealy grain." It is our further subject to trace back the origin and routes of *Daruma* in the near future.

It seems very probable that the short culm varieties developed in the East and the tall culm varieties in the West.

Peripheral Diversity

Cultivated plants must have dispersed from the places of their origins to neighboring places, along with the spread of human culture, overcoming various barriers, geographical and ecological, one after another, until they come to a barrier of extremity, such as a high mountain range, a desert, the seas, or other. During the course of the dispersion, diversity occurred to yield modified forms adaptable to the diverse geographical and ecological conditions encountered. Mutations and introgressive hybridizations took place, resulting in the accumulation of diversity as the spread of the species continued.

It is worth notice here that SCHIEMANN (1939) stated that "Nach unseren experimentellen Erfahrungen wirken aber extreme Aussenbedingungen mutationsausloesend. So wird as Nebeneinander normaler und extremer Bedingungen, wie es sich besonders haeufig in Gebirgsgegenden findet, leicht zur Ausbildung einer Mannifaltigkeit fuehren."

Ultimately a barrier would be reached and not traversed. At the barrier of extremity we should find the greatest diversity. I have proposed to call this "*peripheral diversity*" in my previous paper (Yamashita, 1978). This may be compared to our daily observations;

as waste papers, fallen leaves, sand and other trash are blown about by the wind, it trends to accumulate, in all its diversity, at walls (barrier) and in corners. It is here where the accumulation of diversity of those elements is seen.

Old cultivars may be either eliminated by natural as well as human selection, or replaced by better new cultivars, to meet the demand of increasing human population. This is why the change to new recommended varieties takes place so rapidly in the central densely populated areas, resulting in the loss of valuable gene resources. This is being called genetic erosion. Therefore, the diversity remains accentuated in the peripheral areas.

If the above theory is accepted, some of the questions, if not all, raised in the Vavilovian concept, mentioned before, may be answered. The centers of some of the crops listed comprehensively by VAVILOV (1951) could be the centers of the *peripheral diversities of the present theory* of the far past distribution of ancient crops, spread over a period since the stage of the development of human culture in the middle Stone Age (SCHIEMAN, 1939). They could not be the centers of the formation of cultivated plants of VAVILOV (1951).

The origin and the evolution of wild tetraploid wheats[1)]

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It is the widely accepted theory that A genome parent of the Emmer group (AABB) and the *Timopheevi* group (AAGG) of the tetraploid wheats is *Triticum boeoticum* Boiss. (AA). Regarding to the other genomes (B and G), a number of workers suggested *Aegilops speltoides* Tausch. (SS) as the donor of the B genome to the Emmer (JENKINS 1929, PATHAK 1940, SARKER and STEBBINS 1956, RILEY *et al.* 1958), though there was little evidences that the S genome is homologous to the B genome. The artificial amphidiploid SSAA has been thought to give genomically dissimilar and sterile hybrids with the Emmer wheats. On the other hand, some workers suggested that *Ae. speltoides* is the donor of the G genome to *T. timopheevi* Zhuk. (SHANDS and KIMBER 1973).

In 1966, the senior author has obtained the amphidiploid SSAA from the cross between *Ae. speltoides* and *T. boeoticum*. Data on average chromosome association and seed fertility of the amphidiploid SSAA having 28 chromosomes at F_4, F_8 and F_{12} generations are summarized in Table 1. As shown in Table 1, the chromosome association of the amphidiploid SSAA was very low at the F_4 and F_8 generations indicating cytologically unstable with a large number of univalent formation. The cells with 14 bivalents could not entirely be found. However, at the F_{12} generation after synthesis, it was found that the chromosome association was rather high with the increase of polyvalents but the decrease of univalent formation. This might indicate the possibility of occurrence of some chromosomal and/or genic changes in this unstable amphidiploid at the recent generations.

The F_1 hybrids of synthesized SSAA at earlier generations crossed with the Emmer or the Timopheevi wheats did not show close chromosomal homology and they were highly

Table 1. Chromosome associations and seed fertilities of the amphidiploid SSAA having 28 chromosomes

Generation (year)	No. of plants examined	Chromosome association[1)]							Seed fertility (%)
		I	II	III	IV	VI	VII	VIII	
F_4 (1969)	3	10.01	8.64	0.20	0.03		—		8.5
F_8 (1973)	4	13.98	6.58	0.18	0.08		—		7.8
F_{12} (1977)	1	4.58 (0-13)	8.33 (3-13)	0.67 (0-4)	1.04 (0-4)	0.05 (0-3)	0.02 (0-1)	0.02 (0-1)	11.7

1) Values indicate means and ranges (in parentheses).

1) Contribution No. 13 from the Plant Germ-plasm Institute, Faculty of Agriculture, Kyoto University

Table 2. Chromosome associations and seed fertilities in the F_1 and F_2 hybrids SSAA × *T. dicoccum* and SSAA × *T. araraticum*

Cross combination	No. of PMC's observed	Chromosome association						Seed fertility (%)
		I	II	III	IV	V	VI	
SSAA(F_{11}) × *T. dicoccum*	60	4.44 (1-10)	6.64 (3-12)	1.60 (0-4)	1.27 (0-4)	0.08 (0-2)	—	0.21
F_2	50	2.98 (0-7)	6.96 (4-10)	1.14 (0-3)	1.60 (0-5)	0.16 (0-1)	0.08 (0-1)	4.1
SSAA(F_{11}) × *T. araraticum*	30	2.30 (0-5)	7.03 (3-10)	1.87 (0-4)	1.23 (0-3)	0.10 (0-1)	0.10 (0-1)	0.0

sterile (TANAKA unpublished). However, in 1976, crosses between SSAA at the F_{11} generation and *T. dicoccum* Schübl. or *T. araraticum* Jakubz. were made and two F_1 hybrid combinations were examined cytologically as shown in Table 2. Those hybrids showed rather high chromosome association with a few univalents. Furthermore, one hybrid plant produced two viable seeds though seed fertility of the bagged spikes was very low (0.21%). Two F_2 hybrid plants were also examined cytologically. Among them, one plant with 28 chromosomes showed higher chromosome association than F_1 plants and seed fertility of the bagged spikes increased to some extent (Table 2).

This may indicate the occurrence of genetic changes that were tending toward close genetic constitution to that of the Emmer wheats during the progression of generations in the synthesized SSAA. Although all F_1 plants set no seed in the hybrid between SSAA and *T. araraticum*, it may also be assumed that the similar occurrence of the genetic constitution which will be closer to the Timopheevi wheats might be expected during the advance of generations in the synthesized SSAA.

Furthermore, the above mentioned hypothesis will be supported by the following evidences.

1) F_1 hybrids between *T. araraticum* and *T. dicoccoides* Körn. from a mixed stand in Northern Iraq showed considerably high chromosome associations. Especially, two hybrid combinations showed very high associations and gave very low frequency of univalents (Table 3. See TANAKA and KAWAHARA 1976). These results clearly show that

Table 3. Chromosome associations of F_1 hybrids between *T. dicoccoides* and *T. araraticum* from a mixed stand near Amadiyah, Iraq

Cross combination	No. of PMC's observed	Chromosome association					
		I	II	III	IV	V	VI
8821A×8821B	50	1.26 (0-5)	10.46 (8-13)	1.46 (0-2)	0.36 (0-2)	—	—
8821A×8822	50	1.96 (0-6)	10.64 (8-13)	1.28 (0-3)	0.20 (0-1)	—	0.02 (0-1)

(TANAKA and KAWAHARA 1976)

Table 4. Distribution of seven chromosome types found in strains of *T. araraticum*[1)]

Region		No. of strains observed	Chromosome type						
			A	B	C	D	E	F	G
U.S.S.R.:	Transcaucasus	10	1	8	1				
Turkey:	Hozat	3		3					
	Silvan	2		2					
	Savur	1		1					
Iraq:	Amadiyah	8		7					1
	Rowanduz	14		10		2	1	1	
	Koi-Sanjaq	6		6					
	Sulaymaniyah	14		14					
Iran:	Ravansir	2		2					

1) Including data obtained by TANAKA and ISHII (1975), and KAWAHARA and TANAKA (1977).

the two wild tetraploid wheats in Northern Iraq are cytogenetically more closely related to each other than those reported so far. This may give an evidence to the monophyletic origin of the B and the G genome.

2) *T. araraticum* is known to have various degree of structural differentiations in chromosomes involving several interchanges (SVETOZAROVA 1939, WAGENAAR 1966 TANAKA and ICHIKAWA 1968, 1972, TANAKA and ISHII 1975, KAWAHARA and TANAKA 1977). Recently, the authors found seven reciprocal translocation chromosome types in *T. araraticum*. Number of strains and localities belonging to each type are summarized in Table 4. As shown in this table, chromosome differentiation in *T. araraticum* is more abundant in Northern Iraq than in Transcaucasus.

In contrast, no distinct structural variations of chromosomes in *T. timopheevi* occur, and most *araraticum* and all the *timopheevi* strains in the Tanscaucasus have chromosomes of the B type (TANAKA and ISHII 1975). It was concluded that cultivated *T. timopheevi* has been derived from wild *T. araraticum* having chromosomes of the B type in the Transcaucasus.

Distribution of structural differentiation in chromosomes of the Timopheevi wheats would indicate that they first originated in the eastern part of the Fertile Crescent and that later its distribution area was extended northward to the Transcaucasus (KAWAHARA and TANAKA 1977).

3) Two wild tetraploid species, *T. dicoccoides* and *T. araraticum*, are distributed in southeastern Turkey, Northern Iraq and Western Iran. Morphological differences between strains of *T. dicoccoides* and those of *T. araraticum* collected in these regions are not clear (TANAKA and ISHII 1973). Distribution of some characters in the strains of the two species from these regions are listed in Table 5. In color of ear, glume pubescence and shooting time, a wealth of various forms of both species was encountered in Iraq. Similar results was obtained in the seedling resistance of *T. araraticum* and *T. dicoccoides* to brown rust. According to Saito (unpublished), all strains of *T. dicoccoides* from Palestine,

Table 5. Geographical distribution of morphological and physiological characters in the strains of *T. araraticum* and *T. dicoccodies* collected in Turkey, Iraq and Iran

Region	Species	No. of strains observed	Ear color[1]			Glume[2]		Shooting[3]			No. of strains tested	Reaction to rust[4]		
			ye	br	bl	pu	gl	ea	in	la		R	MR	S
Turkey	*araraticum*	11	2	9	-	10	1	1	4	6	4	2	2	-
	dicoccoides	4	4	-	-	3	1	-	2	2	2	1	1	-
Iraq	*araraticum*	132	37	56	39	91	41	47	67	18	39	27	6	6
	dicoccoides	15	10	2	3	5	10	3	12	-	13	-	-	13
Iran	*araraticum*	5	1	2	2	5	-	-	5	-	2	2	-	-
	dicoccodies	3	3	-	-	3	-	3	-	-	3	-	-	3

1) ye=yellow, br=brown, bl=black. 2) pu=pubescent, gl=glabrous.
3) ea=early, in=intermediate, la=late. 4) R=resistant, MR=moderately resistant, S=susceptible.

Southern Syria, Iraq and Iran were susceptible. However, two strains collected in Turkey were resistant to moderately resistant. While, all the *araraticum* strains collected in the Transcaucasus, Turkey and Iran were resistant or moderately resistant. The majority of the strains of *T. araraticum* in Iraq were resistant or moderately resistant, but six strains were susceptible.

As shown in Table 5, almost all the variation of morphological and physiological characters concentrate in the districts around the Zagros Mountains.

Considering these evidences, the origin and the evolution of the two wild tetraploid wheats, *T. dicoccoides* and *T. araraticum*, is represented in Fig. 1. The two species were originated as the result of disruptive differentiation occured in natural amphidiploid SSAA between *Ae. speltoides* and *T. boeoticum* in the Zagros Mountains.

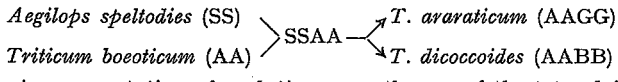

Fig. 1. A representation of evolutionary pathways of the tetraploid wheats.

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Studies on the nature and the possible origin of the spontaneously translocated 1B-1R chromosome in wheat[1)]

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During the last years cytological investigations of a number of hexaploid wheat cultivars revealed the presence of rye chromosome 1R or, at least, parts of it. This alien chromosome substitutes for wheat chromosome 1B (ZELLER and FISCHBECK 1971; BLÜTHNER 1972; ZELLER 1972; ZELLER and SASTROSUMARJO 1972; METTIN *et al.* 1973; ZELLER 1973). It could be demonstrated that almost all of these wheat lines took their origin as derivatives from experimental wheat-rye hybrids bred at Weihenstephan and Salzmünde. The only exception so far being the variety 'Salmon' which derived from a *Triticale* source in Japan (TSUNEWAKI 1964). Because of its fairly good transmission this particular rye chromosome, which provides resistance against rusts and mildew, has been transferred unconsciously by conventional breeding into an increasing number of mostly Europaen wheats.

Previous crossing experiments had already given clear evidence for the existence of two types of spontaneous rye chromosome transfer, i.e. the 1R(1B) whole chromosome substitution and, what is called the 1B-1R translocation. While the presence of the complete chromosome 1R in the substitution lines has been confirmed by the Giemsa banding technique, there are some discrepancies regarding the nature of the 1B-1R translocation (BENNETT and SMITH 1975; FRIEBE 1976; METTIN *et al.* 1976; MÜNZER 1977; JORDANSKY *et al.* 1978).

Further research was thus needed for several reasons. Compiling all cytological data so far available it is evident that cultivars having the 1B-1R translocation are at least as frequent as the 1R(1B) substitution (Table 1). Phytopathological and electrophoretical studies reveal the presence of even more lines (HYZA 1978; SLOVENCIKOVA *et al.* 1978), though cytological checks are still lacking. There is, moreover, some indication that translocations are prevailing against substitutions in the breeders' material. Based on these findings it can be suggested that this particular type of rye introgression might occur also during the development of secondary *Triticale* via substitutional polyploidy.

The interachange status of chromosome 1B-1R has been deduced from meiotic pairing with both chromosomes 1B and 1R resp. (ZELLER and SASTROSUMARJO 1972; BLÜTHENER and METTIN 1973; ZELLER 1973). These data suggested the break point being located near or at the centromere, so that the translocated chromosome contains at least the

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Table 1. List of wheat varieties with identified 1R(1B) substitution or 1B-1R translocation

Country	Substitution	Translocation
Belgium	—	Clement
Bulgaria	Burgas 2	—
GDR	Orlando	Almus
	Saladin	Winnetou
	Salzmünder Bartweizen (Neuzucht, St. 14/44)	
Great Britain	Zorba	—
FRG	Weique	Benno
	Wentzel	Perseus
		Weique
Japan	—	Salmon
The Netherlands	Mildress	—
Roumania	Lovrin 13	Lovrin 10
		Lovrin 12
USSR	Mironovskaja 10	Avrora
		Besostaja 2
		Kavkas
		Predgornaja 2
		Skorospelka 35

major part of the short arm of 1R. Additional evidence has been achieved by using the Giemsa banding technique. While the short arm of chromosome 1B-1R of the translocation lines listed in Table 1 is characterized by the very distinct terminal band together with a subterminal intercalary C-band, the pattern for the long arm is somewhat conflicting, at least in one line. Wheat chromosome 1B has, according to GILI and KIMBER (1974), a medium-sized C-band at the end of the long arm, while the telomeric band on the long arm of 1R is very pronounced. The terminal band on the long arm of the interchange chromosome 1B-1R was found to be wheat-like by most of the authors (BENNETT and SMITH 1975; FRIEBE 1976; JORDANSKY *et al.* 1978). However, MÜNZER (1977) observed a telomeric band being indistinguishable from the appropriate rye band, and suggested thus an intercalary translocation. A re-investigation of most of the translocation lines listed in Table 1 under comparable conditions revealed a medium-sized C-band at the end of the long arm, similar to wheat. Thus, on the basis of the banding pattern as well as the differences in arm length we confirm FRIEBE's results.

So far one of the translocation lines, 'Weique Züchter', has been found deviating from all other by the complete or almost complete lack of the telomeric band of the long arm of chromosome 1B-1R, which is accompanied by an adequate reduction of length (FRIEBE 1976; MÜNZER 1977). At present neither the appropriate meiotic pairing data (Table 2, data taken from ZELLER and SASTROSUMARJO 1972; BLÜTHNER and METTIN 1973; BLÜTHNER and METTIN 1977) nor the Giemsa analyses provide any evidence on the origin of this particular chromosome arm. Actually the data presented in Table 2 only demonstrate the capability of the deviating interchange chromosome to pair with 1RS as well as 1BL. Whether the long arm of chromosome 1B-1R of 'Weique Züchter' is capable to pair with

Table 2 The pairing behaviour of the two types of 1B-1R translocations in comparable crosses

Translocation	Frequency of complete bivalent formation with			
	1R (Weique Sub.)	1R (Zorba)	1B (Chin. Spring)	1BL (Chin. Spring)
Kavkas	82%	61%	53%	86%
Weique Zücht.	87%	62%	47%	100%

1RL has not yet been investigated. And so there is at the moment no reason to speculate about the possible loss of telomeric heterochromatin effecting a bilateral pairing ability similar to the behaviour of the presumed 2D(2R) substitution in 'Rosner' as suggested by KALTSIKES et al. (1977).

On the other hand it seems very likely that the long arm of the common type of the 1B-1R interchange has derived from chromosome 1B completely or almost completely. In addition to previous results SCHLEGEL (unpubl.) by using the Giemsa banding technique was able to demonstrate pairing of chromosome 1B-1R with rye chromosome 1R being restricted to the short arms, i.e. closed bivalents were never observed.

Because of the difficulty to locate the possible breakpoint of the interchange by genetic means, we tried to get some additional evidence by the presumed mode of origin of the 1B–1R interchange. Tracing back the origin of most of the translocation lines listed in Table 1 there is no doubt about the parentage of 1R(1B) whole chromosome substitutions. So it is very likely that the substitution was prior to the translocation. Because substitutions were often crossed to karyotypical ly normal wheats it seems reasonable to suppose a connection between the double-monosomic state for 1B and 1R in the hybrids on the one hand and the origin of the interchange on the other. Considering 1B, 1R double-monosomic wheat hybrids there is a certain probability for centromeric misdivision of the univalents followed by fusion of the telocentrics as shown by MORRISON (1954), SEARS (1972) and SHEPHERD (1973), though casual homoeologous pairing and recombination can no longer ruled out. For that reason some of the prerequisites for either centromeric fusion or recombination have been analyzed.

Taking the amount of telosomic offspring in appropriate wheat lines and hybrids as a measure for centromeric misdivision our previous data show that 1B, 1R double-monosomics yield up to 21% telocentrics. A comparative analysis of the frequency of telosomics in the progenies of wheat hybrids being monosomic for either 1B or 1R indicated a rather high instability of rye chromosome 1R, at least in a wheat background. This suggestion was confirmed in Giemsa-stained metaphase I preparations of 1B, 1R double-monosomics. As shown in Table 3 misdivisions of rye chromosome 1R exceeded by far those of wheat chromosome 1B. Considering the low number of PMC's scored it seems worthwhile to emphasize the occurrence of simultaneous misdivisions of both chromosomes under question, which is the prerequisite for centromeric fusion.

The alternative mode of origin of the 1B-1R interchange by means of homoeologous

Table 3. Analysis of centromeric misdivisions of the univalents in double-monosomic 1B, 1R after Giemsa-staining

Metaphase I-configuration	No. PMC	Frequency of cells with misdivisions of			
		no	1R	1B	1B+1R
$20^{II}2^{I}$	39	79.5%	15.4%	2.6%	2.6%

Table 4. Giemsa analysis of metaphase I-associations in euhaploid and nulli-5B haploid wheat-rye hybrids

Year	Combination	No. PMC	Number of II+III+IV	Total frequency of		
				W-W	R-R	W-R
1976	euphaploid	1451	766	96.74%	1.70%	1.57%
	5B-nullihaplo	159	576	99.47%	0	0.53%
1978	euhaploid	600	514	95.91%	2.33%	1.77%
	5B-nullihaplo	500	2055	92.99%	1.12%	5.90%

recombination must be taken into consideration, since several authors, by using the Giemsa banding technique, have proven the occurrence of wheat-rye pairing even in the presence of wheat chromosome 5B (METTIN *et al.* 1976; DHALIWAL *et al.* 1977; POHLER and KISTNER 1977). Our additional data on a large number of bivalents and multivalents in euhaploid wheat-rye hybrids suggest a figure of about 1.5% wheat-rye pairings of all associations (Table 4). This is, however, the average for the total of the rye chromosomes. Whether or not rye chromosome 1R, having a large amount of telomeric heterochromatin, participates proportionally in the wheat-rye associations must be left open at the moment.

Summarizing all the data available there is a lot of reason to suppose that the 1B-1R interchange derived from the whole chromosome 1R(1B) substitution by means of centromeric fusion. Therefore the breakpoint should be located at or very close to the centromere. This seems to be true, at least, for the common type of the interchange.

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The relationship of the D genomes of hexaploid *Ae. crassa*, *Ae. vavilovii* and hexaploid wheat

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The genome formula $M^{cr}DD^2$ which was assigned by KIHARA (1957) to *Aegilops crassa* Boiss. (2n=6x=42) indicates that two of the three genomes were derived from the D genome of *Ae. squarrosa* (2n=14). Evidence obtained from the meiotic studies of a haploid (CHAPMAN and MILLER 1977) and from hybrids (SIDDIQUI and JONES 1967) showed that the two D genomes of *Ae. crassa* are no longer homologous and that neither is completely homologous with the D genome of *Ae. squarrosa.*

Ae. crassa ssp. *vavilovii* ZHUK. was raised to species rank as *Ae. vavilovii* by CHENNAVEERAIAH (1960), when he found by karyotype studies that it differed from *Ae. crassa* in having only one D genome. The genome formula $M^{cr}DS^p$ was subsequently suggested for *Ae. vavilovii* by KIHARA and TANAKA (1970).

SIDDIQUI and JONES (1967) pointed out that the confusion between the two species could cause the earlier publications concerning the genomes of *Ae. crassa* to be less useful. The investigations reported here were intended to compare the genomes of *Ae. crassa* and *Ae. vavilovii* and to test the homologous relationships of the D and D^2 genomes of *Ae. crassa* and the D genome of *Ae. vavilovii* with the D genome of hexaploid wheat (*Triticum aestivum* L. THELL. 2n=6x=42).

Ae. crassa was crossed with *Ae. vavilvoii* and *Secale cereale* (2n=14). *Ae. crassa* and *Ae. vavilovii* were each crossed with *T. durum* (2n=4x=28) var. Aziziah and with *T. aestivum* var. Chinese Spring. The *Ae. vavilovii* was originally kindly supplied by Dr. TANAKA. The analysis of the meiotic chromosome pairing of the hybrids and the *Aegilops* parents is given in Table 1.

Quadrivalents were seen at meiosis in each of six plants of both *Ae. crassa* and *Ae. vavilovii*, and it seems unlikely, therefore, that these resulted from translocation heterozygosity; however, no multivalents were observed in an earlier meiotic study of *Ae. vavilovii* by CHENNAVEERAIAH (1960). In the hybrid *Ae. crassa* × *Ae. vavilovii* the pairing failure resulted in a mean frequency of more than 11 univalents per cell. The difference between the two species is shown again by a comparison of the meiotic chromosome pairing in hybrids of each species with *T. durum* and with *T. aestivum.* There was little pairing between the genomes of *Ae. vavilovii* and wheat in either hybrid, but the pairing in *Ae. crassa* × *T. aestivum* was much higher than that in *Ae. crassa* × *T. durum.* These results show that *Ae. crassa* and *Ae. vavilovii* differ by approximately one genome and that *Ae. crassa* unlike *Ae. vavilovii*, has chromosomes which pair with chromosomes of the wheat D genome.

Table 1. Mean chromosome pairing at first metaphase of meiosis
(30 cells per plant; ranges in parenthesis)

	Ch. no.	I	II			III	IV
			rod	ring	total		
Ae. crassa	42	0.20 (0-2)	1.87 (0-5)	18.63 (16-21)	20.50 (18-21)	—	0.20 (0-1)
Ae. vavilovii	42	0.03 (0-1)	2.43 (0-6)	18.07 (12-21)	20.50 (18-21)	0.10 (0-2)	0.17 (0-1)
Ae. crassa haploid	21	16.10 (11-19)	2.00 (0-5)	0.20 (0-1)	2.20 (1-5)	0.17 (0-2)	—
Ae. crassa × *S. cereale*	28	21.73 (19-28)	2.67 (0-6)	0.27 (0-1)	2.93 (0-6)	0.13 (0-1)	—
Ae. crassa × *Ae. vavilovii*	42	11.67 (8-20)	2.33 (0-5)	8.23 (8-12)	10.27 (8-14)	2.63 (0-6)	0.43* (0-1)
Ae. crassa × *T. aestivum*	42	31.23 (27-36)	4.00 (2-6)	0.73 (0-2)	4.73 (3-6)	0.43 (0-2)	—
Ae. vavilovii × *T. aestivum*	42	39.70 (36-42)	0.60 (0-3)	—	0.60 (0-3)	0.37 (0-1)	—
Ae. crassa × *T. durum*	35	32.40 (29-35)	1.20 (0-3)	—	1.20 (0-3)	0.06 (0-1)	—
Ae. vavilovii × *T. durum*	35	31.00 (29-35)	0.70 (0-3)	—	0.70 (0-3)	0.57 (0-1)	—

* including 1^{V}.

In order to examine further the pairing of *Ae. crassa* chromosomes with those of the D genome of wheat, hybrids were made between *Ae. crassa* and each of the seven D genome telocentric lines of Chinese Spring. Meiotic chromosome pairing in each of these hybrids is given in Table 2. In all the hybrids, except those for chromosome 7D, the wheat D genome chromosome was represented by its two telocentrics. In the 7D hybrids only the $7D^{s}$ telocentric was present. The mean chromosome pairing was similar in each hybrid, but the frequency of the pairing of the telocentrics, and the configurations in which they paired, varied between hybrids. It can be seen from Table 2 that each of seven chromosomes of *Ae. crassa* pairs with a different wheat D genome chromosome. Trivalents which included two telocentrics demonstrated that 2D and 6D paired in both arms with the corresponding chromosome of *Ae. crassa*. For other chromosomes the pairing was limited to one arm. (7D only one arm tested). There was a maximum of two trivalents per cell in all of the hybrids. In the 3D and 6D hybrids trivalents occurred in which one wheat telocentric was paired. No cells were seen in which the two wheat telocentrics were paired in separate associations although such pairing might have been expected in the 6D hybrid.

The integenomic pairing of chromosomes of *Ae. crassa*, detected by the trivalents in the hybrids with wheat, should be expressed as bivalents in the haploid *Ae. crassa* and might be the cause of the quadrivalents observed at meiosis in *Ae. crassa*.

The action of chromosome 5B could be expected to limit the chromosome pairing to

Table 2. Mean chromosome pairing at first metaphase of meiosis in hybrids of *Ae. crassa* × the D genome telocentric lines of *T. aestivum* var. Chinese Spring (30 cells each of 2 plants per line; ranges in parenthesis)

Telo-centric line	Ch. no.	I	II			III	% cells with telo paried		
			rod	ring	total		II (1 telo)	III (1 telo)	III (2 telo)
1D	43	31.72 (28-35)	4.07 (2-7)	0.85 (0-3)	4.92 (3-7)	0.48 (0-2)	26.70	—	—
2D	43	32.92 (28-37)	3.65 (1-6)	0.47 (0-2)	4.12 (1-7)	0.45 (0-2)	31.70	—	6.70
3D	43	32.05 (27-37)	4.23 (1-7)	0.77 (0-3)	5.00 (2-8)	0.32 (0-2)	11.70	25.00	—
4D	43	33.90 (29-39)	3.58 (2-7)	0.53 (0-3)	4.12 (2-8)	0.38 (0-2)	13.30	—	—
5D	43	33.55 (28-37)	3.43 (2-6)	0.57 (0-3)	4.00 (2-6)	0.48 (0-2)	16.70	—	—
6D	43	31.67 (27-37)	4.28 (2-7)	0.53 (0-3)	4.82 (0-7)	0.52 (0-2)	43.30	3.30	16.70
7D	42	31.52 (26-35)	3.95 (1-6)	0.57 (0-3)	4.52 (1-8)	0.48 (0-1)	43.30	—	—

homologues in the wheat hybrids. However, in *T. aestivum* × *Ae. squarrosa* (RILEY and CHAPMAN 1960) the action of chromosome 5B did not prevent the pairing of chromosomes of *Ae. squarrosa* and wheat D genome chromosomes. The D genome of *T. aestivum* must, therefore, still be very similar to the D genome of *Ae. squarrosa*. The lack of pairing in *Ae. vavilovii* × *T. aestivum* demonstrates that the D genome of *Ae. vavilovii* is greatly modified from the D genome of wheat and, therefore, from that of *Ae. squarrosa*. In *Ae. crassa* × *T. aestivum* there was the equivalent of one paired genome. Our investigations did not produce evidence to show whether the pairing involved chromosomes of either the D, the D^2 or both of these genomes of *Ae. crassa* with the D genome of wheat. It is believed that *Ae. crassa* and *Ae. vavilovii* have in common the genomes D and M^{cr} which they obtained during their evolution from the tetraploid *Ae. crassa* ($M^{cr}D$). If this is correct then this D genome did not pair in *Ae. vavilovii* × *T. aestivum* and may not therefore have paired in *Ae. crassa* × *T. aestivum*. We have been unable to obtain the hybrid *Ae. crassa* 4x×*T. aestivum* which would compare this D genome with the D genome of wheat.

The chromosome pairing in haploid *Ae. crassa* and *Ae. crassa* × *S. cereale* (Table 1) was little more than could be expected from the intergenomic pairing of the chromosomes of *Ae. crassa* which was seen in the wheat hybrids. The absence of further homoeologous pairing, particularly in the haploid, leads us to speculate that a form of genetic control must operate to prevent such pairing.

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The chromosome association between *Triticum urartu* and other diploid or tetraploid wheats[1)]

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A number of workers have been discussing the donor of the B_1 or G-genome to the tetraploid wheats. JOHNSON (1975) suggested that *Triticum urartu* Tum. is the donor of the B-genome. However, JOHNSON's hypothesis has been recently claimed by several authers (CHAPMAN *et al.* 1976, DVORAK 1976, and GERLACH 1977).

The purpose of the present paper is to shed more light on the cytogenetical relationships between *T. urartu* and other wheat species.

Materials and Methods

The following ten strains of *T. urartu* were used:

Strain No.	Localities	Source
199–1～199–4	Transcaucasus	Dr. V. JAASKA
199–5	Turkey	Dr. B.L. JOHNSON
199–6～199–8	Lebanon	〃
199–9 and 199–10	Iran	BEM[2)]

The following eight strains including six wheat species were also used as testers: Einkorn group — Two strains (101–1 and 3620) of *T. boeoticum*, one strain (104) of *T. monococcum.*, Emmer group — one strain (108–3) of *T. dicoccoides*, one strain (125) of *T. durum*, Timopheevi group — two strains (196–1 and 196–2) of *T. araraticum*, one strain (107–1) of *T. timopheevi.*

All materials have been maintained at the Plant Germ-plasm Institute, Faculty of Agriculture, Kyoto University.

The crosses were made between *T. urartu* and other diploid Einkorn group, and between *T. urartu* and tetraploid species of the Emmer group or the Timopheevi group. The F_1 hybrids obtained from these crosses, were grown in the glasshouse and field. They were examined cytogenetically and physiologically. For the cytogenetical observations, young anthers of these hybrids were fixed in Farmer's solution. Chromosome association was observed at MI of PMC's using the aceto-carmine squash method. About 30 cells per hybrid plant were usually observed. The pollen fertility of the hybrids was assessed

1) Contribution No. 15 from the Plant Germ-plasm Institute, Faculty of Agriculture, Kyoto University.

2) The Botanical Expedition to the Northern Highland of Mesopotamia, Kyoto University, 1970.

Table 1. Germination rate in interspecific crosses among diploid and tetraploid species of *Triticum*

Cross		No. of cross combination	No. of florests crossed	No. of seed set	Successful seed set %	No. of seed germinated	Germination rate %	No. of heading plant
Female	Male							
boeoticum	*urartu*	16	1306	825	63.2	435	52.7	0
urartu	*boeoticum*	17	966	609	63.0	49	8.0	17
monococcum	*urartu*	8	762	125	16.4	107	85.5	0
urartu	*monococcum*	8	350	203	58.0	6	3.0	0
Emmer	*urartu*	17	401	139	34.7	72	51.8	72
urartu	Emmer	15	502	310	61.8	7	2.3	0
Timopheevi	*urartu*	27	670	476	71.0	291	61.6	291
urartu	Timopheevi	23	1022	571	55.9	9	1.6	0

Table 2. Germination rate, chromosome association, and fertilites in B_1 hybrids between *T. urartu* and *T. boeoticum*

Cross combination	No. of seed sown	No. of seed germinated	Average chromosome association		Pollen fertility %	Seed fertility %
			I	II		
(*urartu* × *boeoticum*) × *urartu*	25	4[1)]	0.04	6.98	49.9	25
(*urartu* × *boeoticum*) × *boeoticum*	1	1	0.06	6.97	78.3	41

1) One seedling is normal but other three showed lethality.

after staining them with aceto-carmine solution. Seed fertility was calculated from seed setting on the lowest floret of the spikelets of three bagged spikes.

Results and Discussion

The interspecific crosses as shown Table 1 were carried out. In four crosses having *T. urartu* as the female parent, *T. urartu* × *T. boeoticum*, *T. urartu* × *T. monococcum*, *T. urartu* × Emmer, and *T. urartu* × Timopheevi, the germination rate was extremely low, 8.0%, 3.0%, 2.3%, and 1.6%, respectively. Almost all seedlings died at the early stage of growth. But in only one cross combination, *T. urartu* × a strain (3620) of *T. boeoticum*, a high germination rate was observed and seventeen mature plants were obtained. These hybrid plants were very vigorous, but showed complete pollen sterility and set no seeds. However, normal and viable seeds were produced by backcross hybrids, (*T. urartu* × *T. boeoticum*) × *T. urartu* and (*T. urartu* × *T. boeoticum*) × *T. boeoticum*, as shown in Table 2. The backcross hybrids, (*T. urartu* × *T. boeoticum*) × *T. urartu*, showed 49.9% in pollen fertility and 25% in seed fertility. The chromosome association was $0.04_{I} + 6.98_{II}$: The other backcross hybrid, (*T. urartu* × *T. boeoticum*) × *T. boeoticum*, showed 78.3%, 41%, and $0.06_{I}+6.97_{II}$, respectively (Table 2).

Table 3. Chromosome association in hybrids, tetraploid wheat × diploid wheat

Cross combination	No. of cross combination	I	II	III	IV	V
Emmer group						
108–3 × 199	6	9.10	5.89	0.04		
× 101–1	1	8.84	5.60	0.32		
125 × 199	5	8.26	6.37			
× 101–1	1	8.60	6.08	0.08		
Timopheevi group						
107–1 × 199	5	7.38	6.13	0.24	0.16	
× 101–1	1	7.84	5.76	0.44	0.08	
196–1 × 199	7	9.05	5.43	0.23	0.10	
× 101–1	1	7.96	5.84	0.24	0.16	
196–2 × 199	7	7.41	5.75	0.46	0.17	0.006
× 101–1	1	7.92	4.71	1.22		

101–1: *T. boeoticum* 199: *T. urartu* (ten strains) 107–1: *T. timopheevi* 108–3: *T. dicoccoides*
125: *T. durum* 196–1, –2: *T. araraticum*

In two crosses, *T. boeoticum* × *T. urartu* and *T. monococcum* × *T. urartu*, having *T. urartu* as the male parent, seeds produced were small and plumped. The germination rate of those seeds were 52.7% and 85.5%, respectively. Chlorosis was observed in these seedlings and in many cases they died soon.

In the crosses, Emmer × *T. urartu* and Timopheevi × *T. urartu*, having *T. urartu* as the male parent, the germination rate of these seeds were 51.8% and 61.6%, respectively. Chlorosis was also observed in these cross combinations, but almost all plants reached to the mature stage.

Chromosome associations observed at MI of PMCs of F_1 hybrids of Emmer × *T. urartu* and Timopheevi × *T. urartu* are listed in Table 3.

Cytogenetical results obtained in this experiment indicate that the genome of *T. urartu* is homologous with the A-genome of *T. boeoticum*, which is also found in the Emmer and Timopheevi wheats. Therefore, *T. urartu* is not the donor of the B-genome as well as the G-genome.

Also, when *T. urartu* was used for the male parent to the Einkorn group, the germination rate of those hybrids was high, but all plants could not get mature. Chlorosis was observed in all plants.

On the other hand, when *T. urartu* was used for the female parent to the Einkorn group, the germination rate was extremely low. The F_1 hybrids between *T. urartu* and *T. boeoticum* were highly sterile. There clearly exists a reproductive barrier between them. The backcross experiment does not support the hypothesis of JOHNSON *et al.* (1976) and DHALIWAL (1977) that the cytoplasm of *T. urartu* in combination with the genome of *T. T. boeoticum* inhibits the development of viable seeds.

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Addition of *Aegilops umbellulata* chromosomes to seven alloplasmic lines of a common wheat, Chinese Spring

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Among the cytoplasms of 23 *Triticum* and *Aegilops* species, eight plasma types were recognized by TSUNEWAKI *et al.* (1976). As pointed out earlier (TSUNEWAKI and ENDO 1973), individual plasmons (=cytoplasmic genomes) show specific interactions with different nuclei. Thus, it is necessary to use nuclei of variable genetic constitutions in order to reveal every genetic characteristics of the plasmon. Alien chromosome addition to alloplasmic wheats will be one of the possible approaches for it. In each species, its nuclear genome and plasmon are harmoniously interacting with each other resulting in its survival. In order to know the role of individual chromosomes in this nucleus cytoplasm interaction, addition of individual chromosomes of the cytoplasm donor to an alloplasmic line will provide a critical way of approach. The present work is a part of the program, that aims to investigate the above two, i.e., (1) further elucidation of plasmon characteristics, and (2) resolution of the nucleus cytoplasm interaction into the chromosome cytoplasm interactions, in *Triticum* and *Aegilops*.

Materials and Methods

Seven alloplasmic lines of *Triticum aestivum* cv. Chinese Spring (abbreviated as CS) having the cytoplasms of *Aegilops caudata*, *Ae. umbellulata*, *Ae. squarrosa*, *Ae. speltoides*, *Ae. sharonensis*, *Ae. ovata*, and *T. timopheevi*, which represent the C, C^u, D, S, S^1, M^0 and G type plasmas, respectively, were crossed twice to five disomic addition lines of CS with *Ae. umbellulata* chromosomes as the recurrent pollen parent, and the monosomic and disomic addition type plants were cytologically selected in the F_1 and B_1 generation, respectively. The disomic addition lines of CS used as the pollen parent were kindly provided by Dr. G. Kimber, University of Missouri, Columbia, Mo., USA, to whom we would like to express our greatest gratitude.

In the present paper, C^u1 to C^u5 are used to designate the five *umbellulata* chromosomes, which correspond to chromosome A to E in the original KIMBER's designation (KIMBER, 1967).

Results and Discussion

Transmission rates of the five *umbellulata* chromosomes through the female gamete in their monosomic addition type plants are given in Table 1. The transmission rates of the five chromosomes (average of the seven cytoplasms) ranged from 8.5% for C^u1 to 12.1%

Table 1. Number of disomic addition plants obtained and the transmission rate (%) of C^u chromosome through female

Cytoplasm		Chromosome added					Average
		C^u1	C^u2	C^u3	C^u4	C^u5	
caudata	No. disomics	1(37)	3(40)	2(20)	1(16)	1(29)	
	Trans. rate	2.7	7.5	10.0	6.3	3.4	6.0
umbellulata	No. disomics	2(46)	3(35)	3(40)	1(29)	8(35)	
	Trans. rate	4.3	8.6	7.5	3.4	22.9	9.3
squarrosa	No. disomics	3(21)	5(36)	3(17)	4(18)	8(107)	
	Trans. rate	14.3	13.9	17.6	22.2	7.5	15.1
speltoides	No. disomics	2(41)	4(20)	3(18)	2(19)	4(20)	
	Trans. rate	4.9	20.0	16.7	10.5	20.0	14.4
sharonensis	No. disomics	3(20)	3(54)	5(50)	1(19)	1(19)	
	Trans. rate	15.0	5.6	10.0	5.3	5.3	8.2
timopheevi	No. disomics	4(41)	3(38)	1(20)	3(41)	6(39)	
	Trans. rate	9.8	7.9	5.0	7.3	15.4	9.1
ovata	No. disomics	4(47)	2(19)	2(24)	3(22)	6(63)	
	Trans. rate	8.5	10.5	8.3	13.6	9.5	10.1
Average	Trans. rate	8.5	10.6	10.7	9.8	12.1	10.3

( ): Number of examined progenies of monosomic C^u chromosome addition line with an alien cytoplasm crossed by pollen of the corresponding KIMBER's disomic C^u chromosome addition lines of CS.

Table 2. Pollen(P) and selfed seed fertilities (S) of monosomic and disomic C^u chromosome addition line (%)

Cytoplasm		CS nucleus	Chromosome added									
			C^u1		C^u2		C^u3		C^u4		C^u5	
			M	D	M	D	M	D	M	D	M	D
caudata	P	0	95	72	0	-	0	0	0	0	0	-
	S	0	89	60	0	0	0	0	0	0	0	0
umbellulata	P	90	99	90	88	46	93	62	76	76	86	80
	S	39	69	50	44	6	61	19	8	0	44	6
squarrosa	P	96	97	96	96	95	97	95	96	91	97	94
	S	91	98	98	99	94	99	93	99	96	96	76
speltoides	P	96	96	—	99	92	97	91	93	81	92	94
	S	89	95	71*	98	96	80	89	88	70	93	90
sharonensis	P	98	94	96	95	89	98	-	95	87	87	42
	S	98	98	88	91	65	95	75	83	-	79	-
timopheevi	P	0	94	92	0	0	0	-	0	0	0	0
	S	8	78	39	16	0	7	0	0	0	28	0
ovata	P	98	99	90	96	93	98	98	96	90	95	90
	S	94	86	36*	94	90	95	100	88	95	90	61

M: Monosomic addition, D: Disomic addition. *Investigated with plants grown in pots.

Note) Fertilities of alloplasmic CS and its monosomic addition lines were examined in 1977, and those of the disomic addition lines were in 1978.

for C^u5 chromosome, but the difference among the chromosomes was not statistically significant. The transmission rates observed in the seven cytoplasms (average of the five chromosomes) ranged from 6.0% for the *caudata* cytoplasm to 15.1% for the *squarrosa* cytoplasm, but, again their difference was not statistically significant. This fact indicates no cytoplasms induced preferential transmission of the *umbellulata* chromosomes.

Pollen and selfed seed fertilities of the monosomic and disomic addition lines are shown in Table 2, in comparison to those of the normal alloplasmic lines of CS as the control. The *caudata* and *timopheevi* cytoplasms caused complete male sterility in CS, as noticed earlier (TSUNEWAKI *et al.* 1976), while the addition of C^u1 chromosome resulted in remarkable restoration of the fertilities in both cytoplasms. The *umbellulata* cytoplasm caused partial reduction of seed fertility, that was greatly recovered by the same chromosome. Therefore, it can be concluded that the C^u1 chromosome carries a fertility-restoring gene(s) for the above three male sterile cytoplasms. Degree of the restoration was higher in the monosomic than in the disomic addition in all three cases, indicating that a single dose of the gene is as effective as its double dose in fertility restoration. If this gene could be successfully transferred into wheat genome, it will become valuable for hybrid wheat breeding.

All C^u chromosomes tended to reduce fertilities when added in the double dose to fertile alloplasmic lines.

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Fertility and chromosome transmission of synthetic pentaploids involving D,M, or M^u genomes of *Aegilops*

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The concept of genome analysis was introduced by the investigation on AABBD pentaploid plants by KIHARA (1924), and his pioneer works resulted in the identification of twelve basic genomes in *Triticum* and *Aegilops*. Among them, the genomic similarity of analogy was reported among the D of *Ae. squarrosa*, M of *Ae. comosa*, and M^u of *Ae. uniaristata* (KIHARA, 1949).

The authors have been studing on the cytogenetics of the synthetic amphiploids between *T. durum* (AABB) and *Aegilops* species having D, M and M^u genomes (MAAN and SASAKUMA, 1978). The present paper reports the fertility and chromosome transmission of synthetic pentaploids having AABB genome in common and D, M, or M^u genomes.

Materials and Methods

Ae. squarrosa var. *strangulata* (DD), *Ae. comosa* (MM), and *Ae. uniaristata* (M^uM^u) were crossed with *T. durum* Sel. 56–1 (AABB). (*Aegilops* species used in the experiment were originally supplyed by Dr. B. L. JOHNSON, USA). The F_1 plants were treated with 0.01 % colchicine to obtain amphiploids of AABBDD, AABBMM, and $AABBM^uM^u$, where the AABB genome was genetically identical.

The plants with 42 chromosomes and stable pairing conformation were selected from the F_4 progenies of the respective amphiploid, and the reciprocal crosses were conducted among the amphiploids, *T. aestivum* cf Chris (AABBDD), and *T. durum* Sel. 56–1.

Pollen fertility (% of stainable mature pollen grains) and selfed seedset (% of seed-set in 1st and 2nd florets) were examined in each pentaploid obtained. Also, the respective pentaploid plants were backcrossed reciprocally with *T. durum* Sel. 56–1, and the cross-seed production and the somatic chromosome number of BC_1F_1 plants were examined.

Results and Discussion

The crossability in the reciprocal crosses among *T. durum*, *T. aestivum* and the three synthetic amphiploids were summerized in Table 1. The cross-incompatibility was found in the case of $AABBM^uM^u$ (♀)×AABBMM (♂), where the reciprocal cross was successful. The slow or inhibitory pollen tube germination of ABM pollens were observed on the stigma of $AABBM^uM^u$ plant. The similar phenomena to the present observation were observed in the cross between a cytoplasmic substitution Chris having the cytoplasm of *Ae. uniaristata*

Table 1. Crossability among *T. durum* (AABB) and three synthetic amphiploids

♀ \ ♂	AABB	AABBDD	AABBMM	AABBM^{u}M^{u}
AABB	—	○	△	△
AABBDD	○	—	○	○
AABBMM	○	○	—	○
AABBM^{u}M^{u}	○	○	×	—

○: Successful cross producing plump seeds
△: Cross producing shrivelled and inviable seeds
×: Incompatible cross

Table 2. Pollen fertility and seed-set of pentaploid hybrids in the reciprocal backcrosses with *T. durum*

Line	Pollen fertility (%)	Selfed seed-set (%)	Cross with AABB(♀)			Cross with AABB(♂)		
			No. florets pollinated	No. seeds obtained		No. florets pollinated	No. seeds obtained	
				Plump	Shrivelled		Plump	Shrivelled
AABBD	96.5	83.2	60	47	0	128	96	6
AABBM	11.9	1.2	218	78	68	216	104	16
AABBM^{u}	46.4	12.7	112	13	12	452	132	76
AABBDD	98.3	100.0	53	49	0	28	25	0
AABB	98.7	99.7	-	-	-	-	-	-

(♀) and AABBMM amphiploid (♂). Since the cytoplasm of AABBM^{u}M^{u} amphiploid came from M^{u}-donor species, the cross-incompatibility in the cross of AABBM^{u}M^{u}(♀)×AABB MM (♂) may be due to the incompatible interaction between the cytoplasm of *Ae. uniaristata* and M genome. Also, the cross-inviability was noticed when *T. durum* was used as the female parents in the crosses with the two amphiploids involving M and M^{u} genomes. All seeds obtained in these crosses were shrivelled with undeveloped embryos, and did not germinate in petri-dishes. This cross-inviability was reported to be due to the dosage unbalance between the endosperm and embryo genome constitutions, responsible for 5D chromosome of a common wheat to restore the viability (SASAKUMA and MAAN, 1978).

The synthetic AABBD pentaploid was highly fertile and set seeds in 83.2% of florets on the bagged heads. It produced plump and viable seeds in the majority of florets in the reciprocal crosses with *T. durum* (Table 2). On the other hand, the other pentaploids did not show the natural anther dehiscence in general, resulting in low selfed seed-set, because of the low proportion of mature pollen grains in the anthers (Table 2). Less than 50% of seed-sets were observed in these two pentaploids when they were reciprocally crossed with *T. durum*. And the majority of the seeds produced were shrivelled and inviable, except in the case of the cross AABBM×AABB. By considering the misscrossing rate in the control crosses, the male and female fertility are 70.8 and 64.3% for AABBD, 28.3 and 37.4% for AABBM, and only 4.1 and 18.5% for AABBM^{u}, respectively. Being different from the case in the crosses between AABB (♀) and hexaploid amphiploids (♂) having M or M^{u}

genomes, some plump seeds were obtained in the crosses between AABB (♀) and AABBM or AABBM^u (♂). The cytological observation revealed that the plants from the plump seeds had 28, 29 or 33 chromosomes, suggesting a few critical chromosomes of M or M^u genomes may be responsible for seed shrivelness in these crosses.

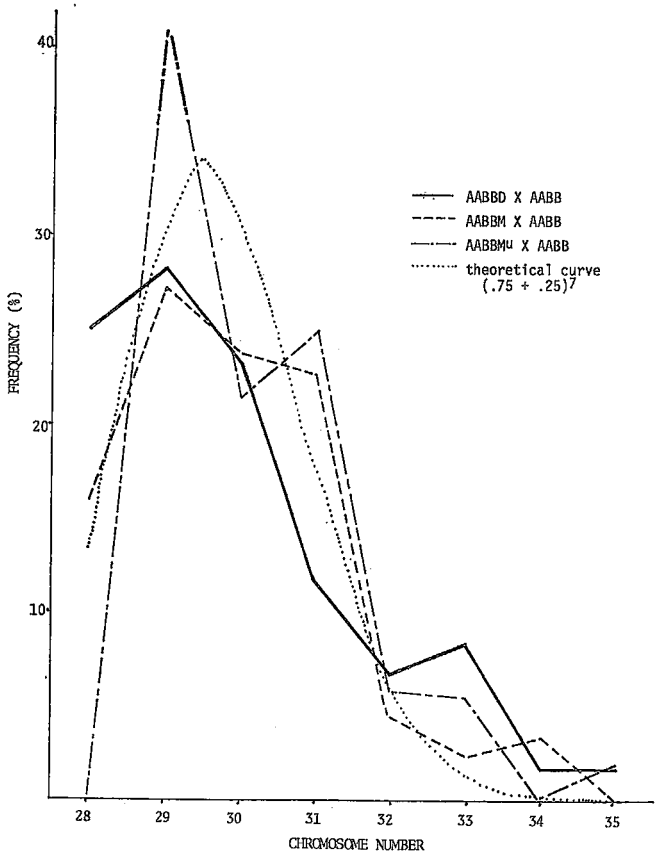

Fig. 1. Distribution of 28–35 chromosome plants in the backcross progenies of three synthetic pentaploids

Fig. 1 shows the chromosome transmission of D, M, and M^u genomes in pentaploids, where only female side could be figured because of small sample size in each reciprocal cross. Since the AABB background in pentaploid crosses were genetically identical, this system employed in the experiment can reveal the direct comparison of chromosome transmission among three genomes of *Aegilops* species. The result showed that the chromosomes of D, M, and M^u genomes were not randomly transmitted through female gametes, but the progenies tended to possess the smaller number of chromosomes. This phenomenon may

be mainly due to the elimination of univalent chromosomes through female gametogenesis. Since the transmission figures of AABBD and AABBM pentaploids did not deviate from the cruve drawn with the equation of $(.75+.25)^7$, the elimination rate of univalent chromosomes in D or M genomes could be estimated about 25%. MURAMATSU (1939) and KIHARA and WAKAKUWA (1935) reported 20–25% of univalent elimination in D genome chromosomes in the pentaploids between *T. polonicum* and *T. Spelta*, or *T. durum* and *T. vulgare*. The present investigation used the artifical amphiploids as the hexaploid parents, and the results indicated that D and M gemones diploid species did not differ significantly from the D genome of common wheat in refference to the pentaploid transmission. On the other hand, the pattern of pentaploid transmission in AABBM^u was different from those of the other two. No 28-chromosome plants was obtained in the backcross of AABBM^u × AABB. The result indicated that there must be an essential chromosome of M^u genome involved to obtain viable progeny in this cross. This can be explained by the fact of incompatible interaction between the cytoplasm of *Ae. uniaristata* and AABB genome reported by MAAN (1977). Probably, some of non-germinating seeds produced in the cross may involve 28-chromosome embryos.

The present experiment showed some similarities and differences among D, M, and M^u genomes of *Aegilops* species. The progenies obtained in the experiment will be used for further genetic analysis of these three genomes.

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Finding of a selectively retained chromosome of *Aegilops caudata* L. in common wheat*

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Selective retention of alien chromosomes in common wheat was discovered with certain chromosomes of several *Aegilops* species, i.e., *Ae. triuncialis*, synthetic *triuncialis*, *Ae. longissima*, and *Ae. sharonensis* (ENDO and TSUNEWAKI, 1975; MAAN, 1975; ENDO, 1978). In each cases severe fertility reduction occurred in plants having such a monosomic *Aegilops* chromosome, and those having disomic chromosomes had normal fertility. This phenomenon was proved to be due to a selective gametocidal action of those *Aegilops* chromosomes on common wheat gametes: When such an *Aegilops* chromosome was monosomically present in common wheat, only gametes having the *Aegilops* chromosome could normally develop to take part in fertilization, while those without it almost completely lost their normal function.

During an attempt to produce addition lines of common wheat having individual chromosomes of *Ae. caudata* L. (2n=14; CC), a chromosome of *Ae. caudata* was found to have been retained selectively in common wheat. Details of this finding will be reported here with regard to its unique breeding behavior in common wheat and effect on the fertility

A cultivar of common wheat, *Triticum aestivum* cv. Jones Fife (2n=42; AABBDD: abbreviated as JF hereafter) was crossed as female with *Ae. caudata* to obtain a tetraploid hybrid (2n=28; ABDC). This hybrid showing vigorous growth and complete sterility was backcrossed to JF, producing four seeds out of 180 florets pollinated (2.2% seed set). Since one of the four B_1 plants was found to have 2n=49 chromosomes with a chromosome configuration of 21″+7′ at MI (consequently, the genome constitution was expected to be AABBDDC), it was employed for the further backcross program to produce the addition lines of JF.

The second backcross of the 2n=49 plant to JF gave rise to a total of 62 seeds on 21 spikes. About half of the B_2 seeds sown germinated (32 in total). Using their root-tips, chromosome numbers of the 30 seedlings were determined, which ranged from 2n=44 to 49 in the following frequencies: two seedlings with 2n=44; seven with 2n=45; eight with 2n=46; ten with 2n=47; two with 2n=48; and one with 2n=49. No monosomic addition plant (2n=43) was found among them.

All the B_2 derivatives with 2n=44 to 2n=49 were used for the third bakcross to JF.

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They all showed severe reduction in crossed seed fertility: eleven plants set no seed; and the highest crossed seed fertility marked in a plant with 2n=44 chromosomes was 15.6%. By selfing only a few plants set seeds very sporadically. B_3 seeds thus produced were sown and all the viable seedlings were cytologically studied to screen monosomic addition plants. A total of 22 seedlings having 2n=43 chromosomes were picked out from the progenies of eight B_2 plants with various chromosome numbers from 2n=44 to 47. Interestingly, those 2n=43 seedlings without exception had a chromosome with a subterminal centromere which must have been derived from *Ae. caudata* (Fig. 1), for common wheat does not have this type of chromosome. Although *Ae. caudata* has three pairs of chromosomes with subterminal centromeres, this fact is not easily explained by a chance occurrence. Some mechanism must have operated to retain this critial chromosome selectively throughout the backcrosses so far made. An 2n=45 plant having the *Ae. caudata* chromosome, for exmaple, produced eight 2n=43 plants having the critical chromosome among its ten backcrossed progeny. In this respect, all the B_2 and B_3 plants, whose chromosome constitutions were fully analyzed, turned out to possess one, two, or three *Ae. caudata* chromosomes with a subterminal centromere.

In order to elucidate the mechanisms of the selective retention of the *Ae. caudata* chromosome in JF, some 2n=43 plants were crossed with JF and/or were self pollinated. Their seed set by crossing or selfing was very sporadical in all cases; the crossed seed fertility was 17.0% on the average (17 seeds from 100 florets pollinated) and in the selfed individual spikes none to 14 seeds were set. Some 2n=43 plants had about 40% pollen fertility, and some were completely pollen sterile. The reduction in fertility of both sexes was probably caused by the monosomic *Ae. caudata* chromosome which has been retained in JF.

Breeding behavior of the *Ae. caudata* chromosome was studied using four 2n=43 plants

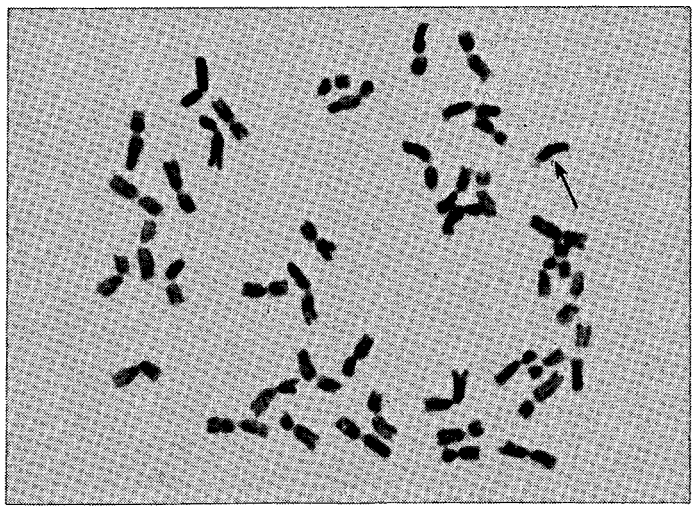

Fig. 1. A chromosome of *Ae. caudata* with a subterminal centromere, which was retained selectively in common wheat (cv. Jones Fife), in shown with an arrow.

Table 1. Frequencies of seedlings with different chromosome constitutions, which were obtained from the cross or selfining of the monosomic addition plants

Cross or self	2n=42	2n=43 (1c)*	2n=44 (2c)*	others
21''+1'(♀)×21''(♂)	1	6	0	1**
21''+1' self	0	0	41	3**

* 1c or 2c in parentheses stands for one or two *Ae. caudata* chromosomes with a subterminal centromere in the chromosome complement.
** This seedling had a chromosome constitution of 2n=42 (1c).
*** Two of them were 2n=43 (2) and one was 2n=42 (1c) including two chromosome fragments.

with partial pollen fertility, which had been proved to be the real monosomic addition type forming 21''+1' at MI, i.e., the univalent must have been the *Ae. caudata* chromosome. The result is shown in Table 1. First, transmission of the *Ae. caudata* chromosome through egg cells was studied in a cross between one of the 21''+1' plants as female and normal JF. Six of the eight plants from this cross had 2n=43 chromosomes including one chromosome with a subterminal centromere. One seedling had the critical chromosome among the 42 chromosomes, and the other 2n=42 seedling did not have such a chromosome. This means that the univalent *Ae. caudata* chromosome is preferentially transmitted through the egg cell. Next, chromosome constitutions of selfed progenies from the four 21''+1' plants were studied. Of the 44 seedlings examined 41 had 2n= 44 chromosomes including a pair of chromosomes with a subterminal centromere. Plants of 2n=42 witn no and 2n=43 with one critical chromosome were not found at all, but two plants had 2n=43 including two critical chromosomes, and one had 2n=42 including one critical and two fragment chromosomes. This in turn indicated the exclusively preferential transmission of the *Ae. caudata* chromosome through pollen as was found in the egg cell.

Accordingly, the exclusively preferential transmission of the *Ae. caudata* chromosome can be attributed to the selective gametocidal action of this chromosome in JF. Namely, only gametes with the *Ae. caudata* chromosome can function normally, but those without it can not function, which results in reduced fertility of the plants having the monosomic *Ae. caudata* chromosome and at the same time causes its selective retention.

Such being the case, it becomes difficult to produce the chromosome addition series of JF which would have the respective chromosomes of *Ae. caudata.*

Since there are three pairs of chromosomes with subterminal centromeres in the karyotype of *Ae. caudata,* it is not confirmed yet whether or not the *Ae. caudata* chromosomes retained through the three backcrosses are the same. Apart from this question, they are similar in morphology and selective gametocidal action to the selectively retained chromosomes of the natural and synthetic strains of *Ae. triuncialis,* one of whose parental species is *Ae. caudata* (KIHARA, 1940; KIHARA and KONDO, 1943). Therefore, the present findings of an *Ae. caudata* chromosome selectively retained in common wheat strongly suggests that the critical chromosome of *Ae. triuncialis* originated from *Ae. caudata.*

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On the genetic mechanism of haploid induction in the cytoplasm substitution lines of common wheat

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Triticum aestivum strain Salmon is a hexaploid derivative of the octoploid *Triticale* (TSUNEWAKI 1964). This strain is different from ordinary common wheat in several respects: It has a 1B/1R translocation, in which the short arm of 1B carrying a nucleolar organizer is replaced by an arm of 1R chromosome of rye (ZELLER 1973), thus having only one pair of satellited chromosomes (6B chromosomes) instead of two pairs in ordinary common wheat (TSUNEWAKI 1964). Also, this strain induces haploids and twin seedlings (mostly diplo-haplo type) at relatively high frequencies when several alien cytoplasms are introduced by repeated backcrosses (TSUNEWAKI *et al.* 1968). So far, the cytoplasms of eight *Aegilops* species, including *Ae. kotschyi*, are known to induce haploids in Salmon (TSUNEWAKI *et al.* 1976).

However, the genetic mechanism of haploid induction in this wheat has not been known yet. The present paper deals with the results of the investigation that was conducted to elucidate this mechanism in Salmon by the cytoplasm of *Ae. kotschyi*.

Materials and Methods

An alloplasmic line of *Triticum aestivum* cv. Chinese Spring (abbreviated as CS) having the cytoplasm of *Aegilops kotschyi* (2n=28, genome constitution $C^uC^uS^vS^v$) has been produced by MUKAI and TSUNEWAKI (1975). This line was crossed with *T. aestivum* strain Salmon (abbrev. Slm) or CS, or self-pollinated, according to the breeding scheme shown in Fig. 1. CS is known to carry a dominant fertility-restoring gene *Rfv1* against the *kotschyi* cytoplasm on the short arm of 1B chromosome (MUKAI and TSUNEWAKI 1979). On the contrary, Slm lacks this gene due to replacement of 1BS arm by a raye chromosome arm, and is designated

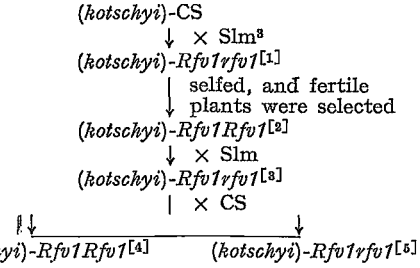

Fig. 1. Breeding scheme. CS for Chinese Spring (genotype *Rfv1Rfv1*), and Slm for Salmon (*rfv1rfv1*).

as *rfv1*. Genotypes of plants obtained in each generation are also indicated in Fig. 1.

The selfed seed fertility was estimated from the number of first and second florets in ten normally developed spikelets, and the number of seeds set in them on spikes which were covered with a paper bag before flowering. Chromosome number was observed in root-tip mitosis, using the ordinary aceto-carmine squash method.

Results and Discussion

As shown in Fig. 1, (*kotschyi*)-CS was crossed three times with Slm's pollen. In the B_2 generation indicated by [1] in the figure, a partially fertile plant was selected that should carry a single *Rfv1* gene. This plant was self-pollinated, raising 14 offspring, of which five were haploid (Table 1). Among nine diploid offspring, seven fertile plants were selected which were assumed to be the homozygote *Rfv1Rfv1* ([2] in Fig. 1). Their selfed seed fertility ranged from 55 to 88%, average being 72% (Table 1). They were crossed with pollen of Slm or some other strain. In total, 353 plants were obtained, but none was haploid (Table 1). The diploids were assumed to be *Rfv1rfv1* ([3] in Fig. 1). The selfed seed fertility of 85 plants was examined, their average being 9% with the range of 0 to 41%. Of those, 82 plants were crossed with CS's pollen, and 1,214 offspring were obtained.

Table 1. Relation of the selfed seed fertility to haploid induction

Line	Selfed seed fertility			Haploid induction			
	No. plants	Ave. %	Range %	No. progenies	No. plants	No. haploids*	%
(*kotschyi*)-*Rfv1rfv1*[1]	—	—	—	1	14	5	35.7
(*kotschyi*)-*Rfv1Rfv1*[2]	7	71.7	55.3- 87.6	7	353	0	0.0
(*kotschyi*)-*Rfv1rfv1*[3]	85	9.0	0.0- 41.3	82	1,214	303	25.0
(*kotschyi*)-*Rfv1Rfv1*[4]	63	97.3	80.0-100.0	18	752	0	0.0
(*kotschyi*)-*Rfv1rfv1*[5]	38	25.7	0.0- 62.5	26	980	34	3.5

*: Diplo-haplo and haplo-haplo twins are included in the haploid.

Detailed classification of those plants is shown in Table 2: 1,154 seedlings were single seedlings, of which 246 were haploid. The remaining 60 seedlings were twins, which were either diplo-diplo, diplo-haplo or haplo-haplo type. In total, 303 seedlings (25%) were haploid, including haploid twins. Plants developed from the diploid seedlings were classified into the fertile and sterile classes, as shown in Table 2, according to their selfed seed fertility observed at their maturity, that is given in the last two rows of Table 1. Two facts must be pointed out from the results: First, the diploid, single seedlings segregated the fertile and sterile in a ratio of 842: 43, greatly deviating from the expected 1:1 ratio. Second, all diploid partners in 56 diplo-haplo twins became sterile, no fully fertile plants being recovered.

The karyotype of 56 haploids was analyzed as to the number of satellited chromosomes in root-tip mitosis. The result is summarized in Table 3. All haploids, whose karyotype

Table 2. Classification of offspring obtained from the cross, (*hotschyi*)-*Rfv1rfv1*[3] × Chinese Spring

Type of seedling	Plants examined		Diploid								Haploid	
	No.	%	Total		Fertile		Sterile		Uncertain		No.	%
			No.	%	No.	%	No.	%	No.	%		
Single	1,154	95.1	908	74.8	842	69.4	43	3.5	23	1.9	246	20.3
Twins	60	4.9	[A] 59	4.9	3	0.2	56	4.6	0	0.0	1	0.1
			[B] 3	0.2	3	0.2	0	0.0	0	0.0	57	4.9
2n–2n	3	0.2	3	0.2	3	0.2	0	0.0	0	0.0	—	—
2n–n	56*	4.6	[A] 56	4.6	0	0.0	56	4.6	0	0.0	—	—
			[B] —	—	—	—	—	—	—	—	56	4.6
n–n	1	0.1	—	—	—	—	—	—	—	—	1	0.1
Total	1,214	100.0	[A]967	79.7	845	69.6	99	8.2	23	1.9	247	20.3
			[B]911	75.0	845	69.6	43	3.5	23	1.9	303	25.0

[A] and [B]: Values obtained when 2n-n twins are regarded as the diploid and haploid, respectively.

* One of them was triplets (2n–2n–n).

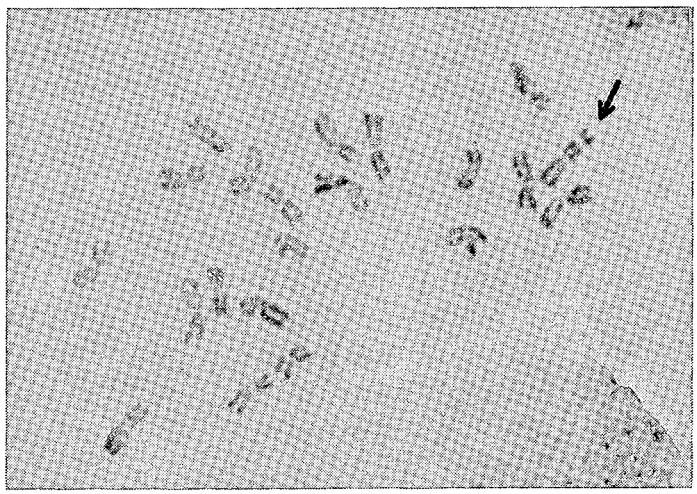

Fig. 2. A metaphase plate of the root-tip mitosis in a haploid plant. Note the presence of only one satellited chromosome (arrowed).

could be studied, had one or no satellited chromosome, none of them having two sat-chromosomes. A typical karyotype of the haploid is shown in Fig. 2. This fact indicates that haploids were derived only from the egg cells carrying 1B/1R translocation chromosome, but not from those with the normal 1B chromosome.

Among the diploid offspring, 101 plants were selected for observation of their fertility. As shown in Table 1, 63 became fully fertile (average seed fertility 97%), and 38

Table 3. Karyotype of haploids

No. haploids examined	No. sat-chromosomes			
	2	1	0	Uncertain
56	0	50	3	3

were partially fertile (average 26%). The former group was assumed to have the genotype *Rfv1Rfv1*, while the latter *Rfv1rfv1* ([4] and [5] in Fig. 1, respectively). Some of them were cross-pollinated with pollen of CS, and the occurrence of haploids was examined. In the offspring of the fully fertile plants, no aphloid was found among 752 plants, while 34 haploids (3.5%) were obtained in the offspring of the partially fertile plants (Table 1).

From the results given in Table 1, it is evident that the presence of *rfv1* allele, i.e., 1B/1R translocation chromosome in the female parent is a necessary condition for haploid production, because even a single haploid was not found among 1,105 offspring of *Rfv1Rfv1* homozygotes. On the contrary, haploids were obtained at variable frequencies (3.5 to 36%) in the offspring of *Rfv1rfv1* heterozygotes.

All these facts point to a fact that only the egg cells carrying the 1B/1R chromosome can develop into the haploid embryos. This directly results in an increase of the relative frequency of 1B (=*Rfv1*)-carrying egg cells for fertilization over 1B/1R (=*rfv1*)-carrying egg cells. Thus, much higher frequency of *Rfv1Rfv1* homozygotes over *Rfv1rfv1* heterozygotes was resulted in the diploid offspring of the heterozygotes crossed with the homozygote (*Rfv1 Rfv1*)'s pollen (rf. the first row of Table 2).

If the *rfv1rfv1* homozygotes (=homozygote of 1B/1R translocation) can be produced, we should expect much higher frequency of haploids in its offspring. The diploid partner of the diplo-haplo twins, which are obtained from a cross, (*kotschyi*)-*Rfv1rfv1* × Slm, should have this genotype, because the chromosome complement derived from the female side must have the 1B/1R chromosome. We already obtained this type of plant, getting haploids (including diplo-haplo twins) at a frequency of as high as 75%: This result will be published elsewhere.

The present result also indicates that a second gene is involved in haploid induction, because two classes of the *Rfv1rfv1* heterozygotes, i.e., [3] and [5] in Fig. 1 and Table 1, showed a remarkable difference in the frequency of haploids. Undoubtedly, Slm carries the second gene for haploid production, of which chromosomal location must be investigated in a future work.

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Cytology and isoenzymes of some *Triticum* auto- and amphiploids

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Introduction

The autotetraploid and the two ssp. *carthlicum* amphiploids have been produced in our laboratory partly for theoretical, (mainly evolutionery), and partly for practical (disease-resistance etc.) purposes. The amphiploid *T. monococcum* L. × *T. timopheevi* Zhuk. we have obtained from the VIR (Leningrad).

As a result of intensive research work, several theories have arisen on the origin and differentiation of wheats. For example, according to SCHRIMPF (1951), and later GORGIDZE (1973), MENABDE (1971) and JOHNSON (1975), the tetraploids have originated by autotetraploidization of diploid wheat species. PERCIVAL (1921), GORGIDZE (1971) and others proposed that the form range of the hexaploid wheat may have been enriched not only by the diploid Ageilops species, but also by the reduced forms of some tetraploid *Aegilops* (e.i. *Ae. ovata, Ae. cylindrica*). In this study we describe results obtained by cytogenetical methods (HADLACZKY and BELEA, 1975) and by the analysis of primary gene products, i.e. enzymes of the above mentioned auto- and amphiploids.

Materials and Methods

The autotetraploid *T. monococcum* was produced by a 0.02 per cent solution of colchicine. Amphiploids of ssp. *carthlicum* were obtained by treating the F_1 hybrid grains with 0.05 per cent colchicine and 10 ppm giberellic acid.

The enzyme extracts were obtained from the flour of mature whole grains by means of an MSE sonicator in 12.5 per cent sucrose solution. Isoelectric focusing on polyacrylamide gels (IEFPA) was performed according to Wrigley (1968, 1969), and polyacrylamide gel electrophoresis (PAGE) by the method of Davis (1964). Visualization of esterases was achieved using the method of Scandalios (1968), with minor modifications.

Results and Discussion

In spite of its 2n=28 chromosomes, the autotetraploid *T. monococcum* resembles morphologically the diploid *T. monococcum* rather than the tetraploid *T. turgidum* L. ssp. *dicoccoides*. The esterase zymograms of diploid and tetraploid *T. monococcum* are pratically identical. The comparison of the zymograms of the autotetraploid and of ssp. *dicoccoides* clearly shows that they are different, although the esterase bands characteristic of genome A are naturally present in ssp. *dicoccoides* too (Fig. 1a).

In the majority of autotetraploid *monococcum* plants in F_2 and mainly in F_3, we observed the reduction of chromosome number to the diploid level, while the polyploid effect still persisted morphologically (BELEA 1969). These plant are characterised by the darker color of leaves as well as by the upright position of leaves and shorter and stronger straw. Later the morphological character of reduced plants became more and more different from that of the tetraploid plants and similar to the original diploid *T. monococcum*.

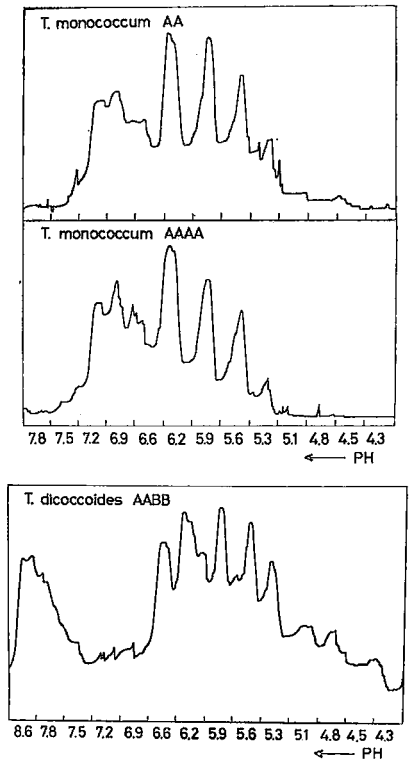

Fig. 1a

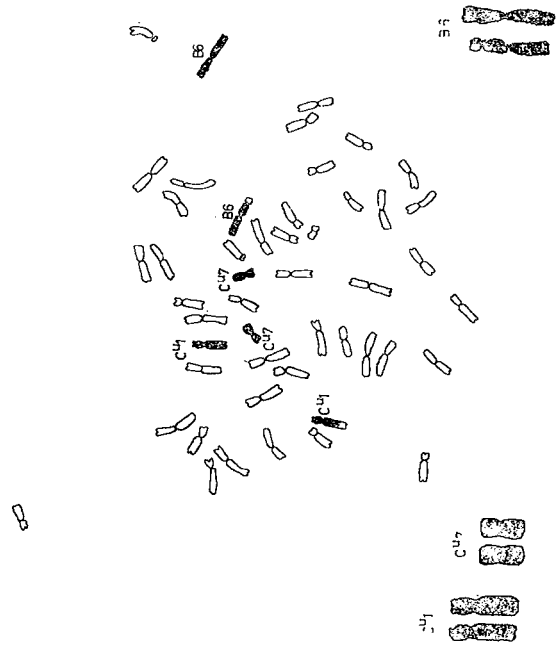

Fig. 1b

Figure 1. a. Denzitometric tracings of IEFPA-isoesterase spectra of *T. monococcum* L., autotetraploid *T. monococcum* and *T. turgidum* ssp. *dicoccoides*
b. Identifiable parent marker chromosomes in the *Ae. ovata* × *T. turgidum* ssp. *carthlicum* amphiploid

The morphological and cytological characteristics of the octoploid (2n=56) F_1 plants of the *Ae. ovata* × *T. turgidum* ssp. *carthlicum* amphiploid were intermediate. The isoesterase spectrum revealed by IEFPA also exhibits an additive effect, which is characteristic for the not reduced amphiploids.

In later generations (F_2-F_6), however, a great reduction of chromosome number was observed (Table 1). Similarly, the fertility was found to decrease temporarily in the F_2,

Table 1 Chromosome number of the reduced plants of the *Ae. ovata* × *T. turgidum* ssp. *carthlicum* octoploid (2n=56)

Generation	chromosome number													Number of plants
	28	42	44	46	47	49	50	51	52	53	54	55	56	
F_1													27	27
F_2									5		4	2	51	62
F_3		1	1	3	1	14	7	16	31	11	13	1	51	150
F_4						6	5	5	6	2	4	1	11	40
F_5		1			4	18	4	6	12		4		7	56
F_6			2	8	7	21	16	15	6		12		4	91
Ae. ovata	50													
ssp. *carthlicum*	45													
Total	95	2	3	11	12	59	32	42	60	13	37	4	151	521
Percent	18.2	0.4	0.6	2.1	2.3	11.3	6.1	8.1	11.5	2.5	7.1	0.8	29.0	

and then to increase. However, the fertility in F_5 was still lower than that in the first generation. This is known to be caused mainly by irregular chromosome pairing which results in sterility.

In the F_2-F_6 generations plants with ears differing in form and color from the intermediate type occured at a high frequency. Among these, no plants similar to hexaploid wheat type were found, not even among the plants with lower chromosome numbers. Because of the presence and high abundance of plants with 2n=49 chromosomes, it was necessary to establish whether the reduction of chromosome number in the amphiploid is the result of the loss of a whole genome or it is caused by random elimination of single chromosomes. By the analysis of the marker chromosomes (*Ae. ovata*: $1C^{u(SAT)}$, $2C^{u(SAT)}$, $7C^{u}$ and $7M^{o}$; *T. turgidum* ssp. *carthlcium*: $1B^{(SAT)}$, $6B^{(SAT)}$ etc) it was established that the reduction was caused by random elimination of single chromosomes from both genomes (Fig. 1b).

A similar phenomenon was observed in the course of the caryotype analysis of the 2n =56 plants occuring at a high frequency (66.9–62.5%) in the F_6-F_{14} generations of the heptaploid (2n=70) of *T. aestivum* × *T. timopheevi*, as it was reported by us at the V. International Wheat Genetics Sympsoium in New Delhi (Fejér and Belea 1978).

Unlike the amphiploids mentioned, the *T. turgidum* ssp. *carthlicum* × *T. timopheevi* octoploid (2n=56) was not reduced even in F_5, an observation which is unambiguously verified by cytological analysis as well as by the esterase spectra obtained by IEFPA. Similarly, no reduction was observed in the F_2-F_4 generations of the hexaploid *T. monococcum* × *T. timopheevi*. The caryotype analysis of this hexaploid and of the parental plants as well as the PAGE esterase spectra support the assumption that the *T. zhukovskyi* species originates from *T. monococcum* and *T. timopheevi* by spontaneous amphiploidization. The so-called "fast moving" esterases of the amphiploid are identical with those of *T. zhukovskyi* obtained under the same conditions.

Besides their theoretical importance, the amphiploids discussed are also of practical

value. We succeeded in transferring the resistance of *T. timopheevi* against leaf and stem rust, powdery mildew etc. into common wheat by way of chromosome addition and in producing resistant lines from different combinations obtained by crossing the above mentioned amphiploids with common wheat varieties.

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Mutiple forms of superoxide dismutase in bread wheat

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Superoxide dismutase (SOD; E.C. 1.15.1.1) provides a defence mechanism against oxygen toxity such as inhibition of photosynthesis, cell killing and oxygen effects of ionizing radiations, to oxygen-metabolizing cells through catalizing the dismutation of O_2^- radical to yield hydrogen peroxide and oxygen. Three kinds of metalloproteins with SOD activity have been isolated from a variety of aerobic and anaerobic organisms; manganese, iron and cupper-zinc enzymes.[1)]

A sensitive staining procedure for localizing SOD on polyacrylamide gel electrophoretograms is now applicable to crude extracts from various materials.[2)] A comparative study of the SOD distribution among tissues of bread wheat has been conducted in the present study from phylogenical and ontogenical interests.

The first leaves and roots emerged under sterile conditions of *Triticum aestivum* cv. Chinese Spring ($2n=42$) were excised from seeds, and the tissues were homogenized in 0.1 M K-phosphate (pH 7.8) and 0.1 mM EDTA (0.1 ml per leaf or per two roots). The supernatant after centrifugation at 13,000 × g for 10 min at 2°C was used as crude SOD extract.

SOD activity was assayed photochemically by inhibition of nitro blue tetrazolium (NBT) reduction due to O_2^- in photoreduction system.[2)] Reduction of NBT, during 6 min of illumination, was measured in terms of increased absorbance at 560 nm, and inhibition (%) caused by SOD was plotted as function of concentration of this enzyme as shown in Fig. 1. Percent of inhibition is not linear with SOD concentration of leaf extracts. This non-linear relationship was also confirmed with crude extracts from roots or other plant materials.[4)]

Polyacrylamide isoelectric focusing was performed by the procedure of Leaback & Rutter[3)] with carrier ampholyte (40 % solution, LKB Ampholine, pH 3–10 range). Electrophoresis was run for 3 hrs at 200 V using 0.2 M HCl and 1% TEMED for the upper cathodal and the lower anodal solution, respectively. Negative staining of SOD bands was achieved according to BEAUCHAM & FRIDOVICH.[2)]

Isoelectric focusing in combination with disc electrophoresis indicates that the SOD activity of the crude extracts is composed of a number of distinct bands. The zymograms of SOD from leaf and root extracts are drawn in Fig. 2.

In leaves, SOD activities were localized at eight sites of the gel with p*I* values of 3.9, 4.8, 5.0, 5.1, 5.6, 5.9, 6.9 and 7.8, whereas the same five active bands with apparent quantitative differences excluding bands with p*I* of 3.9, 5.9 and 6.9 were obtained from root extracts. Any new root-specific band was not observed. The similar change of the band

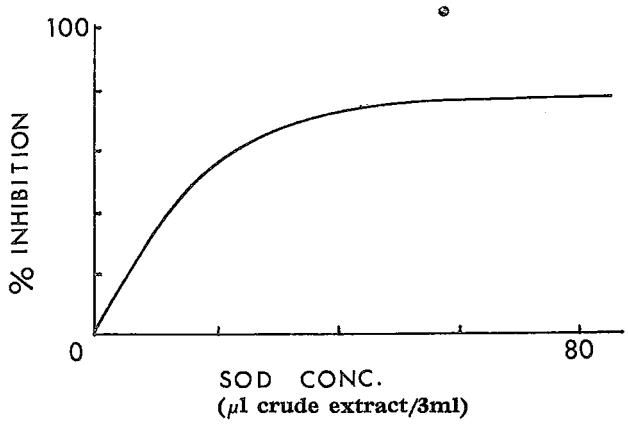

Fig. 1

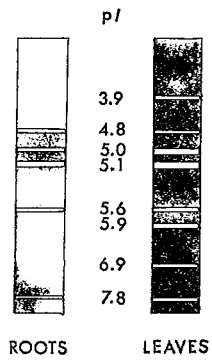

Fig. 2

Fig. 1. Inhibition of NBT photoreduction by crude SOD from bread wheat leaves. The assay mixture contained 28 μM riboflavin, 10 mM methionine, 56 μM NBT, 50 mM potassium phosphate, and indicated amounts of crude SOD in total volume of 3.0 ml (pH 7.8).

Fig. 2. Diagrammatic SOD zymograms of bread wheat. SOD was localized by soaking the gels in 24.5 μM NBT for 20 min., followed by an immersion, for 15 min, in a solution containing 28 mM tetramethylethylenediamine, 28 μM riboflavin, and 50 mM potassium phosphate at pH 7.8. The gels became uniformly blue except at positions containing SOD during illumination for 15 min in test tubes.

pattern was also visible in two other cereals, barley and diploid oats.[4]

The above multiple bands may correspond to different proteins with SOD activity, or different isozymes of a single protein, or a combination of both. Cupper-zinc enzymes are sensitive to cyanide, whereas manganese enzymes are resistant to cyanide and sensitive to treatment with a chloroform-ethanol mixture.[5] The only band with p*I* 3.9 was resistant to cyanide (not shown), and this result suggests that this enzyme seems to be a manganese enzyme, all the remaining being isozymes of cupperzinc SOD.

More detail analyses of metal ions bounded to each SOD band will be necessary to elucidate the organelle specificity.

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Some differential properties of alpha-amylase isozymes in growing and germinating seed of wheat

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All the genes so far identified for alpha-amylase isozymes of germinating seed of common wheat and *Aegilops squarrosa* locate on the chromosomes belonging to either homoeologous group 6 and 7, namely the genes for Band 1, 7 and 9 on chromosome 6D, Band 2 on 6A, Band 3 and 10 on 6B, Band 11 on 7D, Band 13 on 7A and Band 15 on 7B (Nishikawa and Nobuhara 1971, Nishikawa *et al.* 1976, unpublished). In spite of the same substrate specificity, alpha-amylase isozymes specified by the genes on the chromosomes of homoeologous group 6 (group 6 isozymes) differ from those by the chromosomes of group 7 (group 7 isozymes) in some aspects.

As well known, homoeologous chromosomes have been derived from one and the same pivotal chromosome and so called homoeoallelic genes on the respective chromosomes of the same group. The isozyme by definition, no matter whether specified by the allelic or homoeoallelic genes can not tolerate gross modifications of its polypeptide chain. This means in turn that changes of its physical properties, such as isoelectric point, must be within a limited extent. Group 6 isozymes (Band 1 to 10) were higher than group 7 isozymes with regard to isoelectric point, the former being within the zone of about pH 7.1 to 6.1, while the latter within the zone of about pH 5.7 to 5.3. It is evident that the two pI zones do not overlap with each other. Then, in addition to chromosome locations of the genes concerned, non-overlapping zone of pI of group 6 and 7 isozymes proves that group 6 isozymes are specified by a group of homoeoallelic genes and group 7 isozymes by another group of homoeoallelic genes.

In growing seed of common wheat (cv. Chinese Spring) 1 to 21 days after anthesis, weak activity of group 7 isozymes could be detected, but none of group 6 isozymes occurred, as shown in Fig. 1. Band 15 appeared a few days later than two others.

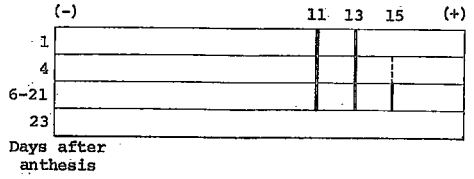

Fig. 1 Change of alpha-amylase zymograms in growing seed of Chinese Spring wheat

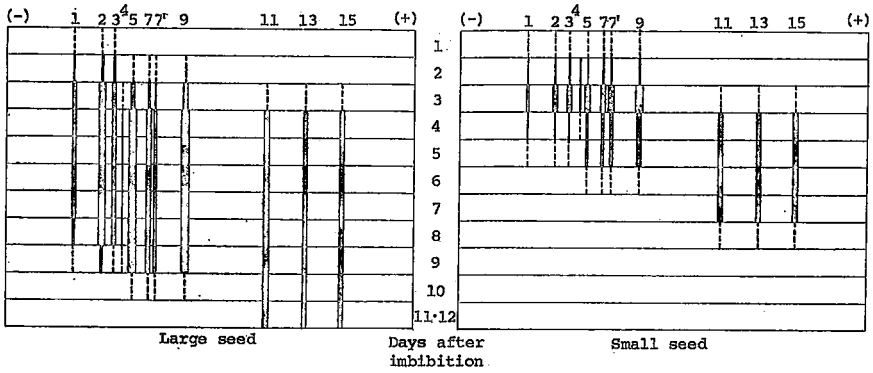

Fig. 2 Changes of alpha-amylase zymograms in germinating seed of Chinese Spring wheat with the lapse of time after imbibition

Group 6 isozymes, on the other hand, were activated in the earlier stage of seed germination than group 7 isozymes as shown in Fig. 2. 1 day after seed imbibition, grop 6 isozymes, Band 1 to 9 (Band 10 does not occur in cv. Chinese Spring) started to be detected and with the lapse of time their catalytic activity increased and continued up to about 10 days after imbibition. While group 7 isozymes were activated about 2 days behind the group 6 isozymes and kept the higher avtivity for at least 10 days thereafter. When small seed was used, in which group 6 isozymes could keep their relatively higher activity for only a few days the alternation of alpha-amylase activity from group 6 to group 7 isozymes was obvious.

From differential activity both in growing and germinating seed as mentioned above, functional differentiation of starch degradation activity of two groups of alpha-amylase isozymes can be reasonably pressumed.

Cytological and electrophoretic analysis of several speltoid and compactoid mutants of *Triticum aestivum*

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Speltoid and compactoid macromutants of common wheat, mostly radiation induced mutants, phenotypically similar in spike morphology with *T. aestivum* subsp. *spelta* and *T. aestivum* subsp. *compactum* respectively, have been the object of serious work as regards their cytogenetic origin (MAC KEY 1954, SEARS 1956, MURAMATSU 1963, SINGH 1968). The information so far available, accepts that the *vulgare* gene *Q*, located on the distal end of 5AL, a gene with speltoid suppressing effect, is chiefly responsible for the mutation rate in irradiated material. This gene is considered to function as hypermoprhic allele of the *spelta* gene q, modified by duplicates in homoeologous loci, and manifesting dose effect due to deficiency-duplication mechanism (KUCKCUK 1959, MURAMATSU 1963). Another gene, the awn inhibitor B_1, been designated to locate also on chromosome arm 5AL, at a distance of 35 crossover units from *Q* locus, has also been known to affect spike morphology (SEARS 1944, 1975).

The causal events which lead to speltoidy or compactoidy have been mostly defined as structural aberrations; however point mutations, though less frequently, can result in giving the same off-types (MAC KEY 1954).

Present work aims at further elucidating the nature of *Q*-influenced or *Q*-associated mutations, by analysing several macromutans both by cytological and electrophoretic procedure. An alteration of enzymes, presumably caused by mutation, would result in differential electrophoretic mobilities of the molecules and provide additional means for designating the particular mutants.

Seeds of two hexaploid wheat cultivars, G–58383 (fully bearded) and G–38290 (beardless), both produced in the Institute of Cereals of Thessaloniki, were irradiated by gamma-rays or thermal neutrons (SKORDA 1971). The progenies were screened on single plant basis, for speltoid and compactoid mutants. After M_3 several mutant types, phenotypically stable and cytologically euploid, have been maintained. Seven speltoid and seven compactoid mutants, selected at the fifth generation, and in addition the two parental varieties, have been the subject of the present work (Fig. 1). The experimental design was chosen, because it offers a basis for comparative study of mutants which derived from the same parent, while it makes it possible to evaluate similar mutants of different varietal origin. Precisely, G–38290 has proved more susceptible in giving speltoids, whereas G–58333 has the tendency to produce compactoid mutants.

All compactoids used in this study are derivatives of the same martyr G–58383 (m_1). Each of them was distinct both in spike density (26–36) and stem height and characterised

by phenotypic uniformity. The majority of speltoids (S_1, S_2, S_5, S_7, S_8) have been also produced from m_1. Among them, mutant S_5 is unique in lacking awns, in contrast to the bearded parental type. Speltoids S_3 and S_4 originated from G–38290 (m_2). The first one is awnless like the parental variety. The second, a spontaneous mutant of G–38290, is distinct in bearing awns.

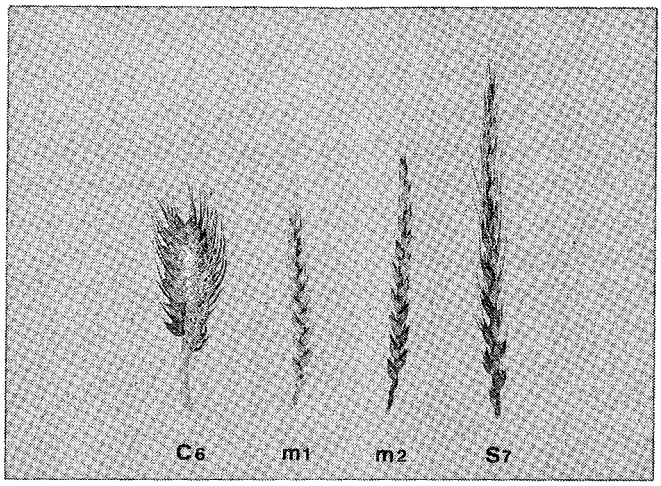

Fig. 1. Photograph of the two parental varieties (m_1, m_2) and two extreme mutant phenotypes (C_6 compactoid, S_7 spelfoid mutant)

Cytological observations

The meiotic analysis revealed two separate group of mutants. Group I includes all compactoids and in addition, S_1, S_2, S_7 and S_8 speltoids. Group II is represented by three speltoid muntants (S_3, S_4, S_5).

All compactoids manifested a polymorphic meiotic spectrum, corresponding with phenotypic grades of compactoidy. Mutant biotypes C_2 and C_3 showed to be the less compactoid off-types. In contrast, mutants C_4 and C_6 were found to possess a typical or extreme compactoid ear. The climax of meiotic behaviour can be set in the following sequence, beginning with the most normal situation (Tab. 1):

Table 1

Mutant	C_2 >	C_3 ≃	C_5 >	C_1 >	C_7 >	C_6 >	C_4
mult. %	3.8	6.1	5.9	11.0	14.2	41.5	46.7
univ. %	10.5	7.7	17.0	8.4	7.3	18.7	20.7

The persisting occurrence of multivalents indicate that the particular compactoid off-types comprise structural mutants. Besides, the fact that the observations have been carried out at the fifth generation after seed irradiation, supports the view that chromosomal interchanges have played an essential role in the maintenance of mutability, by increasing

the probability for further meiotic abnormalities. The commonest process by which multiple dose of *Q* locus is accomplished, might be translocations which involve a segment of 5AL (MAC KEY 1954, HAIR and RIGHT 1968).

Four speltoids (all derivatives of m_1), were also found to be structural mutants having originated by deficiency-duplication process as shown by the observed deviations from meiotic normality. A high frequency of multivalents, associated more or less with univalency, proved to be a common feature. The climax of meiotic indices corresponds to the following sequence, the most normal meiotic situation being the starting point (Tab. 2).

Table 2

Mutant	S_3	$\simeq$	S_4	$\simeq$	S_5	$>$	S_7	$>$	S_8	$>$	S_2	$>$	S_1
mult. %	0.0		0.6		0.0		11.7		10.4		21.7		33.3
univ. %	1.5		5.4		2.2		8.5		12.5		18.1		33.3

Mutant S_1, the most unstable speltoid of the group, is clearly distinct morphologically by possessing the most lax spike (D 11, 5) and cytologically by containing a high proportion of univalents (up to 12 per cell). In addition, sporadic aneuploid cells (2.9%) as well as two quadrivalents in one cell (2.7%) have been recorded.

Speltoid S_7, the less "speltoid" mutant in the series (D 16), showed a high proportion of normal meiocytes, but it was distinct in containing a persisting heteromorphic bivalent, usually rod-bivalent, including a telocentric member. However, as it was never found to participate a quadrivalent, it might not be considered to be involved in the system affecting the speltoid character.

The findings were strikingly different with speltoids belonging to the group II. All three manifested normal meiotic behaviour, almost approximating that of the martyrs (Table II). This is an indication that gross chromosome changes, implicating interchanges within genome do not account for their evident speltoid form. The bearded character of the S_4 mutant, the spontaneous derivative of the awnless m_2, could be expected among the offspring of a variety like G–38290, resembling in chromosome structure and meiotic attitude with Chinese Spring (COUCOLI and SKORDA 1966). Therefore it would be more likely to suggest that the three speltoids arose due to point mutations. This conclusion has been strongly supported by the electrophoretic analysis of the material.

Analysis of the zymograms

Taking into consideration the whole spectrum of zymograms as revealed by both enzyme system studied, in association with all tissues used in the procedure, 7–9 esterase bands and 4–7 peroxidase bands were separated.

The two parental forms (m_1 and m_2, Fig. 2) appeared to differ 1) in three bands of shoot esterase zymograms (slow bd. 2 absent in m_1, present in m_2; slow bd. 4 and fast bd 9 present in m_1, absent in m_2). 2) in three esterase bands of the coleoptile pattern (weak band

1 present only in m_2, intense band 3 present only in m_1, fast band 9 being substantially weaker in m_2) and 3) in one zone of endosperm peroxidase pattern (band 3 present in m_1 and absent in m_2).

In compactoids, isozymic patterns of both enzymic systems, as revealed by all tissues studied, did not show any intermutant variation or any variation between any mutant and the parental variety m_1. For the same organ the enzymic bands were common to all compactoids as regards both number and density.

The above mentioned findings concerning the similarity of zymograms, suggest that biosynthesis of the two investigated enzymic systems is presumably controlled by other genetic sites, different from the segment of 5AL which carries the *Q* and B_1 genes (MITRA and BHATIA 1971). Thus, there was found no genic alteration or inactivation interfering with compactoid character.

Speltoid mutants showed intermutant variation as well as variation between mutants and varieties in their isoenzymic patterns. The situation was of small degree for the structural mutants S_1, S_2, S_7, S_8 (Group I) which differed from their common parental variety m_1 only by separating the slow band 1 in shoot esterase spectrum (Fig. 2).

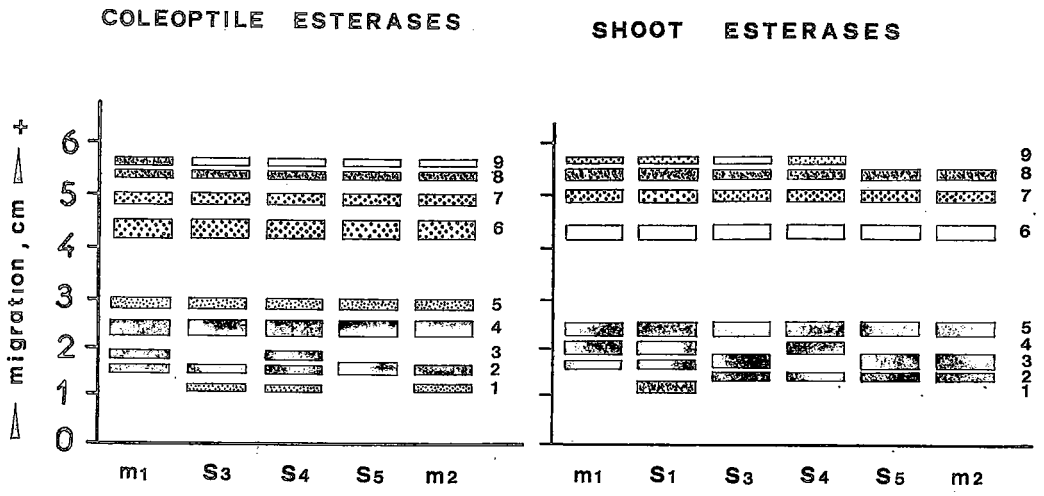

Fig. 2. Schematic representation of starch gel zymograms showing the electrophoretic patterns of esterase activity in 10-day-old seedlings (two martyrs and four speltoid mutants)

The variation was significant as regards the mutants belonging to group II, and it proved to be associated with concrete phenotypic differences. It chiefly concerned: 1) bands 4 and 9 of shoot esterase patterns and 2) and 3 of the coleoptile esterase pattern (Fig. 2). In detail, mutant S_3 revealed the typical electrophoretic spectrum of m_2 (parental type) and, in addition, the fast band 9 (found in m_1 and all mutants, apart S_5). Besides, as regards shoot peroxidase zymogram, mutant S_3 was exceptional in lacking the slow band 3, which was identified in both varieties and in all other mutants.

Mutant S_4, the awned derivative of the awnless m_2 separated 1) in shoot esterase pattern, the zones 4 and 9, lacking from m_2, but present in m_1, 2) in coleoptile esterase spectrum the slow zone 3, also typical for m_1. On the contrary, mutant S_5, the awnless derivative of the awned m_1 lacked bands 4 and 9 of shoot esterase patttens (Fig. 2) as well as band 3 of the coleoptile zymogram. This absence was characteristic of m_2. Therefore the three bands seem to be phenotypically associated with awning, having been recognised in m_1 and all awned mutants, yet not all separating either in m_2 or in the awnless mutants S_3 and S_5.

The results provided by meiotic and electrophoretic analysis lead to the conclusion that the diverging mutants S_3, S_4 and S_5 represent situations in which irradiation had mostly affected genes controlling awn character. Such genes had been recognised to locate in chromosome arms 4BS (Hd), 5AL (B_1) and 6BL (B_2), so that epistatic interaction between them or between each of them and various promoter genes can result to the appearance of awns (McIntosh 1973).

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Amino acid compositions of ferredoxins isolated from common wheat and the relatives

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Plant-type ferredoxin is a low molecular, iron-sulfur protein and functions as an electron carrier in the fundamental metabolisms of plants, such as photosynthesis and nitrate assimialtion. They distributed in a wide taxonomical range from higher plants to blue-green algae. Because of these situations of ferredoxin, the protein has been considered to be a particularily suitable component to study on the biochemical evolution of plants. Matsubara and his colleagues (MATSUBARA *et al.*, 1978, WAKABAYASHI *et al.*, 1978) have investigated primary structures of ferredoxins isolated from many plants, including from higher plants to blue-green algae, and proposed the phylogenetic tree of ferredoxin. On the other hand, KIHARA (KIHARA, 1924, KIHARA and LILIENFELD, 1949) has established that common wheat, possessing genome complement of AABBDD, is originated

Table 1. Amino acid composition of ferredoxins isolated from common wheat and the relatives*

Amino Acid	*Triticum aegilopoides*	*Triticum durum*	*Triticum aestivum*	*Aegilops squarrosa*	*Aegilops ovata*	Nearest. Integer.	*Hordeum vulgare*
	Number of amino acid residues per molecule						
Lysine	4.78	5.31	5.21	4.94	5.27	5	4.44
Histidine	2.33	2.11	2.09	2.04	2.18	2	2.22
Arginine	1.16	1.22	0.74	0.97	0.92	1	1.11
Aspartic acid	10.59	10.75	10.65	10.73	11.17	11	11.77
Threonine	4.85	5.04	4.92	5.10	4.72	5	5.11
Serine	6.76	7.19	7.00	6.88	6.75	7	7.11
Glutamic acid	18.30	18.19	18.11	18.47	17.80	18	19.11
Proline	4.99	4.58	4.72	5.22	4.70	5	4.37
Glycine	6.32	6.36	6.39	6.56	6.25	6	6.66
Alanine	7.23	7.42	7.48	7.31	6.94	7	7.11
Cysteine**	5.18	4.56	5.09	4.50	4.53	5	—
Valine	6.69	6.62	6.82	6.51	6.40	7	9.60
Methionine	1.03	1.01	1.06	1.02	1.07	1	0.90
Isolecuine	4.17	4.07	4.41	4.22	4.03	4	5.11
Leucine	7.43	7.28	7.10	7.41	7.34	7	9.11
Tyrosine	3.83	3.70	3.54	3.81	4.08	4	4.66
Phenylalanine	0.92	0.88	1.09	1.05	0.85	1	1.07
Tryptophan	0.92	0.88	1.01	1.09	1.09	1	—
Total						97	

Numbers are average values obtained after hydrolysis for 22 and 42 hr. The values for threonine and serine were extrapolated to zero time hydrolysis. ** Cysteine was determined as cysteic acid.
* The analysis data were in part appeared in the previous paper (SHIN *et al.* 1979).

as an amphidiploid of a hybrid between a species of emmer wheat (AABB) and *Aegilops squarrosa* (DD). It is, therefore, of considerable interest to study whether the genealogical relationships in wheat plants bring any change on the chemical composition of ferredoxin in these plants.

For the present interest, amino acid compositions were analyzed for ferredoxins isolated from three species of *Triticum*, *T. aegilopoides* var. *boeoticum*, *T. durum* ver. *apulicum*, and *T. aestivum* cultvar. *Shirasagi*, and two of *Aegilops*, *Ae. squarrosa* var. *typica* and *Ae. ovata*. as shown in Table I. The analysis data appear to indicate that these five ferredoxins are all idintical. For comparing with other ferredoxins, amino acid composition of *Hordeum vulgare* is also shown in the same table. Differences can be seen in the contents of glutamic acid, valine, isoleucine and leucine.

It is, therefore, likely that one molecular species of ferredoxin is distributed through two genera of *Triticum* and *Aegilops*, and that ferredoxin molecule has remained unaltered during the evolution of wheat plants.

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Genetic effects of 25 alien cytoplasms on plant height and its component parts in common wheat

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By repeated backcrosses, the cytoplasms of 25 species of *Triticum* and *Aegilops* have been introduced into 12 strains of five common wheat species (TSUNEWAKI *et al.* 1978). The nucleus donors used were as follows: *T. aestivum* var. *erythrospermum*, strain P168, cv. Chinese Spring, cv. Norin 26, strain Salmon, cv. Jones Fife, cv. Selkirk, cv. S-615, *T. sphaerococcum* var. *rotundatum*, *T. compactum* cv. No. 44, *T. spelta* var. *duhamelianum*, and *T. macha* var. *subletschchumicum*.

All these cytoplasm substitution lines were grown in an experimental field under a split plot design with four replications, in which 12 nuclei were placed in the major plots and 26 cytoplasms (25 alien and a common wheat cytoplasm) in the subplots. In each subplot two plants were grown, average of which was regarded to represent the subplot value.

Number of internodes over 3 cm, lengths of three culm internodes from the top, ear length and plant height were measured in each plant using its tallest culm. Analysis of variance revealed that all six characters were influenced by alien cytoplasms. Average deviations of 12 cytoplasm substitution lines with the same cytoplasm from their corresponding normal lines are shown in Table 1. All nine cytoplasms belonging to A, C^u, M and S^1 plasma types reduced every character to a great extent; all reductions were significant at the 1% level. C and G type plasmas reduced the first internode length and plant height, and most D type plasmas reduced the number of internodes. M^o type plasma increased number of internodes but reduced the first and second internode lengths and plant height. In general, S type plasmas did not show a remarkable effect on any character. From these results it became evident that cytoplasms of the different types exert very specific effects on plant height and its component parts.

A representative cytoplasm was selected from each plasma type, and the relative effects it had on plant height and the component parts were calculated as shown in Table 2. From these data, it became clear that three cytoplasms of C^u, M and S^1 type almost uniformly depressed all characters, while the cytoplasms of C, G and M^o type had great influence on only certain characters. Two cytoplasms of D and S type did not show any effect. From those results, we may conclude that A, C^u, M and S^1 type cytoplasms depress general growth vigor of common wheat, while C, G, M^o and probably D type plasmas have stage-specific effects on wheat growth: S type plasmas do not have any such effects.

In order to reveal the relative contribution of the cytoplasm to genetic variability, genetic variances attributable to the nucleus, cytoplasm and their interaction were

Table 1. Deviation of the cytoplasm substitution lines from the corresponding normal lines of common wheat (Average of 12 lines having different nuclei)

Cytoplasm	Plasma type	No. internodes (>3 cm)	Internode length (cm)			Ear length (cm)	Plant height (cm)
			3rd	2nd	1st		
boeoticum	A	−1.25**	−6.1**	−12.7**	−29.8**	—	−58.8**
caudata	C	−0.02	0.1	−1.1*	− 3.3**	0.1	− 5.9**
syn-triuncialis	〃	−0.20**	−0.2	−0.7	− 3.2**	0.3	− 3.7**
umbellulata	C^u	−0.27**	−1.6**	−2.9**	− 8.8**	−1.2**	−20.0**
triuncialis	〃	−0.37**	−2.1**	−3.8**	− 9.0**	−1.1**	−21.5**
biuncialis	〃	−0.38**	−2.3**	−3.9**	−10.8**	−1.8**	−24.6**
columnaris	〃	−0.37**	−2.0**	−3.4**	−10.3**	−1.0**	−22.8**
triaristata 4x	〃	−0.67**	−2.8**	−4.3**	−15.2**	−1.8**	−29.0**
〃 6x	〃	−0.27**	−2.0**	−3.4**	−11.3**	−1.2**	−23.5**
squarrosa	D	−0.16*	0.2	0.0	0.8	0.2	− 0.1
cylindrica	〃	−0.32**	0.0	−0.3	− 0.7	−0.3	− 4.4**
ventricosa	〃	−0.27**	−0.6	−1.3*	1.5	0.9**	− 2.9*
juvenalis	〃	−0.17*	0.0	0.2	− 0.3	0.0	− 1.2
crassa 6×	〃	0.03	0.5	1.4**	0.1	0.1	1.5
vavilovii	〃	−0.23**	0.2	0.7	− 0.9	0.0	− 1.9
nudiglumis	G	−0.12	0.3	0.3	− 4.8**	0.4	− 4.5**
timopheevi	〃	−0.09	−0.1	−0.3	− 5.3**	0.4	− 4.8**
comosa	M	−0.22**	−1.7**	−5.8**	−13.8**	−0.7**	−24.7**
ovata	M^o	0.49**	0.2	−2.7**	−11.3**	0.2	−11.7**
speltoides	S	0.00	0.1	−0.3	− 1.7*	0.1	− 2.3
dicoccoides	〃	−0.11	0.0	−0.5	− 1.5	−0.1	− 0.5
dicoccum	〃	−0.13	0.0	0.2	0.0	0.2	− 0.5
kotschyi	〃	−0.08	0.2	0.4	− 1.6	0.0	− 1.3
variabilis	〃	−0.19*	0.0	−0.3	− 1.8*	0.1	− 4.4*
aestivum	〃	0.00	0.0	0.0	0.0	0.0	0.0
sharonensis	S^1	−0.43**	−1.6**	−2.1**	− 6.6**	−1.0**	−17.7**
5% l.s.d.		0.15	0.68	1.03	1.69	0.41	2.74
1% l.s.d.		0.20	0.89	1.36	2.22	0.54	3.60

Table 2. Relative effects of the 8 representative cytoplasms to each character, expressed by [(NC hybrid)-(Normal)]/(Normal) in per cent

Cytoplasm	Plasma type	Intenode length			Ear length	Plant height
		3rd	2nd	1st		
caudata	C	1	− 4	− 7	1	− 5
umbellulata	C^u	−12	−12	−19	−11	−18
squarrosa	D	1	0	2	2	0
nudiglumis	G	2	1	−10	4	− 4
comosa	M	−12	−23	−30	− 6	−22
ovata	M^o	1	−11	−24	2	−10
speltoides	S	1	− 1	− 4	1	− 2
sharonensis	S^1	−12	− 8	−14	− 9	−16

calculated, which are shown in Table 3. The variance attributable to genetic differences among the cytoplasms of 26 *Triticum* and *Aegilops* species was only 2 to 20%, with an average of 15%, of the variance attributable to the nuclear differences among 12 common wheat strains. This fact supports our general belief that a large part of the genetic

Table 3. Relative genetic effects of the alien cytoplasm on 6 characters of common wheat

Character	σ_N^2	σ_C^2	$\sigma_{N\times C}^2$	σ_C^2/σ_N^2	$\sigma_{N\times C}^2/\sigma_N^2$
No. internodes (>3 cm)	0.295	0.030	0.021	0.10	0.07
3rd internode length	5.078	0.751	0.837	0.15	0.17
2nd 〃 〃	13.411	2.781	2.581	0.21	0.19
1st 〃 〃	93.812	20.961	12.754	0.22	0.14
Ear length	14.609	0.302	0.523	0.02	0.04
Plant height	403.857	86.171	45.714	0.21	0.11

variability owes to the nucleus.

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Performance and selection of wheat mutants for some quantitative characters

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Plant height, culm diameter and tillers per plant have evolutionary significance (LARIK, 1978) and are important from breeders point of view because of their direct influences on crop yield (ROMERO and FREY, 1973; JOPPA, 1973; SHUKLA, 1974). At present, in breeding programmes concentration is being made on the development of semi-dwarf selection with one gene only (ALLAN and PRITCHETT, 1973). Semi-dwarf and stiff straw traits, are doubly beneficial in wheat production because short plants are lodging resistant and have high grain-straw ratio (VOGEL *et al*, 1956). Semi-dwarf lines also produce more tillers than the tall lines, and as expected, environments have large effects on the number of tillers. Environments that induce the highest number of tillers also produce the highest yields (JOPPA, 1973).

The present studies are concerned with an evaluation of phenotypically stable wheat mutants for plant height, culm diameter and tillers per plant, isolated from one locally bred cultivar and two cultivars of Mexican origin. Such studies can be instrumental in producing genotypes and populations with high genetic homeostatis (LERNER, 1954) and ultimately in enhancing the yield of bread wheat. The magnitude of genetic variability and response to selection among these mutants are also reported.

Materials and Methods

The material originated from different doses of gamma rays (20, 25 and 35 kR) and ethyle methane sulphonate (EMS) of varieties C–591 (locally bred), Nayab and Indus-66 (Mexican origin) of bread wheat *Triticum aestivum* L. Phenotypically stable mutants were evaluated for plant height, culm diameter and tillers per plant in M_9 generation grown in the field in Tandojam during Rabi 1977–78. Seeds of these genotypes were procured from the Department of Botany and Plant Breeding, Sind Agricultural University, Tandojam. Sowing of homogeneous seeds of mutants and cultivars was done by dibbling single seed per hole at 30.5 cm intervals, in single rows each 3.1 m long with 30.5 cm interrow distance with path ways 1.0 m wide between blocks of a plot in randomized block design with four replications. Thus 50 plants were studied from each mutant genotype and cultivars respectively. Mean values for the mutant populations for each character were compared with the control means by using *t* tests.

To make effective and efficient use of mutant genotypes in advanced generations through selection, estimates of broad sense heritability and expected genetic advance with selection

intensity of five percent have been computed for these quantitative characters.

The broad sense heritability (h) of a character was estimated similarly to LARIK (1978) as under:

$$\% h = \frac{\sigma^2 g}{\sigma^2 t} \times 100$$

where $\sigma^2 g$=induced genetic variance and $\sigma^2 t$ is the total phenotypic variance calculated from mutant population.

The estimates of genetic advance (GA) at 5% selection intensity was based on the relation suggested by LARIK (1978) and computed by the following formula:

$$GA = (K)(\sigma p)(H)$$

where σp=phenotypic standard deviation from the mean performance of mutant population, H=heritability coefficient and K=2.06 constant for selection differential.

Table 1. Estimates of mean values, genotypic coefficient of variation, heritability and expected genetic advance with selection intensity (K)* of five percent for plant height and culm diameter of hexaploid wheat cultivars and their mutant strains

Genotype/Treatment/ Origin	Mean	C.V. (p) %	C.V. (g) %	Heritability (b.s.) %	Genetic advance % of means
		Plant Height (cm)			
C–591 (Control)	118.45	16.80	—	—	—
M– 7 EMS 7 hr	105.80**	18.52	13.80	29.90	14.49
M–28 EMS 7 hr	113.35*	17.83	12.56	15.80	12.72
M–38 EMS 7 hr	100.45**	18.75	13.95	25.50	13.78
Mayab (Control)	83.24	17.29	—	—	—
M–10 20 kR	79.95*	18.42	13.54	27.90	15.08
M–27 35 kR	76.12**	17.98	12.45	15.10	13.04
M–44 25 kR	80.11*	17.80	12.73	15.75	14.09
Indus-66 (Control)	70.44	16.04	—	—	—
M–13 20 kR	68.31	17.25	12.53	15.80	11.95
M–37 20 kR	66.10*	18.26	15.05	34.50	20.36
		Culm Diameter (mm)			
C–591 (Control)	3.3	3.63	—	—	—
M– 7 EMS 7 hr	3.5	8.33	7.64	14.70	8.90
M–28 EMS 7 hr	3.8**	15.85	17.31	25.00	14.28
M–38 EMS 7 hr	3.9**	20.43	22.78	27.79	12.49
Nayab (Control)	3.5	9.12	—	—	—
M–10 20 kR	3.5	10.34	16.98	40.08	16.68
M–27 35 kR	3.8*	13.53	18.85	45.60	20.67
M–44 25 kR	3.7	12.10	20.88	48.35	25.86
Indus–66 (Control)	3.6	10.50	—	—	—
M–10 20 kR	3.8	15.70	18.80	30.58	17.40
M–37 20 kR	4.0**	17.37	20.67	48.59	21.84

(K)*=5%=2.06

*,** denote significant at 5% and 1% level of probability respectively.

Table 2. Estimates of mean values, genotypic co-efficient of variation, heritability and expected genetic advance with selection intensity (K)* of five percent for tillers per plant of hexaploid wheat cultivars and their mutant strains

Genotype/Treatment/ Origin	Mean	C.V. (p) %	C.V. (g) %	Heritability (b.s.) %	Genetic advance % of means
C–591 (Control)	19.10	12.04	—	—	—
M– 7 EMS 7 hr	21.20**	15.70	18.40	50.56	16.79
M–28 EMS 7 hr	19.50	13.37	17.10	48.30	15.83
M–38 EMS 7 hr	22.50**	17.38	19.60	55.90	17.89
Nayab (Control)	18.50	10.60	—	—	—
M–10 20 kR	19.80	12.30	17.25	45.20	15.75
M–27 35 kR	21.38**	15.56	19.10	52.55	17.83
M–44 25 kR	23.35**	17.30	21.45	58.38	19,35
Indus–66 (Control)	18.70	15.08	—	—	—
M–13 20 kR	19.90	16.85	18.50	50.53	16.90
M–37 20 kR	18.80	16.75	16.78	38.90	15.30

(K)*=5%=2.06
** denote significant at 1% level of probability

Results and Discussion

Plant height in all the mutant populations was significantly (P>0.05, 0.01) reduced from that of controls whereas, culm diameter and tiller per plant revealed significant (P> 0.05, 0.01) increase in mutants, except mutant No. 7 of C–591; mutant No. 10 and 44 of Nayab and mutant–13 of Indus–66 for culm diameter and mutant No. 28 of C–591, mutant No. 10 of Nayab and mutant No. 37 of Indus–66 for tillers per plant (Table 1 and 2).

These mutant strains showed an increase over respective controls, but this was not statistically significant. Significant shift in mean values of these agronomicaly important traits is in good agreement with the findings of LARIK (1975a, b; 1978) and SIDDIQUI (1972).

The mean height of the mutants of Nayab and Indus–66 were reasonably homogeneous except mutants of C–591, in which mutant No. 28 was clearly taller than the rest of mutants whereas, mutant No. 38 was dwarf which showed a reduction of 18 cm in plant height along with an increase of 0.6 microns in culm diameter. A combined persual of the effects of data with respect to ethyle methane sulphonate (EMS) upon plant height and culm diameter would reveal that if the height of plant declined, the girth of culm increased. Reduction in plant height, increase in culm diameter and tillers per plant in wheat, *Triticum aestivum* are desirable attributes from breeders point of view as these are associated with stiffness of the straw, efficient utilization of nitrogen, loding resistance and grain yield (HEAR and WETTSTEIN, 1973; LARIK, 1978; SIDDIQUI, 1972)

The highest genotypic coefficient of variation (18.26%) for plant height and culm diameter was given by mutant No. 37 of Induss–66, which also had the highest heritability (48.59%) and genetic advances (21.84%). This indicates the potential for the improvement and greater gains from selection for these characters are anticipated in mutant No. 37 (CHAFOOR ARAIN, 1973, PATIL, 1972). Low heritability estimates, genetic advance and genetic variation was given by mutant No. 7 of C–591 for culm diameter and mutant No. 13

and 37 of Indus–66 for plant height and tillers per plant respectively. These results indicate that the character could be transmitted to future generation however, no significant gain could be achieved through selection in early generation. The magnitude of these estimates among the treated lines of different cultivars varied widely (Table 1 and 2).

The present studies conclude that from breeders point of view selection for superior genotypes for agronomically important traits can only be made among mutant strains for those attributes which reveal high heritability values and high genetic advance. The present studies have also provided an evidence on the induction of genetic variability connected with these quantitative characters among different mutant strains of wheat cultivars derived from gamma rays and EMS-treatment. The genetic variability thus, induced can effectively be exploited for evolving mutant strains possessing desirable attributes.

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V. Editorial Remarks

Announcement for Future Issues

WIS Nos. 49 will appear soon and No. 50 will be planned for publication in December 1979. – No. 50 will possibly be made for double page issue. Manuscripts for this issue are most welcome and accepted any time, not later than September 30, 1979.

WIS is open to all contributions regarding methods, materials and stocks, ideas and research results related to genetics, breeding and cytology of *Triticum*, *Aegiolops*, *Secale*, *Haynaldia* and related genera. Manuscripts should be typewriten in English, and submitted with duplicates. One article should not exceed five printed pages, including one textfigure (smaller than 7×7 cm^2). Lists of stocks are exempted from this page limit. Authors receive 50 reprints of their contributions free of charge. Extra copies are printed by order at cost price. Communications regarding editorial matters should be addressed to:

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Membership Fee

Due to the economic situations, the yearly Membership Fee has been raised up to ¥ 1,000 for foreign as well as Japanese members from the fiscal year beginning April 1978. The money should be paid by the Foreign Postal Money Order, otherwise considerable loss is caused due to the bank charges. Back numbers are available.

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The Managing Editor

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Explanation of the Figure on the Cover

A bowl of charred wheat grains excavated in Mohenjodoro (3,000 years B.C.), exhibited in the Archaeological Museum in Mohenjodaro, Pakistan (Rf. page 3 in the article of present issue of WIS, by K. YAMASHITA.)

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