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I. Research Notes

On the origin of Triticum carthlicum NEYSKI (=Triticum persicum VAV.)

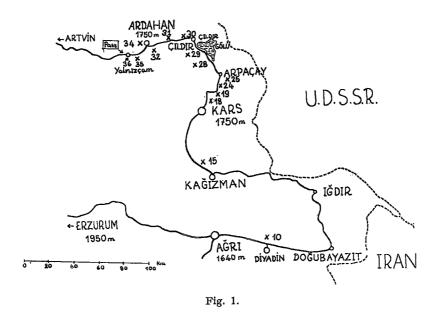
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Triticum carthlicum is very distinct in its morphology from the other free threshing tetraploid wheats, such as Triticum durum, turgidum, turanicum, iranicum and polonicum. As it looks very much like the wheats of T. aestivum ssp. vulgare, it was classified at first as an hexaploid species. A striking feature is the awned glume, so all the spikelets show four awns. Later, on account of its resistance to mildew and rust and the chromosome number with 2n=28, T. carthlicum was recognized to be a tetraploid species (Schiemann 1948).

As in 1953, in Iran, I met wheats with 4 awns I had the illusion to have made the first findings of T. carthlicum in Iran, up to now still unknown in this country. But chromosome number proved an hexaploid wheat. Later Dr. Gökgöl, at that time chief of Plant Breeding Institute in Istanbul-Yelsiköy taught me how to distinguish between the true tetraploid T. carthlicum and the hexaploid T. aestivum ssp. carthlicoides: the awns of the glumes of T. carthlicum are longer than those of carthlicoides. From that time I became particularly interested in the problem of the relationship of these two species and of the origin of T. carthlicum. In 1967 the Turkish Sugar Trust gave me the chance to carry out a collecting excursion through the eastern part of Turkey along the boundary to the U.d.S.S.R. and Iran by providing me with transportation and guidance. This region is distinguished by a tremendous genetic variation in wheat including T. dicoccum, T. carthlicum and T. aestivum ssp. macha which are grown to some extent resp. still had been grown at that time according to the information I received from Dr. Gökgöl.

The route of the collecting excursion which started in Erzurum is mapped in Fig. 1. Samples were taken at 38 localities designated with consecutive numbers by selecting single ears out from the populations directly in the field. However only such populations are marked up on the map where populations with T. carthlicum, T. aestivum ssp. carthlicoides or



T. dicoccum are grown. These localities are situated at a latitude between 39°30' and 41°10', on a longitude between 41°50' and 43°40' and on an altitude of about 1800 m.

In 1968 progenies of the collected ears were grown in Hannover but only such progenies are listed in Table 1 from which the somatic chromosome number of the mother ear have been checked up in order to make sure that the morphological classification into the two groups carthlicum and carthlicoides have been correct. The analysis revealed the existence of 3 different populations:

- 1. populations in which probably exclusively tetraploid *carthlicum* types are included such as the collection numbers 19, 24, 28, 29, 32, 34 and 35. They are concentrated between Cildir and Ardahan.
- 2. populations in which only hexaploid carthlicoides types could be found; collection number 10 and 25.
- 3. populations with *carthleium* and *carthleoides* types; collection number 18 and 36. Of particular interest are the two *dicoccum* populations near Çildir, locality 30 and 31. They are characterized by some admixtures of an hexaploid spelt type, probably of *T. aestivum* ssp. *macha*. Unfortunately they were not yet ripe and I did not succeed in getting seeds after the harvest.

In Hannover field observations were carried out in 1968 as to the resistance resp. susceptibility to powdery mildew, *Erysiphe graminis tritici* El. Marchal, and having been scored with 1–5. As far as it is possible to draw any conclusion from one year-observation without any replication the more resistant types prevail in the tetraploid group. Some exceptions do occur, particulary in collection 32 and 33. The reaction of

Table 1. Chromosome number of the selected ears and the reaction of their progenies to Erysiphe graminis tritici El. Marchal and Puccinia striiformis West

	H	Ear	E. graminis	P. stv	iiformis	
Field No. 1968	Selected	Chromosome	Field	Field	Greenhouse	
1000	from	No.		Race 8	Race 20A	
	collection	2n	1968	1969	1970	
3023	10 c /1.	42	2			
3024	10 c /2	42	2			
3025	10 c /3	42	. 2		IV	
3027	10 c /5	42	2		IV	
3032	10 c/10	42	2		0	
3033	10 c /11	42	ō		IV	
3034	10 c / 12	42	ő			
3036	10 c /14	42	2		i-0	
3037	10 c /15	42	2		i-0	
3038	10 c /16	42	2		i-0	
3039	10 c /17	42	1		10	
3054	15/3	28	0		1	
3055	15/4	42			1	
3056	15/5		0			
3057		42	0			
	15/6 15/5	42	2			
3058	15/7	42	0		1	
3101	18/1	28	0			
3102	18/2	42	2			
3103	18/3	42	2		0+	
3104	18/4	42	3			
3105	18/5	42	3			
3106	18/6	28	1			
3107	18/7	28	0			
3108	18/8	28	0		i-0	
3109	18/9	42	0			
3110	18/10	28	0			
3111	18 / 1 ₁	28	0		i-0	
3112	18/1 ₂	28	0		i-0	
3126	19/3	28	0			
3128	19/5	28	1		IV	
3129	19/6	28	0		0+	
3130	19/7	28	i			
3132	19/9	28	ō			
3142	24/5	28 ?	2			
3143	24/6	28 ?	2			
31,44	24/7	28	3			
3149	25/5	42	3		i	
3150	25/6	42	3		1	
3153	28/1	28	0		0+	
3155	28/3	28	1		0+	
3156	28/4	28	ō		IV	
3157	28/5	28	o		i-0	
3158	28/6	28	0		1-0	
31.59	28/7	28	0		IV	
3160	28/8	28	0		i-0	
3166	29/1	l I	0		1-0	
	29/1 29/2	28		0		
3167		28	0	U	I	
3169	29/4	28	1		0.77	
3170	29/5	28	2		0-II	
3171	29/6	28	0		īV	
3172	29/7	28	2		0	

Table 1 (Continued)

	E	ar	E. graminis	P. stri	iformis			
Field No. 1968	Selected from collection	Chromosome No. 2n	Field 1968	Field Race 8 1969	Greenhouse Race 20A 1970			
3173	29/8	28	2					
3176	29/11	28						
3182	32/4	28	0	0	II			
3183	32/5	28	2		IV			
3184	32/6	28	2 .					
3185	32/7	28	2		0-11			
3186	32/8	28	3	0				
3187	32/9	28			II+			
3188	32/10	28	2 3 2 3		0+			
3189	32/11	28	2					
3190	33/1	28						
3193	33/4	28	0					
3194	33/5	28	3	1				
3195	33/6	28	1.		0			
3196	33/7	28	1	0.	II			
31.97	33/8	28	3	0	I			
3201	34/3	28	0	0	0+			
3202	34/4	28	2					
3203	34/5	28	0		1			
3204	34/6	28	3					
3205	34/7	28	0					
3206	34/8	28	0	0	0-II			
3207	34/9	28	0		IV			
3214	35/2	28	1					
3215	35/3	28	0		0+			
3216	35/4	28	0					
3217	35/5	28	0					
3218	36/1	42	1					
3219	36/2	42	4		TT 337			
3220	36/3	28	0		II-IV			

x) The experiments with *Puccinia striiformis* were performed by Mrs. Dr. E. Fuchs in Biologische Bundesanstalt, Braunschweig

0=without pustules, chlorosis, necrosis
0+=sporadic pustules, chlorosis, necrosis
I=small pustules, chlorosis, necrosis
II=intermediary pustules, chlorosis, necrosis

III=large pustules, chlorosis
IV=large pustules without chlorosis or necrosis } susceptible

i=immune or unsuccessful infection

some progenies to *Puccinia striiformis* WEST. was tested by Mrs. Dr. E. Fuchs; the seed-ling stage in greenhouse to race 20 A which is very common in the Near East, and in the field to race 8. Although the results are to small to draw any conclusion, but there might be some indication that resistant types are more frequent in the *carthlicum* group than in the *carthlicoides* group. On the basis of the analysis of these findings I would like to propose the following hypothesis as to the origin of *T. carthlicum*: the hexaploid *T. aestivum* ssp. *carthlicoides* should be considered as the elder (original) species. *Spontaneous* crosses between both species, *T. dicoccum* and *T. aestivum* ssp. *carthlicoides* are assumed. As both

species are still spread over the same area to-day, such an hybridization is rather likely. In the following generation of the pentaploid hybrid, 2n=35, with the genome formula AABBD the chromosomes of the D-genome were eliminated. By recombination and crossing over between the chromosomes of the A-genome as well as between these of the B-genome T. carthlicum as a new recombinant among many other genotypes was evolved. In this species genes responsible to the particular morphology of the hexaploid parent are combined with the genes for resistance to rust and mildew by which the tetraploid T. dicoccum is distinguished.

MACKEY (1954) stated in his research work on the Spelta problem that T. carthleium is the only 4x species with the so called Q-factor, the suppressor of the typical spelt characteristics; Q is present in all free threshing hexaploid wheats and is located on chromosome IX of the B-genome. According to Sears (1956) T. carthlicum differs from T. dicoccum by the same gene Q as distinguishes T. aestivum ssp. vulgare from ssp. spelta. These facts might give support to the proposed hypothesis that the 6x ssp. carthlicoides should be considered as the original and elder genotype from which genes for the particular morphology of the ear were transferred together with the Q-factor to T. carthlicum. The prolongation of the glume awns in T. carthlicum might be due to the interaction of genes resp. the lack of the D-genome.

Acknowledgement

I am grateful for the support of Mrs. Dr. Eva Fuchs, Braunschweig, in resistance-testing, of Mrs. Ruth Peters in chromosome counting and last but not least to the Turkish Sugar Trust for transportation and guidance.

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Chromosome location of the "kinky neck" character established by crossing durum wheat × monosomics of Chinese Spring

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The chromosome location of genes in durum wheat is still a difficult task to be overcome, partly because of its tetraploid nature and partly due to the lack of suitable aneuploid lines. So far few attempts have been made in trying to utilize the monosomics of bread wheat (Allan and Vogel, 1960; Kuspira and Millis, 1967; Bozzini and Giorgi, 1971). In durum wheat it happens very often to come across a variety in which the part of peduncle bearing the spike appears to some extent bended and twisted, namely kinky. In a previous work (l. c.) aimed at locating genetic factors in durum wheat the cultivar Capeiti, still widely grown in Italy, was crossed with 14 monosomics lines of Chinese Spring. Obviously, only the chromosomes of the genomes A and B were involved in this kind of monosomic analysis. From the F₁'s two types of hybrids can be separated by means of chromosome counting in root tips of the seedlings. One type has 35 chromosomes and represents straight way the normal pentaploid hybrid. The other type with 34 chromosomes comprises 14 monopentaploid hybrids in which one chromosome, in turn, is missing. Therefore, in each monopentaploid hybrid one chromosome is represented by a single dose, coming from the durum wheat parent, while the corresponding chromosome of

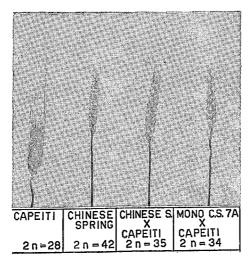


Fig. 1.

bread wheat is absent. In such a situation the recessive and hemyzigous effective genes carried by the single durum type chromosome can express themselves in F₁ generation. The effect of a certain number of genes has been beautifully depicted in this way.

Among the parameters studies and rechecked the characters "kinky neck" seems associated with the chromosome 7A. It appears that a major recessive and hemyzygous effective gene controls this characters as evidenced by the spike of CS mono 7A × Capeiti (Fig. 1). From time to time plants of the remaining monopentaploid hybrids show very slightly the "kinky neck" character, thus indicating that minor genes or modifiers can be present, spread throughout the genomes of durum wheat.

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A data base of meiotic analyses in wheat

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The study of the meiosis of hybrids has been used extensively in determining the genomic, taxonomic, and evolutionary relationships of species. In the wheat group this type of work has been conducted on a scale and with a precision unmatched in other genera. The relative simplicity of hybridization, the large and easily stained chromosomes, and the commercial importance of the *Triticinae* have all led to an extensive bibliography, yet the last listing of the literature and the data of which the author is aware was in 1954 (Anon.).

Concomittant with the advent of computers it has become common practice to store and search data and literature references in various ways. Recently, with the development of microprocessors and their associated peripheral equipment it has become practical to design and maintain small, specialized data banks appropriate to specific bibliographic needs. This paper birefly outlines the establishment and operation of such a system in which both meiotic analyses and their related bibliographic references are stored, can be searched in various ways and printed upon request.

At the time of writing the data base contains some 658 meiotic analyses and 200 journal references. The data are stored in coded form on mini-floppy magnetic disks. The data can be recovered, formatted and printed with the aid of various specially written programs. Since the data is written upon the disks in random order the addition of new references and meiotic analyses does not affect the sorting process. The meiotic analyses are always printed in the order the sorting program finds them but the references are both alphabetized and placed in chronological order before printing.

The meiotic data are stored as a string of numbers and, if necessary, a single line of of remarks in a series of files each of which has up to 12 entries. Each entry is identified by an eight- or nine-symbol alphanumeric code which is stored in a separate file. Each entry in the code file has two letters representing the female parent, two letters for the male parent (one of the parents is always a *Triticum* according to the 1967 classification of Morris and Sears) and a single number indicating the ploidy level of the hybrid. It is from this combination of four letters and one number that the searches are conducted. The remaining three or four alphanumeric characters of this code are the file name and entry number.

To make a search these codes are read and compared to the combination desired. If a match is made the meiotic data are located and printed. A second code (the ref. code) is

also read with the meiotic data and is stored in a temporary file. If, at the completion of the search for meiotic data, a request is made to print the references appropriate to the meiotic data already printed then the reference codes are alphabetized, the references are located and are printed. The meiotic data can be associated with the appropriate reference because the ref. code is printed with both.

The hybrid data base can be searched in eight different ways:

- 1) All hybrids with a specified female and male parent.
- 2) All hybrids with a specified female parent irrespective of the male parent.
- 3) All hybrids with a specified male parent irrespective of the female parent.
- 4) All hybrids in which one particular species is found, irrespective of whether it is the male or female parent.
- 5) All hybrids of a specific combination, irrespective of which species is the male or female parent.
- 6) All hybrids of a particular ploidy level.
- 7) All hybrids with a specified genome in the female and a specified genome in the male.
- 8) All hybrids with a specified genome common to both the male and female parents.

The reference data base can also be examined independently of the search for meiotic data. All the references can be alphabetized and printed or all the references of a particular author, irrespective of whether he is the first or subsequent author, can be located and printed.

It is proposed to attempt to keep this data bank up-to-date and to make searches of the data for other workers. Requests for searches should match one of the eight categories listed above.

The author would appreciate receiving new or inadvertentely omitted results for addition to the existing lists.

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Source of meiotic abnormalities in barley-wheat hybrids

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Hybrids between Betzes barley and Chinese Spring wheat were first reported by Islam et al., (1975) and subsequently other authors (Fedak 1977a; Cauderon et al., 1978). The hybrid plants in all cases had the expected somatic chromosome number of 28 and an irregular meiosis. Occassional PMC's with more than 28 chromosomes and some with up to 23 ring bivalents were reported by Islam et al. (1975). Similarly PMC's with chromosome numbers from 28 to 63 were reported in Betzes × Chinese Spring hybrids (Fedak 1977b) and from 28 to 56 in the reciprocal cross (Fedak 1980). Backcrossing of Chinese Spring onto the latter gave progeny with somatic chromosome numbers of 44 to 60, although 49 or less would have been expected. These progeny with excessive chromosome numbers undoubtedly arose from the union of 21 chromosome Chinese Spring gametes with hyperploid gametes from the hybrid that likely arose from hyperploid products of meiosis.

Premeiotic mitosis in the hybrids was examined as a possible origin of hyperploid PMC's. Spikes collected at 72 hours prior to the PMC stage contained cells at prophase and metaphase of mitosis. Anthers for mitotic studies were squashed in acetocarmine or pretreated with Snow's solution prior to squashing in acetocarmine as in PMC studies.

The majority of cells at premeiotic mitosis had 28 chromosomes, showed a 28–28 disjunction at anaphase, the products of which would presumeably produce normal gametes. A small proportion of cells, however, showed unequal disjunction at anaphase as shown in Fig. 1 which would lead to deficiency duplication PMC's; the latter eventually forming hyperploid gametes. Deficient cells likely were inviable since PMC's with less than 28 chromosomes were not encountered in the present study.

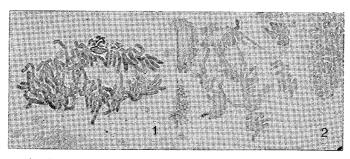


Fig. 1. unequal disjunction of chromosomes at anaphase.

Fig. 2. multipolar anaphase.

Several other cytological abnormalities were detected in studies of meiosis of barley-wheat hybrids and their progenies. Isochromosomes were observed in PMC's of Betzes × Chinese Spring hybrids (Fedak, 1977b) and telocentric chromosomes in backcross progenies of the same hybrids. Telocentrics would result from misdivisions of the centromere and isochromosomes would result from them. Multipolar anaphase as shown in Fig. 2 was observed at premeiotic mitosis and could have caused misdivision of centromeres leading to the formation of the chromosome fragments observed.

A number of *Hordeum* and *Triticum* species and varieties have now been intercrossed and cytological peculiarities have been reported for a number of these combinations. The hybridization of Chinese Spring by H. bulbosum is followed by a sequential elimination of chromosomes of the latter at a post zygotic stage (Barclay, 1975). At later stages such as mitotic metaphase in hybrids between H. vulgare cult. Manker \times T. turgidum, chromosomal instability is manifest as anaphase bridges, aberrant chromatid separation and finally somatic cells with chromosome numbers of 14, 16, 17, and 18 instead of the expected number of 21 (Mujeeb et al., 1978). And finally, abnormalities at gametogenesis such as those reported herein occur at still later stages.

Thus far, there are no reports of chromosome doubling in *Hordeum* × *Triticum* hybrids to produce fertile amphiploids. It is possible that the chromosomal instability described for the hybrid material may persist in the amphiploids, thus affecting gametogenesis and reducing fertility. In view of this possibility, a more practical approach to the transfer of alien loci between species may be the manipulation of meiotic pairing control genes to affect recombination followed by backcrossing and selection of desired traits rather than the production of the raw amphiploids.

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A very high frequency of nullisomics in selfed monosomic population for chromosome 3A of *T. aestivum* var. Pb. C 591

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Chlorophyll synthetic gene (s) CSG3A has been located on chromosome 3A of T. aestivum var. Pb. C 591 by Singh and Joshi (1979), on the basis of the observation that nullisomic albina seedlings occur only in the monosomic line for chromosome 3A.

An attempt was made to calculate frequencies of disomics, monosomics and nullisomics in this monosomic line of Pb. C 591. Three hundred to four hundred seeds, obtained from cytologically identified 3A monosomic plants, were grown every year in petri dishes. The number of green and albina seedlings were recorded for every plant progeny separately. Albina represented nullisomics (Singh and Joshi, 1979). All the green seedlings were transplanted in the field. At the time of maturity all the plants were harvested and threshed separately. The frequencies of disomics and monosomics were determined on the basis of segregating plant progenies for green and albina seedlings (only monosomic plants segregated). Data for eight years are given in Table 1.

Table 1. Frequencies of albina, monosomics and disomics in monosomic line 3A of Pb. C 591

	Seeds germinated	Albina	Monosomics	Disomics
1971	350	45	211	94
1972	350	41	217	92
1973	350	42	212	96
1974	350	39	218	93
1975	400	49	243	108
1976	350	46	213	91
1977	300	3 4	187	79
1978	400	47	238	115
Total	2850	343	1739	768
%		12.03	61, 02	26, 95

In all, two thousand eight hundred and fifty plants were sown during the span of eight years. It was observed that 343 were albina seedlings (12.03%) and 2507 were green plants which were transplanted in the field. Out of these 2507 plants, 1739 plants segregated for albina and green seedlings, representing monosomics and 768 produced only green seedlings representing disomics. Percentage for disomics, monosomics and nullisomics thus obtained was 27% (21)", 61% (20"+1') and 12% (20"), respectively.

Frequency of albina plants was calculated on a total of 19039 seedlings – 16754 were green and 2285 were albina seedlings. The overall frequency of albina was thus 12.00%.

Sears (1958) proposed a general model of breeding behaviour of monosomics. The frequencies proposed were disomics (21'')=24%, monosomics (20''+1')=73% and nullisomics (20'')=30%, when a normal monosomic plant is selfed. In the present data a very high frequency of nullisomics (12%), a marginal increase in disomics (27%) and significant reduction in the frequency of monosomics (61%) was observed as compared with the frequencies expected by Sears (1958).

The high frequency (12%) of nullisomics indicates that deficient male gamete functioned in about 18% of the cases as compared with a frequency of 4% that was observed, in general, by Sears (1958). Functional female gametes were transmitted with a frequency of 67%, while this was 75% as reported by Sears (loc. cit.). On the basis of this observation, the breeding behaviour of line monosomic for chromosome 3A in Pb. C 591 appears to be as proposed in Table 2.

Table 2. Breeding behaviour of monosomic 3A of var. Pb. C 591

	Male						
Female	21-chromosome 82%	pollen	20-chromosome 18%	pollen			
21-chromosome Eggs 33%	Disomics	27%	Monosomics	6%			
20-chromosome Eggs 67%	Monosomics	55%	Nullisomics	12%			

Total: Disomics (21")=27%

Monosomics (20"+1')=61%

Nullisomics (20")=12%

High transmission rate (18%) of deficient male gamete indicates lesser involvement of chromosome 3A in the post meiotic activities. Decrease in the transmission rate for the female gamete deficient for chromosome 3A suggests its greater involvement in prefertilization activities.

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Monosomic analysis of some morphological characters in wheat (*Triticum aestium* L. em. THELL)

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Introduction

Monosomic analysis was invented by Sears (1954) in wheat, to reduce the complexity of genetic analysis by reducing genetic duplication. This method has been employed for critical cytogenetic analysis in recent years. Dwarf plant stature of Mexican dwarf varieties which have wider adaptability is one of the important attributes of their excellency. Therefore, Allen et al. (1968) have stressed the need for a deeper understanding of the nature of inheritance of plant height.

Days to heading is a complex character in wheat and is dependent on several factors like date of sowing, day length, latitude and day and night temperature. Its nature of dominance is still controversial. Spike length is under the control of mostly additive genes while a few cytogenetic investigations are available with respect to tillering ability of plant. Therefore, cytogenetic analysis was carried out to investigate these complex characters whose results are presented in this paper.

Material and Methods

The material for the present study comprised of 19 of the possible 21 monosomic F_2 populations (except 1A and 4A), disomic population and the parents. Monosomic F_2 populations were derived from the cross of corresponding monosomic lines of Pb. C591 with UP. 301. The material was grown in a randomised block design with three replications, in Botany Garden, College of Agriculture, Dharwad during 1976 rabi season. A spacing of 25 cm \times 10 cm was given and a fertilizer dose of 100: 62.5: 37.5 kg of N, P_2O_5 and K_2O per hectare was supplied. Irrigation was given at 15 days interval till maturity.

Observations on plant height, spike length and number of tillers per plant were recorded at maturity. The day on which the basal most spikelet of the spike emerged from the boot leaf was taken as the date of heading from which days to heading was calculated.

Mean and standard error for each population were calculated. To detect the critical monosomic populations means of the monosomic populations were compared with the disomic mean by 'Z' test given by Sundararaj et al. (1972).

Results

Monosomic populations 7A, 3B, 3D, 4D and 7D registered significant reduction in plant

height indicating the presence of dwarfing genes on these chromosomes of UP 301. Three monosomic populations viz., 7A, 3D and 7D were earlier than disomic population while monosomic population 5A was significantly late (Table 1).

Eight monosomic populations showed significant deviation from the disomic mean. Of these, populations monosomic for 2B and 4B had longer spike length whereas populations 1B, 3A, 3B, 3D, 5B and 7D had shorter spike length as compared to disomic mean. With regard to number of tillers per plant, monosomic populations 3D and 4D showed fewer tillers than disome, while populations 2B, 7B and 6D had more tillers (Table 2).

Table 1.	Means of monosomic and disomic F ₂ populations and parents
	with respect to plant height and days to heading

Population	Plant height (cm)	Days to heading
1B	78,66±1,27	73, 42±1, 23
1D	77.07 ± 1.72	73.26 ± 1.55
2A	79.36 ± 1.91	73.73 ± 1.39
2 B	81.91±1.30	76.75 ± 1.24
2 .D	79.05 ± 1.60	$76,31\pm1,55$
3A	76.09 ± 1.12	$73,61\pm0,99$
3B	72,49±1,83**	73.50 ± 1.93
3 D	73.48±1.27**	$69.72 \pm 1.17**$
4B	$78,10\pm1,18$	75.55 ± 1.20
4D	75.29±1.08*	73.94 ± 1.07
5A	78.68 ± 1.38	$79.38\pm1.22**$
5 B	77,73±1,33	$71,25\pm1,31$
5 D	81, 31±1, 38	76.71±1.11
6A	78,77±2,05	73.77 ± 1.61
6B	78, 69±4, 1i	74.91 ± 1.90
6D	76.37±1.36	74.67 ± 1.25
7 A	74.48±1.02**	69.73±0.93***
7 B	75.56 \pm 1.20	75.73 ± 1.26
7 D	74.89±1.42*	68,94±1,41**
Disome	78.33 ± 1.03	73.94 ± 0.94
Pb. C591	94,56±0,88	77.79 ± 0.55
UP 301	55.05 ± 0.45	$61,03\pm0,30$

^{*} Significant at 5 per cent level

Discussion

Genetic investigations of plant height in wheat are numerous but not conclusive. Plant height has been reported to be under polygenic control with innumerable modifiers (Allan and Vogel, 1963 and Allan et al., 1968). Cytogenetic investigations have led to the location of genes affecting plant height on almost all chromosomes in one or the other variety. Sears (1954) identified homoeologous groups I, II, III, IV and 6A possessing genes for plant height determination in Chinese Spring. Chromosomes 2A and 4D of Sonora-64 and chromosome 6D of Lerma Rojo have been identified carrying genes for dwarfness (Jea and Swaminathan, 1969). But Bhowal (1970) using Cadet monosomic series found 15 chromosomes (i.e, 1A, 1B, 5A, 5D, 6A, 7A and homoeologus groups II, III and IV)

^{**} Significant at 1 per cent level

Table 2. Mean spike length and number of tillers per plant of monosomic and disomic F_a populations and parents

Population	Spike length (cm)	Number of tillers per plant		
1B	9.41±0.11*	15.82 ± 0.69		
1D	9.74 ± 0.17	12,65 \pm 0,96		
2A	10.02 ± 0.14	$14,88\pm0.83$		
2B	10.22 ± 0.16 *	17, 11 ±1, 13*		
2 D	9.94 ± 0.14	16.90 ± 1.08		
3A	9.45±0.10*	14.62 ± 0.57		
3B	8.95±0.19**	$13,66\pm1,35$		
3D	$9.04\pm0.17**$	12 , 09±0, 75**		
4B	$10.20\pm0.14*$	16.62 ± 0.87		
4D	9.68 ± 0.14	$10.02\pm0.78**$		
5A	9.93 ± 0.14	15.64 ± 0.95		
5B	9.36±0.14*	14.95 ± 0.87		
5D	10.14±0.14	13.33 ± 0.76		
6A	9.92 ± 0.22	14.65 ± 1.07		
6B	10.02 ± 0.24	15.36 ± 1.08		
5 D	9.64±0.17	17.54±0.93**		
7A	9.63±0.10	14.01 ± 0.48		
7 B	9.95±0.13	18, 13±0, 89**		
7 D	9. 2 8±0. 14**	$13,01\pm0,77$		
Disome	9.80 ± 0.12	14.66 ± 0.53		
Pb. C 591	8.80±0.09	17.81±1.28		
UP 301	9.48 ± 0.09	11, 17 ± 0.47		

^{*, **} indicate significent deviation at 5 per cent and 1 per cent levels respectively

affecting plant height in Sonora-64. Sadananda (1976) associated a gene for dwarfness with chromosome 3D of Sharbati Sonora. Thus all the genes for dwarfness identified in the present study, except the one on 7D, were identified in Sonora-64 which very well agrees with the evolution of UP 301 from the cross between Lerma Rojo and Sonora-64. However, the major dwarfing genes identified in Lerma Rojo and Sonora-64 (Jha and Swamina-Than, 1969) except the one on chromosome 4D, were not identified in the present combinations. There is no report of a gene on chromosome 7D affecting plant height. But other two members of the homoeologous group VII (namely 7A and 7B) have been known to carry genes affecting plant height (Bhowal, 1970; Halloran, 1974 and Sadananda, 1976). Thus the identification of a dwarfing gene on chromosome 7D of UP 301 again demonstrates the functional relationship between the members of the homoeologous group.

Days to heading is under polygenic control with additive gene action (Paroda et al., 1972). In the present study, monosomic populations 7A, 3D and 7D were early indicating the presence of genes for earliness on these chromosomes of UP 301. The presence of a gene for lateness on 5A was expressed by delayed heading of 5A monosomic population. Chromosome 7D carrying a factor for earliness has been reported by Driscoll and Jensen (1964). As UP 301 is derived from a cross involving Sonora-64, the identification a gene for earliness on chromosome 3D of UP 301 supports the view of Pirasteh and Welsh (1975) who suspected chromosome 3D of Sonora-64 to carry a gene for earliness. The association

of a gene for earliness with chromosome 7A of UP 301 also agrees with the findings of Bozzini and Giorgi (1971). The gene for late heading identified in the present study is also reported by Driscoll and Jensen (1964) and by Law et al. (1976).

Spike length is predominantly controlled by polygenes with additive gene action (Johnson et al., 1966 and Kosnev and Bares, 1975). The disomic F₂ population exhibited longer spike length than either of the parents. This may be because of the complex interaction of the genes controlling this character. Monosomic populations 2B and 4B had longer spike length as compared to disomic mean indicating the presence of gene(s) increasing spike length on these chromosomes of UP 301. Whereas monosomic populations 1B, 3A, 3B, 3D, 5B and 7D were found to carry genes for reduced spike length. The chromosomes of A and B genomes which have been identified in the present study to carry factors affecting spike length were also reported by Bozzini and Giorgi (1971) in Triticum durum variety Capeti. In Sonora-64 chromosomes 3B, 4D and 5D decreased spike length (Sharma and Bhowal, 1973) of which only one gene on 3B was identified in the present cross combination. Kosnev and Bares (1975) associated genes for short spike to chromosomes 3A and 4B. The present study agreed with the results obtained by Kosnev and Bares (1975) with respect to chromosome 3A which was associated with short spike, but differed with respect to chromosome 4B which is found to carry a gene for increased spike length.

Number of tillers per plant shows low heritability (Panigrahi, 1962 and Selim, 1963). Atleast five genes controlled tillering ability differences between Pb. C591 and UP 301. Monosomic populations 3D and 4D had genes for low tiller number per plant, while 2B, 6D and 7B had genes with opposite effects.

In the variety Chinese Spring, chromosomes 2B, 3D (SEARS, 1954) and 7B (LAW, 1967) have been associated with high tillering ability. The present study agreed with respect to 2B and 7B, but showed opposite effect for 3D.

Thus, chromosome 3D of UP 301 seems to carry many desirable genes affecting morphological characters.

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Thirtyfive-chromosome plants obtained by successive deletion of A-genome chromosomes from common wheat

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In the process of successive deletion of A-genome chromosomes from Chinese Spring wheat by using nullisomic lines (Mochizuki and Shigenaga 1964), three kinds of sextuple monosomics were crossed with the seventh nullisomics for obtaining the septuple monosomic, that is a pentaploid plant (2n=35, 14''+7', ABBDD). Five 35-chromosome plants could be cytological selected in the F_1 (Table 1 and Table 2).

Table 1. Fertility of three cross combinations between sextuple monosomics and nullisomics of Chinese Spring wheat, and germination of the F_1 seeds

Cross	Florets pollinated	Seed set (%)	Seeds sown	Germination (%)
$\begin{array}{l} m1Am2Am4Am5Am6Am7A\times n3A\\ m1Am2Am3Am4Am5Am6A\times n7A\\ m1Am2Am3Am4Am6Am7A\times n5A \end{array}$	410	59. 5	244	76. 2
	808	31. 8	257	81. 7
	494	64. 3	328	90. 2

Table 2. Number of plants with different chromosome numbers in the F_1 of the three crosses between sextuple monosomics and nullisomics of Chinese Spring wheat

0	Chromosome numbers								
Cross	35	36	37	38	39	40	41	54	Total
$\begin{array}{l} m1Am2Am4Am5Am6Am7A\times n3A\\ m1Am2Am3Am4Am5Am6A\times n7A\\ m1Am2Am3Am4Am6Am7A\times n5A \end{array}$	2 1 2	18 12 35	43 49 85	49 69 89	42 53 58	24 21 17	7 5 10	1	186 210 296
Total	5	65	177	207	1.53	62	22	1	692

Each hypoaneuploid dealt with in the present paper is symbolized for brevity by the letter m and n, indicating the monosomic and nullisomic condition, respectively, followed by the designation of the chromosome for which it is deficient, as was done in the previous papers (Shigenaga 1968a, b, and 1976). For exmaple a nulli-3A plant and a plant sextuply monosomic for chromosome 1A, 2A, 4A, 5A, 6A and 7A were designated as n3A and m1Am2Am4Am5Am6Am7A, respectively.

Two 35-chromosome plants obtained from the cross between m1Am2Am4Am5Am 6Am7A and n3A, and a 35-chromosome plant from the cross between m1Am2Am3Am4Am 6Am7A and n5A grew well. The former two were designated in this paper as Plant No. 1

and Plant No. 2, respectively, and the latter as Plant No. 3. Other 35-chromosome plants died as seedlings.

The chromosome configurations, however, were unexpectedly 15''+5' in both Plant No. 1 and Plant No. 2, and 1'''+13''+6' in Plant No. 3 (Fig. 1). No other configurations than the above in each plant were observed and most bivalents were of the closed type. Trivalents involved in Plant No. 3 were also closely associated and formed figure in the shape of V.

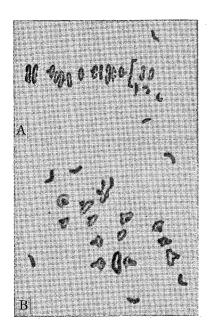


Fig. 1. First meiotic metaphase plate
A: 15"+5' in Plant No. 1
B: 1"'+13"+6' in Plant No. 3

Accordingly, plant No. 1 and No. 2 are considered to have the same chromosome constitution which is quintuply monosomic for A-genome chromosomes, nullisomic for another chromosome of the same genome and disomic for all other chromosomes of common wheat. Plant No. 3 should be considered as the aneuploid which is sextuply monosomic for A-genome chromosomes, nullisomic for another chromosome of the same genome, trisomic for a chromosome of B- or D-genome and disomic for all other chromosomes.

Some morphological characteristics at maturity are shown in Table 3. In Plant No. 1 and No. 2 all spikes were pollinated with normal disomic pollen. Rather large number of seeds set in these plants shows that they had enough function in fertilization in their female organs. On the other hand all spikes of Plant No. 3 were self-pollinated. Its smaller number of seeds obtained is attributable to poor function of male gamete in consideration with the score of 36.6 per cent of stainable pollen in this plant.

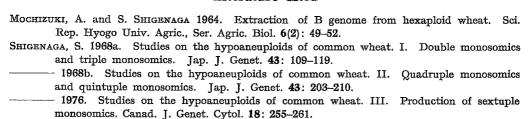
The 35-chromosome plants obtained in the present experiment are considered to be originated from occasional fertilization of pollen which has unusual chromosome constitution resulted from pairing failure of homologous chromosomes or non-disjunction in meiosis of nullisomics used in the cross.

Table 3. Some morphological characteristics at maturity of three 35-chromosome plants in Chinese Spring wheat

Plant	Chromosome configuration at MI in meiosis	Plant height (cm)	No. tillers	No. seeds obtained
No. 1	15"+5'	100	12	135*
No. 2	15"+5'	110	27	396*
No. 3	1"'+13"+6'	81	29	23**

^{*} By pollination with normal disomic pollen

Literature Cited



^{**} By self-pollination

A line with a deletion on the long arm of chromosome 6B isolated in *Triticum aestivum* cv. Chinese Spring.

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A wide range of aneuploid lines, nullisomics, monosomics, telosomics, isosomics, trisomics, tetrasomics and nulli-tetrasomics compensating stocks have been developed in *T. aestivum* cv. Chinese Spring by SEARS (1954). Other aneuploids and naeuploid derivatives involving other varieties have been intensively searched during the past 25 years.

So far, homozygous deletions which might be exstremely useful for genetic analyses, either have not been sought, or have been overlooked for various reasons. However, an interstitial and small deletion involving the *Ph* gene located on the long arm of chromosome 5B seems to have occurred following radiation treatment both in bread (Sears, 1977) and in *durum* wheat (Giorgi, 1978).

In a routinary work based on chromosome counting of monosomic lines of Chinese Spring a spontaneous heterozygous deletion involving the long arm of chromosome 6B was noticed. It was easily recognizable because such a deletion deals with a statellited chromosome in which about 2/3 of the long arm is lacking. In the progeny of a selfed heterozygote plant, 3 out of 18 carrying deletion homozygote plants were recovered. All of them have spikes with shrot awans just like CS ditelo 6BS.

Morphologically this lines (henceforth called CS Df 6BL) is quite similar to the ditelo 6BS, being however a little more vigorous. Yield and yield components of this line, CS

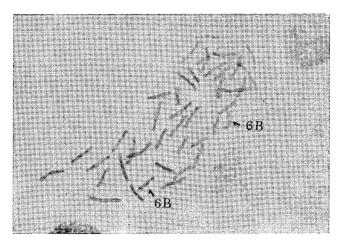


Fig. 1

ditelo 6BS, CS ditelo 6BL and Chinese Spring euploid were analyzed and compared in a field experimental based upon a single plant randomisation.

The results reported in Table 1 show that the absence of the distal part of the 6B long chromosome arm affects as much severely the overall growth as the lack of the entire long arm.

Table 1. Means and standard deviation of aneuploids lines lacking different regions of chromosome 6B as compared to the euploid Chinese Spring

Lines	Numbers of plants analyzed	Ear-emer- gence time	Tiller number	Plant height (cm.)	yield per plant (gr.)	100 grain weight (gr.)
Chinese Spring	25	10, 5, 77	4, 2 ±1, 10	110±10.5	5.5±1.21	3.3±1.06
CSDT 6BL	26	10.5.77	4.3 ± 1.08	95± 9.7	3.2 ± 1.03	2.5±0.94
CSDf 6BL	21	13, 5, 77	3.4 ± 1.05	75± 6.3	2.0 ± 0.90	2.1 ± 0.72
CSDT 6BS	24	14. 5. 77	3.0 ± 1.02	73± 7.1	1.7 ± 0.75	1.8±0.71

The presence of awns in the spikes of CS Df 6BL proves that the awn inhibitor B2 must be located in the distal part of the long arm of the chromosome 6B.

In addition, the above cytologically marked lines show a different picture as to types, structure and distribution of cuticolar waxes.

This is an interesting aspect which deserves further investigation.

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Selective gametocidal action of a chromosome of Aegilops cylindrica in a cultivar of common wheat*

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Preferential transmission of alien chromosomes has been reported in some alien chromosome addition (or substitution) lines of common wheat which had a certain chromosome derived from Aegilops species, such as Ae. triuncialis (2n=28, CCC^uC^u), synthetic triuncialis (2n=28 CCC^uC^u), Ae. caudata (2n=14, CC), Ae. longissima (2n=14, S^lS^l), and Ae. sharonensis (2n=14, S^lS^l) (Endo and Tsunewaki 1975, Endo and Katayama 1978, Maan 1975). The preferential transmission of those Aegilops chromosomes was proved to be caused by selective fertilization or selective gametocidality in those addition lines, and the presence of the monosomic Aegilops chromosome itself was responsible for the selective gametocidality: Gametophytes to which a certain Aegilops chromosome was not distributed became difficult (or impossible in some cases) to develop normally, and those carrying the critical chromosome developed successfully into normal gametes. As the selective gametocidal action was effective on microspores as well as megaspores, self-pollination of the monosomic addition line gave rise to mostly disomic addition plants, which consequentially showed normal fertility. It was also demonstrated that differences in cytoplasm does not affect the selective gametocidal action.

A chromosome of Ae. cylindrica (2n=28, CCDD) was found to be selectively retained in some cytoplasm substitution lines of common wheat. An F_1 hybrid between Ae. cylindrica as female and a common wheat variety was repeatedly backcrossed to various kinds of common wheat in order to produce various cytoplasm substitution lines with different nuclei of common wheat. One of them, which had been backcrossed five times to a common wheat cultivar, Triticum aestivum cv. Jones Fife, was noticed to produce plants aberrant in appearance. The line was found to include in the chromosome complement a chromosome with a subterminal centromere which was suggested to be derived from Ae. cylindrica, since common wheat has no chromosome of that type. This line had a poor seed-set in every backcross generation, which indicated a relationship between partial fertility and selective retention of this cylindrica chromosome.

The *cylindrica* chromosome was then transferred into a background of normal cytoplasm by reverse backcross to Jones Fife, using the cytoplasm substitution line as the pollen parent (this line has partial pollen fertility).

A plant with 2n=43 was selected and crossed with Jones Fife's pollen or self-pollinated, producing 2n=43 plants and 2n=44 plants from the cross and selfing, respectively. The

^{*} The work was supported in part by a Grant-in-Aid (No. 476005) from the Ministry of Education, Japan.

2n=43 plants had this *cylindrica* chromosome and a meiotic configuration of 21"+1' (Fig. 1A). The 2n=44 plants had two such chromosomes and showed 22" at MI. In both addition lines, however, the chromosome pairing at MI was unstable, thus producing a trivalent and quadrivalent in some PMC's (Fig. 1B). The *cylindrica* chromosome may have had some effect on homoeologous pairing.

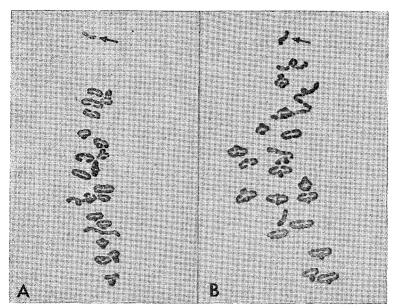


Fig. 1. MI configurations of the monosomic cylindrica chromosome addition line of Jones Fife: A, 21"+1'; B, 1^{iv}+1"'+17"+2'. The univalent shown with an arrow is supposed to be the cylindrica chromosome.

The plants of the monosomic addition line and the disomic addition line both showed very characteristic appearances. They had rather shorter culms and selenderer spikes. This aberration was evidently caused solely by the added *cylindrica* chromosome(s).

Table 1 shows the effects of the added cylindrica chromosome (or chromosomes) on the fertility of Jones Fife. The monosomic addition line set a few plump seeds and many aborted ones on a spike by either artificial pollination or self-pollination. The aborted seeds were flattened and seemed to have no embryo and endosperm; they did not germinate at all. Therefore, the seed-set ratios of viable seeds (plump ones) were only 14.9% (23 seeds set out of 154 florets) by crossing and 12.3% (37 out of 300) by selfing. The pollen fertility of the monosomic addition line on the other hand was almost normal in appearance. In contrast, the disomic addition plants had a nearly normal fertility of both sexes. They set seeds in 76.9% of florets by crossing (20 out of 26) and 81.7% of florets by selfing (98 out of 120). They did not produced aborted seeds. In short, the monosomic addition of the cylindrica chromosome to Jones Fife reduced the seed fertility strikingly, while disomic addition of that chromosome exerted no effect on the fertility of Jones Fife.

Table 1. Effects of the addition of the monosomic or disomic cylindrica chromosomes on the fertility of Jones Fife

Addition	Pollen fert. (%)	Crossed seed fertility*		Selfed seed fertility*	
		No. florets pollinated	No. seeds set (%)	No. florets examined	No. seeds set (%)
Monosomic Disomic	94 99	154 26	23 (14, 9) 20 (76, 9)	300 1 20	37 (12, 3) 98 (81, 7)

^{*} The 1st and 2nd florets of the middle spikelets of a spike were used for the study.

In respect to transmission of the *cylindrica* chromosome, chromosome constitutions of the viable offspring of the monosomic addition line were examined, and the results are given in Table 2. All the offspring except three (16 plants) had 2n=43 chromosomes which included the *cylindrica* chromosome when the monosomic addition line was crossed as female with normal Jones Fife. One of the two plants with unexpected chromosome constitutions had 2n=42 chromosomes including the *cylindrica* chromosome, and the other had 41 whole chromosomes and a small telocentric one. Therefore, the *cylindrica* chromosome was confirmed to be transmitted to 17 plants out of 19.

When the monosomic addition line was self-pollinated, almost all offspring (20 out of 22) were disomic addition plants with 2n=44 chromosomes including a pair of the *cylindrica* chromosomes. One of the unexpected chromosome constitutions was 2n=45 including a pair of the *cylindrica* chromosomes, and the other was 2n=44 including two *cylindrica* chromosomes plus an aberrant chromosome with a subterminal centromere which was smaller than the *cylindrica* chromosome.

Table 2. Chromosome constitutions of the offspring obtained from crossand self-pollination of the monosomic *cylindrica* chromosome addition line of Jones Fife

0.4	No. plants having 2n=				
Offspring	42	43	44	unexpected	
21"+1'(우)×21"(含) 21"+1' self	1 0	16 0		2 2	

Note: Chromosome complements of 2n=43 and 2n=44 plants included one and two *cylindrica* chromosomes, respectively.

The results shown in Table 2 suggested that the *cylindrica* chromosome had been transmitted exclusively through egg cells and pollen. The unexpected chromosome constitution might have originated from the unstable chromosome pairing of the monosomic addition line.

The above-mentioned results on fertility and chromosome constitution indicated a mechanism for the selective retention of the *cylindrica* chromosome in the *cytoplasm* substitution line of Jones Fife having the *cylindrica* cytoplasm. When the *clyindrica*

chromosome exists in a monosomic condition in Jones Fife, female gametes to which the *cylindrica* chromosome is not distributed will not be successfully fertilized, and only those carrying that chromosome will be fertilized. This selective fertilization (or sterilization) was proved to be caused by the *cylindrica* chromosome by itself, not by an interaction between the *cylindrica* chromosome and the *cylindrica* cytoplasm. Although the aborted seeds produced in the monosomic addition line were supposed to originate mostly from egg cells lacking the *cylindrica* chromosome, the presence of the *cylindrica* chromosome in zygotes would not offer a sufficient condition for their normal development; because among the offspring obtained from self-pollination of the monosomic addition plants were found no viable 2n=43 plants that would have received the *cylindrica* chromosome through pollen. Therefore, it follows that egg cells lacking the *cylindrica* chromosome were defective; they were not fertilized at all or unsuccessfully fertilized to develop into abortive seeds.

Selective fertilization was also seen on the male side. It is evedent from the chromsome constitutions of the selfed-offspring of the monosomoic addition line (see Table 2) that the pollen carrying the *cylindrica* chromosome exclusively took plart in the fertilization. It could not be ascertained whether or not the pollen grains lacking the *cylindrica* chromosome had lost its function; they may have been functioning, but just unable to compete in certation with those carrying the *cylindrica* chromosome.

Thus the *cylindrica* chromosome was demonstrated to be selectively transmitted to the next generations in Jones Fife through both egg cells and pollen, and, at least on the female side, it had selective gametocidal action which is independent of the *cylindrica* cytoplasm. The selective gametocidal action of the *cylindrica* chromosome, however, turned out to be dependent on the kind of common wheat into which the chromosome was introduced. The *cylindrica* chromosome in hybrids between Jones Fife and some kinds of common wheat (e. g., cv. Chinese Spring) lost its function and was quickly eliminated in the following generations.

Genome analysis demonstrated that Ae. cylindrica is an amphidiploid with C genome from Ae. caudata and D genome from Ae. squarrosa (2n=14, DD) (Kihara 1949). As the D genome of Ae. squarrosa has no chromosome with a subterminal centromere, the cylindrica chromosome is supposed to have derived from the C genome of Ae. caudata in which three pairs of chromosomes with subterminal centromeres are included, one of which is very similar to the cylindrica chromosome (Chennaveeralah 1960).

The selective gametocidal chromosomes of Ae. triuncialis and of synthetic triuncialis were revealed to be almost the same as those of Ae. caudata in their morphology, pairing homology, selective gametocidality, and effects on plant growth (unpublished data). The cylindrica chromosome, however, was found to be different from the foregoing three chromosomes in some respects: A characteristic appearance and many aborted seeds distinguished the plants with cylindrica chromosome from the others having the caudata chromosome and others; the centromere of the cylindrica chromosome is not so extremely subterminal as those of the caudata chromosome and others; the selective gametocidal action of the cylindrica chromosome is not effective in the kinds of common wheat that the caudata chromosome

and others exert their action in. In respect of the selective gametocidal chromosome, therefore, the C genome of Ae. cylindrica is farther differentiated from that of Ae. caudata than that of Ae. triuncialis is.

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Rapid method of transferring alien genetic variation to wheat by substitution and recombination

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The related genera of bread wheat (T. sestivum L.) such as Aegilops, Agropyron and Secale have many genetic attributes of agricultural potential, specially disease resistance. A few method, such as, amphidiploidy, alien addition, induced translocation, alien recombination and alien substitution have been employed to introduce genetic variation to wheat. Amongst these there are rare reports of application of last two methods in India and many other countries excepting a few European and North American countries. Long procedure involved in these two methods and also non-availability of monosomic lines in suitable background may be limiting factors. In this Institute we are following two modified methods for alien chromosome substitution and alien recombination. The methods essentially involve the introduction of alien material in partially developed monosomic lines instead of waiting till the monosomic lines are fully developed in a variety. By following these methods, we expect to cut short the standard long procedures substantially. It will also be possible to develop the alien substitution and recombination lines in any sutiable

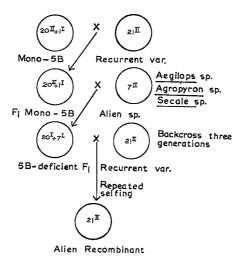


Fig. 1 Schematic presentation of the procedure for inducing alien recombination in absence of 5B

background desired. The methods are birefly described and schematically presented (Figs. 1 & 2).

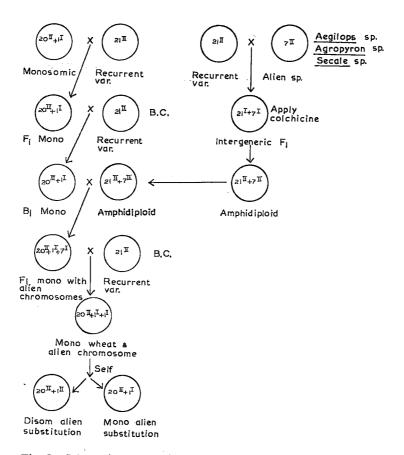


Fig. 2. Schematic presentation of the procedure for producing alien substitution lines

I. Alien recombination

- 1. Cross the recurrent variety with mono-5B of Chinese Spring.
- 2. Identify F₁ mono-5B and cross with the desired alien species (from Aegilops, Agropyron, Secale etc.).
- 3. Select 5B- deficient 27-chromosome hybrid. In absence of chromosome 5B pairing between wheat and alien chromosomes would take place leading to recombination. Backcross with the recurrent variety for at least three generations.
- 4. Self the last back-cross progeny, Select the fertile 2n=42 chromosomes derivatives. The selfed progeny is expected to have many alien recombinants in the recurrent variety.

II. Alien Chromosome substitution

- Corss the recurrent variety as male with the monosomic lines of Chinese Spring.
 Also cross the variety with the desired alien species of Aegilops, Agropyron or Secale.
- 2. Identify F_1 monosomics (2n-1=41) and back cross them as female with recurrent variety. Grow intergeneric F_1 and apply colchicine to induce amphidiploids, (2n=56).
- 3. Select B_1 monosomics from the backcross progenies and cross them as female with amphidiploid.
- 4. Identify the F_1 monosomics with the alien chromosomes having the chromosome constitution, $20^{11}+1^1+7^1$. Back cross them with recurrent variety.
- 5. Grow the back cross progenies. Identify plants which are simultaneously monosomic for a specific wheat chromosome and an alien chromosome (20^{II}+1^I+1^I) and self them.
- 6. Screan the selfed progenies for alien monosomic (20^{II}+1^I) and disomic (20^{II}+1^{II}) substitutions.

In the alien chromosome substitutions initially developed following the proposed scheme it will not be known which of the foreign chromosomes has substituted a specific wheat chromosome, unless there are some cytological or genetical markes. However, the alien chromosomes can be identified by applying some cytological technique.

Behrain, a semi-dwarf spring rye

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In recent years with the development of fertile hexaploid triticale lines, capable of giving high yield, the need for height reduction has become very important. The reduction in plant height of hexaploid triticale was first achieved by Dr. N.E. Borlaug through incorporating the Norin-10 genes from wheat (Zillinsky and Alfonso 1973). In rye a shrot statured line Snoopy was reported but its use in the triticale breeding programme remained limited mainly due to its poor performance particularly late maturity and susceptibility to disease (Zillinsky and Alfonso 1973). A dominant factor for short straw spontaneous mutant EMI was reported in Vytaka X Kung II (Kobylyanskii 1972), and another dwarfing source of winter rye UC-90 was reported by Gustafson et al. (1973). The present source of height, reduction being discussed here was isolated from a population of spring rye endemic to district of Swat in North West Frontier Province of Pakistan.

Materials and Methods

Netherland Pakistan Germaplasm Expedition to the districts of Chitral and Swat, Pakistan was organised during 1976. Rye mixture was quite common in most of the wheat samples collected from these places. However accession NPE 120 collected from Behrain located at an altitude of 1510 metres showed predominance of rye seeds in wheat. The seeds from this sample were sown at Nuclear Institute for Agriculture and Biology, during November, 1976. Data on individual plant basis for plant height, spike and grain characters were recorded at maturity in this population.

Results and Discussion

The plant height of 124 rye plants raised from accession NPE 120 ranged from 98 cm to 168 cm showing a normal distribution (Fig. 1). The semi-dwarf plants were stout and showed resistance against lodging. The semi-dwarf plants whose height ranged from 98 cm to 113 cm. on an average had 20 gm 1000 grain weight as compared to the normal height plants whose average 1000 grain weight was 25 gm. Similarly the difference in spike length was also obvious. The average spike length of the semi-dwarf plants was 10.5 cm as compared to the tall plants (15.0 cm). The seed colour ranged from amber to dark showing a large variation for this character in both the semi-dwarf and tall growing populations.

Next year separate populations comprised of only semi-dwarf and mixture of semi-dwarf and tall plants will be raised in isolation and lines with different height levels and

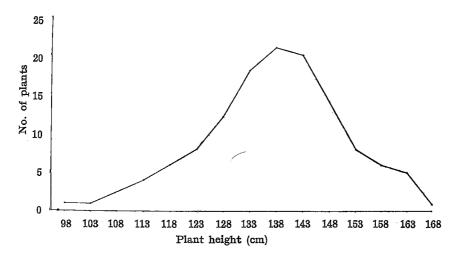


Fig. 1. Frequency distribution of plant height of rye plants in the compsite sample NPE 120

grain colour will be extracted. The short statured rye Behrain, may serve as a new source of height reduction in triticale and rye breeding programmes.

The seed is available for distribution to the interested breeders on request.

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Amber grained and awned mutations in wheat variety, Yaqui-50

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A spring wheat variety Yaqui-50 has been maintaining resistance to wheat rusts for more than 50 years, as reported by CIMMYT, Mexico. For conducting an irradiation experiment, seeds of this variety were obtained from Dr. Raja RAM, CIMMYT, Mexico. This variety is tall, has red kernels and is awnless.

Five hundred seeds of Yaqui-50 were irradiated with 30 kR of gamma rays. After irradiation the seeds were planted in the field. In the M₁ many chimeras were observed. Fortyfour spikes were observed to be hetero-spelta type and 4 spikes showed homospelta characteristics. Some spikes had spelta type of earhead with awns. No chlorophyll mutations were detected.

To raise M₂ population, first two tillers were taken from all the M₁ plants. Individual spike progenies were sown separately. In the M₂ population no detectable chlorophyll deficient mutations were observed indicating that Yaqui-50 may have tetrasomic or hexasomic conditions for chlorophyll synthesis. In all, 3562 plants were screened for isolating amber seeds and awn character. Seven amber seeded and awnless plants were isolated, which were observed in seven different progenies. Eight plants were observed with fully developed awns. Out of these, 6 plants with fully developed awns were from one spike progeny. One plant was observed with amber seeds and fully developed awns.

Amber mutants in wheat have been isolated by JAIN et al. (1970) BANSAL et al. (1972) in M₁ generation. VARUGHESE and SWAMINATHAN (1967) found amber mutants in M₂ generation in the material studied by them.

In the present study no amber mutant was detected in M_1 generation. In M_2 the frequency of amber and awned mutants was found to be comparable.

Normal square head spike in T. aestivum is due to the suppression effect of gene (QQ) located on chromosome 5A. In the absence of one chromosome of 5A the spike is spleta suggesting that Q locus is hemizygous ineffective. The F_1 chimeras in the present study resemble chromosome 5A deficient spikes. It indicates that one of the 5A chromosome or part of it, where Q locus is situated, got deleted by gamma rays, since the frequency of spelta forming spike is very high. It suggests that physical mutagens, in most of the cases, produce changes by deletion or translocation or due to the loss of full chromosome.

A very high frequency of amber and awned mutants in Yaqui-50 suggests that both these terminally located genes get deleted from the chromosome with a very high frequency which

leads to the production of amber mutants, awned mutants and amber and awned mutants.

On the basis of comparable frequencies of amber awnless and red awned mutants (terminally located) in the M₂ generation, it may be postulated that all the genes which are terminally located, can get deleted by physical mutagens in equal proportions. To test this hypothesis work is under progress which will be published elsewhere.

Yield performance of amber awnless, red awned and amber awned mutants of Yaqui-50 as compared to the parent variety is yet to be tested. Seeds of these mutants are available for distribution.

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Correlation and path coefficient analysis of yield components in mutants of *Triticum aestivum*

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Complex character such as grain yield is polygenic (Bhatt, 1973; Dewey and Lu, 1959; Larik, 1978) and is greatly influenced by environmental factors (Kheradnam and Niknejad, 1974). Adequate knowledge of interrelationship of factors influencing such complex character is essential for designing an effective plant breeding programme (Worley et al., 1976). Studies of correlations of agronomic and morphological characters are helpful in the identification of the components of a complex character such as yield but they do not provide precise information on the relative importance of direct and indirect influences of each of the componential characters (Larik, 1978). Thus with increasing number of variables it becomes essential to measure the contribution of various variables to the observed correlation and to partition the correlation coefficient into components of direct and indirect effects (Pandey and Gitton, 1975).

Path coefficient analysis provide an effective means of partitioning correlation coefficients into unidirectional pathway and alternate pathways. The analysis thus permits a critical examination of specific factors that produce a given correlation and can be successfully employed in formulating an effective selection strategy. The technique of path coefficient analysis developed by Wright (1921) has been extensively used by conventional breeders (Bhatt, 1973; Jain et al., 1975; Lyrene and Shands, 1975) and most probably is being employed first time by a mutation breeder. The present paper elucidates the interrelationship of factors influencing grain yield of the mutants isolated at this University through path coefficient analysis.

Material and Methods

The material originated from the gamma rays and ethyle methane sulphonate (EMS) treatments of three cultivars C-591 (Locally bred), Nayab and Indus-66 (Meixcan origin) of bread wheat *Triticum aestivum* (2n=6x=AABBDD=42). Fifteen phenotypically stable mutants classified on the basis of grain yield in M₉ generation (Table 1) and three mother cultivars were grown during Rabi 1977-78 in a randomized block design with four replications at Sind Agricultural University, Tandojam, Pakistan. Homogeneous seeds of these mutants and cultivars was drilled in single row each 300.5 cm long with 30.5 cm row to row and plant to plant distance. The data were collected on 10 randomly selected plants in each replication for four quantitative traits. Thus 40 plants were studied from

Table 1. Mean yield (g/plot) of mutant strains and their respective control strains

Sr. No.	Strain No.	Strain/treatment/origin	Mean yield (g/plot)
1	32	Nayab (Control)	455, 00
2	1.0	" 20kR	358, 40
3	44	" 25kR	605.50**
4	40	" 30kR	520, 81
5	27	" 35kR	465, 10
6	43	C-591 (Control)	430,00
7	38	" EMS 7hr	440.00
8	7	" EMS 7hr	425, 80
9	28	" EMS 7hr	390,00*
10	45	" EMS 3 1/2hr	400.00
1 .1	14	" EMS 7hr	450,00
12	20	" 20kR	375, 00
13	11	" 30kR	395,00
14	2	Indus-66 (Control)	410.74
15	13	" 20kR	300.50**
16	37	" 20kR	350,00*
17	39	" 20kR	491.00
18	5	" 25kR	510.40

^{*, **:} Mutant strains significantly different from respective control strains (P≥.05 and .01 respectively) by L.S.D. method.

each mutant and mean values of each mutant were used for calculating phenotypic correlations which were partitioned into path coefficients using the technique outlined by Dewey and Lu (1959). This technique involves partitioning of correlation coefficients to determine direct (unidirectional pathways 'p') and indirect influences through alternate pathways (pathways 'p' × correlation coefficient 'r') of various variables and grain yield. Grain yield was considered as the resultant variable. The path coefficients were calculated through the solution of the following equations.

- 1. $r_{14} = r_{11}p_{14} + r_{12}p_{24} + r_{18}r_{84}$
- 2. $r_{24} = r_{12}p_{14} + r_{22}p_{24} + r_{23}p_{34}$
- 3. $r_{84} = r_{18}p_{14} + r_{23}p_{24} + r_{88}p_{84}$
- 4. $p_{\times 4} = \sqrt{1 (p_{14}^2 + p_{24}^2 + p_{34}^2 + 2p_{14}p_{24}r_{12} + 2p_{14}p_{34}r_{18} + 2p_{24}p_{34}r_{23})}$

Results and Discussion

Simple correlation coefficients (phenotypic) between all possible combinations of four quantitative traits were estimated (Table 2). Results reveal that grain yield per plant exhibited a strong positive correlation (P \geq .01) with tiller number per plant and seeds per spike. The correlations reported by Bhatt (1973), Virk and Verma (1972) and Larik (1978) also revealed similar associations. Seeds per spike were positively correlated (P \geq .05) with spike length but negatively correlated with tiller number per plant. However, negative correlation of seeds per spike with tiller number per plant did not reach the significance level.

Table 2. Phenotypic correlation coefficients among all possible combinations of four different quantitative characters

du

ha wl m Pi

Characters correlated	Tiller number per plant (1)	Spike length (2)	Seeds per spike (3)	Crain yield (4)
Tiller number per plant Spike length Seeds per spike Grain yield	1.000	0.0531 1.000	-0.0364 0.2854* 1.000	0.6074** 0.0924 0.6675** 1.000

^{*, **} Denote significance at P≥.05 and P≥.01 respectively.

The high positive correlation coefficient indicates that selection based on tiller number per plant and seeds per spike could be more rewarding and will equally improve the grain yield. Non-significant positive correlation between spike length and grain yield indicate that the selection on the basis of longer spikes do not guarantee the high yield. Out of 6 possible combinations, only one combination produced negative relationship. A negative correlation occur when two developing structures of a plant compete for a common nutrient supply and a negative correlation may arise if one structure is favoured over the other in amount of nutrient supply (ADAMS, 1967).

The pathways through which the three yield components operate to produce their phenotypic associations with grain yield reveal their direct and indirect contributions (Table 3) and are demonstrated diagramatically in Fig. 1. The path coefficient analysis showed that the direct effect of tiller number on grain yield was high and positive (0.6013). The indirect effect via spike length (0.0083) and seeds per spike (0.0893) was negligible. The total correlation coefficient (0.6074) between grain yield and tiller number was mainly

Table 3. Direct and indirect influences of tiller number, spike length, and seeds per spike on grain yield in bread wheat

	Pathways of association	Direct effect path coefficient (p)	Indirect effect path coefficient (p×r)	Correlation coefficient (r)
1.	Grain yield and Tiller number per plant Direct effect (p ₁₄) Indirect effect via spike length (p ₂₄ T ₁₂) via seeds/spike (p ₃₄ T ₁₈) Total effect	0.6013	0.0083 0.0893	0.6074
2.	Grain yield and Spike length Direct effect (p ₂₄) Indirect effect via tiller number (p ₃₄ r ₂₃) via seeds/spike (p ₁₄ r ₁₂) Total effect	0.0435	0.1108 0.1223	0.0924
3.	Grain yield and Seeds/spike Direct effect (p_{34}) Indirect effect via tiller number ($p_{14}r_{13}$) via spike length ($p_{24}r_{23}$) Total effect Residual effect (x)	0.7234	0.0806 0.0512	0.6675 0.7320

due to direct effect. Other workers (Bhatt, 1973; Larik, 1978 and Virk and Singh, 1972) have also concluded that tiller number per plant is an important yield component in wheat mutants. Indeed under most agricultural environments tillering is a valuable mechanism to enable the crop to exploit fully the environment (Kirby and Faris, 1972). Production of effective tiller has also evolutionary significance (Larik, 1978) and spikes per plant are known to exert a preponderant effect upon yield in wheat (Jaimini et al., 1974).

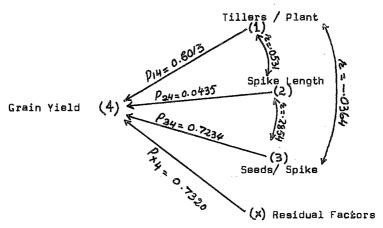


Fig. 1. Diagrammatic representation of factors influencing grain yield in wheat.

Doublearrowed lines indicate correlation coefficients and the single-arrowed lines indicate direct path coefficients.

The direct effect of spike length on grain yield was positive but not so pronounced (Table 3). The indirect effect via tiller number and seeds per spike was also positive but very low in magnitude. Hence the total effect of spike length on grain yield remained rather low. Therefore spike length cannot be used as a reliable criterion in the selection of high yielding mutant genotypes.

In contemporary model of yield (Worley et al., 1976) seed is recognised as the basic unit of yield. Semi-dwarf cultivars of wheat have achieved their yield advantage over tall cultivars primarily because of seeds per spike (Diehl and Welsh, 1972). All the genotypes included in the present study are classified as semi-dwarf (Larik, unpub.) and therefore, the highly significant (P \geq .01) positive association of seeds per spike with grain yield is quite understandable (Table 2). This behaviour was also confirmed by path coefficient analysis in which seeds per spike have shown highest direct effect (0.7234) on grain yield (Table 3). However, indirect effect via tiller number (-0.0806) and spike length (-0.0512) have somewhat diluted the direct effect. A number of complex and interlocking systems (Walton, 1972), contribute to the expression of a quantitative character like yield. The high residual effect observed in present studies (Fig. 1) suggest that the path coefficient obtained within the constraint of the construct do not reflect the influences of the second order components.

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Comparative yield performance and digestibility of triticale and other small grain forages¹⁾

U.R. BISHNOI and G.A. PATEL²⁾

Regardless of similarity in growing environment and stage of growth, the dry matter composition and digestibility of a plant can be greatly influenced by its genetic constitution. Triticale (X Triticosecale Wittmack) (a wheat-rye amphiploid) has the potential of being alternative source of winter grazing in areas having mild winters, although it was developed as a food grain crop. There are several agronomically promising triticale cultivars developed by plant breeders (5, 6, 8) that are available for use. The potential of using triticale as a supplemental forage (3), silage (2) or grain (7, 8) has been studied; but work on its agronomic performance and forage digestibility is needed. The grain and forage production capabilities of rye (Secale cereale L.), wheat (Triticum aestivum L.) oats (Avena sativa L.) and barley (Hordeum vulgare L.) have been discussed (9); however, information concerning the capabilities of triticale is limited (1, 3). Brown and Almodares (3) reported that triticale cultivars produced as much forage as oats and wheat but less than Athens Abruzzi rye. They also reported that cell wall content of triticale cultivars was lower than rye and that crude protein content of triticale forage was similar to rye, wheat and oats. BARNETT et al. (1) concluded that yields of most initially developed triticale cultivars were not comparable to rye in North Florida; but they conceded that some of the more recently developed cultivars were narrowing the gap. From clipping experiments in Southern Kansas, SAPRA et al. (8) reported that the forage productivity of triticales were equal to wheat, barley and rye with triticale producing forage few weeks later in the spring than wheat. The experiments reported here were designed to compare forage and grain yields and forage digestibility data on a number of triticale cultivars with the better and well adapted cultivars of rye, wheat, oats and barley.

Materials and Methods

Seven triticale cultivars; '6TA 131', '6TA 298' developed by Jenkins Research Foundation, (Salinas, California), 'AM 2149', 'AM 2855', 'AM 2870', 'AM 3760', 'AM 3761' (developed at Alabama A&M University) and one adapted cultivar each of what; 'Arthur', rye; 'Bonel', 'barley; 'Barsoy' and oats; 'Coker 66–22' were planted on September 8 in 1975 and again on September 12, in 1976. These newly developed triticale cultivars are leafy-forage types, disease resistant, and are better grain yielding types. The experiments were planted in 4-row plots 5 m long with rows 25 cm apart, on Decatur silty clay loam soil

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(Rhodic Paleudult) at Huntsville, Alabama. All cultivars were seeded at a rate of 70 kg/ha in a randomized complete block design with five replications. 300 kg/ha of 13–13–13 fertilizer was applied before planting. The plots were clipped when plants were 18–20 cm tall. Plots were fertilized with 20 kg/ha of N as NH₄NO₃ after each clipping. After the last clipping, N at 25 kg/ha was top dressed in mid to late March of each year for grain production. A 4 m × 30 cm area from each plot was clipped four times (October 14, November 8, February 20 and March 14) in 1975 and three time (October 25, November 16 and March 10) in 1976, using hand clippers. After fresh forage weights were recorded, samples for dry matter determination were dried in a forced air dryer at 65C. Yields were calculated on an oven dry basis. From 1976 crop, a 15 gram sample of dry forage from first clipping of each plot was ground for quality analysis. Crude protein content, ash, crude fiber, ether and N-free extracts and total digestible nutrients (TDN) were determined according to the method outlined by Harris (4). Analyses of variance were performed and comparison of means were made by using the Duncan's New Multiple Range Test.

Results and Discussion

A. Forage and Grain Yields:

Forage and grain yields of seven triticale cultivars and one each of wheat, rye, barley and oat are shown in Table 1. Triticale 'AM 2855', for both years, produced significantly higher forage yield than other triticales or the other small grain cultivars. This cultivar also exhibited an upright type of growth during the winter whereas triticales, '6TA 131' and '6TA 298' had prostrate type of growth. These two cultivars produced a very profuse growth in mid February to March and produced maximum forage at the third and fourth

Table 1. Total forage and grain yields of seven Triticales and other small grain cultivars in 1975 and 1976 growing seasons

a 111	Fora	age	Gra	in
Cultivar	1975	1976	1975	1976
		(kg	g/ha)	
Triticale				
6TA 131	2412 bc*	2216 b	2597 a	2401 abc
6TA 298	2567 b	2048 bc	2607 a	2418 ab
AM 2149	2493 b	2120 bc	2183 bcd	2318 bc
AM 2855	2729 a	2502 a	2338 b	2403 abc
AM 2870	2434 bc	2090 bc	2221 bc	2321 bc
AM 3760	2209 d	$1976 \mathrm{cd}$	2173 bcd	2007 e
AM 3761	2285 cd	1786 de	2099 cd	2240 bcd
Arthur wheat	1981 e	1656 ef	2174 bcd	2202 cde
Bonel rye	2323 cd	2088 bc	2670 a	2598 a
Barsoy barley	1691 f	$1820\mathrm{d}$	2017 d	2016 e
Coker 66-22 oats	1680 f	1612 f	2244 bc	2108 de
C.V., %	13. 1	11.3	12.5	10.4

^{*} Means within each column followed by the same letter are not significantly different at 5% level according to Duncan's New Multiple Range Test.

clippings. Low forage yield by oats, barley and wheat with spring type growth have been reported by Brown and Almodares (3). They also found that winter triticales produced more forage than other small grains at the fourth clippings. AM 3760 and AM 3761 triticales, 'Coker 66–22' oats, 'Barsoy' barley, and 'Arthur' wheat had the lower forage production during both growing seasons.

'Bonel' rye produced highest grain yield during both growing seasons but triticale '6TA 131' and '6TA 298' in 1975 and '6TA 131'., '6TA 298', 'AM 2149' and 'AM 2855' in 1976 exhibited similar yields. Among triticales 'AM 3760' had the lowest grain yield in the 1976 growing seasons; however, the yield of 'Arthur' wheat was comparable with most triticale cultivars. 'Barsoy' barley, during both growing seasons and 'Cocker 66-22' oats in 1976 produced significantly lower grain yields than 'Bonel' rye and the triticale cultivars. In comparative study on the performance of grain yields, Oplinger and Young (7) reported similar differences among the spring type cultivars of triticale, wheat, oats and rye. The exceptionally low yield from barley, oats and wheat can be further explained by more winter killing after several days of hard freeze particularly during the 1976 winter which also affected the yield of all the cultivars. Grain yields and stands of barley, wheat and oats were also substantially lower by the time of the fourth and third clippings in late March of 1975 and 1976, respectively.

B. Forage Digestibility:

Concentrations of ash, ether extract, crude fiber, crube protein, nitrogen free extract and percent digestibility of forage harvested at comparable stage of growth are given in Table 2. Ash and crude fiber in the forage of 'Bonel' rye was numerically highest. All triticales except AM 3760 and AM 3761 were significantly lower in ash concentration than rye. Five of the seven triticale cultivars and 'Arthur' wheat exhibited significantly higher ether extract than the other small grains. Crude protein concentration of the

Table 2. Proximate analysis of forange from triticale and other small grain cultivars grown in 1976

					•	•	
Cultivar	Mostiure	Ash	Ether Extract	Crude Fiber	Crude Protein	N-Free Extract	Digestibility (TDN)
				%		-	<u> </u>
Triticale							
6TA 131	13 , 2 a*	10, 2 c	3.8 ab	18.1 b	28.0 ab	26.7 bcd	86, 2 abc
6TA 298	10.2 b	10.8 bc	3.9a	19. 3 ab	27.9 ab	27. 9 ab	87.4 ab
AM 2149	9,8b	11. 1 bc	4.1a	21.9 a	28. 5 ab	24. 6 de	88.6 a
AM 2855	9.8b	11. 4 bc	3. 4 cd	18. 2 b	29.3 a	28. 2 ab	84. 9 bcd
AM 2870	9.5 bc	10.8 bc	3. 5 bcd	21.9a	27.9 a	27.8 abc	85.3 abc
AM 3760	8.1 c	1". 4 ab	4.0a	18.1 b	28.7 ab	27. 2 abc	87.1 abc
AM 3761	9.6 bc	12.8 ab	3.9 a	22.0 a	27.6 ab	23.0 e	85, 8 abc
Arthur wheat	10,7b	11. 1 bc	3.7 abc	21.0 ab	27. 9 ab	25. 6 cd	82.6 cd
Bonel rye	7.3 c	13.8 a	3.3 d	22.1 a	24.9 c	28, 6 ab	80.7d
Barsoy barley	10.6b	11. 9 abc	3.3 d	19.8 ab	26.7 bc	27. 7 abc	70.0e
Coker 66-22 oats	7.7 с	12.4 ab	3. 2 d	18, 9 ab	28, 6 ab	29. 2 a	71.3 e
c.v., %	7.0	5.7	7.6	8.3	6.7	6, 4	7.2

^{*} Means within each column followed by the same letter are not significantly different at 5% level according to Duncan's New Multiple Range Test.

triticale forage was significantly higher than 'Barsoy' barley but was similar to 'Arthur' wheat. Oats forage showed the highest nitrogen free extract which was significantly higher than wheat and triticale '6TA 131', 'AM 2149; and 'AM 3761' cultivar. Very high ash concentration and low ether extract (fat %) in rye, oats and barley forage may be attributed to their low digestibility in comparison to wheat and triticale cultivars. The total digestible nutrient (TDN) concentration (88.6%) in forage of 'AM 2149' was highest among all cultivars used in this study. The forage of other small grains were significantly lower in TDN concentration than most triticales.

Results of this study show that triticale produced as much or more forage as rye, whereas rye produced higher grain yields. Crude protein concentration of triticale forage at comparable stage of growth was about 2 to 3 percent higher than barley and rye. The total percent digestibility of triticale was higher than that of barley, oats and rye.

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Chlorophyll synthetic gene(s) in T. aestivum (var. Pb. C 591)

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A monosomic series was developed by Swaminathan et al. (1968) in a hexaploid strain of T. aestivum (var. Pb. C 591), with the help of monosomic series of Chinese spring developed by Sears (1954). Both these monosomic series are being used in cytogenetical studies at the Indian Agricultural Research Institute, New Delhi. Utilizing these monosomic series, several genes have been located on specific chromosomes (Swaminathan et al., 1968; Sawhney et al., 1978).

In the present communication we report about chlorophyll synthetic gene(s) in T. aestivum var. Pb. C 591.

Since the production of monosomic series, we have observed albina seedlings in monosomic line 3A of Pb. C 591. Appearance of albina seedlings in the line mono 3A was presumed to be a spontaneous mutation which was being maintained in heterozygous condition. This assumption was based on the findings of NATARAJAN (1958) who for the first time found albina mutants in the M₂ population of this variety. To confirm the spontaneous mutation theory, a number of monosomic plants were identified cytologically. Seeds of monosomic and disomic plants of line 3A were germinated separately and segregation was observed at seedling stage, since the albina seedlings can be easily identified. All the discomic plants produced only green seedlings. Monosomic plants on the other hand segregated for albina and green seedlings with a variable frequency of 9% to 15%. Expected monogenic ratio of albina: 3 green was not observed, which suggested that the segregation of albina plants in monosomic line 3A was not due to spontaneous mutation at this locus.

To ascertain their somatic chromosome number, roots from different albina seedlings were analysed and it was found that all the albina seedlings had nullisomic (2n=40) chromosomal constitution. Somatic preparations of green seedlings showed that they had either 2n=41 (monosomics) or 2n=42 (disomics).

Since albina seedlings are nullisomic (i.e. chlorophyll synthetic gene(s) bearing chromosomes are absent) for chromosome 3A, it can be suggested that chlorophyll synthetic gene or gene complex is located on chromosome 3A of *T. aestivum* var. Pb. C 591.

STALDER (1929) observed that no chlorophyll deficient mutations are obtained in hexaploid wheat. He therefore suggested that there are more genes which regulate chlorophyll synthesis in hexaploid wheat. SEARS (1954), on the basis of aneuploid analysis, suggested that group 3 chromosomes control the synthesis of chlorophyll in hexaploid wheat.

To facilitate genetical studies in detail, on the system of chlorophyll synthesis in wheat, the following gene symbols are being proposed:—

For A genome, CSG3A (chlorophyll synthetic gene on chromosome 3A); for B genome, CSG3B (chlorophyll synthetic gene on chromosome 3B) and for D genome, CSG3D (chlorophyll synthetic gene on chromosome 3D).

Identification of only one chromosome (3A) in wheat variety Pb. C 591 explains as to why albina plants are obtained after mutagenic treatment in this variety and not in others (NATARAJAN et al., 1958).

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Genetic variability in aluminum tolerance of Triticinae

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Differential tolerances of species and cultivars to aluminum have been reported (Foy, 1974). Campbell and Lafever (1976) and Foy et al. (1974) found varying degrees of aluminum tolerance between wheat cultivars. Slootmaker (1974) studied the tolerance to high soil acidity in wheat and related species, and concluded that the A-genome of Triticum species contributes to tolerance. Sapra et al (1978) reported that some triticale cultivars are tolerant to aluminium while others are highly sensitive. In another study Sapra et al (unpublished) found that rye homoelogous chromosomes 3R and 4R/7R contribute to aluminum tolerance. The present study was undertaken to determine the degrees of Aluminum tolerance in wheat, rye and triticale species.

Materials and Methods

Several diploid and tetraploid species of wheat were acquired from germplasm laboratory, USDA, Beltsville, MD. Rye species were supplied by Dr. J.C. CRADDOCK, USDA, Beltsville, MD. Additional diploid species of wheat were supplied by Drs. B.L. Johnson and J. Waines, University of California, Riverside, California. Several accessions of both diploid and tetraploid species were included in the study. Four uniform seedlings of each accession were planted in 32 litre plastic tanks (53×27×27 cm) containing 1/5 Steinberg nutrient solution as modified by Foy et al. (1967). Four replications of each accession were used. Each accession was randomized within each replication. Two levels of aluminum (0 and 8 ppm) were used to differentiate the response of roots to aluminum. The solutions were adjusted twice daily to pH 4.5±0.2. After ten days of growth in nturient solution, the mean root lengths were recorded and the relative root lengths (8/0 ppm) were calculated.

Results and Discussions

The mean root lengths, range and relative root lengths of different diploid and tetraploid species are presented in Tables 1 and 2, respectively. The relative root length of diploid species T. monococcum (AA) and Agropyron (EE) were 47 and 27 percent, respectively. A elongatum was found to be highly sensitive to aluminum. Slootmaker (1974) reported similar results for T. monococcum and T. boeticum. However, he did not study A. elongatum. In our study T. boeticum was intermediate in tolerance, similar to those results found by Slootmaker (1974) in barley medium. We found that greater diversity exists between and within diploid species (Fig. 1).

Table 1. Mean root length, range and ratio of different wheat species in 0 & 8 ppm aluminum

Consider	G	No. of 0 ppm		-	Ratio		
Species	Genome	accession	Ā	Range	Ī	Range	Ratio
Triticum monococcum	AA	14	8, 47	6, 87-15, 77	4.05	2, 35-5, 55	47
n boeticum	AA	4	7.19	4.87-10.66	4.11	2, 75-6, 55	57
" urartu	AA	3	6,45	5,75-7,60	3,82	3, 45-4, 07	59
n speltoides	BB	2	8.46	6, 40-12, 30	5, 91	3,80-8,30	70
" squarrosa	DD	4	17.02	13, 10-20, 50	8.57	8.30-9.20	50
Agropyron elongatum	EE	7	9, 35	7.6 -13.5	2, 56	2,00-3,70	27

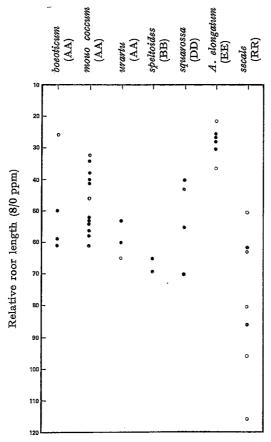


Fig. 1. Relative root length (8/0 ppm) of Triticinae.

Among tetraploid species a greater diversity was noticed between and within species T. turanicum being the only cultivar sensitive to aluminum. This species had a mean relative root length of 37 percent in comparison to relatively tolerant species T. dicoccum (70%) (Table 2). Slootmaker (1974) reported that T. dicoccum was sensitive to aluminum in wheat medium but intermediate in barley medium. T. durum showed less

Table 2. Mean root length, range and ratio of different wheat species in 0 & 8 ppm aluminum

C.	Species	C	No. of 0 pp		0 ppm	pm 8 ppm		
ວງ		Genome	accession	Ā	Range	X.	Range	Ratio
Triticum	durum	AABB	8	11.82	7, 50-16, 25	6.42	4, 22-11, 50	54
//	dicoccum	AABB	5	11,90	11, 30-11, 57	8.37	7,05-11,05	70
"	dicoccoides	AABB	4	11, 56	8,77-15,00	5, 93	4,70-8.00	51
"	timopheevi	AAGG	9	12, 91	8, 17 - 15, 92	7,66	4,87-12,27	59
"	turanicum	AABB	7	16,16	15.00-18.00	6.08	2.50- 9.50	38

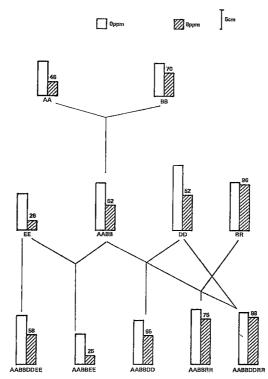


Fig. 2. Root length of wheat and its relatives.

tolerance than *T. dicoccum*. Durum cultivars showed varying responses to aluminum, some were highly tolerant while others highly sensitive. Similar observations have been made in durum wheats by Foy (personal communication). Other tetraploid species such as *T. dicoccoides* and *T. timopheevi* were intermediate in reaction (Table 2).

Among hexaploid species, Agropyron elongatum (AABBEE) was highly sensitive to aluminum due to presence of E genome. Similar response to aluminum was noticed at the other ploidy level of A. elongatum (AABBDDEE) (Fig. 2). In this octaploid elongatum, the degree of tolerance was probably contributed by the presence of D genome. SLOOTMAKER (1978) showed that gene or genes carrying aluminum tolerance are located on D genome in

hexaploid wheats. In this study, we did not try to discuss the variation that exists for this trait in triticale as authors have already reported these trends (SAPRA et al., 1978). In general, octaploid triticales were more tolerant than hexaploid triticales. Rye showed highest degree of tolerance in comparison to wheat species but rye species responded differently to aluminum (Fig. 1)

The present study reveals that genomes A and E of triticinae contribute to the aluminum sensitivity in wheat and related species. In recent years plant breeders have been utilizing the E genome as a bridge species in developing new hexaploid wheats and transferring disease resistance, winter hardiness and forage characters. The effect of E genome (Agropyron elongatum) carrying aluminum toxicity should be studied further especially in those areas with high acid sub-soils. Plant breeders and soil scientists should be aware of the role of A, B and D genomes as pointed out by Slootmaker (1974) and of E genome reported in our findings. Additional work on the role of these genomes to other mineral stress levels (salinity etc.) should be studied further. Such efforts are being made in our laboratory.

Acknowledgements

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Aminoacid composition and species relationships in genus Triticum

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The genus *Triticum* is composed of di-tetra- and hexa-ploid species including both wild cultivated types. Based on evidence from chromosome pairing in F1 hybrids and on gross morphological and karyotype comparisons, three basic genomes-A, B and D- have been recognised in the cultivated types. Tetraploids – AABB – are thought to be originated by amphiploidy between diploids AA and BB (Jenkins, 1929; Sarkar and Stebbins, 1956; Sears, 1956; Riley, et al., 1958), probably before the advent of agriculture, while exaploids – AABBDD – emerged later as a result of amphiploidy between a tetraploid AABB and diploid DD (Kihara, 1944; McFadden and Sears, 1944).

The problem of confirming the parents of polyploid types is intensified by the genetic heterogeneity accumulated by them in centuries of evolution.

In recent times, numerous biochemical parameters, such as phenolic compounds (Dass, 1972; Frost and Holm, 1977), proteins (Johnson and Hall, 1965, 1966), isoenzyme (Nakai, 1973; Mitra and Bhatia, 1971; Jaaska, 1978) and immunochemical methods (Bozzini *et al.* 1973) have been used for studying the phylogenetic relationships in wheats.

The present investigation on quantitative differences in the aminoacids, from hydrolyzed proteins, of different species of *Triticum* was undertaken in order to assess the biochemical bases of the species relationships.

Material and Methods

33 samples of different species of T-riticum -3 samples of T. monococcum, 10 samples of T. durum, 11 samples of T. aestivum, 1 sample of T. speltoides, 2 samples of T. tauschii, 2 samples of T. longissimum and 4 samples of T. dicoccoides - were included in the analysis.

Seeds were derived from a cultivation performed in the same place during the same year. Protein content was determined, by microkjeldahl method, as a crude nitrogen times 5.7; aminoacid composition was determined by an ion exchange chromatography on the hydrolized meals. Aminoacid content was expressed as a % of protein content. Methionine and cystine were not determined.

Analysis of variance was performed for each aminoacid; correlation coefficients and canonical analysis were determined on mean values per species.

Results and Discussion

Aminoacid composition of the analyzed species is shown in Table 1. Species did not show any difference for aspartic acid, isoleucine, tyrosine; differences

Table 1. Aminoacid composition in different species of Triticum

Amino acid	T. monoco- ccum	T. durum	T. aestivum	T. speltodies	T. tauschii	T. longis- simum	T. dicoc- coides
Lysine	2, 81 ab	3.01 a	2.84 ab	2, 54 b	2.78 ab	2, 81 ab	2, 54 b
Histidine	2.19 c	2.38 abc	2, 33 bc	2, 38 abc	2,63 a	2. 45 ab	2, 40 abc
Argine	4.52 a	4.96 a	4.88 a	4.38 b	4.70 a	4.74 a	4.46 a
Aspartic acid	5.35	5.37	5. 25	4.94	5, 05	5. 44	5.09
Threonine	2,82 b	3, 06 ab	2.98 ab	3, 12 ab	3, 16 a	3, 16 ab	2,93 ab
Serine	4.33	4.78 e	4.80 de	5, 32 abc	5, 37 a	5. 36 ab	5. 16 abcd
Glutamic acid	28, 50 de	28. 64 de	28. 94 d	37.80 a	36, 20 ab	34, 66 bc	34. 41 bc
Proline	9, 31 d	9.71 cd	9.77 cd	11, 65 ab	12, 53 a	11, 29 b	10, 90 bc
Glycine	3.49 с	3.94 bc	4.08 ab	3, 73 bc	4.37 a	3, 98 b	3.75 bc
Alanine	3.37 b	3.72 a	3, 63 ab	3, 36	3. 63 ab	3, 56 ab	3, 34 b
Valine	4. 27 ab	4. 16 ab	4.08b	4. 26 ab	4. 75 a	4.15 b	3. 95 Ъ
Isoleucine	3.65	3.40	3. 27	3, 39	3.57	3, 34	3. 22
Leucine	6.43	7.06 abcd	6. 97 bd	7.48 a	7. 46 ab	7. 29 abcd	7.38 ab
Tyrosine	2.84	2.84	2, 96	3, 23	3.08	2, 96	3.19
Phenylalanine	4.63 bc	4.51 c	4.46 c	5, 39 a	5. 15 ab	5, 24 ab	5.03
Protein content	14. 52	13, 29	13. 92	21. 35	17.00	21.30	19, 55

among species were significant at 1% level for all the other aminoacids.

Correlation coefficients shown in Table 2 indicate that lysine was positively associated with arginine, aspartic acid, alanine and negatively with tyrosine; histidine was positively associated with threonine, serine, proline, glycine and leucine, while arginine was associated to alanine in addition to lysine. Leucine was also associated with threonine, serine, glutamic acid and proline; serine was associated also with threonine, glutamic acid and proline; this later was associated with glutamic acid.

Results of canonical analysis indicate that the variability accounted for by the first three characteristic roots was over 93%. The first characteristic root (47%) was positively correlated with serine, glutamic acid and proline, the second (39%) was negatively associated to glutamic acid and positively to glycine, threonine, serine, alanine and leucine.

Table 2. Correlation coefficients among

	MLYS	MHIS	MARG	MASP	MTHR	MSER	MGLU
MLYS MHIS MARG			.89**	. 76*	.80*	. 83*	
MASP MTHR MSER						.83*	00**
MGLU MPRO							. 90**
MGLY MALA MVAL							
MILEU MLEU MPHE							

The values of the first three canonical variables, for the analyzed samples are graphically reported in Fig. 1.

Two clusters seem to emerge from the obtained picture. The first cluster is formed by T. speltodies, T. longissimum and T. dicoccoides, and the second by T. durum and T.

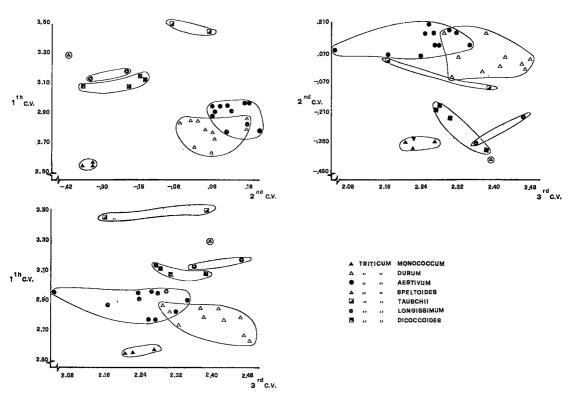


Fig. 1. Relative distribution of species, according the first three canonical variaties.

aminoacid in different species

MPRO	MGLY	MALA	MVAL	MILEU	MLEU	MTIR	MPHE
.87*	. 83*	.82* .95**			.80*	 91**	
. 91** . 93**					.77* .96** .85*		
						.78*	

aestivum. While the relationships among these two latter were rather obvious, the similarity (closeness) between longissimum and dicoccoides seems to be rather interesting, although expected. On the basis of immunochemical data and α -amylase inhibitors a possible involvement of T. longissimum in the speciation of emmer wheats was considered by Konarev et al. (1976) and Vitozzi and Silano (1976) respectively. Isoenzyme patterns Jaaska reporting (1978) suggested that T. dicoccoides could represent a cytogenetically stabilized and evolutionary-wise very successful recombinational segregant of a hybrid between initial amphiploids, involving ancestral forms or precursors of the contemporary diploids among which T. longissimum.

Samples of T. monococcum represent a rather independent cluster, which shows, by the second and third characteristic roots, some closeness with the cluster formed by T. dicoccoides, T. longissimum and T. spelloides.

Worth of mentioning is also the fact that, according to the second and third characteristic roots, T. tauschii samples lie very close to the durum-aestivum cluster. Since these two characteristic roots are considered to have more biological meaning than the first one (Blackith and Reyment, 1971) and closeness of T. tauschii, donor of D genome (Kihara, 1944), to the T. aestivum, could be considered as an additional indication of the reliability of the aminoacid composition in studying species relationships. Interesting for the implication it could have in practical breeding seems also the rather large variation shown by T. tauschii.

In conclusion, the present study of species relationships in *Triticum*, based on aminacid composition, seems to confirm some of the earliest hypothesis, and provide a criterion of genetic affinity which, in cooperation with other criteria, could allow inferences on evolutionary relationships. However, due to the limited number of samples utilized and species analyzed, additional studies would be necessary before a definite usefulness of the method may be assessed.

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Stem rust resistance in accessions of *Triticum timopheevi* and three *Triticum aestivum* lines with resistance from *timopheevi*

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Triticum timopheevi (Zhuk.) Zhuk., a tatraploid wheat (2n=28) has been known as a vital and diverse soruce of resistance to a number of common bread wheat pathogens. The tetraploid wheats are also believed to carry a more valuable resistance to rusts (Watson & Luig, 1968). However, there are limited successful attempts in transferring disease resistance from T. timopheevi to bread wheat.

Studies on accessions of *T. timopheevi* and *T. aestivum* stocks having genes derived from *T. timopheevi* indicate the presence of more than three distinct designated genes for low reaction to *Puccinia graminis tritici*, when tested with three North American cultures at the University of Missouri (U.S.A.) and four Australian cultures at the University of Sydney (McIntosh and Gyarfas, 1971). An assessment of a number of *timopheevi* accessions for genetic diversity in resistance to Indian stem rust strains is presented in this communication.

Table 1. Infection types produced on various T. timopheevi lines and T. aestivum

Accession No.	Source -					7 24	
		17	21	21A-1	24	34	
T. timopheevi:							
PI 119442	Turkey	0;-1	0;-1	0;-2+	0;	0;	
PI 288033	Australia	0;-2	0;-1	1	0;-1	0;-1	
PI 326318	U.S.S.R	0;-1	0;	1-2	0;	0;	
PI 110972	Spain	3	3	0;-1	0;-2	0;	
PI 221421	Yugoslavia	3 3	0;-2	0;-2+	0;	3	
PI 251017	U.S.S.R	3	3	0;-2+	0;-2	0;-2	
PI 251018	"		-	3	-		
PI 272523	Hungry	3	0;-2	3	0;-2	0;-1	
PI 272530	Poland	0;-1	0;-1	1-2	0;	0;-1	
PI 286073	"	3 3	0;.2	3	. 3	0;-1	
PI 290518	Hungry	3	3	0;-2+	3	0;-1	
PI 297030	"	0;-2	0;	0;	0;	3	
PI 306557	Romania	0;	0;	0;-2	0;	3	
CI 11651	U.S.S.R	0;-1	0;	0;-2	0;-2	0;-1	
CI 14133	Unknown	3	3	0;-2+	0;-2	1-2	
T. aestivum:							
CI 12632 (S/Tt1)	U.S.A	4	4	4	4	0;	
Timvera (Tt1)	Australia	4	4	0; -1	3	0;	
Line W (SrTt2)	"	0;-1	1-2	0;	0;-1	0;-2	

Resistance=0;, 0;-1, 1-2, 0;-2, 0;-2+ - = reactions not available Fifteen accessions of *T. timopheevi* and three *T. aestivum* stocks with genes for resistance, derived from *T. timopheevi* supplied by Dr. R.A. McIntosh, University of Sydney, Australia, and being maintained at the Division of Genetics, Indian Agricultural Research Institute, New Delhi, were tested in the seedling stage with 14 strains of stem rust pathogen (*Puccinia graminis tritici* (pers.) Eriks and Henn.) viz., 17, 21, 21A-1, 24, 34, 40, 42, 117, 117-A, 122, 184, 194, 222 and 295. The infection types produced on these lines were recorded following (STAKMAN & LEVINE, 1922). The data obtained are presented in Table 1. The important conclusions drawn were:

- 1. CI 11651 (SrTtl & SrTt2) was observed resistant to all the Indian strains of stem rust. The resistance of CI 11651 to race 40 to which both SrTtl and SrTr2 were found susceptible indicates the possibility of some additional factor in CI 11651. This observation is supported by McIntosh & Gyarfas (1971) who have also reproted some additional factor in this line when tested with a few selected North American and Australian cultures of stem rust.
- 2. The pattern of infection produced on PI 119442, PI 288033 and PI 326318 was identical suggesting the probable presence of same gene(s) for resistance to Indian stem rust strains although the source of these lines is different.
- 3. A number of *T. timopheevi* lines (PI 119442, PI 221421, PI 272523, PI 272530, PI 286073, PI 288033, PI 297030, PI 306557, PI 326318 and CI 11651) were resistant to race 21 that happens to be most prevalent race in the major wheat growing areas in India. The

(having T. timopheevi resistance) when tested with Indian stem rust cultures

Cul	tures							
40	42	117	117A	122	184	194	222	295
0;	0;	4	3-4	0;-1	0;-1	0;-2	0;	0;-1
0;-2	0;	. 4	4	0;-2	0;	0;-1	0;	0;
0;	0;	3	3	0;	0;	0;-1	0;	0;-1
3	4	4	4	0;-1	0;-1	0;	0;-1	0;-2
3	0;	0;-2	0;-2	0;-1		1-2	0;-1	0;
3 3 3	0;	4	4	3	3-4	2-3	3	0;-2
	0;	<u> </u>		_		3-4		-
3	0;	4	4	3	0;-1	0;-2+	0;	3
3	0;	0;	0;	0;-1	0;-1	_	0;-1	0;
3	0;	0;-1	0;-1	0;-2	0; ·2	3		0;
3 3 3 3	0;-2	3	3	0;-2	0;-2	3 3	_	3
0;-1	0;	3-4	0;	0;	0;	1-2+		0;
3	4	0;	0;	0;	0;-1	3	 .	<u> </u>
0;-2	0;-2	0;	0;	0;-2	0;	0;	0;-2	0;-2
3	3	4	4	0;-2	Ŏ;	0;-2+	0;	3.4
	Ü	*	7	0, 2	, ,,	0,21	0,	2.4
3 3 3	0;	0;	0;-1	0;-2	0;-1	0;	0;	0;-1
3	0;-1	0;	0;-1	0;	0;	0;	0;	0;-1
3	0;-2	0;	3	1-2	0;	1-2	0;	0;-2

Susceptible=3, 3-4, 4

exploitation of these sources could be useful both in protecting the crop from the most prevalent race and in transference to diversity for resistance to stem rust.

- 4. Of the three *T. aestivum* lines, the reaction pattern on CI 12632 (SrTt1) and Timvera (SrTt1) was identical except that Timvera was found resistant to the strain 21A-1 to which CI 12632 is susceptible (IT 3). This observation suggests that perhaps Timvera carries an additional factor(s) effective to strain 21A-1, an Indian sub-biotype of race 21.
- 5. In the regular Rust Secreening Nurseries, CI 12632 showed a fair degree of resistance to both the stem and leaf rusts at the adult stage which perhaps is due to some additional factor(s) operative at the adult stage. The use of this line in breeding rust resistant cultivars is suggested.

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Plant regeneration from stem-derived calluses of wheat

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Regenerated plants from the wheat cultures would be useful for genetic studies and for improving the quality of wheat. With wheat (*Triticum aestivum*), however, plants have been obtained from wheat cultures derived from various organs only sporadically (Shimada et al. 1969, Dudits et al. 1975, O'hara and Street 1978). Recently, I obtained cultures capable of regeneration from the young embryos of wheat.

This paper describes cultures capable of regeneration derived from stem tissues of various species of wheat. Many restored plants have been obtained from long-term subcultured calluses of *T. dicoccoides*.

Materials and methods

Plant materials were: Triticum aestivum cv. Chinese Spring, T. dicoccoides spontaneonigrum, T. carthlicum stramineum, T. durum (Gulab), Aegilops squarrosa strangulata, Ae. squarrosa typica No. 2 and synthesized wheats; ABD-1 (T. dicoccoides spontaneonigrum × Ae. squarrosa typica No. 2), ABD-4 (T. carthlicum stramineum × Ae. squarrosa typica No. 2), ABD-12 (T. dicoccoides spontaneonigrum × Ae. squarrosa strangulata), ABD-14 (T. durum (Gulab) × Ae. squarrosa strangulata) and ABD-16 (T. durum (Gulab) × Ae. squarrosa meyeri). These strains were kindly provided by Dr. M. Tanaka, Plant Germ-plasm Institute, Kyoto University, and Dr. J. Tabushi, Kyoto Bunkyo College.

The stem pieces (2 mm long) were taken 5 cm below the ear neck from the uppermost internode of the culum, and were placed aceptically on an agar slant media in test tubes, each containing 10 ml of RM-64 medium (LINSMAIER and SKOOG 1965) supplemented with 2,4-D at 2.0 mg/1. They were incubated at 25-28°C under continuous illumination.

Results and Discussion

Stems of Dinkel, Emmer, synthesized wheats and Aegilops were cultured on RM-64 medium containing 2.0 mg/1 of 2,4-D. The results after one month of incubation are shown in Table 1. Calluses were induced from stems of all species tested. In some species, shoots redifferentiated from the callusses after one month of incubation. The frequencies of calluses with shoots were 5.0, 12.0, 5.0 and 16.0% in T. dicoccoides, ABD-1, ABD-4 and ABD-12, respectively. Shoot redifferentiation did not occur in the calluses of T. aestivum, T. durum, T. carthlicum and Ae. squarrosa, and the calluses of ABD-14 and ABD-16 whose parents are T. durum and Ae. squarrosa did not show shoot redifferentiation.

Table 1. Callus formation and shoot redifferentiation of various wheats and Aegilops

M	aterials*	Callus formation**	% calluses with shoots		
Dinkel:	Triticum aestivum cv. Chinese Spring	. #	0		
Emmer:	T. dicoccoides	++	5.0		
	T. carthlicum	+	0		
	T. durum	#	0		
Aegilobs:	Ae. squarrosa	+	0		
Amphiploid:		#	12,0		
ppo	ABD-4	#	5, 0		
	ABD-12	#	16, 0		
	ABD-14	 ±	0		
	ABD-16	+	0		

^{*} For explanation of the varieties, see the text.

These results suggest that the differences in the efficiencies of regeneration among the species depend on the genotypes.

Stem calluses of *T. dicoccoides*, showing localized chlorophyll development, were subcultured every 30 to 40 days on RM-64 medium containing 2.0 mg/l of 2,4-D. When these calluses subcultured for 1.5 years were transferred to 2,4-D-free RM-64 medium, they formed many leaves and roots. And when the differentiated plantlets grew about 10 cm long, they were planted in soil. Most of them grew normally in the greenhouse. Some differentiated plantlets had white stripes on their leaves. The chromosome numbers in the root tip cells of regenerated plantlets were normal diploid (2n=28). These calluses derived from the stem are similar to those from the embryo of *T. aestivum* with respect to the capability of regeneration (Shimada and Yamada 1979).

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^{** ±:} occasional callus formation, +: constituent callus formation, +: large callus formation.

An interspecific cross-incompatibility system in diploid and tetraploid Aegilops

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Unsuccessful interspecific crosses are mostly caused by abortion of hybrid seeds. Recently, Nishiyama and Yabuno (1978, 1979) have well explained its biological mechanism in the genus Avena in terms of a hypothesis 'polar-nuclei activation'. The hypothesis is based on the facts that the abortion of hybrid seeds is primarily due to abnormal development of the endosperm which has been found by many authors in their histological studies, and this is also supported by successful culture of young embryos excised from abortive crossed ovaries. Development of the endosperm, especially early formation of the endosperm enclosing proembryos, seems to be closely related to an interaction between two polar nuclei and a male nucleus at double fertilization, because it probably initiates mitosis of the primary endosperm nucleus. Then, the intensity of activating action of the male nucleus and reaction of the polar nuclei is indicated 'activating value (AV)' and 'response value (RV)', respectively. The degree of activated polar nuclei is designated 'activation index (AI)=AV/2RV (or × 100)'. In selfed plants the activation index of the polar nuclei (or the primary endosperm nucleus) is always 1/2=0.5 or 50% where AV=RV, and the primary endosperm nucleus could be harmoniously activated for normal development of the endosperm or the seed. AV is a gametophyte character, and may show quantitative differences in different species. Then, in interspecific crossing AI sometimes varies from less to more than 50%, being due to hypo- and hyperactivating action of the male nucleus, respectively. Such unbalanced activations may induce disturbance of the embryogenesis, and results in the formation of deformed or inviable seeds, following the extent of AI deviated from normal 50 per cent.

The hypothesis was successfully applied to the cross incompatibility in the genus *Triticum* (NISHIYAMA 1979).

The present paper represents a further application of the hypothesis to interspecific crosses in diploid and tetraploid Aegilops. I owed the crossing data using six diploid (2n=14) and five tetraploid (2n=28) Aegilops to many earier workers (Percival 1932, Katayama 1933, Kihara and Lilienfeld 1932, Kihara 1937, 1949, Kihara and Tanaka 1954, Berg 1937, Sears 1941). The results were simply summarized in a model of the diallel cross (Table 1). No detail of the development and germination (%) of hybrid seeds was reported in most of the crossing experiments. Accordingly relative activating values were arbitrarily estimated only by a comparative analysis of cross-combinations from a standpoint of hybrid-seed viability. They varied from 0.6 for Ae. squarrosa to 2.2 for Ae. cylindrica and Ae. triuncialis. In Ae. caudata 1.4-1.7 were estimated, but 1.4 was chosen in Table 1. As AV=1 of

Triticum boeoticum was employed as a standard the activating values may be available in intergeneric crosses between Aegilops and Triticum which will be reported in the following paper.

Table 1 shows activation indices in 110 cross combinations among 11 species of which 83 were actually examined to give viable seeds (successful cross, marked with +) or inviable seeds (unsuccessful cross, marked with *). In the crossing experiments AI indicated a wide variation of 15.9–183.3% as compared with 50% in selfed plants. The results were more briefly shown in a diagramatic illustration (Fig. 1). That is, AI was divided in classes

Table 1. Relationship between polar-nuclei activation index (%) and seed viability of interspecific crosses in diploid and tetraploid Aegilops

			-								
∂ AV ♀ RV	squa. 0.6	unia. 0.7	umbe. 0.9	como. 1.1	caud. 1.4	spel. 1.5	vent. 1.6	ovat. 1.65	tria. 2.1	cyli. 2.2	triu. 2.2
squarrosa, 2x, 0.6		58.3 ¹⁾ +	75, 0 *	91.7	116.7 *	125.0 *	133.3 +	137.5 *	175.0	183.3 *	183.3 *
		K-37	K-37	Ka-33	K-37	Ka-33	K-49	K-37	,	K-37	K-37
uniaristata, 2x,0.7	42, 9 +		64.3 +	78.6	100.0	107.1 *	114.3	117.9 *	150.0	157.1	157.1 *
	K-37		P-32		K-37	K-37		K-37			K-37
umbellulata, 2x, 0.9	33, 3 +	38.9 +		61.1 +	77.8 *	83.3 *	88.9 t	91.7 *	116.7 *	122. 2 *	122, 2 *
,	K-49	B-37		K-37	K-37	K-37	K-37	K-37	K-37	K-37	Ķ-37
comosa, 2x, 1.1	27.3 +	34.8 +	40.9 +		63.6 +	68.2 *	72, 7 t	75.0	95.5	100.0	100.0
,	Ka-33	K-37	K-37		K-37	K-37	K-37				
caudata,	21.5	25.0	32, 1	39.3		53, 6	57,1	58.9	75.0	78.6	78,6
2x, 1.4-(1.7)	+	+	+	+		+	+	+	_+	+	+
	S-41	K-37	K-37	K-49		K-37	K-37	K-37	P-32	KT-54	K-37
speltoides, 2x, 1.5	20.0 *	23.3 +	30.0 +	36.7 +	46.7 +		53, 3	55.0	70,0	73, 3	73, 3
	K-37	S-41	K-37	S-41	Ka-33		ļ		ĺ		1
ventricosa,	18.8	21.9	28.1	34.4	43.8	46.9		51.6	65 6	68.8	68.8
4x, 1.6	*		+	t	17.07			+		+ KL-32	*
	K-37		K-37	K-37	K-37			Ka-33		ļ	K-37
ovata, 4x, 1.65	18, 2	21.2	27.3 +	33, 3 +	42, 4 +	45.5 +	48.5 +		63.6	66.7 +	66.7 +
4x, 1.03	K-49	K-49	K-37	K-49	K-37	K-37	Ka-33		P-32	KL-32	K-37
triaristata.	14.3	16.7	21.4	26, 2	33, 3	35.7	38,1	39.3		52, 4	52, 4
4x, 2.1		+	*		+	+	}	+		+	+
		K-49	K-37		K-37	K~49		K-37		K-37	K-37
cylindrica,	13.6	15.9	20, 5	25.0	31.8	34.1	36.4	37.5	47.7		50.0
4x, 2.2		+ V-27	+ K-37		+ K-37	+ Ka-33	+ Ka-33	+ Ka-32			+ Ka-33
		K-37							47.7		Na-55
triuncialis, 4x, 2.2	13.6	15.9	20.5	25, 0	31.8 +	34.1	36.4	37, 5 +	47.7	50.0 +	
4A, 4.4			K-37		K-49	K-37	Ka-33	Ka-33		Ka-33	

¹⁾ AI(%), + viable seeds, * inviable seeds, t death of young seedlings, B-37 Berg 1937, Ka-33 Katayama 1933, K-37, -49 Kihara 1937, 1949, KL-32 Kihara and Lilienfeld 1932, KT-54 Kihara and Tanaka 1954, P-32 Percival 1932, S-41 Sears 1941.

differing by 10%, e.g. the class 50–60% containing AI with 51 to 60%, and so on. There was given the frequency distribution of crosses where abortive one was marked with*. The AI series was arbitrarily divided into four groups, 10–20, 20–70, 70–90 and 90–190% in which the seed germination was generally variable, stable, variable and nothing, respectively. In the last group only one cross, Ae. squarrosa × ventricosa, was successful though some authors failed to get viable seeds. This is merely to make a special case of the general feature of cross incompatibility. Only a few data were available in abortive crosses of the first and second group. Therefore it has need to check them in detail.

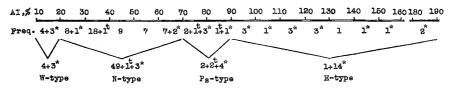


Fig. 1 Illustration of frequency distribution of crosses and seed viability in connection with activation index.

* abortive cross, t young seedlings killed.

Without a knowledge of detailed seed development it is speculative to make a further discussion in connection with activation index. However, based on a comparative investigation with that of *Avena* and others, the following is probably assumed as shown in Fig. 1. In general the AI 20–70% give nearly normal or normal seeds (N-type), and more than 90% produce empty, shrivelled seeds (E-type). The AI 70–90% show an intermediate type of seeds (Ps-type) between them. In the AI 10–20% small and weakly developed seeds are obtained and their germination is usually low (W-type).

The polar-nuclei activation hypothesis is almost successfully applied to the seed abortion in interspecific hybridizations of *Aegilops*. The result of some unexamined crosses in Table 1 will be expected by their activation indices in advance.

The supplement of some appropriate crossing data, indicating hybrid-seed development and germination (%) would assist the establishing of a more perfect cross-incompatibility system in the genus *Aegilops*.

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Alteration of growth habit and variation of heading time induced by the alien cytoplasm in common wheats¹⁾

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Based on the extensive studies on nucleo-cytoplasmic substitution in wheats and their relatives, various cytoplasmic effects on genome manifestation have been reported (Kihara 1951, Fukasawa 1953, Maan 1975, Tsunewaki et al. 1976). Recently Kihara (1973, 1975) has suggested the possible utilization of the nucleo-cytoplasmic hybrid as a mean of plant breeding for nucleo-cytoplasmic heterosis, as it was revealed that the alloplasmic common wheats with Aegilops squarrosa cytoplasm provided complete pollen fertility and vigorous growth. Semenov (1978) reported the alloplasmic common wheat with Ae. ovata cytoplasm which had economically useful characters.

In this paper, the authors clarified the cytoplasmic effect on the growth and flowering habits by using the alloplasmic common wheats with the cytoplasm of Ae. ovata. In addition, effects of the other cytoplasms such as Ae. squarrosa, Ae. umbellulata, Ae. vavilovii were also investigated both in the field and under the controlled environment.

The alloplasmic common wheats used in the experiments are given in Table 1a. They have been established by the successive backcross method. After the proposal by Tsunewaki (1969), alloplasmic lines are expressed as the following example in the text; (ovata)-Chinese Spring indicates the nucleo-cytoplasmic substitution line of Triticum aestivum cv. Chinese Spring with cytoplasm of Ae. ovata. Field experiments were carried out in Sapporo (N43°, E142°) and Kurasahiki (N35°, E134°) in Japan. Winter and spring wheats were sown in September and in April in Sapporo, respectively, while the both cultivars were sown in November in Kurashiki, with 20 cm×40 cm spacing. The autors wish to express their sincere thanks to Prof. S. Yasuda and Mr. Fukuyama for their co-operation in the experiment at Kurashiki.

1. Heading time in the fields

The nucleo-cytoplasmic substitution lines and their nucleus donors were grown in Sapporo and Kurashiki from 1977 to 1978 for the comparative observation of their heading time. Table 2 shows the heading dates of the cytoplasmic substitution lines and the deviation from their nucleus donors in two places. When the cultivar Chinese Spring was compared with the alloplasmic lines with Ae. ovata, Ae. squarrosa, Ae. umbellulata and Ae. vavilovii, significant differences were observed in the heading time. Among the alloplasmic lines of Chinese Spring, the heading time of (ovata)-Chinese Spring was most remarkably

¹⁾ The study is conducted as a part of The Co-operative Project on NC-heterosis initiated by Kihara Institute for Biological Research.

Table 1. Cytoplasmic substitution lines of common wheats and indicator strains for classifying the grade of growth habit

a) Cytoplasmic substitution lines

Cytoplasm donor	Nucleus donor ¹⁾				
Ae. ovata	Chinese Spring (SB ₁₈), P168 (SB ₁₀)				
Ae. squarrosa	Chinese Spring (SB ₈), P168 (SB ₆) Norin 26 (SB ₅),				
•	Selkirk (SB ₅), Bison (SB ₆), Jones Fife (SB ₇), Salmon (SB ₆),				
	T. vulgare erythrospermum (SB ₅),				
	T. compactum Humboldti (SB ₅), T. spelta duhamelianum (SB ₇),				
	T. spelta Rumania (SB ₆)				
Ae. umbellulata	Chinese Spring (SB ₁₇), P168 (SB ₁₀)				
Ae. vavilovii	Chinese Spring (SB _s), P168 (SB ₄)				

 Numeral given in parentheses indicates the number of times of substitution back crosses.

b) Indicator strains for the grade of growth habit

Grade ²⁾	Indicator strain	Genotype		
I	Triple Dirk	Vrn ₁ Vrn ₁ , Vrn ₂ Vrn ₂		
I	Triple Dirk (D)	Vvn ₁ Vvn ₁		
II	Triple Dirk (E)	Vrn ₃ Vrn ₃		
III	Triple Dirk (B)	Vrn ₂ Vrn ₂		
III	Shirasagi	·		
IV	Aoba			
V	Nambu			
V-VI	Oku			

2) I-III: spring growth habit, IV-VI: winter growth habit.

delayed as compared with the nucleus donor, by 35.2 days in Sapporo and 11.0 days in Kurashiki. The similar effects of Ae. ovata cytoplasm to Chinese Spring was noticed in the heading time in P168. In both lines, a considerable number of unemergent and sterile tillers were observed in Sapporo.

Data in Table 2, also, shows that some alloplasmic common wheats with Ae. squarrosa cytoplasm headed significantly earlier than their nucleus donors. Fukasawa (1953) firstly reported the significant delay of heading time in alloplasmic emmer wheat (T. durum) with Ae. ovata cytoplasm, and Kihara (1975) proposed the possible usefulness of cytoplasmic substitution lines by taking advantage of cytoplasmic effect on maturity in wheat breeding. The results in the present experiment indicates that heading time could be varied by introduction of alien cytoplasm into wheat varieties. Though the cytoplasmic effect on heading time varies depending on the nucleus donors and the locations of experiments, the degree of influence by the alien cytoplasms was in the order of Ae. ovata>Ae. umbellulata>Ae. vavilovii>Ae. squarrosa.

2. Alteration of growth habit

The delay on heading time of alloplasmic common wheats with Ae. ovata cytoplasm was manifested more remarkably when those alloplasmic lines were grown in Sapporo by

Table 2. Heading dates of the cytoplasmic substitution lines and the deviations from their nucleus donors

	Headin	ng date ¹⁾	Deviation		
Cytoplasmic substitution line	Sapporo (July)	Kurashiki (May)	Sapporo	Kurashiki	
(ovata)-Chinese Spring ("")-P168 (squar.)-Chinese Spring ("")-P168 ("")-T. vulgare erythro. ("")-Norin 26 ("")-Selkirk ("")-T. compactum Humbol. ("")-T. spelta duhamel. ("")-T. spelta Rumania ("")-Jones Fife²) ("")-Bison²) ("")-Bison²) ("")-Salmon²) (umbel.)-Chinese Spring ("")-P168 (vavil.)-Chinese Spring	36.5 49.3 2.3 9.4 5.2 -2.5 -1.9 11.9 15.4 11.1 -14.2 -19.7 -15.4 4.0 10.5 3.9	15.4 5.6 12.7 12.4 -4.4 4.3 10.9 14.8 17.8 14.3 8.8 10.9 11.3	35, 2** 40, 9** 1, 0** 1, 0* -0, 2 0, 1 0, 3 1, 8** -1, 1 -0, 1 -0, 3 0, 7 0, 3 2, 7** 2, 1** 2, 6**	11.0**	

¹⁾ Numerals indicate the differences in days from July 1 (in case of Sapporo) and from May 1 (in case of Kurashiki).

spring sowing than in Kurashiki by fall sowing (Table 2.). Therefore, it is implied that the venalization during winter in Kurashiki affect the reduction of the delayed period for heading time in alloplasmic common wheats with Ae. ovata cytoplasm. The strains shown in Table 1b were used as the indicators in the experiment to examine the effect of vernalization in alloplasmic common wheats with Ae. ovata cytoplasm. Before the trans-planting into the field at Sapporo (in case of spring sowing), the seedlings of the single leaf stage were treated with low temperature (8°C) under continuous illumination for 40 days for vernalization.

Table 3 shows the heading dates of vernalized and non-vernalized plants of (ovata)-Chinese Spring and (ovata)-P168, together with the four indicator strains for the growth habit. Chinese Spring and P168 are of spring growth habit, but the heading date of two alloplasmic lines resembled that of the winter wheat Oku after the vernalization. On the other hand, the treatment shortened the duration until heading in (ovata)-Chinese Spring and (ovata)-P168 by 11.2 and 12.8 days, respectively, which was quite similar to the case of Aoba.

It has been proved in barley and wheat that the time of flag leaf emergence correlats closely with the grade of spring and winter growth habit, under the condition of continuous illumination with high temperature (TAKAHASHI 1943, YASUDA and SHIMOYAMA 1965). Therefore, an experiment was conducted to examine the effect of alien cytoplasm on the growth habit in controlled environment of growth chamber. Materials were grown under con-

²⁾ Fall (September) sowing in Sapporo.

^{*, **:} significance at 5% and 1% levels, respectively.

Table 3. Acceration of heading time by the vernalization (40 days)1)

Ct	Headin	Acceration		
Strain (Grade) ²⁾	Non-vernal.	Vernalized	(days) ³⁾	
Shirasagi (III)	June 27	June 20	7.1	
Aoba (IV)	July 17	July 1	15.4	
Nambu (V)	Sep. 16	July 4	89.5	
Oku (V–VI)	4)	July 26	_	
(ovata)-Chinese Spring	Aug. 6	July 25	11.2	
(ovata)-P168	Aug. 18	Aug. 6	12.8	

- Vernalization treatment was initiated at the single leaf stage.
- Grade of growth habit, I-III; spring habit, IV-VI; winter habit.
- Average days of about 20 plants.
- Remained in rosette state without heading.

tinuous illumination with the temperature of 20°C, and days until the flag leaf emergence from seeding were scored. The degree of spring or winter habits were classified into five grades based on the time of the flag leaf emergence; I (extreme spring habit) – less than 30 days for flag leaf emergence, II (spring habit) -31~40 days, III (weak spring habit) -41~50 days, IV (weak winter habit) -51~90 days, and V or over (winter habit) - more than 91 days.

Result of the experiment were summerized in Table 4. Most of the cytoplasmic substitution lines remained in the same grade as their nucleus donors. (ovata)-Chinese Spring, however, showed grade IV in spite of that the control Chinese Spring was ranked in grade III together with the other alloplasmic lines of Chinese Spring. This fact suggests Ae.

Table 4. Grade of spring and winter growth habit classified by the days until flag leaf emergence from seeding under the condition of continuous illumination and high temperature

Grade

I. Extreme spring habit (<30 days)*</p>

Triple Dirk, Triple Dirk (D), Selkirk, (squarrosa)-Selkirk

II. Spring habit (31-40 days)*

Triple Dirk (E), P168, (squarrosa)-P168, T. vulgare erythrospermum, (squarrosa)-T. vulgare erythrospermum, T. spelta duhamelinaum, (squarrosa)-T. spelta dauhamelianum, T. spelta Rumania, (squarrosa)-T. spelta Rumania

III. Weak spring habit (41-50 days)*

Triple Dirk (B), Chinese Spring, (squarrosa)-Chinese Spring, (vavilovii)-Chinese Spring, (umbellulata)-Chinese Spring, Norin 26, (squarrosa)-Norin 26,

T. compactum Humboldti, (squarrosa)-T. compactum Humboldti

IV. Weak winter habit (51-90 days)*

(ovata)-Chinese Spring, Salmon, (squarrosa)-Salmon

V or over. Winter habit (>91 days)*

Jones Fife, (squarrosa)-Jones Fife, Bison, (squarrosa)-Bison

^{*} Days until flag leaf emergence from seeding in growth chamber.

ovata cytoplasm caused the alteration of growth habit from spring habit to winter habit in Chinese Spring. In this connection, (ovata)-Chinese Spring were survived and produced plump kernels when it had been sown in September, 1978 in Sapporo, although some plants were killed during the winter.

3. Requirement of vernalization

In the next experiment, the periods requiring for the full vernalization were examined. The seedlings of alloplasmic lines of Chinese Spring and three indicator strains were treated with low temperature (8°C) under continuous illumination (about 2,000 lux) for the different periods ranging from 10 to 50 days. After the treatment, plants were transfered into the growth chamber (Koitotron KG–106 HL-D type), which was controlled with the luminous intesity of 28,000 lux for 17 hours (20°C) and about 10,000 lux for 7 houres (18°C) a days. In each plot, ten individuals were planted in a dense space (5 cm×3 cm).

Table 5 shows the average days until the flag leaf emergence after the end of the treatment of low temperature. According to the experiment by Gotoh (1976), the completion of vernalization is achieved when the days until flag leaf emergence become less than 34 days under the condition of continuous illumination with high temperature, after the treatment of low temperature. Based on this criterion, Chinese Spring and three alloplasmic lines of Chinese Spring with Ae. squarrosa, Ae. umbellulata and Ae. vavilovii cytoplasm required the vernalization for 10 days, in which category the indicator Shirasagi (grade III) was included. While (ovata)-Chinese Spring required the vernalization for 50 days to achieve the criterion, even the indicators Aoba (grade IV) and Nambu (grade V) achieved the criterion by vernalization for 25 days and 30 days, respectively. This result alone might lead to conclude that (ovata)-Chinese Spring have stronger winter habit than that of Aoba or Nambu.

Table 5. Days until the flag leaf emergence under the condition of continuous illumination with high temperature after various days of vernalization¹⁾

Strain	Duration of vernalization (days)								D
	0	10	20	25	30	35	40	50	Degree
Chinese Spring	50	33	32	26	29	25	24	21	III
(squar.) -C. Spring	46	31	32	25	29	23	24	20	"
(umbel.)-C. Spring	44	31	30	26	28	22	21	19	"
(vavil.) -C. Spring	41	31	32	26	30	24	22	21	"
Shirasagi	46	29	28	2 3	24	20	19	17	"
(ovata)-C. Spring	67	54	51	46	47	40	37	35	IV
Aoba	73	67	41	33	32	25	26	21	"
Nambu	72	72	63	44	32	32	32	25	v

¹⁾ Broken line indicates the boundary of minimum requirement for effective vernalization.

²⁾ Degree of vernalization requirement was determined by comparing with three indicator strains.

However, since (ovata)-Chinese Spring headed later by 11 days than the control Chinese Spring in the field experiment at Kurashiki where the full vernalization must have been achieved during winter, it is concluded that the vegitative growth period was extended by 11 days by the introduction of Ae. ovata cytoplasm in Chinese Spring. Considering the extension of vegitative growth period, it is estimated that about 45 days until the flag leaf emergence could be the criterion to achieve the full vernalization in case of (ovata)-Chinese Spring at the experiment in the growth chamber. Then, (ovata)-Chinese Spring required the treatment of low temperature for 25 days to achieved the criterion of full vernalization, which is equivalent to the indicator Aoba (grade IV). Consequently, it can be concluded that the degree of vernalization requirement of Chinese Spring is altered by the effect of Ae. ovata cytoplasm from grade III (weak spring habit) to grade IV (weak winter habit).

The results of the present experiments suggest that the interaction between the plasmon of Ae. ovata cytoplasm and the plasmon-sensitive gene or genes in T. aestivum cv. Chinese Spring is responsible for not only the extention of vegetative growth but also the alteration of growth habit from spring habit to winter habit.

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Specificity of nucleo-cytoplasmic interactions in *Triticum* and *Aegilops* species (a review)

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Cytoplasmic differences among related plants are inferred from the different phenotypes of hybrid progenies from reciprocal crosses, because hybrid genotypes are assumed to have differential sensitivity to the parental cytoplasms. Certain hybrid genotypes may not produce noticeable differential phenotypic effects if they share certain nuclear genes which control cytoplasmic effects of both parental cytoplasms. In such cases, parental plants are assumed to have the same or similar cytoplasms, until another nuclear genotype produces differential sensitivity to one or both of these cytoplasms. Cytoplasms of related species are considered the same or similar until they are shown to be different. For example, TSUNEWAKI et al. (1976 and 1978) assumed cytoplasmic similarities between diploid Ae. squarrosa and 5 polyploids with the D-genome, and they based their conclusions on the interactions observed between T. aestivum genomes and the cytoplasms of these Aegilops species. However, interactions involving T. durum genomes indicated cytoplasmic differences among these Aegilops species. Accordingly, Ae. squarrosa was assumed to have contributed the cytoplasm as well as the D-genome to Ae. cylindrica and Ae. ventricosa, and Ae. uniaristata was assumed to have contributed the cytoplasm as well as the M genome to Ae. crassa and Ae. juvenalis (MAAN, 1978). In this case, T. aestivum genomes did not differentiate these cytoplasms and the T. durum genome had differential interactions which separated these Aegilops species into two groups: 1) Ae. squarrosa, Ae. cylindrica, and Ae. ventricosa and 2) Ae. uniaristata, Ae. crassa, and Ae. juvenalis.

In general, intraspecific cytoplasmic differences are controlled by one or two nuclear genes. Occasional mutants or off-type genotypes lacking these critical nuclear genes have detrimental cytoplasmic effects and are eliminated immediately or gradually depending on the traits affected and the magnitude of the cytoplasmic effects; most incompatable or inviable gametes or zygotes, and male-sterile or weak plants may be eliminated each generation and the proportion of less prolific genotypes may be gradually reduced over several generations. Therefore, a species population would be expected to have all of the cytoplasm-specific nuclear genes in homozygous condition. A close linkage between cytoplasm-specific nuclear genes would ensure that (like the cytoplasmic genes) all essential genes will be inherited together. This will contribute to the stability of the nucleocytoplasmic mechanisms and would enhance the fitness of the population. Cytoplasmic and the cytoplasm-specific nuclear gene mutations would persist only if they are followed by

specific compensating nuclear gene or cytoplasmic mutations. Certain cytoplasm non-specific homoeoalleles may partially compensate for the effects of a cytoplasmic mutation, until a complementary nuclear gene mutation has a chance to appear and spread in the population. A mutation with small effect may have a greater chance to survive because a complementary mutation may not be immediately required for the survival of the affected individual. Most mutations producing major phenotypic alterations may be eliminated before a complementary mutation has a chance to appear. Mutations with small phenotypic effects may accumulate in intraspecies populations. The related species populations may differ in the number and kinds of cytoplasmic and cytoplasm-specific nuclear genes, because complementary cytoplasmic and nuclear gene mutations may proceed independently among species. Therefore, interspecific cytoplasmic differences in well-differentiated species are polygenically controlled, and close linkage among these genes may contribute to the development and operation of the interspecific genetic isolating mechanisms.

The presence of the species-specific nuclear genes can be inferred only from their sterility or incompatibility interactions with other species-specific genes in interspecific hybrids. Therefore, hybrid progenies from crosses involving related polyploids may be examined to study hybrid sterility components which may include cytoplasmic, sporophytic, chromosomal, or genomic sterilities, because stability and expression of the species-specific nuclear genes may be modified in an alien cytoplasmic and genomic backgrounds.

The satellited chromosomes or their homoeologous in T. aestivum are reported to have gene(s) controlling cytoplasmic effects, even though satellites are not known to have any mapped genes. Kihara (1951) reported that a satellited Ae. caudata chromosome, which was homoeologous to group 1 of the wheat chromosomes, had a major gene or genes controlling male fertility restoration to the alloplasmic wheat plants with Ae. caudata cytoplasm. MAAN (1977b, 1978) reported that the long arm of chromosome 1D had a gene or genes controlling the effects due to Ae. squarrosa, Ae. ventricosa, or Ae. cylindrica cytoplasms. Bahl and Maan (1972) reported that several of the independently derived wheat lines from crosses involving cytoplasm donor species had male fertility restoring gene(s) on chromosome 1A and on other satellited wheat chromosomes or their homoeologues. This evidence may indicate that genes controlling metabolic activity of the nucleolar organizer may be directly or indirectly involved in coordinating nucleo-cytoplasmic interactions. The relative expressivity of these genes in alien cytoplasms may correspond to the genetic distance between related species, if gene products of the nuclear organizer are species-specific. Possibly, mutations in the satellited chromosome segment are viable only if they are accompanied or followed by complementary cytoplasmic mutations. This may explain relative stability of the nuclear and the cytoplasmic systems and the lack of marker genes on the satellited chromosome segments.

Possibly different sets of species-specific recessive genes control nucleo-cytoplasmic interactions resulting in normal fertility and normal plant growth in related diploid species. Interactions among these genes result in sterility, inviability of hybrid progenies even though meiotic abnormalities in F_1 resulting from chromosomal structural

differences between the parental species are reduced or eliminated in certain hybrid plants. The plasma-sensitive nuclear genes are not directly transferable from one diploid to another diploid species, even when the sterility of the interspecific hybrids is bypassed via polyploidy or by bridging crosses. For example, Kihara (1959) reported that Ae. umbellulata genome could not be substituted into the Ae. speltoides cytoplasm, because it was an inviable nuclear cytoplasmic combination. Also, KIHARA (1963) reported that Ae. uniaristata (2n= 14; M^uM^u) genome could not be substituted into Ae. comosa (2n=14; MM) cytoplasm, because all functional female gametes of the Ae. comosa $\mathcal{P} \times Ae$. uniaristata \mathcal{F}_1 had a complete set of the M-genome chromosomes. Female gametes with Mu-genome chromosomes did not function in Ae. comosa cytoplasm of F_1 plants. All plants from a backcross with Ae. uniaristata had MM^u-genomes and resembled F₁ plants. All plants resembling Ae. comosa were obtained from $F_1 \times Ae.$ comosa, because all viable seeds from this backcross had embryos with MM-genome. Reciprocal F₁ was not obtained because Ae. uniaristata as a female was cross-incompatable with Ae. comosa. Therefore, characteristics of Ae. uniaristata cytoplasm were not examined from direct crosses with Ae. comosa. However, different interactions were obtained between T. durum genome and cytoplasms of Ae. uniaristata or Ae. comosa which indicated that these diploids had different cytoplasms (MAAN, 1978). T. durum plants with Ae. uniaristata cytoplasm were viable only if they retained a critical Ae. uniaristata chromosome arm (1977a). These plants were male sterile and produced a few plump and viable seeds, and a larger number of shrivelled and inviable seeds when crossed with T. durum as a male parent. The plump and viable seeds again produced malesterile plants with maternal chromosome number which included the critical Ae. uniaristata chromosome (arm). These results indicated that seeds having embryos with ciritical Ae. uniaristata chromosome arm were viable and embryos without the critical telocentric were inviable in Ae. uniaristata cytoplasm. However, alloplasmic T. durum plants with Ae. uniaristata cytoplasm and without the critical Ae. uniaristata cytoplasm were obtained when T. aestivum with Ae. uniaristata cytoplasm was used as the cytoplasmic source to develop T. durum with Ae. uniaristata cytoplasm. T. aestivum with Ae. uniaristata cytoplasm was fertile and did not contain critical Ae. uniaristata telocentric. These results indicated that: 1) the presence of the critical Ae. uniaristata chromosome in T. durum genome having Ae. uniaristata cytoplasm controlled the abortion of seeds whose embryos lacked that telocentric. This telocentric had gene or genes which restored vigor to T. durum plants with Ae. uniaristata cytoplasm, because weak alloplasmic T. durum plants were obtained when alloplasmic T. aestivum was used as the source of Ae. uniaristata cytoplasm, 2) hexaploid T. aestivum genome was not cytoplasm-specific and had homoeolleles which compensated for the critical cytoplasm-specific nuclear genes of Ae. uniaristata. Therefore, hexaploid T. aestivum genome is more compatable and less cytoplasm-specific than tetraploid T. durum genome, and T. durum genome is less cytoplasm-specific than diploid genomes of Ae. uniaristata or Ae. comosa.

LAMPRECHT (1945) reported similar results in interspecific hybrids of *Phaseolous* species. He obtained sterile plants when *Hyp* (hypogeal cotyledons) and *Ext* (exterior

stigma) genes of P. multifluorous were transferred to the nuclear genome of P. vulgaris in P. vulgaris cytoplasm. All other genes examined were reciprocally transferred from one species to the other by backcross and selection procedures. He suggested that Hyp and Ext genes were plasma-specific, and produced male sterile P. vulgaris plants in P. vulgaris cytoplasm. Also, Hyp and Ext were unstable in P. vulgaris cytoplasm and frequently mutated to Epi and Int alleles, respectively. These alleles normally occur in P. vulgaris. Similarly, Kihara (1951) reported that the gene controlling black glume color was preferentially transmitted and frequently mutated to an allele for yellow glume in T. aestivum cytoplasm (and produced mosaics) when transferred from an Ae. caudata chromosome to a T. aestivum chromosome. In these instances species-specific nuclear genes could not be transferred from one diploid species to another, because of incompatable nucleo-cytoplasmic interactions. However, species-specific nuclear genes of the diploid species can be transferred to the nuclear genome of the related polyploid species. The resulting alloplasmic plants with critical nuclear genes from different diploid species can be crossed with one another or with critical diploids to determine the specificity of the nucleo-cytoplasmic interactions. For example, Maan and Lucken (1972) reported that wheat R-lines derived from crosses involving T. boeoticum-Ae. squarrosa amphidiploid did not restore fertility to alloplasmic T. aestivum with Ae. speltoides or T. araraticum cytoplasms, where as wheat R-lines derived from crosses involving Ae. speltoides or T. araraticum did restore fertility to wheat with cytoplasms of these species. These results indicated that Ae. speltoides and T. boeoticum have different cytoplasms and Ae. speltoides and T. araraticum have similar cytoplasms. Therefore, T. aestivum lines with cytoplasm and critical nuclear genes from diploids can be used to study nucleo-cytoplasmic interactions in the genetic background of hexaploid T. aestivum. Also, alloplasmic wheats having cytoplasm of diploid species and with or without the critical nuclear genes may be crossed with other related diploids (which are cross-incompatable at the diploid level) and their interactions may be examined in F₁ hybrids.

Possibly, nuclear genomes of the polyploid species (i.e. T. aestivum) have substantial inter-genomic variability because of the heterogeneity (or multiplicity) of the homoeoalleles derived from the diploid parental progenitor species. Therefore, polyploid species genomes may be less species-specific in their interactions with certain alien cytoplasms than the genomes of the diploid progenitors. Interactions between polyploid nuclear genomes and the cytoplasms of two or more of the related species may result in apparently similar plant phenotypes, or different genotypes of a polyploid species may produce apparently different phenotypes in their interactions with the same cytoplasm. For example, T. aestivum plants with the cytoplasms of T. boeoticum (Maan and Lucken 1970) or S. cereale (Maan and Lucken, 1971) had male sterility, greatly reduced vigor and reduced seed viability; the similar phenotype indicated similar interactions between Triticum genomes and T. boeoticum or S. cereale cytoplasms. Also, the difference in the extent of male sterility and delayed maturity of alloplasmic T. aestivum cvs. Chris, Selkirk, and Chinese Spring lines with Ae. ovata cytoplasms indicated that these nuclear genotypes give different interactions

with Ae. ovata cytoplasm (MAAN, unpublished). These examples of apparent non-specificity of nucleo-cytoplasmic interactions between hexaploid T. aestivum genomes and T. boeoticum, S. cereale or Ae. ovata cytoplasms can be explained as follows: The Ae. ovata cytoplasm has similar effects on the expression of various T. aestivum genotypes; alloplasmic plants have reduced male fertility and delayed maturity. The magnitude of the cytoplasmic effects is modified by the nuclear genes in the three T. aestivum cultivars. Similarly, alloplasmic T. aestivum with the cytoplasms of T. boeoticum or S. cereale can be distinguished by a closer examination of anther size and spore development. Alloplasmic plants with T. boeoticum cytoplasm have smaller anthers with 0% stainable pollen grains and plants with S. cereale cytoplasm have fairly well developed anthers with some stainable pollen grains. Therefore, apparent non-specificity of the interactions between T. aestivum genomes and the cytoplasms of T. boeoticum, S. cereale, Ae. ovata or certain other species does not distract from the other evidence for the specificity of interspecific nucleo-cytoplasmic interactions.

Even though certain interactions between T. aestivum genomes and the alien cytoplasma may appear to be less species-specific, the use of the T. aestivum genome as a tester allows greater flexibility in the choice of cytogenetic techniques that can be used, because aneuploid stocks allow study of chromosomal location of nuclear genes controlling cytoplasmic effects and relatively easy transfer of alien genes to wheat chromosomes. Also, inherent heterogeniety of the parental genomes and the homoeoalleles makes 6x T. aestivum more compatable with alien cytoplasms than 4x T. durum. For example, T. aestivum with cytoplasms of Ae. squarrosa, Ae. cylindrica, Ae. ventricosa, Ae. crassa, Ae. juvenalis or Ae. uniaristata is fertile and of near-normal vigor. T. durum is not viable in the cytoplasms of Ae. squarrosa, Ae. cylindrica, or Ae. ventricosa. Plants of T. durum in Ae. crassa, Ae. juvenalis or Ae. uniaristata cytoplasms have greatly reduced vigor. Interactions with T. durum genomes and the cytoplasms of these 6 Aegilops species indicate cytoplasmic similarity between diploid Ae. squarrosa and tetraploid Ae. cylindrica or Ae. ventricosa, and between diploid Ae. uniaristata and polyploids Ae. crassa or Ae. juvenalis. Obviously, T. durum is more species-specific than T. aestivum in its interactions with alien cytoplasms (Maan, 1978).

Specificity of these nucleo-cytoplasmic interactions was also indicated by the following observations: An addition of chromosome 1D to the T. durum genome was essential for viability of T. durum with the cytoplasm of Ae. squarrosa, Ae. cylindrica, or Ae. ventricosa. Therefore, chromosome 1D has critical nuclear genes controlling effects conditioned by these cytoplasms. These genes were not essential for viability of T. durum with the cytoplasms of Ae. uniaristata, Ae. crassa or Ae. juvenalis. Apparently, chromosome 1D or another D-genome chromosome has homoeoalleles which make T. aestivum fertile in the cytoplasm of Ae. uniaristata, Ae crassa, or Ae. juvenalis, even though alloplasmic plants of T. aestivum in these three cytoplasms are less productive than those with cytoplasms of Ae. squarrosa, Ae. cylindrica, or Ae. ventricosa. The critical gene(s) on an Ae. uniaristata chromosome arm which restored plant vigor to T. durum with Ae. uniaristata cytoplasm did

not have male fertility restoring genes (MAAN, 1977a). These plants were male sterile, and the effect of the critical Ae. uniaristata chromosome remains to be examined in the cytoplasms of Ae. crassa or Ae. juvenalis. These results further indicate that polyploid nuclear genomes may be useful in the study of nucleo-cytoplasmic interactions involving specific nuclear genes or chromosome segments and alien cytoplasms.

In the studies of nucleo-cytoplasmic interactions between Triticum genomes and alien cytoplasms, the cytoplasm donor species are crossed as females, and Triticum species are used as the recurrent male parents. Two types of plants appear in the backcross progenies. In the first type of plant, all of the nuclear genes from the cytoplasm donor species are eliminated, and the nuclear genome of the recurrent male parent is substituted into the alien species cytoplasm. Plants so obtained may have cytoplasmically inherited male sterility or other cytoplasmic effects such as reduced plant vigor and enhanced sensitivity to environmental conditions. The male-sterile plants may be maintained by repeated backcrossing with the recurrent male parent. In the second type of plant, certain critical nuclear genes from the genome of the female cytoplasm donor are transferred to the genome of the recurrent male parent when parental chromosomes pair in the F₁ or in the backcross plants. Alternatively, a chromosome or a chromosome arm with critical nuclear gene(s) is transferred to the genome of the recurrent male parent, if parental chromosomes do not pair in the F₁. Plants of the second type have noticeably improved male fertility and/or plant vigor when compared to the first types and may be maintained by selfing, if fertile. Usually most of the fertile alloplasmic plants are less vigorous, and less productive than euplasmic controls used as the recurrent male parent; either the critical nuclear gene(s) from the cytoplasm donor species are not fully expressed when transferred to the wheat genome, or not all of the genes necessary for complete control of cytoplasmic effects to produce a normal phenotype are transferred to the wheat genome by the backcrossing procedures. However, alloplasmic plants comparable to euplasmic controls in plant vigor or productivity can be produced by repeated selection and intercrossing of plants with maximum expression of the critical nuclear genes controlling cytoplasmic effects. In plants having normal vigor and fertility, certain genes with detrimental effects may be eliminated during backcrossing and selection procedures, or certain genes in T. aestivum may complement specific nuclear genes in improving nucleo-cytoplasmic interactions.

Most interspecific hybrids from crosses between species with well-differentiated genomes are highly sterile due to interactions between the specific genes of the parental species, which complement sterility due to meiotic irregularities. Only natural or induced amphidiploids and some of the progenies from backcrosses with parental species or from out-crosses with other related species are fertile, and these progenies can be used for the analysis of the hybrid sterility components. Sterility may be due to hemizygosity of the species-specific genes in the F_1 , and fertility is restored when these genes become homozygous in the amphidiploid, or sterility genes from one of the parents may be eliminated in certain fertile backcross progenies. If parental species differ cytoplasmically, then cytoplasm-specific nuclear genes from the genome of the cytoplasm donor species may be transferred to the

chromosomal complement of the recurrent male parent which usually is T. aestivum or T. The use of polyploid T. aestivum facilitates the transfer of the alien genes to wheat chromosomes because a greater variety of the aneuploid gametes and zygotes produced are viable and functional, and the effects of aneuploidy and sterility due to meiotic irregularities are minimized. Of course, only those alien genes which are expressed in the genetic background of T. aestivum would be identified and examined. Others, which are not transferred to wheat, or remain unexpressed, or those having minor effects will remain unidentified. Genes controlling most easily noticeable cytoplasmic effects like restoration of male fertility and vigor of hybrid plants are examined most often. In most species, the genes controlling restoration of male fertility and plant vigor appear to be closely linked or are located on the same arm of a critical chromosome of the cytoplasm donor species (MAAN, 1977b). The presence of the alicn chromosome in wheat plants can be readily detected when derived hybrid progenies are crossed with alloplasmic wheat lines having cytoplasm of the same donor species from which the critical nuclear genes were extracted, and F₁'s are cytologically examined for lack of pairing between wheat and alien chromosome(s) and from other phenotypic effects.

Usually, a large number of the plant traits are modified as a result of interaction between a Triticum genome and alien cytoplasms. The magnitude of cytoplsmic effects depends on the nuclear genotype as well as the environmental conditions in which plants are grown. Possibly, several plasma-sensitive nuclear genes in the Triticum genome may produce observed phenotypic alterations, and a similar number of the critical nuclear genes from the respective cytoplasm donor species control the effects on the expression of the plasmasensitive genes. A majority of the critical nuclear genes remain closely linked because of their location on an alien chromosome segment which may not (or may less often) pair with a homeologous wheat chromosome segment. For example, the 43-chromosome (monosomic-addition) wheat plants with T. boeoticum cytoplasm and a critical T. boeoticum chromosome have near-normal fertility and plant vigor (MAAN, unpublished). They produce a few plump and viable seeds having embryos with the critical T. boeoticum chromosome, but a majority of the seeds lack the critical chromosome and are shrivelled. Some of the shrivelled seeds are viable and they produce male-sterile plants of greatly reduced vigor. After one or two additional backcrosses, only inviable seeds are produced. Similar results are obtained from the 43-chromosome (monosomic-addition) wheat plants with a critical Secale cereale chromosome and S. cereale cytoplasm (MAAN and LUCKEN, 1972). The T. boeoticum and S. cereale cytoplasms induce male sterility and reduction of plant vigor in wheat plants. The plants with T. boeoticum cytoplasm have sterile pollen grains and smaller anthers than those with S. cereale cytoplasm. Therefore, T. boeoticum and S. cereale cytoplasms affect different plasma-sensitive genes of T. aestivum. Also, nuclear genes on the critical T. boeoticum chromosome do not control effects due to S. cereale cytoplasm and genes on critical S. cereale chromosome do not control effects due to T. boeoticum cytoplasm. Therefore, the species-specific plasma-sensitive genes of T. aestivum which interact with T. boeoticum cytoplasm may be different from those which interact with S. cereale cytoplasm,

and specific nuclear genes on critical T. boeoticum or S. cereale chromosomes control effects due to these cytoplasms.

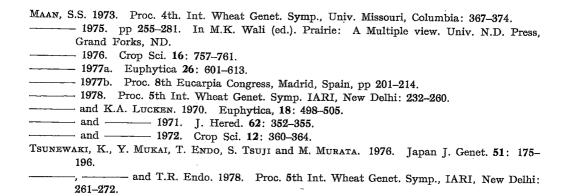
Nucleo-cytoplasmic interactions involving *Triticum* genomes and *Aegilops* cytoplasms indicate that several species-specific plasma-senstive genes from the cytoplasm donor species control these interactions. Since interspecific hybrid sterility and loss of plant vigor of hybrid progenies are among the major genetic isolating mechanisms in related plant species, the interspecific nucleocytoplasmic differentiation may be intimately involved in the evolutionary processes separating species. Therefore, interspecific and intergeneric nucleocytoplasmic interactions may indicate relative genetic relationships among the species of *Triticum* and *Aegilops*. The inviability of *T. aestivum* in the cytoplasms of *T. boeoticum* or *S. cereale* in the absence of specific nuclear genes from the respective cytoplasm donors and specificity of the cirtical nuclear genes controlling cytoplasmic effects indicates a remote genetic distance between *T. boeoticum* and *S. cereale* and between each of these two species and *T. aestivum*.

Results from the study of interactions involving *T. durum* or *T. aestivum* genomes and cytoplasms of related *Triticum* and *Aegilops* species can be summarized briefly (Maan, 1978):

1) All diploid *Triticum* and *Aegilops* species having cytogenetically distinct genomes also have different cytoplasms, 2) certain polyploid species are cytoplasmically similar to only one of their putative diploid progenitors; this observation indicates that this particular diploid contributed cytoplasm as well as the nuclear genome to that polyploid. These results lead to the following conclusions:

- 1. Cytyplasmic and genomic differences existed among the diploid species of *Triticum* and related general before some of them participated in the origin of polyploids.
- 2. Cytoplasmic and genomic similarities have persisted between related polyploids and their respective cytoplasm donor species. Cytoplasmic and genomic changes have been slow since the origin of the polyploids. Perhaps, cytoplasmic mutations were matched by compensating nuclear gene mutations and vice versa. The residual genetic similarities indicate that the cytoplasmic and nuclear genetic systems have been equally table during the evolution of related diploid and polyploid species, and major modifications may have occurred in the genomes contributed by the male progenitors, and
- 3. Nucleocytoplasmic compatibility may have been an important factor determining the success of the natural amphidiploids and polyploidy may be an evolutionary bypass to interspecific sterility due to cytoplasmic and genomic differences among the diploid species.

Literature Cited



II. Editorial Remarks

Words for WIS No. 50, a memorial 25th anniversary issue.

During my visit at WSU in Pullman, Washinton, U.S.A., 1951–53. it happened to me to see "Drosophila Information Service" which contained many scientific informations mainly on *Drosophila* genetics, and I was very much impressed by its valuable contributions. I thought of the similar publications concerning wheat genetics.

Returning to Japan in 1953, I proposed to publish "Wheat Information Service," and my proposal was accepted. The coordinating committee was organized with Dr. H. Kihara as the chairman. WIS No. 1 appeared in October 1954 and since then, two issues have been published yearly. The cost of the publication has been defrayed partly by the Grant in Aid for Publishing Results from the Ministry of Education, Government of Japan, and partly by the contributions from the Flour Miller Association, Tokyo, Japan. I wish to express my sincere thanks to those organizations.

During the past twenty-five years, the research notes and principal scientific informations totalling 578 have been published as follows:

Nos. of WIS	Papers published	Year
1–10	155	1954–1959
11-20	108	1960-1965
21-30	109	1966-1970
31-40	102	1970-1675
41–50	104	1976–1979
Total	578	·

I would also like to express my sincere gratitude for favorable comments regarding WIS Nos. 1–49, and valuable contributions for the present issue. Increased contributions and support would be appreciated.

December 15, 1979

Kosuke Yamashita
The Managing Editor

Announcement for future issues

WIS No. 51 and 52 will be planned for publication in December 1980 and March 1981. Manuscripts for thoses issue are accepted any time, not later than September 31, 1980, and January 31 1981 for No. 52.

WIS is open to all contributions regarding methods, materials and stocks, ideas and research results related to genetics, breeding and cytology of Triticum, Aegilops, 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 cm²). 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:

Kosuke Yamashita Wheat Information Service, Kihara Institute for Biological Research, Mutsugawa 3–122, Minami-ku, Yokohama 232, Japan

Membership Fee

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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Explanation of the Figure on the Cover

Cf. text figure in page 10 of an article by G. Fedak.

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