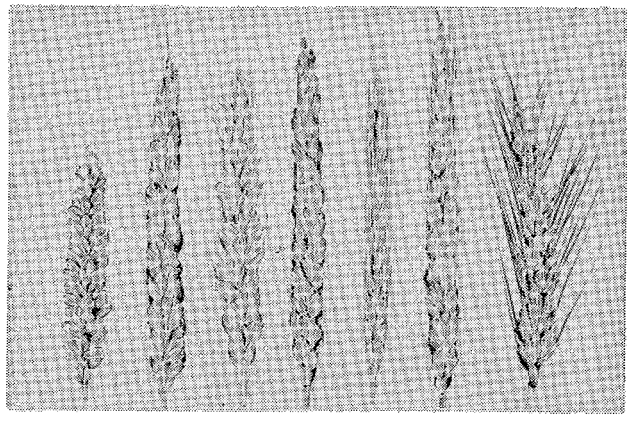
WHEAT INFORMATION SERVICE



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I. Research Notes

Cytoplasmic relationship between *Triticum boeoticum* and *T. urartu*

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The nucleus of one species can be substituted into the cytoplasm of another related species by repeated backcrossing. Information on male fertility/sterility interactions from such nuclear substitution lines has been used to establish cytoplasmic relationships among various *Triticum* and *Aegilops* species (MAAN and LUCKEN 1970, 1971 and SUEMOTO 1973). The cytoplasmic relationship between the diploid wheats *T. boeoticum* and *T. urartu*, based upon nucleo-cytoplasmic interaction, has not been reported thus far. In spite of the fact that *T. urartu* is reproductively isolated from *T. boeoticum* throughout the range of their sympatric distribution in Transcaucasia, Turkey, Iran, Iraq and Lebanon; it was not previovsly considered a distinct species but a different form of *T. boeoticum*. Recently, *T. urartu* has also been considered as the B genome donor to the tetraploid wheats (JOHNSON 1975, DHALIWAL and JOHNSON 1976). This paper reports a study of the cytoplasmic relationship between *T. boeoticum* (2587) and *T. urartu* (1545) following development of nuclear substitution lines.

To substitute the *T. urartu* genome into *T. boeoticum* cytoplasm, *T. boeoticum* was used as the female parent and *T. urartu* as the pollen parent. The *boeoticum* × *urartu* F_1 hybrid was completely male sterile. The sterile F_1 hybrid was used as the seed parent and backcrossed with its parental *urartu* line. The first backcross progeny (BC_1F_1) segregated for sterility with plants ranging from completely sterile to a few partially fertile. The completely sterile BC_1F_1 plants were backcrossed with *T. urartu*. The BC_5F_1 plants resembled *T. urartu* on several morphological characters e.g. glabrous leaves, glabrous leaf sheath, glabrous glumes, presence of a third awn in the spikelet, short and divergent awns, and dense spike indicating that the *T. urartu* genome was almost completely reconstituted in the *boeoticum* cytoplasm. Theoretically 98.43% of the *urartu* genome should have been substituted after five backcrosses. Three plants obtained in the BC_5F_1 were morphologically uniform and were completely male sterile in spite of normal meiosis with seven bivalents at metaphase I. Anthers were irregularly developed and never protrude from the florets.

The plants were, however, female fertile as partial seed set was obtained on backcrossing with either *T. urartu* or *T. boeoticum*.

The complete male sterility of plants produced by substituting the *T. urartu* genome into *T. boeoticum* cytoplasm suggested that the two speceies have different cytoplasms. Male sterility of the *urartu* genome in *boeoticum* cytoplasm may be due to the failure of *boeoticum* cytoplasm to translate or to activate a fraction of the *urartu* genome responsible for male gametophyte development as effectively as that of the *urartu* cytoplasm. These results are consistent with the observed difference in behaviour of reciprocal crosses involving *T. boeoticum* and *T. urartu* JONSON and DHALIWAL, in press. When *T. boeoticum* is used as the female parent and to *urartu* as the pollen parent, the F_1 hybrid seeds are extremely reduced in size but are viable whereas in the reciprocal cross, the F_1 seeds are of normal length but are shrivelled and non-viable. Frequently such differential phenotypic effects in reciprocal crosses of related species are attributed to differences in their cytoplasms.

A few plants of the hybrid involving *T. urartu* (1545) as the female parent and *T. boeoticum* (1195) as the male parent were obtained by embryo culture. The sterile *urartu* × *boeoticum* hybrid is being backcrossed with *T. boeoticum* in order to substitute the *boeoticum* genome into *urartu* cytoplasm. The second backcross progeny from this substitution is only partially male sterile.

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Specific interaction between the D genome and the three alien cytoplasms in wheat

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KIHARA (1973) reported that emmer wheat (AABB) with the cytoplasm of *Aegilops squarrosa* (DD) is very weak and highly male sterile. Since common wheat (AABBDD)

with this cytoplasm shows high fertility and normal growth, his results imply that the D genome should have the restoring genes to the *squarrosa* cytoplasm for both growth vigor and male fertility. Moreover, common wheat with the cytoplasms of *Ae. cylindrica* (CCDD) or *Ae. crassa* ($DDD^2D^2M^{cr}M^{cr}$) also manifests high fertility and normal growth. It is thus concluded that the cytoplasm of both species is derived from *Ae. squarrosa* (TSUJI and TSUNEWAKI 1974, MURATA and TSUNEWAKI 1975). From this conclusion, we can expect the same kind of nucleo-cytoplasmic interactions between the nuclei of emmer or common wheat and the cytoplasms of *Ae. cylindrica* and *Ae. crassa* as that found between these wheats and the *squarrosa* cytoplasm.

We, therefore, started to analyze the specific interactions between the D-genome and the cytoplasms of the above three species having D-genome in common, in the following two ways: (1) Removal of the D-genome from common wheat with each of the three alien cytoplasms, and (2) production of the aneuploid series of D-genome chromosome in common wheat with the alien cytoplasm. Although these works have not yet been completed, their outlines and the results so far obtained are reported here. Materials used are the three alien cytoplasm substitution lines of *Triticum aestivum* cv. Chinese Spring (CS in abbrev.).

The first approach will be carried out by the successive backcrosses with emmer wheat. In the spring of 1975, F_1 pentaploid hybrids (AABBD) between the three cytoplasm substitution lines of CS and *T. durum* var. *melanopus* were produced and investigated (Fig. 1). Selfed seed fertilities of the hybrids ($5x$) and of the corresponding cytoplasm substitution lines ($6x$) are given in Table 1. The pentaploids with the three alien cytoplasms manifested considerably reduced fertilities as compared with the reciprocal hybrids between normal CS and *T. durum* var. *melanopus*. All three cytoplasms clearly showed the same pattern of response. This confirms that these three cytoplasms are similar to one another.

In the second approach, it is attempted to produce mono-, nullitetra- and ditelosomics of the cytoplasm substitution lines of CS, only for D-genome chromosomes. Although

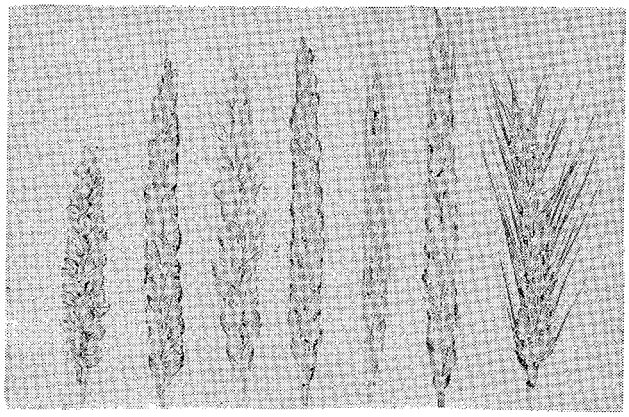

Fig. 1. Spikes of normal CS, F_1 pentaploid hybrids with CS, *durum*, *squarrosa*, *cylindrica* and *crassa* cytoplasms, and *T. durum* var. *melanopus* (from left to right).

Table 1. Average selfed seed fertilities (%) of the normal and three cytoplasm substitution lines of *T. aestivum* cv. Chinese Spring, and their F_1 hybrids with *T. durum* var. *melanopus*

Nucleus	Cytoplasm				
	squarrosa	*cylindrica*	*crassa*	*durum*	*aestivum*
AABBDD (CS)	99.3	97.5	99.1	–	100.0
AABBD (5♂ hybrid)	32.3	30.0	20.0	64.1	80.0

Table 2. Average selfed seed fertilities (%) of the F_1 monotrisomics from the crosses, cytoplasm substitution lines of CS × nullitetrasomic CS

Monotrisomics	Cytoplasm		
	squarrosa	*cylindrica*	*crassa*
1D1A	94.0	94.2	–
2D2A	100.0	100.0	–
3D3B	95.0	100.0	96.9
4D4A	98.8	96.0	93.8
5D5A	–	87.5	–
6D6B	98.3	94.0	86.1
7D7A	96.7	100.0	92.4

MAAN and LUCKEN (1967, 1968) has produced the monosomics with the *T. timopheevi* cytoplasm by crossing ms-Bison with monoiso- and monotelosomics as the male parent, we adopted a different method. In the spring of 1974, three cytoplasm substitution lines of CS were first crossed with the nullitetrasomic series (♀), resulting in the monotrisomics ($19_{II}+1_I+1_{III}$) with three alien cytoplasms. All monotrisomic plants investigated in 1975 were highly fertile and vigorous in spite of the deficiency of one D-chromosome (Table 2).

When the monotrisomics are backcrossed with nullitetrasomics, we can find the nullitetrasomics among the offspring. At the same time, when they are crossed with normal CS (♂), three types of the segregants, *i.e.*, 41-, 42- and 43-chromosome individuals, will be obtained. The 41-chromosome plants of each line are expected to be the monosomics of a D-genome chromosome. If the female transmission rates of the univalent and an extrachromosome of the trivalent in the monotrisomics are assumed to be 25% and 40%, respectively (SEARS 1944, 1953), we can expect the ratio of the three segregants to be 9:9:2. Their frequencies were investigated in a small population (Table 3). The segregation ratio observed fitted fairly well to the expected one, and about a half of the offspring was the monosomic which we wanted to obtain. It, therefore, can be said that this method is available for production of the monosomic series with an alien cytoplasm.

The data on the pentaploids indicate that the restoring genes for fertility and plant vigor to the three cytoplasms exist in the D-genome of common wheat. From the results given in Table 2, it seems probable that the fertility restoration to each alien cytoplasm is controlled by multiple factors rather than by a single dominant factor, because no single

Table 3. Chromosome constitution of the offspring from the crosses, (cytoplasm substitution lines of CS × nullitetrasomic CS) F_1 × normal CS

Monotrisomic parent	Cytoplasm											
	squarrosa				*cylindrica*				*crassa*			
	No. plants obs.	Chrom. no.			No. plants obs.	Chrom. no.			No. plants obs.	Chrom. no.		
		41	42	43		41	42	43		41	42	43
1D1A	9	2	6	1	10	5	4	1	9	5	4	0
2D2A	9	4	4	1	8	3	5	0	-	-	-	-
3D3B	9	6	2	1	9	3	5	1	10	5	5	0
4D4A	9	6	3	0	7	2	5	0	8	4	4	0
5D5A	-	-	-	-	5	4	1	0	-	-	-	-
6D6B	9	5	3	1	8	5	3	0	6	4	2	0
7D7A	7	1	4	2	9	3	5	1	10	2	6	2
Total	52	24	22	6	56	25	28	3	43	20	21	2

line of the monotrisomics showed clear reduction of fertility. Although the monosomic lines obtained by our method might also give the same results as the monotrisomics did for fertility, these lines will be useful in studying the specific nucleo-cytoplasmic interactions, *e.g.*, by crossing them with other lines such as ditelosomics of CS or emmer wheat.

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The effect of the S genome of *T. speltoides* on the pairing of homologous chromosomes of *T. aestivum*[1)]

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T. speltoides has been considered to have donated the B genome to *T. aestivum*. Recent work has caused a reconsideration of the evolution of polyploid wheats and has shown that it is doubtful that *T. speltoides* donated the chromosomes comprising the B genome in *T. aestivum* (KIMBER and ATHWAL, 1972; DVORAK, 1972). KIMBER and ATHWAL observed variation in the amount of pairing in *T. aestivum* × *T. speltoides* hybrids. The amount of pairing was classified as high, intermediate, or low and averaged the equivalent of 10.60, 5.65, and 0.70 bivalents per cell, respectively.

In the low-pairing hybrid, which formed the basis for the rejection of *T. speltoides* as the B genome donor, the reduction in chromosome associations may be attributed to a reduc-

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tion in either homologous or homoeologous pairing, or both. If the low pairing was due to a reduction in homologous associations, then the decrease in bivalent formation might be accounted for by genetic regulation and not be indicative of a lack of homology between the chromosomes of *T. speltoides* and the B genome of *T. aestivum*. Some evidence concerning the nature of the reduction in pairing in low-pairing hybrids was given by KIMBER and ATHWAL (1972) by examination of the configurations in a 54-chromosome amphiploid of an F_1 hybrid between *T. aestivum* and *T. speltoides*, in which chromosome-5B was represented by a pair of telocentric chromosomes for the long arm. The amphiploid showed regular bivalent formation, which indicated that homologous pairing may take place in the presence of the genome of *T. speltoides* inducing low-pairing in hybrids. Also, in all three types of hybrids of Chinese Spring with *T. speltoides*, heteromorphic bivalents were observed showing that the pairing of homoeologous chromosomes may occur even in the presence of low-pairing *T. speltoides*.

KIMBER and ATHWAL state, "Since homoeologous chromosome pairing is not completely prohibited in any of the hybrids, it must be concluded that homologous chromosome pairing is not precluded either." While this infers that homologous pairing is not affected, it is necessary to perform a more definitive test of the effect of *T. speltoides* on homologous pairing.

The purpose of this contribution is to report investigations on the effect of the S genome of *T. speltoides* on the pairing of homologous chromosomes of *T. aestivum*. To examine the effect an isochromosome of wheat, having arms with identical constituent gene loci and structure, was used to estimate the frequency of homologous pairing. Internal pairing of an isochromosome occurs when the two homologous arms of the chromosome pair with each other to produce a ring univalent. This ring univalent has the advantage of being readily recognizable at meiosis and distinguishable from other wheat chromosomes. Thus, the frequency of pairing of an isochromosome may reflect the frequency of homologous pairing. However, DRISCOLL and DARVEY (1970) have reported differences in the pairing of isochromosomes and homologous chromosomes in the presence of colchicine. By producing hybrids of *T. aestivum* with the various pairing forms of *T. speltoides*; high, intermediate, and low, and having one of the wheat chromosomes in an isosomic condition, any effect of *T. speltoides* on the pairing of homologous chromosomes of wheat might be detected by differences between the hybrids in the frequency of formation of a ring univalent.

Table 1 shows the mean and range of chromosome associations observed per cell in the hybrids between *T. aestivum*, monoisosomic for either chromosome-1A or 6D, and three forms of *T. speltoides*. Also, the mean and range of the frequency of pairing in the aneuploid monoisosomic-1A Chinese Spring is given. In the table the frequency of univalent ring formation is given for both the hybrids and the aneuploid. Since the sibling plants in any one type of hybrid were so similar, the data for each type of hybrid were summarized.

The data for the hybrids made with monoisosomic-1A and the three pairing forms of *T. speltoides* show a close correspondence with the three classifications of KIMBER and ATHWAL (1972) and may be termed low-, intermediate-, and high-pairing-hybrids. While

Table 1. The mean and range of chromosome pairing in hybirds of monoisosomic Chinese Spring-1A and -6D with *T. speltoides* and in monoisosomic-1A Chinese Spring and the frequency of formation of an isochromosome ring

Plant	#Cells	#Plants	I*	II Rod	II Ring	III	IV	V	VI	I Ring
Monoiso-1A Chinese Spring × *T. spletoides* (Low Pairing)	20	2	27.00 24-28	0.50 0-2						0.90
Monoiso-1A Chinese Spring × *T. speltoides* (Intermediate Pairing)	180	9	14.99 5-26	4.46 1-9	0.86 0-4	0.72 0-3	0.05 0-1			0.93
Monoiso-1A Chinese Spring × *T. speltoides* (High Pairing)	60	3	6.96 1-13	4.52 1-9	2.32 0-6	1.70 0-4	0.48 0-2	0.05 0-1	0.02 0.1	0.87
Monoiso-6D Chinese Spring × *T. speltoides* (Low Pairing)	60	3	25.48 22-28	1.18 0-3	0.05 0-1	0.02 0-1				0.92
Monoiso-1A Chinese Spring	20	1	1.00 1	5.50 3-10	14.50 10-17					0.90

*I, II Rod, II Ring, III, IV, V, VI, and I Ring represent univalents, rod bivalents, ring bivalents, trivalents, quadrivalents, quinquivalents, sexivalents and a ring formed by an isochromosome pairing on itself, respectively.

the three hybrids showed differing amounts of pairing of chromosomes, the formation of a ring univalent by the internal pairing of an isochromosome is nearly identical for all three hybrids. In addition, the data from the cross of monoisosomic-6D × low-pairing *T. speltoides* corresponds to the hybrid of monoisosomic-1A with low-pairing *T. speltoides* with respect to both the frequency of multivalent formation and the formation of a ring univalent. When the data from these hybrids are compared to the formation of a ring univalent in the aneuploid monoisosomic-1A Chinese Spring, no significant difference is seen.

By comparing the frequencies of ring-univalent formation in hybrids involving different pairing forms of *T. speltoides* with the pairing in monoisosomic-1A Chinese Spring, it appears that the genomes of the accessions of *T. speltoides* investigated have no effect on the pairing of homologous chromosomes in *T. aestivum*. Further, there is no supporting evidence that the low-pairing seen in hybrids with *T. aestivum* may be attributed to the presence of synaptic genes in *T. speltoides* which have affected the pairing of homologous chromosomes.

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The D genome dependent isozymes of α-amylase in wheat

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In our first report (NISHIKAWA and NOBUHARA 1971) out of sixteen isozyme bands of α-amylase detected in the germinated seeds of hexaploid wheat, six have been genetically defined, *i.e.*, Band 1 is specified by the gene on 6Dβ (β arm of chromosome 6D), Band 2 on 6Aβ, Band 3 on 6BL (long arm of chromosome 6B), Band 11 on 7DL, Band 13 on 7AL and Band 15 on 7BL, respectively. Afterward, a minor modification of the buffer solution for enzyme extraction made it possible to separate Band 7 from Band 7′, both being superimposed on each other in the previous work. The facts that Band 7 was absent in the zymogram of Tetra Canthatch as well as *Triticum durum reichenbachii*, while it was present in most of strains of *Aegilops squarrosa* so far tested (NISHIKAWA 1973), would indicate that Band 7 is possibly dependent on the D genome.

Out of eight lines ditelosomic for the respective arms of the D genome chromosomes now available in Chinese Spring, ditelosomic for 6Dα showed the zymogram lacking either Band 1 and Band 7 (Fig. 2). This means that the respective genes for Band 1 and Band 7 locate on the same chromosome arm, 6Dβ. But there is no linkage datum of these genes, yet.

As already reported (NISHIKAWA and NOBUHARA 1971) Prelude, a cultivar of common wheat showed a different zymogram from Chinese Spring in Band 1 absent and Band 3 minor (Fig. 3). Another cultivar, Thatcher was very similar to Prelude as to α-amylase zymogram (Fig. 5). Tetra Prelude (Fig. 4) and Tetra Thatcher (Fig. 6), both were kindly provided by Dr. P.J. KALTSIKES, University of Manitoba, Winnipeg, Manitoba, Canada, which had got rid of all the D genome chromosomes showed the α-amylase zymograms almost identical to each other and very similar to *T. durum reichenbachii* (Fig. 7). Namely, the zymograms of these three strains or variety, in contrast to their hexaploid counterparts, showed absence of Band 1, 7 and 11. These results porve in agreement with the previous works that Band 1, 7 and 11 are the D genome dependent α-amylase isozyme bands.

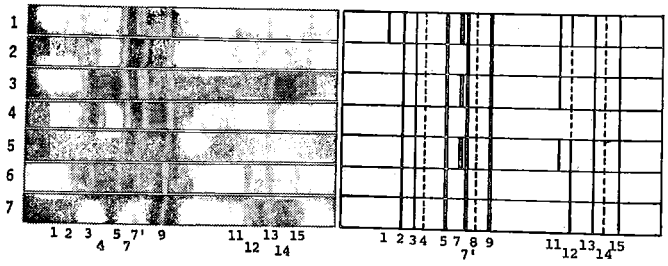

Fig. 1–7 α-amlyase zymograms of germinated seeds in wheat. 1: Chinese Spring disomic, 2: diletosomic for 6Dα, 3: Prelude, 4: Tetra Prelude, 5: Thatcher, 6: Tetra Thatcher, 7: *Triticum durum reichenbachii*.

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The meiotic analysis of the hybrid *T. timopheevii* var. *zhukovskyi* × *Secale cereale*[1)]

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The species *Triticum timopheevii* var. *zhukovskyi* is unique amongst the polyploid wheats in that it is an autoallohexaploid. The genomic analysis of this relatively newly identified species was undertaken by UPADHYA and SWAMINATHAN (1963 and 1965). They concluded that it had arisen as a result of hybridization and amphiploidy between *T. monococcum* and *T. timopheevii*. This conclusion is supported both by the sympatric distribution of these two species and the morphology of *zhukovskyi*. Thus, genomically, it would be AAAABB (or AAAAGG). The hybrid *T. timopheevii* var. *zhukovskyi* × *T. monococcum* has not been made, and thus the conclusions are based on the indirect evidence of comparisons of the meiosis of hybrids *T. timopheevii* × *T. monococcum*, *T. timopheevii* var. *zhukovskyi* × *T. timopheevii* and *T. aestivum* × *T. timopheevii* var. *zhukovskyi*. The evidence showing that the A and not the B genome is duplicated rests mainly on comparisons of satellite morphology by UPADHYA and SWAMINATHAN (1963). Hybrids that will allow the resolution of this situation have been made by the present authors and will be reported upon later.

Clear recognition of the presence of a duplicated genome in *zhukovskyi* is difficult

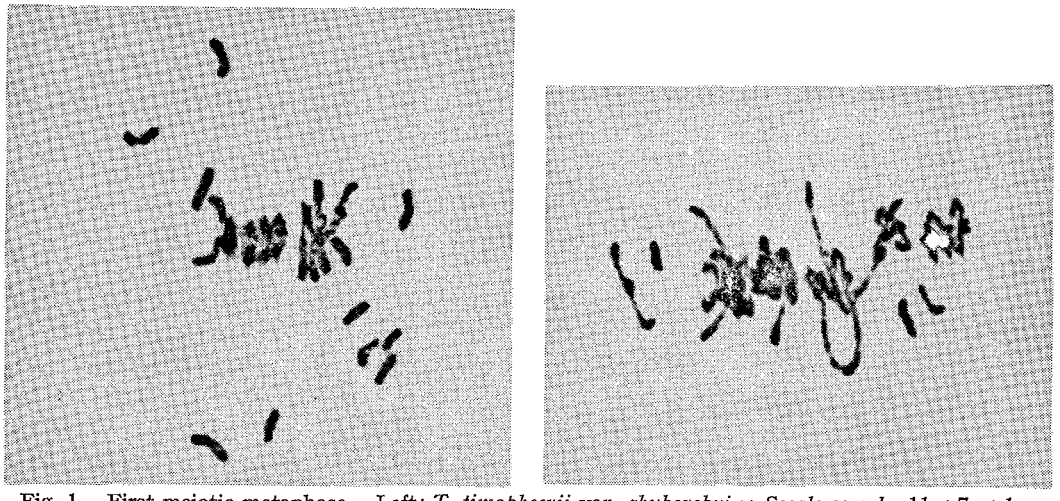

Fig. 1. First meiotic metaphase. Left: *T. timopheevii* var. *zhukovskyi* × *Secale cereale*, $11_I+7_{II}+1_{III}$ Right: *T. timopheevii* var *zhukovskyi*, $2_I+17_{II}+1_{IV}$

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because the formation of quadrivalents does not reach expectation (UPADHYA and SWAMINATHAN, 1963). In induced autotetraploids in the genus the frequency of multivalents also does not reach the theoretical expectation (KIMBER and LARSON, 1973) with approximately 50% of the possible multivalents being observed. Further, polyhaploids of *zhukovskyi*, which would allow the easy recognition of a duplicated genome, are unknown. However, it is possible to make a hybrid situation which, in some ways, simulates a haploid. By crossing *T. timopheevii* var. *zhukovskyi* with an unrelated species, the genomes of *zhukovskyi* are rendered effectively hemizygous and any duplicated genome should be recognized by bivalent formation. At first metaphase of meiosis in the hybrid *T. timopheevii* var. *zhukovskyi* × *Secale cereale* (Table 1), the number of paired chromosomes per cell approximated to 14 (the equivalent of seven bivalents). In fact, in only one cell were there more than 14 univalents, and in both cells with only four bivalents two multivalents were also recorded. Clearly the chromosome pairing in this hybrid is consistent with the hypothesis of a duplicated genome in *T. timopheevii* var. *zhukovskyi*. Interestingly the presence of trivalents and quadrivalents must indicate translocations between chromosomes of the genome that is duplicated in the hybrid and that which is hemizygous.

Table 1. The mean and range of meiotic configurations in the hybrid *T. timopheevii* var. *zhukovskyi* × *S. cereale*

I	II Rod	II Ring	II Total	III	IV	Number of cells
12.65 11-16	3.50 2-7	2.65 0-4	6.15 4-8	0.95 0-2	0.05 0-1	20

The meiosis of *T. timopheevii* var. *zhukovskyi* is tabulated in Table 2.

Table 2. The mean and range of meiotic configurations in *T. timopheevii* var. *zhukovskyi*

I	II Rod	II Ring	II Total	III	IV	V	VI	Number of cells
1.10 0-2	4.10 2-7	10.90 9-13	15.00 10-14	1.10 0-2	1.50 0-3	0.20 0-1	0.10 0-1	10

Results of an analysis of the meiotic chromosome configuration of *zhukovskyi* (Table 2) closely paralleled the findings of UPADHYA and SWAMINATHAN (1963). The total number of chromosomes paired is very similar, but there are small increases in the number of multivalents in the present example. The observation of occasional quinquevalents and sexivalents in our data most probably represents the translocations inferred from the trivalents and quadrivalents seen in the hybrid with rye. Also the frequency of trivalents and quadrivalents in *zhukovskyi* is lower than that expected from the frequency of bivalents in the hybrid with rye. It is possible that there is some selection pressure towards increased

bivalent frequency in *zhukovskyi*, and it could be anticipated that this would be of selective advantage. If this reduction in multivalent formation had a genetic basis and was not simply a physical or spatial limitation on synapsis, it could represent an early stage in the cytological diploidization of the species.

It is also possible that *T. timopheevii* var. *zhukovskyi* carries a regulator of chromosome pairing similar, if not identical, to that in *T. aestivum*. FELDMAN (1966) demonstrated the presence of such a mechanism in *T. timopheevii*, and assuming this species is involved in the evolutionary history of *zhukovskyi*, then it is reasonable to assume that the same allele would be found in *zhukovskyi* also. UPADHYA and SWAMINATHAN (1965) investigated hybrids of *zhukovskyi* with *T. aestivum* with and without chromosome 5B and concluded that *zhukovskyi* did not have a gene equivalent to that on chromosome 5B of *T. aestivum*. However, there was relatively little difference between the meiotic configurations of the two hybrids. In the 5B deficient cross there were only 3.02 more chromosomes paired than in the hybrid which included chromosome 5B. SHANDS and KIMBER (1973) also observed the meiotic configuration of a hybrid *T. timopheevii* var. *zhukovskyi* × *T. aestivum*, and this had only 0.09 paired chromosomes per cell less than the 5B deficient hybrid of UPADHYA and SWAMINATHAN (1963). It would thus appear that there is in fact a mechanism regulating chromosome pairing in *T. timopheevii* var. *zhukovskyi*.

Clearly an increase in bivalent formation and a concomitant reduction in multivalent frequency must offer some selective advantage to *zhukovskyi*. Even with the current reduction, the odd-numbered multivalents and asymetric segregation from even-numbered complexes will give rise to aneuploid gametes and zygotes. The somatic chromosome numbers of 7 progeny of the *zhukovskyi* plant analyzed in Table 2 were distributed as follows; 41–2, 42–4, and 43–1.

From the investigations reported in this contribution and from those of other workers, it is apparent that the genomic constitution of *T. timopheevii* var. *zhukovskyi* is that anticipated of an autoallohexaploid. Further, there is some evidence of a reduction of multivalent configurations not anticipated from the meiotic data of the hybrid with rye. This, together with other, circumstantial evidence indicates that there may be some genetic regulation of chromosome pairing. Additional investigations have already been undertaken.

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Chromosomal location of a gene for male sterility in wheat (*Triticum aestivum*)

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In 1970, FOSSATI and INGOLD isolated in M_2 a male sterile mutant of the variety Probus after applying 24 kR of X-rays to seed. The sterility is due to a single recessive gene, which is normally inherited. They proposed the designation ms^{a1} for this gene.

Chromosomal location of a recessive gene can be done in F_1 from crosses between a monosomic serie and in this case plants heterozygous for the ms^{a1} gene. For 20 chromosomes, there will be no segregation in F_1. The critical chromosome will be segregated in about 35% of sterile plants.

To locate this gene, crosses are made between the 21 monosomics of Probus, a part of the monosomics of Cappelle (kindly provided by Dr. C.N. LAW, Cambridge) with male fertile plants, heterozygous for the ms^{a1} gene. The F_1 is cultivated on the field. Observa-

Table 1. Segregation for male fertile and male sterile plants among the F_1's from crosses of the 21 monosomics of Probus, a part of the monosomics of Cappelle with male fertile plants heterozygous for the ms^{a1} gene

Chromosome	Monos. of Probus		Monos. of Cappelle		Total		Total
	Fertile	Sterile	Fertile	Sterile	Fertile	Sterile	
Probus					47		47
$ms^{a1}ms^{a1} \times$ Prob. (F_2)					81	16	97
Capp. $\times$ $Msms^{a1}$ (F_1)					42		42
1A	37		57		94		94
2A	69		46		115		115
3A	70		32		102		102
4A	40	7			40	7	47
5A	49		19		68		68
6A	27				27		27
7A	49				49		49
1B	43		29		72		72
2B	27		82		109		109
3B	58		52		110		110
4B	69				69		69
5B	46				46		46
6B	86		40		126		126
7B	85		53		138		138
1D	109		39		148		148
2D	86				86		86
3D	49		90		139		139
4D	97				97		97
5D	89		67		156		156
6D	48		28		76		76
7D	21		21		42		42

tions are made during flowering time. The florets of the male sterile plants remain broadly open. The anthers are typically thin and slightly curved, staying mostly in the flower and are not dehiscent. The results of the analyses in F_1 are given in Table 1. In two cases, male sterile plants were found: in the F_2 of the cross male sterile plants with Probus and in the F_1 of the cross mono 4A with heterozygous male fertile plants. Microscopical examination of the anthers of these plants showed nearly only empty pollen. Thus, this recessive gene for male sterility is located on chromosome 4A. The segregation ratios of the F_2 and chromosome 4A do not very well fit in with the expected values. An explanation of this is difficult to give. A lot of plants were lost with an attack by the larvae of an insect (*Agriotes* sp.).

As chromosome 4A is one of the chromosomes carrying a gene or genes for male fertility (SEARS, cited by DRISCOLL, 1973), it might be possible that the male sterility of this mutant is due to a small deletion, behaving as a recessive gene.

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Inheritance of seed coat color of six spring wheats (*Triticum aestivum* L.)

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It has been reported that seed coat color in wheat (*Triticum aestivum* L.) is controlled by three independent genes located on chromosomes 3A, 3B and 3D and the red color is dominant to the white (NILSSON-EHLE 1909, SEARS 1944, ALLAN and VOGEL 1965, METZGER and SILBAUGH 1970). Our present study was to examine the genetics of seed coat color of six spring wheat varieties, with special reference to Sharbati Sonora, presumably an induced white-seeded mutant (VARUGHESE and SWAMINANTHAN 1967), and Lerma Blanco 70, a spontaneously derived white-seeded mutant found in a population of Lerma Rojo 64 by the authors at Davis, California.

Materials and Methods

In 1970 four white-seeded varieties, Safed Lerma, Sharbati Sonora, Chhoti Lerma, and Lerma Blanco 70, one light red-seeded variety, Lerma Rojo 64, and one dark red-seeded variety, Sonora 64, were chosen and used in a diallel cross at Davis, California. The Indian white-seeded varieties, Safed Lerma and Chhoti Lerma, were selected from CIMMYT crosses with the parentage of II 15444={ (Y50×N10-B)L52} Lerma Rojo^3 for Safed Lerma and

II 15929=Lerma Rojo 64 (sib) × Humantla Rojo for Chhoti Lerma. The F_1's and F_2's were then grown in 1971 and 1972 at Davis, respectively. One spike per plant was sampled for all the 15 F_2 populations and the threshed seeds were visually observed and recorded according to the color. The X^2 test was used to test the goodness of fit to the theoretical ratios.

Results and Discussion

Table 1 shows the seed coat color of the parents, F_1 and the segregation of the F_2 populations. No red-seeded plants appeared in the F_1 and F_2 populations of the white (W) × white (W) crosses which indicated the lack of any red alleles in Safed Lerma, Sharbati Sonora, Chhoti Lerma, and Lerma Blanco 70. For the red (R)×W or W×R crosses, the F_1 plants produced red seeds with the same degree of redness of their red-seeded parents. In all these crosses, the red alleles showed very strong dominance over the white alleles. The F_2 populations of R×W and W×R crosses segregated with a ratio of 3 red to 1 white indicating that both red parents have one pair of dominant red genes in homozygous condition. The F_1 seed coat color of the R×R cross showed dark redness same as its dark red-seeded parent Sonora 64. Theoretically, its F_2 should show darker seeds than either of the parents; however, this could not be detected by visual observation. Probably a better method is necessary to determine the slight differences in color. The F_2 population of the R×R cross segregated into 15 red to 1 white indicating that each variety carried one pair of dominant red-seed genes, probably located on different chromosomes.

Based on the segregation situation discussed above, the suggested genotypes for the

Table 1. Segregation of seed coat color in the F_2 populations

Cross	No. of Plants		Expected ratio	χ^2
	red	white		
W×W†				
Safed Lerma × Sharbati Lerma	0	148		
Chhoti Lemra × Sharbati Lerma	0	138		
Chhoti Lerma × Safed Lerma	0	151		
Lerma Blanco 70× Sharbati Lerma	0	135		
Lerma Blanco 70× Safed Lerma	0	180		
Lerma Blanco 70× Chhoti Lerma	0	171		
R×W *or* W×R				
Lerma Rojo 64 × Sharbati Sonora	89	26	3:1	0.004
Lerma Rojo 64 × Safed Lerma	108	28	3:1	1.412
Lerma Rojo 64 × Chhoti Lerma	118	32	3:1	1.075
Lerma Blanco 70× Lerma Rojo 64	141	44	3:1	0.146
Sonora 64× Sharbati Lerma	149	36	3:1	3.029
Sonora 64 × Chhoti Lerma	137	30	3:1	4.418*
Sonora 64 × Safed Lerma	157	42	3:1	1.610
Sonora 64 × Lerma Blanco 70	149	54	3:1	0.277
R×R				
Sonora 64 × Lerma Rojo 64	168	14	15:1	0.646

* $.01<P<.05$ † R=red seed; W=white seed

six varieties used are as follows: Safed Lerma, Sharbati Sonora, Chhoti Lerma, and Lerma Blanco 70, $r_x r_x r_y r_y$; Lerma Rojo 64, $R_x R_x r_y r_y$; Sonora 64, $r_x r_x R_y R_y$. The intensity of red color is less with $R_x R_x$ of Lerma Rojo 64 than $R_y R_y$ of Sonora 64. From these results it is not possible to assign the genotypes to the specific R-loci, viz. R_1, R_2, and R_3.

The discovery of the spontaneous mutation of red-seeded Lerma Rojo 64 to white-seeded Lerma Blanco 70 indicated the possibility of utilizing naturally occurring white-seeded mutants in a breeding program and the possibility of a rather high mutation for the R-locus. Sharbati Sonora was reported by VARUGHESE and SWAMINATHAN (1967) as the direct result of γ-irradiation without any backcrossing after being identified from an M_2 population of 48,500 plants, and it resembled Sonora 64 in all respects except seed coat color. It seems quite possible that Sharbati Sonora could have also arisen as a spontaneous mutant just as Lerma Blanco 70.

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Preliminary location of some chlorina mutants in wheat[1)]

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Chlorophyll mutants received from Dr. Calvin KONZAK (5 mutants) and from Dr. Horst GAUL (20 mutants) were grown in the greenhouse at Columbia, Missouri, and observed. Two of the Konzak mutants and nine of GAUL's could be easily distinguished under our conditions. They were crossed into our test variety Chinese Spring for a varying number of generations. In the second and later generations, heterozygotes were used for the crosses. These were identified by checking that their selfed seed segregated the mutant phenotype. From a selfed generation, mutants were selected to be crossed with monosomics of Chinese Spring.

Since these were all chlorina mutants, and previous work at Missouri and at the University of New South Wales had shown that three such mutants were located on chromo-

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Table 1. Segregation in F_2 from Monosomic F_1's

Cross	Super Chlorina		Chlorina			Green			
	Total No.	No. Mono.	Total No.	No. Dis.	No. Mono.	Total No.	No. Dis.	No. Mono.	No. Null.
685									
×7A			4	1	3	16	-	2	-
×7B			5	4	-	15	-	2	-
×7D	1(died)		3	3	-	16	1	1	-
691									
×7A	2	2	2	2	-	16	1	1	-
×7B			6	4	-	14	-	2	-
×7D	2(died)		2	-	1	16	-	2	-
693									
×7A						20	2	2	-
×7B			5	4	-	2	-	2	-
×7D			3	-	3	17	1	1	-
694									
×7A			3	2	-	17	-	-	1
×7B			5	4	-	15	-	2	-
×7D			8	4	-	12	1	-	-
695									
×7A	1	1	3	1	1	15	-	1	-
×7B	1	1	3	1	2	15	-	2	1
×7D			4	-	1	16	1	1	-
679									
×7A			2	2	-	18	-	1	2
×7B			8	1	2	12	2	-	-
×7D			1(died)	-	-	19	-	3	-

some 7A and one on chromosome 7D, they were crossed to monosomics of group 7 as a first approach to their location. Also, in the past it had been found that sometimes the absence of a homoeologous chromosome resulted in a more extreme phenotype. Thus whenever "super" (extreme) chlorinas were found among the F_2, this was considered an indication that the gene was not on the chromosome tested but on one of its homoeologues. Table 1 lists the results obtained.

For mutant 685 the analysis of the chlorina offspring placed this gene on chromosome 7B or 7D, but in the F_2 of the cross with 7D there was a disomic green plant and also one superchlorina. This makes it unlikely that chromosome 7D is the critical one. Thus mutant 685 is most likely located on chromosome 7B. The same is true for mutant 691. Mutant 693 is almost certainly located on chromosome 7B, since disomics were found among green offspring of the crosses with 7A and 7D. Mutant 694 could be on chromosome 7A or 7B, but 7B seems more likely, so the mutant will first be checked against the others now believed to be on chromosome 7B. These four mutants will be crossed with each other to see whether the same locus in involved.

Mutant 695 is being rechecked, since the results listed in the table were inconclusive. The fact that super chlorinas were found in the crosses with 7A and 7B would favor a location on chromosome 7D; however, in the 7D F_2 the one chlorina analyzed was monosomic, and one of the green seedlings was disomic. There is a strong possibility that monosomic shift caused these results.

Mutant 679 is most likely on chromosome 7A. It will be crossed with one of the mutants that has been confirmed to be located on chromosome 7A.

Morphology and cytology of teratological floral organs of wheat hybrids having *Aegilops caudata* cytoplasm

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Cytoplasmic male sterility (CMS), as a phenomenon responsible for sterility of male reproductive organs of the flower has developed in the course of plant evolution (ZHUKOVSKY 1964). CMS in wheat was first produced experimentally by the Japanese scientists H. KIHARA (1951) and H. FUKASAWA (1953). By translocating the wheat nucleus to alien cytoplasm, they obtained plants which, although manifesting sterility, retained female fertility. This made it possible to pose the problem of utilizing heterosis in wheat breeding.

Since 1962 experiments have been made at the Laboratory of Experimental Biology of Agricultural Plants on the transfer of wheat genomes to different cytoplasms. Both male sterility and the specific effect of alien cytoplasm were found in the CMS wheat hybrids. Thus, plants having *Triticum timopheevi* cytoplasm possess good viability and a normal growing period. *Aegilops ovata* cytoplasm causes a longer vegetative period and a vigorous growth of vegetative material. Hybrids having *Aegilops caudata* cytoplasm are characterized by reduced female fertility. The findings of some researchers (KIHARA and TSUNEWAKI 1964, KIHARA 1967, PORTER, KEITH and ATKINS 1965) and our observations show that the development of the female organs in these hybrids is disturbed as a result of the transformation of stamens into pistils and pistillody is manifested.

Analysis of published data on the transformation of male sex into female demonstrates that it can be caused by a number of reasons, such as unfavourable ecological factors (TUTAYUK 1969) or produced experimentally (BRESLAVETS 1936, 1938, 1946, MININA 1952, LVOVA 1963) as well as during hybridization (LUBIMOVA 1951, 1968).

As mentioned above, we have come across genetically-based transformation of stamens into pistils in our studies of a CMS hybrid having *Aegilops caudata* cytoplasm and *Triticum aestivum* nucleus (var. *erythrospermum*, the 16th backcross). The hybrid seeds

were received from Professor H. KIHARA by Academician I.E. GLUSHCHENKO who kindly offered them for our work.

During 1970～1972 this hybrid having *Ae. caudata* cytoplasm was crossed with spring wheat varieties including Saratovskaya 29, Moskovka, Krasnozernaya and others. It is interesting to note that under new growing conditions in Moscow crosses between this hybrid and *T. aestivum* varieties retained the CMS trait and also showed pistillody. This phenomenon was observed in a large number of florets. Analysis of florets in spikes of hybrid plants is given in Table 1.

Table 1. Morphology of florets in CMS wheat hybrid having *Ae. caudata* (B_{18} *S. caudata* × Moskovka)

Total number of spikes studied	Total number of florets studied	Including							
		Florets with 1 pistil and 3 stamens		Florets with 2 pistils and 2 stamens		Florets with 3 pistils and 1 stamen		Florets with 4 pistils without stamens	
		Number	% of total	Number	% of total	Number	% of total	Number	% of total
10	203	31	14.5	60	29.5	70	30.4	42	21.6

The Table shows that 85.5% of florets were pistilloid, i.e. had 2, 3 or 4 pistils and fewer stamens, and only 14.5% had normally a single pistil and 3 stamens with sterile pollen grains in the anthers. It should be noted that degeneration of pollen grains in the anthers of pistilloid florets not affected by the transformation proceeds similarly to that in CMS hybrids. Analysis of florets along the spike shows that basal florets have generally four pistils while apical florets-one or two.

Pistillody of the hybrids studied manifests itself in the transformation of stamens into pistils and involves one, two or all the three stamens. Depending on this the floret becomes two-, three- or four-pistilled while the number of stamens reduces to two, one or is missing altogether. A pistil can be formed on a stamen at the apex of the anther, in the middle or basal part of it or even in the filament. The stamen thus resembles a female floret in appearance.

Among polygynous florets, transitional forms are found which carry the traits both of stamens and pistils. Stamens with hardly noticeable pubescence at the terminal part as well as well-defined stigmas with characteristic hairs were observed among them. In some stamens the transformation into pistils involved one half of the anther while the other remained unchanged. There was a numerous group of stamens whose basal part turned into the ovary. Finally, there was another group of stamens which completely turned into pistils where the stigma and ovaries were differentiated.

Transitional forms from male to female sex are of interest cytoembryologically. For the sake of convinience, we shall dwell on the results of studying florets with a single pistil and three stamens, then on pistilloid florets with two, three and four pistils. During the

study of permanent preparations made by standard cytological methods, normally developed ovules were found in the ovaries of florets with three stamens and a single pistil. The ovules had outer and inner integuments, a nucellus with an embryo sac containing the egg-apparatus of two synergids, and an egg cell (Fig. 1). Polar nuclei in the embryo sacs were normally positioned under the egg cell, and ten to twelve antipodal cells either in the chalazal area or at one of the lateral sides. The ovaries with the ovules containing normally structured embryo sacs were considered fertile, capable of forming grain as a whole.

However, there were embryo sacs with changed antipodal cells compared to fertile plants. The changes occured in the cytoplasm, nucleus and nucleolus of the antipodal cells. In most cases the cytoplasm was more vacuolized compared to the normal state. Large vacuoli were formed as a result of fusion of smaller ones. Clumps of chromatin appeared in the nuclei which did not resemble chromosomes in form. The nucleoli differed in size and form. They were much larger not round as usual, but rod-like elongated and not vacuolated.

Since such changes in the antipodal cells were found in the embryo sacs of CMS

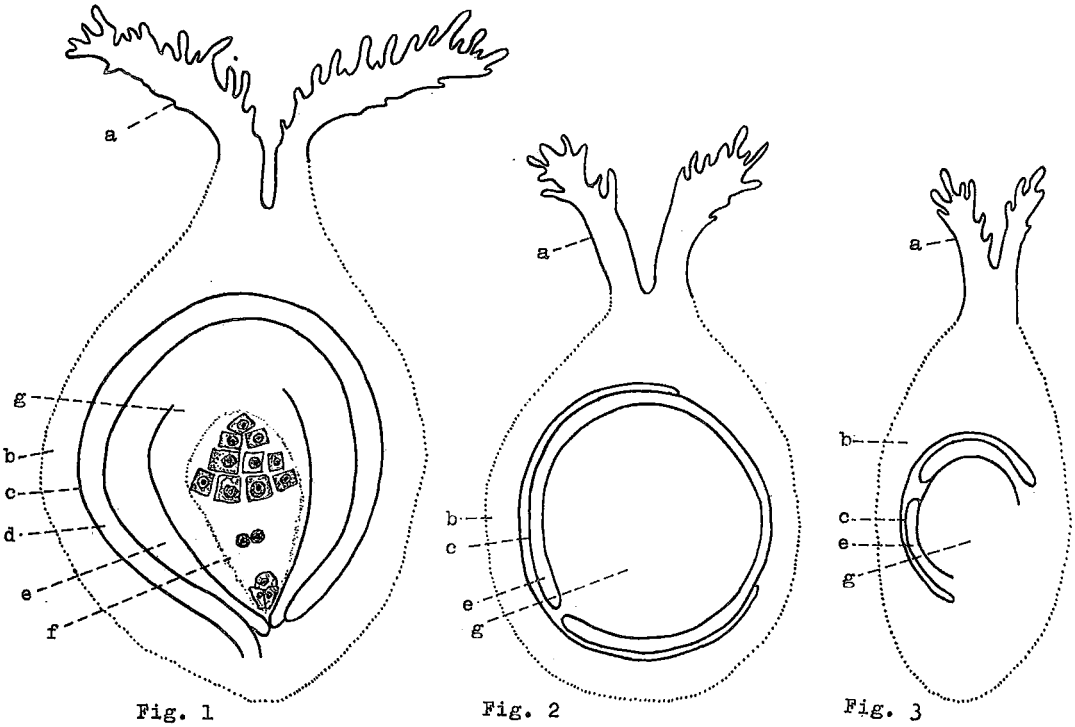

Fig. 1 Fig. 2 Fig. 3

Fig. 1. Schematic representation of the morphology of the pistil of a monogynous floret of the wheat hybrid B_{18} *S. caudata* × Moskovka
a) stigma, b) ovary, c) ovule, d) outer integument, e) inner integument, f) mature embryo sac, g) nucellus of the ovule.
Fig. 2. Main pistil of a pistilloid flower of the same hybrid (the same designations as in Fig. 1)
Fig. 3. Additional pistil transformed from the stamen (the same designations).

plants and were not observed normally, they may be related to the manifestation of the cytoplasmic factor responsible for pollen sterility.

In florets with one pisitil of interest is also the fact that some ovules were underdeveloped: the mother-cells of the macrospores in them were not differentiated, i.e. the cells whose development results in the long run in the formation of the embryo sacs.

Studies of polygynous florets show that one pistil, the central (we term it the main pistil) in all pistilloid florets is normal, a pubescent stigma is clearly seen in its upper part and the ovary in the lower part. Investigations revealed that the ovules were formed in the ovaries (Fig. 2). However, the ovules cease the development. The outer coats do not develop, the mother cells of the macrospores and embryo sacs do not differentiate. The ovules of the main pistils should be considered sterile. It should be noted that the ovaries were fixed in the period of expected maturity of the embryo sacs.

Of particular interest were studies of additional pistils transformed from stamens with well defined stigmas and ovaries. They were somewhat smaller in size compared to the main pistils. In additional pistils the ovules in the ovaries were more elongated than those in the main pistils. The peculiarity of the ovules in additional pistils was that only the inner integument was formed while the outer one did not develop (Fig. 3). Mother cells of the macrospores in the ovules were not differentiated and no embryo sacs were formed. Thus, they were as sterile as ovules in the main pistils. Sterility of the ovules in both cases in polygynous florets must be attributed to the manifestation of specific interaction of wheat genome with alien cytoplasm. Some authors indicate low seed set (14 to 20%) typical of CMS hybrids having *Ae. caudata* cytoplasm (PORTER, KEITH, ATKINS 1966; KIHARA, TSUNEWAKI 1964 and others). In our experiments with controlled pollination of non-emasculated bagged florets in 1973, the percent of seed set ranged from 8 to 28%. Evidently in this case seed set is determined by florets with one pistil which occured approximately in the same proportion (Table 1). As embryological studies indicate, they had normally developed ovaries, ovules and embryo sacs. Our findings show that pistillody clearly expressed in wheat hybrids having *Ae. caudata* cytoplasm, disturbes the development of female generative sphere, sterilises the ovaries of the main and additional pistils. This is one of the reasons why seed set is low.

Decreased fertility resulting from the disturbance of the female generative organs is the only case of the total number of CMS wheat lines studied and it reflects the specific nature of the interaction between *Ae. caudata* cytoplasm and wheat genomes used as a parental form for backcrossing.

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Persistent modifications and their genetic importance for spring wheat breeding

Part I

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In biology there circulates an opinion that modificational variability does not affect genetical characters and properties of organisms (I).

Carrying out a number of experiments some scientists have come across the facts that made them introduce amendments into the notion about the modificational variability. The term "persistent modifications" has been firmly established in science for a long time. This term designates the fact of retaining during a number of generations the changes induced by the environment. These changes are retained when the influencing agent is eliminated and they are inherited by the maternal lines.

For a long time many investigators have been interested in the following problem: can persistent modifications turn into hereditary changes and is it possible by having studied this phenomenon to make it solve the problems of breeding? As far back as 1932 N.I. VAVILOV dwelled at length on the problem of theoretical and practical importance of

studying the phenomenon of persistent modifications, of elucidating their nature and types, and the factors inducing these modifications. N.I. VAVILOV wrote: "Of great theoretical interest is the problem of persistent modifications changing into mutations, the influence of persistent modifications on the mutational ability of the organism....". However the phenamenon of persistent modifications has been studied very poorly up to now and it occupies rather vague position in the hereditary science. Experimental material on this problem, accumulated by microbiologists, protistologists, entomologists and plant breeders, deserves thorough study.

During many years of research (1965–1975) in spring wheat we have obtained evidence that persistent modifications are not only observed in seberal generations, but also can turn into hereditary changes. It has been shown that the variability of the character "winter habit – spring habit", induced by partial vernalization and spring sowing of winter varieties under uncontrolled (field) conditions, is expressed in two directions – as common modifications and as persistent modifications. The latter are consolidated from the third to the fifth generations and become stable later on. The influence of extreme conditions at the earlier stages of plant development both during the year of vernalization and during the growth of successive generations has been the decisive factor of this complicated process. The influence of unusually high temperatures, long day and other factors at the early stages of organogenesis disturbs the normal reaction of the organism as a result of which a homogeneous variety turns into a heterogeneous population in which there are created preconditions for the genetical change of the character "winter habit" into "spring habit".

This shows that the cropped up modifications can autoreproduce, intensify, and serve as a basis for a hereditary change of a certain character and property, which is of great interest for breeders.

The problems associated with the genetical transformation of the character "winter habit – spring habit" in a number of wheat varieties are stated below.

For the experiment there were taken varieties with different length of the vernalization stage (Kavkaz and Bezostaya 1, 40 days; PPG 186, 55 days; Mironovskaya 808, 60 days; IGEN 3, 80 days). The seeds of these winter varieties were vernalized during different number of days (from 5 days to complete vernalization) and sown at the beginning of May. The number of shoots was counted. On all heading plants of the first, second, and often third generations paper bags were put. The numbers of heading and shooting plants were counted once a month.

In successive years the seeds of heading plants were sown during the first ten days of May by families without extra vernalization.

We have shown that the dynamics of the vernalization stage has its turning points, at which the influence causes the highest effect. The highest possible reformation of developmental rhythms is observed, as a rule, in plants which were vernalized lesser number of days when compared with the date that caused mass plant heading.

The importance of partial vernalization for the transformation of the "winter habit" character

Partial vernalization and sowing winter plants in spring makes labile plant material even during the first year. Growth and developmental conditions determine whether the offspring will be spring-habited or become in time winter-habited. The influence of the conditions of different years (for instance, favourable summer in 1971 and very hot summer in 1972) on the vernalization of winter wheat seeds of the variety Kavkaz is seen from the data of Table 1.

Table 1. Heading in winter wheat plants of the variety Kavkaz in different years of vernalization and growing[1)]

Treatment (number of vernalization days)	1971			1972		
	Number of plants	Headed plants, %	Date of heading	Number of plants	Headed plants, %	Date of heading
10	114	1.7	29. VIII	257	8.4	22. VII
15	135	3.0	17. VIII	228	12.5	20. VII
20	110	9.1	30. VII	279	47.0	19. VII
25	110	30.0	15. VII	343	93.3	10. VII
30	115	49.6	10. VII	330	94.3	26. VI
35	123	96.5	5. VII	334	95.3	28. VI
40	78	100	8. VII	228	100.0	28. VI
Control	1125	0.4	30. VIII	1250	4.1	26. VIII

1) The sowing took place on the 5th of May.

As it is seen from the given data, in 1971 the process of complete vernalization under field conditions did not go so easily as in 1972. In the second case the partial vernalization (10, 15, 20, 25 and 30 days) induced heading of 2; 3 and even 4 fold greater number of plants than in the previous year. Maximum of headed plants was observed when seeds were vernalized during 20 and 25 days. The heading also began a little earlier. One can suppose that plants will also behave differently in the next generations. This is proved by the study of the first generation obtained from partial vernalization of seeds of the variety Kavkaz (Table 2).

The given data show that the conditions in 1971 ensured better heading of the first generation when compared with the year 1972. Almost in all treatments the number of spring plants was a little higher in the complete vernalization treatment in 1971 than in 1972. For instance 10 days of vernalization gave in the first case 39.7% of headed plants and in the second case only 18.7%, while 30 days of vernalization gave 39.5 and 0% of headed plants respectively. Very interesting is also the fact that partial vernalization during 20 and 30 days in 1971 ensured complete heading, 1.9 and 47.7% of total families respectively, while in the first generation from the vernalization in 1972 this was not the case.

Similar data were obtained in the experiments with the variety Bezostaya 1. The

Table 2. Heading in the first generation plants of the variety Kavkaz in different years of vernalization[1)]

Number of vernalization days	Year of sowing	Total number of families	Number of spring families, %	Number of semispring families, %	Total number of plants	Number of plants, %	Data of heading
10	1972	15	0	33.3	78	39.7	18. VII
10	1973	3	0	33.3	16	18.7	26. VI
15	1972	6	0	16.6	20	10.0	2. VII
15	1973	6	0	33.3	37	10.8	20. VII
20	1972	52	1.9	34.7	185	24.9	2. VII
20	1973	22	0	31.7	360	17.7	13. VII
25	1972	17	0	82.3	263	29.7	15. VII
25	1973	50	0	2.0	958	0.1	4. VII
30	1972	42	47.7	52.3	570	39.5	29. VI
30	1973	5	0	0	165	0	–

1) The sowing took place from the 5th to the 8th of May.

vernalization during 25, 30 and 40 days in 1968 ensured mass and early heding of the first generation plants, grown in 1968 (96.6, 78.9 and 50.5%). The partial vernalization in 1969 gave considerably less headed plants in the first generation (10.5, 10.0 and 2.1%), the heading took place almost a month later.

The examined material allows us to come to a conclusion that the influence of the conditions of the first year of growing on the vernalized seeds difines the extent of the transformation of the character "winter habit – spring habit" in subsequent generations.

Persistent modifications and their genetic importance for spring wheat breeding

Part II

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Transformation of the character "winter habit - spring habit" in wheat varieties with different length of the vernalization stage

The study of the variability of the character "winter habit" in short-staged (Bezostaya 1) and long-staged (PPG–186, Mironovskaya 808 and IGEN 3) wheat varieties has shown considerable differences. The work on the winter wheat Bezostaya 1 was begun in 1965. The experiments were repeated many times with nearly the same results. The chromosomal apparatus was studied in the spring forms of the fifth generations. All plants had normal chromosome numbers (2n=42). The monosomal analysis of the transformed

material was begun in the same generation. There were analysed F_1 and F_2, obtained from crossing the lines 5A, 2B and 5D of Chinese Spring wheat with the spring whest Bezostaya 1. The analysis confirmed the stability of the transformed spring forms.

At present breeding work has been carried out on the transformed tenth generation of the spring wheat Bezostaya 1 and on the seventh generation of the spring wheat Mironovskaya 808.

We shall examine at greater length the third generation of the varieties Bezostaya 1, Mironovskaya 808, PPG–186, IGEN–3, partial vernalization of which took place in 1970. This experiment particularly shows the differentiation of the characters of "winter habit" and "spring habit" when compared with the preceeding generations. During all three years experimental plants were grown under individual isolation.

Unlike the experiments of the preceeding years the change in the character of Bezostaya 1 has taken place in the treatments having longer periods of vernalization (Table 3). Thus, 35 days of vernalization in the third generation gave 85.3% of spring plants, 40 days of vernalization induced restoration of the character "winter habit", and 45 days of vernalization consolidated the character "spring habit" in all experimental plants.

Of special interest is the work on the variety Mironovskaya 808. The data given in Table 4 show that all the plants in the third generation of the 15 days treatment restored winter habit, though the rate of spring forms in the two preceeding generations was rather high. In the treatment of 50 and 55 days of vernalization all the plants were transformed into spring plants. Short periods (three days) of mass and early (from the 20th to the 23d of June) heading in the third generation show that three years suffice to transform the plants of the variety Mironovskaya 808 into spring forms.

The plants of the variety PPG–186 behaved differently. The number of spring

Table 3. Dynamics of heading in the winter variety Bezostaya 1 in three generations

Generation	Number of vernalization days	Year of sowing	Total number of families	Number of spring families %	Number of semispring families %	Total number of plants	Number of spring plants, %	Data of heading
1	35	1971	123	0	4.9	1142	2.6	30. VII
2	35	1972	12	0	100.0	86	47.7	28. VI
3	35	1973	5	40.0	60.0	129	85.3	3. VII
1	40	1971	146	0	0.7	1242	0.9	2. VIII
2	40	1972	3	0	100.0	21	47.7	5. VII
3	40	1973	1	0	0	13	0	-
1	45	1971	146	0	4.8	1136	18.6	10. VII
2	45	1972	5	0	80.0	54	40.7	8. VII
3	45	1973	10	100.0	0	141	100.0	13. VII
Control								
-	0	1971	-	-	-	1401	3.4	6. VIII
-	0	1972	-	-	-	3475	4.1	18. VIII
-	0	1973	-	-	-	398	7.0	14. VIII

Table 4. Dynamics of heading in the winter wheat of the variety Mironovskaya 808 in three generations

Generation	Number of vernalization days	Year of sowing	Total number of families	Number of spring families, %	Number of semispring families, %	Total number of plants	Number of spring plants, %	Data of heading
1	15	1971	3	0	66.7	21	33.9	16. VII
2	15	1972	3	33.3	33.3	33	48.4	23. VI
3	15	1973	6	0	0	87	0	-
1	50	1971	161	0	1.2	1316	0.6	9. VII
2	50	1972	4	0	100.0	69	85.6	24. VI
3	50	1973	9	100.0	-	177	100.0	20. VI
1	55	1971	47	0	10.1	727	3.4	30. VI
2	55	1972	4	75.0	25.0	47	58.4	26. VI
3	55	1973	18	100.0	-	496	100.0	20. VI
Control								
-	0	1971	-	-	-	2325	0.08	30. IX
-	0	1972	-	-	-	1250	0.9	27. IX
-	0	1973	-	-	-	453	0	-

forms increased in the second generation when compared with the first generation, but in the third generation the plants of 35 and 55 days of vernalization had complete restoration of winter habit. In the treatment of 30 days of vernalization the rate of spring plants decreased to 1.2%. In the treatment of 40 days of vernalization the number of spring plants increased and amounted to 97.4% in the third generation. Three years of spring resowing are not enough for making stable spring habit in the plants of this variety.

In a number of experiments we have not succeeded in transforming plants of the most long-staged variety IGEN-3 into spring plants. The plants which headed during previous years restored their winter habit in the second or third generations. The first reassuring results were obtained in the treatments of 40 and 65 days of vernalization which took place in 1970. Early and mass heading of the plants after 40 days of vernalization favoured persistent spring habit in successive generations.

The analused material allowed to draw a conclusion that directed transformation of winter forms into spring forms is possible.

Persistent modifications and their genetic importance for spring wheat breeding

Part III

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Persistent modifications obtained during the transformation of winter habit into spring habit

In our work modificational variability preceeded hereditary consolidation of the studied character. As it had already been said, transformation depended on the number of days of seed vernalization, on the state of plants, and the conditions of the year, both during seed vernalization and during growing the first and the second generations. It is precisely this that accounts for considerable differences in plant behavior during vernalization in different years, their change towards spring habit or their restoration of winter habit.

Thus, in the first generation of the variety Bezostaya 1 out of 415 sown families of the treatments 35, 40 and 45 days of vernalization 85.9% families (98.4% of plants) remained winter-habited. In the second generation 20 families were sown and all of them turned out to be semispring-habited. Out of 161 plants in the experiment 54.8% restored their winter type of development. In the third generation 16 families were sown and 56.3% of them were winter-habited. Out of 273 plants 11.7% turned out to be winter-habited.

In the first generation of the variety Mironovskaya 808 out of 211 families of all treatments 95.7% families (98.2% out of 2064 plants) remained winter-habited. The second generation was represented by 11 families; one family become completely winter-habited (45 plants out of 149 plants or 30.3%). In the third generation, comprising 33 families, 6 families or 18.8% were winter-habited. Out of 760 plants 87 (11.5%) turned out to be winter-habited (on account of the treatment of 15 days of vernalization in which all plants reversed towards winter-habit).

In the first generation of the variety PPG–186, 253 families were sown; out of them 94.6% of families (98% of plants) remained winter-habited. In the second generation one family out of 21 retained its winter habit. Out of 140 plants 33.2% restored their winter habit. In the third generation out of 67 families 26.9% of families (19.3% of plants) were winter-habited.

Modificational variability is expressed specifically by different varieties in different years. Thus, if in the variety IGEN–3 it ends more often in the second generation and in Mironovskaya 808 in this generation there takes place a strongly pronounced differentiation into winter and spring forms, in Bezostaya 1 it is observed up to the fifth generation. Thus, in the experiment with partial vernalization, begun in 1965, the rate of spring plants

of the variety Bezostaya 1 increased from the first to the fifth generations and equaled 16.3, 27.0, 43.4, 98.5. and 100% respectively. In the similar experiment, repeated in 1968, in the fifth generation 61.3% out of 6121 studied plants were spring-habited, and 38.7% of plants reversed to winter habit.

It follows from the above mentioned that transformation of persistent modifications into genotypical changes is accomplished in some varieties in the early generations and in the others in fairly late generations.

Control plant material

Control plants of the initial varieties of winter wheat, sown in spring without vernalization of seeds, differed by their vernalization stage. In August and September there was observed in short-staged varieties (Bezostaya 1) heading of a small rate of plants. In 1969, 7.9% of headed plants were observed in the control; small part of them gave half-mature seeds. When sown for the second time in spring (the first generation), 87.5% of spring-habited plants were obtained. In the second generation the rate of spring-habited plants decreased to 23.1, in the third and forth generations it equaled 82% and 83.9% respectively. In another treatment of the experiment the headed plants in the control of Bezostaya 1 variety equaled 1.1%, in the first generation 34.4%, and in the third generation all of them restored their winter habit.

Thus, the control plants of short-staged varieties behave similarly to the experimental plants; according to natural conditions of complete vernalization they can give spring offspring or restore their winter habit.

In long-staged varieties we have another situation. For instance in the control plants of Mironovskaya 808 there headed in 1969 by the 15th of September only one plant, in 1970 on the 30th September – only one plant, in 1971 two plants shooted, in 1972 one plant shooted, in 1973 no shooting and no heading was observed. The number of plants in the control in all years equaled 7253. Similar data are also obtained in other long-staded varieties (PPG–186, IGEN–3).

If under Moscow district conditions transformation of the character "winter habit" into "spring habit" can occur when Bezostaya 1 plants are sown in spring (without preliminary vernalization), the desirable result in the varieties Mironovskaya 808, PPG–186 and IGEN–3 can be obtained only by partial vernalization.

The importance of transformation method for plant breeding

The change of winter habit is not an independent process; this change involves the change of other biological and morphological properties and characters and in particular the length and strength of the stem, resistance to lodging, the form and length of the ear, grain quality, etc.

Similar results have been obtained by twice performed partial vernalization of the variety Mironovskaya 808 in 1968 and 1970. In both cases spring forms were obtained in

the third generation. The diversity of plants in the fifth generation has been studied (Table 5). The treatment of 35 days of vernalization comprised 26 families which differed by the studied characters. There were also short-stemmed families among them (26.9%). Approximately one half of the plants had the stem of medium thickness, which usually ensures better resistance to lodging. There were observed differences in ear length (7–11 sm.), 1000 kernel weight (30–40 g.), grain characters (61% of the lines had vitreous grain) and even in maturing (one family was late-maturing). Similar variability was also observed in the other treatments (50 and 55 days of vernalization).

Table 5. Characteristics of the fifth generation of the variety Mironovskaya 808, the rate of families possessing the characters mentioned below

Number of vernalization days	Number of families	Plant height, sm			Straw		Resistance to lodging		Ear form	
		60–70	71–80	81–100	Medium	Thin	+	–	Prismatic	Spindle-like
35	26	26.9	15.4	57.7	42.3	57.7	19.2	80.8	0	10.0
50	21	19.1	38.2	42.7	85.7	14.3	23.8	76.2	0	100
55	50	20.0	38.0	42.0	72.0	28	22	78	0	100

Ear length		1000 kernel weight, g		Grain characteristics		Maturing	
7–9	10–11	30–35	35–40	Vitreous grain	Semivitreous grain	Early	Late
84.5	15.5	92.3	7.7	61.5	38.5	96.2	3.8
90.5	9.5	100	0	85.7	14.3	100	0
92.5	8.0	96.0	4.0	88.0	12.0	100	0

Will these differences disappear in later generations? In order to give an answer to this question we have studied the eighth generation of Bezostaya 1, obtained from the treatments of 28, 35 and 41 days of vernalization in 1965. Here we have found still greater differences. All three treatments had dwarf forms with length up to 60 sm (4.4–52.7%). The ear form in general retained; small number of plants had spindle-like ears (from 0 to 10.5%). The length of the ear greatly varied (from 4 to 12 sm.). Most of the families had vitreous grain and some of the lines had semi-vitreos grain. The difference in 1000 kernel weight between some families equaled 12 g. They also differed in their vegetative period; parallel with extremely early families there have been obtained late-maturing families (up to 6.3%).

Of special interest is grain quality. The grain of the transformed spring wheat Bezostaya 1 was sent for technological analysis. Initial winter wheat Bezostaya 1 and the strong spring variety Saratovskaya 29 were used for comparison.

The results show that protein content in grain varied from 14.88 to 17.96% (in the winter control Bezostaya 1 it equaled 12.37%), raw gluten content from 32.5 to 45.6% (25% in the control,) flour strength from 246 to 454 g. (194 J. in the control), sedimentation

index from 8.2 to 10.8 ml. (4.1 ml. in the control), bread volume yield from 486 to 544 sm^3 (488 sm^3 in the control). Saratovskaya 29 in all indices of the analysis, except flour strength, was inferior when compared to spring forms of Bezostaya 1.

The given data indicate wide divergence of characters, which is very important for breeders.

In this connection in 1974 the transformed forms of wheat (33 spring lines of the sixth generation of the variety Mironovskaya 808 and 25 spring lines of the sixth and nineth generations of the variety Bezostaya 1) were sent to Mironovka Institute of Wheat Breeding for breeding evaluation. As the obtained data indicate, 27 spring lines of the variety Mironovskaya 808 (82%) were superior in yield when compared with the standard variety; the increase in most cases equaled 5–10 and up to 14 c/ha. 18% of the lines were inferior in yield when compared with the standart. 20 lines of Bezostaya 1 (80%) exceeded the standard in their yield; the increase amounted to 12 c/ha. Later the best lines were included into competitive trials.

Consequently the method of obtaining directed mutations can be broadly used in breeding both winter and spring wheats.

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A synthetic hexaploid wheat with fragile rachis[1)]

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It is generally believed that no wild form of hexaploid wheat exists – that this species is completely dependent on man for its dispersal. Whereas the wild diploid and tetraploid wheats have a fragile rachis that allows the spike to shatter into segments when ripe, the spike of the common wheats and even the presumed ancestral hexaploid wheats, the spelta wheats, is non-fragile. The hexaploids thus lack an adequate means of seed dispersal.

Since hexaploid wheat evidently did not originate until after man had already begun to cultivate diploid and tetraploid wheat, it might be assumed that no wild type ever existed. Strong support for this view was provided by the report of MCFADDEN and SEARS (1947) that the amphiploid between wild emmer and *T. tauschii* (=*Aegilops squarrosa*), which reconstitutes spelta wheat, has a non-fragile rachis. Such a result was not unexpected in view of SEARS's previous finding (1941) that the amphiploid between wild einkorn and *T. tauschii* has a relatively tough rachis. The rachis breaks in different places in the two parents, and the amphiploid is intermediate in its tendency to break at each place. Since wild emmer has the same type of fragility as wild einkorn, its amphiploid with *T. tauschii* could also be expected to be non-fragile.

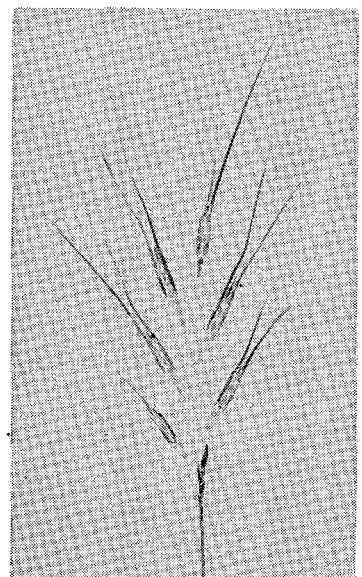

Fig. 1. Spike of a sterile hybrid between wild emmer and *Triticum tauschii*.

However, DEKAPRELEVICH (1961) reported finding a hexaploid, fragile-rachised wheat growing wild in Russian Georgia. Subsequently, it became clear that the supposed wild emmer used by MCFADDEN and SEARS in resynthesizing spelta wheat was not really wild at all but had a tough rachis and was therefore a cultivated emmer. This led to the question whether an amphiploid between a truly wild emmer and *T. tauschii* would have a fragile rachis even though wild einkorn × *T. tauschii* does not. With the B genome present and presumably acting toward the same type of fragility as that determined by the A genome, it

1) Cooperative investigations of the Agricultural Research Service, U.S. Department of Agriculture, and the Missouri Agricultural Experiment Station. Journal Paper No. 7410 of the Missouri Station.

seemed possible that the fragility of the wild emmer might be epistatic in the amphiploid between it and *T. tauschii*. It was this emmer type of fragility that DEKAPRELEVICH found in the Georgian wheat.

If the amphiploid wild emmer × *T. tauschii* has a fragile rachis, then as KUCKUCK (1964) has suggested, the wheat of DEKAPRELEVICH may have originated as such an amphiploid, independently of the cultivated hexaploids, which are believed to have involved cultivated emmer as their tetraploid parent. Both wild emmer and *T. tauschii* are native to the area concerned.

When 40 spikes of a true wild emmer (from Israel) were pollinated by *T. tauschii*, two viable seeds were obtained. These were kindly germinated on nutrient agar by Dr. W. F. SHERIDAN.

The two plants obtained proved semi-lethal, too weak for treatment with colchicine. Both eventually flowered, however, and although they were completely sterile, the spikes could be observed to be fragile (Fig. 1). Since the effect of sterility is to make the rachis less, not more, fragile, it seems safe to conclude that a fertile hybrid between wild emmer and *T. tauschii* would have fragile spikes. Whether DEKAPRELEVICH's wild hexaploid actually originated in this way or as a segregate from a cross of a cultivated hexaploid with wild emmer remains uncertain.

Seven other synthetic hexaploids reported by MCFADDEN and SEARS (1941) had the supposedly wild tetraploid wheat as one parent. One involved *T. speltoides* (=*Ae. speltoides*) and had a "relatively nonfragile" rachis. Presumably if a truly wild tetraploid had been the wheat parent, this amphiploid would have been fragile.

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Origin of *Triticum zhukovskyi*

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The parentage of a polyploids of recent origin can be confirmed if the hybrid involving the polyploid and the synthetic amphiploid between its presumable parents is fertile. This has been accomplished in the case of *T. aestivum* ssp. *spelta* (MCFADDEN and SEARS 1944). Evidence from karyotype studies (UPADHYA and SWAMINATHAN 1963) and protein electrophoresis (JOHNSON 1968) suggested that *T. zhukovskyi* ($A^zA^zA^tA^tB^tB^t$) presumably originated as an amphiploid between *T. timopheevi* ($A^tA^tB^tB^t$) and *T. monococcum* (AA). However, this has not been established unequivocally by artificial synthesis of *T. zhukovskyi*. WATANABE *et. al.* (1956) synthesized the *T. timopheevi* – *T. monococcum* amphiploid but it was not test crossed with *T. zhukovskyi*. Subsequent attempts to synthesize *T. zhukovskyi* were unsuccessful (UPADHYA and SWAMINATHAN 1965).

In this article we are reporting chromosome pairing and fertility of synthetic amphiploids involving *T. araraticum* (wild prototype of *T. timopheevi*) and *T. boeoticum* (presumed wild prototype of *T. monococcum*), and F_1 hybrids between the amphiploids and *T. zhukovskyi*. Results reported here confirm the previous finding that *T. zhukovskyi* originated as an amphiploid between *T. timopheevi* and *T. monococcum*.

Materials and Methods

To synthesize the amphiploids, triploid hybrids were made between *T. araraticum* (1767, 2659) and *T. boeoticum* (1815, 2578) instead of between their cultivated types *T. timopheevi* and *T. monococcum*. In order to induce polyploidy the seedlings of the *araraticum* × *boeoticum* triploid hybrids were treated by dipping their plumules into 0.4% aqueous colchine solution for 45 minutes. Alternatively, seedlings (0.5 cm plumule) were treated with nitrous oxide gas for 24 hrs. at 8 atmospheres pressure and were transplanted directly into the soil. Two of the three *araraticum-boeoticum* amphiploids were crossed with *T. zhukovskyi* (986). Sporocyte material was fixed in Cornoys fluid (6:3:1) for 8 hrs. and anther squashes were made in 1% propiono-orcein. Chromosome association was scored from meiotic metaphase I cells.

Results and Discussion

Results of chromosome association and fertility of *T. zhukovskyi*, *T. araraticum* × *T. boeotocium* hybrids, *araraticum-boeoticum* amphiploids and F_1 hybrids between *T. zhukovskyi* and the amphiploids are given in Table 1.

A high frequency of multivalents in *T. zhukovskyi* (0.35 III+1.35 IV) indicates that it is not completely diploidized like other polyploid wheats. The multivalent association could

Table 1 Average and range (parenthesis) of chromosome association at metaphase I of meiosis and male and female fertility

Species	No. of cells studied	Frequency of						Fertility %	
		I	II		III	IV	V or higher association	Male	Female
			Ring	Rod					
*T. zhukovskyi**	48	1.42 (0-6)	16.89** (11-21)	—	0.35 (0-2)	1.35 (0-4)	—	80.00	63.80
F_1 hybrid *T. araraticum* × *T. boeoticum*									
1767×2578	52	9.22 (6-13)	2.20 (0-5)	2.45 (0-7)	0.26 (0-3)	0.03 (0-1)	—	0.00	0.00
2659×2578	50	7.70 (4-13)	1.60 (0-3)	3.12 (0-6)	0.30 (0-3)	0.02 (0-1)	0.02 (0.1)	0.00	0.00
Amphiploid *araraticum-boeoticum*									
1767×1815	30	1.34 (0-4)	14.45 (10-18)	4.32 (0-8)	0.17 (0-2)	0.69 (0-2)	—	92.19	93.40
1767×2578	38	0.55 (0-4)	16.34 (12-19)	2.74 (0-7)	0.06 (0-1)	0.77 (0-2)	—	91.89	91.42
2659×2578	20	0.53 (0-2)	16.58 (12-19)	2.39 (0-6)	0.00	0.95 (0-2)	—	82.81	58.06
F_1 hybrid *T. zhukovskyi* × *araraticum-boeoticum* amphiploid									
986×amph. 1767×1815	20	1.15 (0-6)	11.46 (8-15)	4.15 (1-7)	0.54 (0-2)	2.00 (0-3)	—	82.92	42.85
986×amph. 1767×2578	35	1.09 (0-3)	12.09 (8-16)	4.35 (1-8)	0.50 (0-2)	1.50 (0-5)	0.09 (0-1)	57.89	30.00

* Data from UPADHYA and SWAMINATHAN (1963) ** Total of both ring and rod bivalent

be attributed to homologous pairing presumably between its two similar A genomes. However *T. zhukovskyi* is more diploidized than would be expected if it had two similar genomes particularly since it is believed to be of recent origin. Furthermore, the possibility that the multivalents represent homoeologous association can be eliminated as *T. zhukovskyi* apparently inherited a Ph gene system from its tetraploid parent equally as efficient as that of *T. aestivum* (FELDMAN 1966). which completely suppresses homoeologous association.

The *araraticum-boeoticum* amphiploids resemble *T. zhukovskyi* very closely with respect to chromosome association and fertility (Table 1). The amphiploids have a rather high frequency of bivalents and a lower frequency of univalents and multivalents as compared with *T. zhukovskyi*. They are completely male and female fertile. They also resemble *T. zhukovskyi* in anther morphology (DHALIWAL and JOHNSON 1976). However the amphiploids do not resemble *T. zhukovskyi* with respect to general spike morphology and leaf coloration. These characteristics are present only in *T. timopheevi* but not *T. arraticum*.

High preferential diploid pairing in the synthetic amphidiploid (AA $A^tA^tB^tB^t$), with two A genomes, strongly suggests that the A^t genome of *T. araraticum* (contributed by *T. boeoticum*) might have been modified in relation to the A genome of *T. boeoticum*. In

two *araraticum* × *boeoticum* triploid hybrids homology between the *T. boeoticum* genome and one genome of *T. araraticum* does not appear to be complete as there is a very low frequency of closed bivalents and a high frequency of multivalents (Table 1). A change in homology between the A genome of *T. araraticum* or *T. timopheevi* and A of *T. boeoticum* presumably was responsible for nearly complete diploidization of the synthetic amphiploids as well as of *T. zhukovskyi*.

A low frequency of univalents and high fertility in the F_1 hybrids between the *araraticum-boeoticum* amphiploid and *T. zhukovskyi* (Table 1) confirms that the latter indeed is an amphiploid between a tetraploid of the *timopheevi* group and an A genome diploid. *T. timopheevi* is implicated on morphological grounds, *T. monococcum* is inplicated on the basis of a pair of chromosomes with small satellites (UPADHYA and SWAMINATHAN 1963). The F_1 hybrids have a slightly higher frequency of multivalents and a lower frequency of bivalents as compared with *T. zhukovskyi* and amphiploids (Table 1). The fertility of the F_1 hybrids was not as high as would be expected. The higher frequency of multivalent association and lower fertility of the F_1 hybrids may be attributed to reciprocal translocations between the particular *T. timopheevi* (parent of *T. zhukovskyi*) and *T. araraticum* (1767) used in the amphiploids. This is possible because a high frequency of reciprocal translocations was observed in crosses involving *T. araraticum* and *T. timopheevi* (unpublished, H.S. DHALIWAL). The F_1 hybrids showed only a slight deviation from 21:21 disjunction at anaphase I indicating that the univalents occurred mostly due to precocious separation of chromosomes from bivalents and quadrivalents rather than due to lack of their synapsis.

The complete diploidization and high fertility of the synthetic hexaploids with two A genomes suggest that completely fertile hexaploids involving cultivated tetraploid wheats such as *T. durum* and wild A or B genome diploid wheats could also be synthesized and exploited commercially.

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Effect of chromosomes on distribution of protein fractions in bread wheat seeds determined by monosomic technique

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In genetic studies of wheat, techniques using aneuploids are often applied to locate genes on chromosomes. Summaries on gene location on chromosomes were published by MORRIS (1970, 1971, 1973).

Recently, electrophoretic techniques are used for the genetic study of proteins. Successful results has been already achieved by a number of workers. JOHNSON (1967, 1968, 1972) and JOHNSON *et al.* (1967) compared electrophoreograms of endosperm proteins and obtained information on phylogenetic relations. Effect of individual chromosomes on the protein distribution in wheat was studied by BOYD and LEE (1967), EASTIN *et al.* (1967) and SHEPHERD (1968). KALTSIKES *et al.* (1968) demonstrated the importance of the D genome, and specifically the 1D chromosome for the breadmarking quality. MATTERN *et al.* (1968) studied the solubility of protein fractions in various solvents by means of chromosome substitution from the cultivar Cheyenne to Chinese Spring. SHEPHERD and JENINGS (1971) applied electrophoretic technique for the study of wheat and rye proteins in addition lines and amphidiploids of rye and wheat. NADA and TSUNEWAKI (1972) have located an effect on three protein fractions on chromosome arms of the homeologous group 3 by comparing the cultivar Chinese Spring and 20 ditelocentric lines of Chinese Spring.

Material and methods

The Czechoslovak spring wheat Zlatka (*Triticum aestivum* L., var. lutescens) was used in this study. This cultivar originated from the cross (Janetzskis Früh × Marquis) × Heines Koga. The set of Chinese Spring (*Triticum aestivum* L.) monosomic lines was applied.

Monosomic analysis was used to determine the effect of individual chromosomes F_2 generation after crossing monosomic lines of Chinese Spring with Zlatka was studied. Seeds of the lines developed in this way were thoroughly mixed within the line to obtain an average sample and used to the study of grain protein composition by electrophoretic technique. Details of this procedure were deseribed earlier (ŠAŠEK 1972).

Electrophoreograms were evaluated visually and zone identification was carried out by numbers according to mobility, so that the closest zone in the direction to the anode was designated by number "1".

For the reason of simplicity results are presented in the form of sketched schemes, where following subjective evaluation has been applied.

very intensively stained zone – full
intensively stained zone – dense lines

zone of medium stain intensity– rare lines
zone of low stain intensity – no lines
traces – dashed line

Note: intensity of the zone staining is in correlation with the concentration of the present proteins.

Electrophoreograms of each line were compared with electrophoreograms of the cultivars Zlatka, Chinese Spring and the disomic cross.

Results and discussion

Distinct differences between the cultivars Zlatka and Chinese Spring has been revealed in the gliadine zone where particularly zones 26 and 27 differ expressively. Zone 26 is intensive in the cultivar Zlatka, whereas zone 27 in Chinese Spring. Both these critical zones are intensive in the disomic cross (fig. 1).

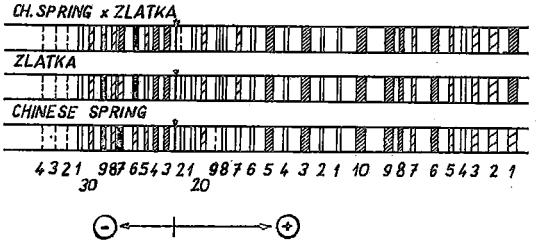

Fig. 1 Electrophoretic diagram of "Zlatka", "Chinese Spring" and their disomic hybrid

Of the 21 lines mono-Chinese Spring × Zlatka (fig. 2) that were investigated only small differences from the disomic cross were found in 19 lines (lines 2A, 3A and 6A show a slight increase of the synthesis in gliadine zones, whereas line 2D a slight decrease). Other differences are within the limits of errors of the technique applied.

Distinct differences were found in lines 1D and 5D. In line 1D a considerable intensity decrease of synthesis can be observed in the gliadine zone. Zone 27 was slight in this line that posses the critical chromosome 1D only from the cultivar Zlatka. (in a homozygous or hemizygous combination), like in the cultivar Zlatka. This demonstrates the effect of a gene or a gene complex located on chromosome 1D causing an increase of gliadine synthesis intensity, particularly zone 27 in the cultivar Chinese Spring; the opposite is true in the cultivar Zlatka.

The result obtained by us is in agreement with the findings by BOYD and LEE (1967) who described differences in less mobile protein zones located on the arm of chromosome 1D of ditelocentric lines of Chinese Spring. Effect of chromosome 1D has been also demonstrated in the study on protein differences in ditelocentric and nuli-tetrasomic lines of Chinese Spring (SHEPHERD 1968). Connection between chromosome 1D and protein changes, eventually changes in breadmaking quality was observed by MATTERN *et al.* (1968), KALTSIKES (1968) as well.

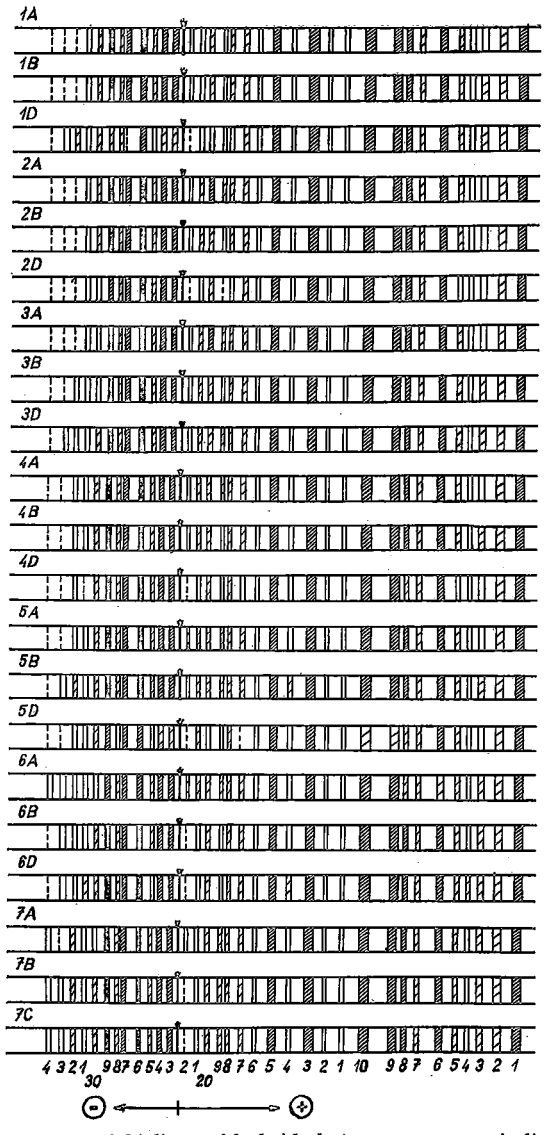

Fig. 2 Electrophoretic diagram of 21 lines of hybrids between monosomic lines of "Chinese Spring" and "Zlatka" in generation F_2

An additional difference – lower of zones both in the gliadine and albumine zones – was found in line 5D. This difference may be in connection with the general negative effect of chromosome 5D in the cultivar Zlatka. Negative effect of this chromosome on other traits like 1000 kernel weight and length of the ear has been described earlier (BAREŠ, KOŠNER 1974). Therefore the assumption that the lower synthesis of proteins results from the generally unfavourable chromosome 5D in the cultivar Zlatka may be justified.

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Induced variation in quantitative traits in bread wheat (*Triticum aestivum* L.)

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Introduction

The use of ionizing radiation is now an acceptable tool to supplement conventional breeding methods with field crops. The extensive literature on the production of varieties resulting from screening irradiated material for desirable deviates has been summarized by

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GAUL (1965) and VIGLASI (1968). It is now of interest to explore and examine the possibilities of the practical application of induced mutation through different mutagens applied in different doses.

Many workers (ABIDI and BALUCH 1969; BHATIA and SWAMINATHAN 1962; D'AMATO *et al.* 1964; DONINI 1968; GAUL 1965; GOUD 1967; KUMAR 1972; KRISHNASWAMY 1967; RAJPUT 1974 and YAMAGATA 1964) have attempted to assess radiation induced variation in quantitative characters and have reported significant improvements in these characters.

The present paper reports the results of M_2 studies on plant height, culm diameter, days to heading and seed index.

Materials and methods

Seeds from M_1 generation of four cultivars of *Triticum aestivum* L.; namely Wisconsin Supermo, No. 43, Kenya Plume and Kenya Hunter were received through the courtesy of the Department of Botany and Plant Breeding, College of Agriculture, Tandojam, Pakistan. Two hundred and forty seeds from each of three radiation treatments (25, 35 and 45 kR) and 60 seeds for the control for each of the cultivars were sown in plots uniformly treated. Sowing was done in four blocks, by dibbling single seed per hole at 30 cm intervals in rows 3.6 m long and 30 cm apart. Every block consisted of 75 rows, of which 60 were sown with treated seeds and 15 with the respective control.

Data collected on individual plants in the M_2 generation for four characters, viz. plant height, culm diameter, days to heading and seed index were analysed according to a one-way classification for each variety and treatment separately. The mean values of all the treated populations for character and varieties were compared with the respective control means by using t test.

The total phenotypic variance ($\gamma^2 t$) calculated from the treated plants for each character was partitioned into an environmental variance ($\gamma^2 e$) and radiation induced genetic variance ($\gamma^2 g$) by subtracting the variance of the control plants from the variance of treated plants.

% heritability was calculated from $\frac{\gamma^2 g}{\gamma^2 t} \times 100$

The estimates of the expected genetic advance at 5% selection intensity was based on the relation suggested by JOHNSON *et al.* (1965) where

$$\text{Genetic advance (G.A.)} = K \times \frac{\gamma^2 g}{\sqrt{\gamma^2 g + \gamma^2 e}}$$

Where $K=2.06$ at 5% selection differential. The genetic advance was expressed as a percentage of the means for the purpose of comparison. For the seed index (1000 grain weight) three random samples were drawn from each treated and control seed bulks, and an analysis of variance made.

Results and Discussion

Plant Height: The data in Table 1 shows that irradiation generally decreased plant

Table 1. Mean values, co-efficient of variation, heritability and expected genetic advance for plant height in M_2 generation of four Kenya wheat varieties under different doses of gamma radiation

Material and dose	Means (cms)	C.V. (p) %	C.V. (g) %	Heritability %	Genetic advance % of means
1. Wisconsin Supremo					
Control	140.39	9.78	—	—	—
25kR	134.93**	10.84	3.72	11.80	2.64
35kR	108.91**	18.43	14.80	57.92	23.20
45kR	127.77**	12.25	5.88	23.02	5.81
2. No. 43					
Control	119.01	10.08	—	—	—
25kR	118.58	10.19	1.24	1.48	0.31
35kR	117.10	11.94	6.12	26.32	6.47
45kR	110.84**	12.69	6.63	27.26	7.13
3. Kenya Plume					
Control	122.71	13.71	—	—	—
25kR	121.82	15.49	7.02	20.54	6.56
35kR	117.16**	14.49	1.92	1.76	0.53
45kR	119.99	14.29	2.70	3.58	1.05
4. Kenya Hunter					
Control	102.48	11.42	—	—	—
25kR	99.04*	14.59	8.54	34.33	10.32
35kR	97.99**	13.98	7.21	26.62	7.67
45kR	92.80**	13.00	3.11	5.72	1.53

C.V. (p) Phenotypic co-efficient of variation
C.V. (g) Genotypic co-efficient of variation
* Significant at 5 per cent level
** Significant at 1 per cent level

height, being significant at 5% and 1% level at all doses for varieties Wisconsin Supremo and Kenya Hunter. The different responses to radiation by varieties No. 43 and Kenya Plume on the one hand and varieties Wisconsin Supremo and Kenya Hunter on the other indicate varietal responses displayed by wheat varieties due to their polygenomic constitution. Under 35 kR Wisconsin Supremo was the most adversely affected and No. 43 the least, a fact which may lead to the assumption that for certain characters, mutations with a deterimental effect occur more frequently. The co-efficient of variation, heritability and genetic advance was enlarged in all the radiation treatments. The maximum reduction in height was given by variety Wisconsin Supremo at 35 kR. The lowest mean height is given by Kenya Hunter at 45 kR, which is 92.80 cm. There is evidently considerable scope for selection for shorter straw following radiation. Similar plant height reductions by different radiation doses have been observed earlier (Goud *et al.* 1969; Krishnaswamy 1967; Rajput 1974; and Viglasi 1968).

Reduction in plant height is desirable for the evolution of lodging resistant varieties provided yield is not affected.

Clum Diameter: The character for culm diameter displayed negative response to radiation, but no dose relationship with the character could be detected (Table 2). This trend of

Table 2. Mean values, co-efficient of variation, heritability and expected genetic advance for culm diameter in M_2 generation of four Kenya wheat varieties under different doses of gamma radiation

Material and dose	Meanss (milimeters)	C.V. (p) %	C.V. (g) %	Heritability %	Genetic advance % of means
1. Wisconsin Supremo					
Control	4.29	10.25	—	—	—
25kR	4.03**	11.31	2.34	4.40	1.01
35kR	4.03**	12.03	4.76	15.97	1.07
45kR	4.01**	14.46	9.42	42.42	12.65
2. No. 43					
Control	5.81	6.71	—	—	—
25kR	5.18**	9.36	5.40	33.98	6.49
35kR	5.13**	12.30	9.64	61.68	15.60
45kR	5.20**	9.01	4.32	24.89	4.37
3. Kenya Plume					
Control	4.88	13.32	—	—	—
25kR	4.55**	13.75	—	—	—
35kR	4.80	14.65	5.91	16.41	4.93
45kR	4.69**	16.29	8.74	29.09	9.71
4. Kenya Hunter					
Control	5.22	9.15	—	—	—
25kR	5.15	9.95	4.28	18.65	3.80
35kR	4.85**	11.30	5.87	27.43	6.33
45kR	4.61**	11.03	4.25	15.36	3.43

C.V. (p) Phenotypic co-efficient of variation
C.V. (g) Genotypic co-efficient of variation
** Significant at 1 per cent level

general deterioration in the diameter of culms is indicative of the frequent occurrence of polygenic mutations. The co-efficient of variation, heritability and genetic advance was increased in all the varieties due to irradiation. GREGORY (1968) reported an increase in variance in irradiated populations without appreciable change in mean values indicating that mutations for polygenes occurred equally in plus and minus direction.

Similar results were also reported by SHAHANI (1969) for culm diameter in wheat. Decrease in culm diameter is liable to lead to lodging and irradiation is therefore less promising here; nevertheless there is considerable induced variation and rare mutants giving thicker straw may be present.

Days to Heading: It could be observed from the results (Table 3) that heading was hastened due to radiation treatments. Data reveal varietal responses to irradiation. Variety Wisconsin Supermo was comparatively less affected for the initiation of spikes, while on the contrary, variety No. 43 displayed greater susceptibility to radiation showing maximum response of 10.18 days earliness with 45 kR treatment. There was a significant decrease in the mean values of treated populations as compared to control. Highest genotypic co-efficient of variation was observed in 35 kR of variety Wisconsin Supremo with (93.79%) heritability and (17.89%) genetic advance.

These results agree with those of MACKEY (1960) and YAMAGATA (1964), who reported

Table 3. Mean values, co-efficient of variation, heritability and genetic advance for heading days in M_2 generation of four Kenya wheat varieties under different doses of gamma production

Material and dose	Means (days)	C.V. (p) %	C.V. (g) %	Heritability %	Genetic advance % of means
1. Wisconsin Supremo					
Control	100.27	2.12	—	—	—
25kR	100.10	4.83	4.33	80.54	8.00
35kR	92.32**	9.26	8.96	93.79	17.00
45kR	99.00**	3.72	3.01	66.32	5.06
2. No. 43					
Control	95.84	6.56	—	—	—
25kR	90.37**	7.28	2.10	8.32	1.247
35kR	89.88**	7.39	2.33	9.97	1.517
45kR	85.66**	6.98	—	—	—
3. Kenya Plume					
Control	120.64	1.68	—	—	—
25kR	117.12**	3.53	3.08	76.19	5.54
35kR	115.30**	2.37	1.59	42.25	2.20
45kR	114.50**	2.57	1.86	52.79	2.79
4. Kenya Hunter					
Control	133.07	1.61	—	—	—
25kR	129.00**	3.50	—	—	—
35kR	126.11**	3.03	2.05	48.17	3.005
45kR	129.51**	2.31	2.29	52.49	3.33

C.V. (p) Phenotypic co-efficient of variation
C.V. (g) Genotypic co-efficient of variation
** Significant at 1 per cent level

Table 4. Seed index in grammes of M_2 populations of four Kenya wheat varieties given different radiation doses

Culture	Treatments			
Varieties	Control	25kR	35kR	45kR
Wisconsin Supremo	37.60	37.80	39.83	38.40
No. 43	53.50	53.70	54.50	53.93
Kenya Plume	46.10	46.12	46.40	46.20
Kenya Hunter	28.10	30.20	30.80	32.50

earliness in heading date due to X-ray treatment in cereals.

Earliness in heading is somewhat valuable in the areas where winter is mild and short, and as such it is necessary to evolve early maturing varieties of wheat to conform to the requirements of grain development.

Seed Index: Seed index data (Table 4) and analysis of variance (Table 5), show that all the effects are highly significant against error (M.S.). The variety and treatment interaction was also highly significant. The treatment sum of squares has been split, firstly with a component for the difference between treated and control, and secondly into its linear and quadratic components of dosage. The analysis shows that both linear and

Table 5. Analysis of variance of seed index (1000 grain weight) in M_2 populations of four Kenya wheat varieties

Item	d.f.	Mean square	V.R. interacting against M.S. error	V.R. interacting against interaction error
a) Treatments	3	6.55	23.38**	2.78
Control vs irradiation treatments	1	13.15	47.00**	5.60*
Among irrad. treatments	2	3.25	11.60**	1.38 N.S.
Linear	1	4.16	14.86**	1.77 N.S.
Quadratic	1	2.34	8.35**	9.99 N.S.
b) Varieties	3	1225.58	4377.07**	
c) Varieties × treatments	9	2.35	8.39**	
Control vs irradiated treatment × varieties	3	3.78	13.5 **	
Among irrad. treatments × Varieties	6	1.63	5.82**	
Linear	3	1.48	5.28**	
Quadratic	3	1.78	6.35**	
d) Errors	32	0.28		

* Significant at 5 per cent level
** Significant at 1 per cent level
N.S. Not significant

quadratic components are significant at 1% level. The treatment effect was, however, not significant against interaction (M.S.). This shows that varieties by and large reacted differently under different doses. Irradiation has slightly increased the seed index of all four varieties and at all dosages. Similar results were also reported by RAJPUT (1974) with mung beans.

The results of these radiation studies are therefore promising. In three important characters of height, earliness and grain weight there are fairly consistent changes in the required direction in all four commercial varieties of wheat.

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Chromosome substitutions, genetic recombination and the breeding of hexaploid triticale

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During the passed 15 years increasing attention has been paid to triticale as a potential cereal crop. This is mainly the result of the successful breeding efforts in several countries such as Hungary, Canada, Mexico and the USSR. These programs have shown that triticale has many agronomically valuable properties such as high yield potential, good

nutritional quality, good disease resistance, drought resistance and winter-hardiness. The breeding has so far led to the release of varieties in some countries e.g. Canada, USA and Spain. In Hungary triticales have been in practical cultivation for several years. CIMMYT of Mexico counts on practical cultivation of triticale within some years.

Early triticale breeding programs were restricted to octoploid lines from breadwheat and rye. This material usually could not compete with wheat and rye. The selection of improved hexaploid lines from crosses between octoploid and hexaploid triticales was reported by PISSAREV (1963) and by KISS (1966). JENKINS (1966), and ZILLINSKY and BORLAUG (1971) reported the same thing from crosses between hexaploid triticale and bread wheat. These results underlined the importance of *Triticum aestivum* germplasm in the breeding of hexaploid triticale. Among triticale breeders, 42-chromosome triticales that have *Triticum aestivum* in their genetic background are referred to as secondary hexaploids (KISS 1966).

The superiority of secondary hexaploids has been explained along three different lines: genic, cytoplasmic and chromosomal. Most probably all three explanations are valid and the superior performance of secondary hexaploids is the result of an interaction between factors on the genic, chromosomal as well as cytoplasmic levels.

The genic explanation (PISSAREV 1963, MÜNTZING 1972, THOMAS and KALTSIKES 1972) is based on the assumption that the A and B genomes of hexaploid and tetraploid wheats are not genetically identical, because they have had a long period of separate evolution behind them. The A and B genomes of bread wheat are supposed to be better adapted to the presence of a third genome. This should make them cooperate better with the rye genome in the triticales.

By means of reciprocal triticale F_1 hybrids LARTER and HSAM (1973) have shown that triticales with cytoplasm from hexaploid wheat in several respects are superior to those with cytoplasm from tetraploid wheat. This indicates that the incorporation of bread wheat cytoplasm is of importance in the breeding of triticale.

The substitution of rye chromosomes by D genome chromosomes is the basis of the chromosomal explanation of the superiority of secondary hexaploids. ZILLINSKY and BORLAUG (1971), on plant morphological and physiological grounds, presumed that the Armadillo triticales were the result of a spontaneous outcross between triticale and bread wheat. GUSTAFSSON and ZILLINSKY (1973) proved the presence of the 2D chromosome in an Armadillo line. The F_1 between this line and the ditelo 2D of Chinese Spring wheat showed a heteromorphic bivalent in the first meiotic metaphase. Based on the meiotic pairing in the F_1 between the Armadillo and bread wheat they concluded that the 2D had replaced the 2R.

The Giemsa staining techniques for chromosomal heterochromatin have proved to be very valuable for triticale, since they permit the exact identification of the seven pairs of rye chromosomes. The terminal localisation of the heterochromatin of rye chromosomes makes them easy to distinguish from wheat chromosomes (MERKER 1973). This facilitates the identification of lines where rye chromosomes are substituted by wheat chromosomes.

By means of this technique MERKER (1975), in the CIMMYT triticale program, has isolated 42-chromosome hexaploid lines, which have from one pair to seven pairs of rye chromosomes. Among the most valuable lines were genotypes with four, five, six and seven pairs of rye chromosomes. The third genome of most of these valuable lines is of a mixed composition. One to three pairs of rye chromosomes have been substituted by homoeologous D genome chromosomes.

There is a high number of theoretically possible homozygous and stable chromosome combinations. Under the presumption that the substitutions are restricted to homoeologous rye and D genome chromosomes the number can be calculated from the general formula 2^n. In this case n is 7, that is the number of chromosome pairs in each of the participating genomes. The distribution of different possible chromosome combinations will be the following:

A:	7	6	5	4	3	2	1	0
B:	0	1	2	3	4	5	6	7
C:	1	7	21	35	35	21	7	1

A represents the number of rye chromosome pairs and B the number of D genome chromosome pairs (or vice versa). The sum of A and B is seven, that is a full genome. C represents the number of different possible chromosome combinations. E.g. there are seven different combinations of six rye and one D genome chromosome, since each of the seven rye chromosomes theoretically can be substituted by its homoeologous D genome chromosome. In addition to these 128 different R-D combinations there is the possibility of substitutions between the wheat genomes. A line with e.g. four pairs of rye chromosomes does not necessarily have three pairs of D genome chromosomes. It could have more, since D genome chromosomes can substitute for chromosomes of the A and B genomes. This means that the production of secondary hexaploid triticale opens the possibility of a far reaching reorganisation of the chromosomal and genomic composition. Hexaploid triticale crossed to bread wheat seems to be the most suitable combination for the selection of different chromosome types. Maybe the optimal chromosome composition of hexaploid triticale has not yet been isolated.

In practice, however, there are indications that a specific F_1 between hexaploid triticale and bread wheat is limited in its chromosome substitution possibilities (MERKER 1975). There are two plausible explanations for this: One is gene interaction and the other is lack of homoeology between rye and wheat chromosomes. A pair of D genome chromosomes in a certain line may lack a specific gene that is essential for the successful replacement of a rye homoeologue, or have a specific gene that makes it impossible as a substitute for a rye homoeologue. Cultivated rye, *Secale cereale*, is differentiated from species of wild rye by reciprocal translocations involving either two or three chromosome pairs (see KRANZ 1963). F_1:s between different wheat cultivars reveale the presence of a varying number of reciprocal translocations (see LARSEN 1973). These structural differences disturb the homoeology between rye and wheat chromosomes and counteract full compensation and

balanced genotypes when chromosomes are substituted.

If more variation is introduced into the crosses by making double crosses (F_1 hexaploid triticale $\times$ F_1 bread wheat) there should be a better chance to obtain different chromosome combinations, since all gametes forming the hybrids have a different genetic content and there is a higher chance of introducing structural differences. The use of amphidiploids with wild rye could increase the chromosomal variation, but has the disadvantage of introducing agronomically inferior characters.

Also from a recombination point of view the double cross is preferable in this case. The F_1 between hexaploid triticle and bread wheat has the genomic constitution AABBDR. Only the A and B genomes have the opportunity to pair in meiosis and exchange alleles. The chromosomes of the single D and R genomes are inherited without recombination. This decreases the over all recombination by one third. If a double cross is made, all genomes have the possibility to take part in recombination, which results in a wider variation in segregating generations.

In octoploid $\times$ hexaploid triticale crosses it is also advisable to use double or three way (octoploid F_1 $\times$ hexaploid) crosses to increase recombination and the chances of substitution. In this type of cross the D genome has no opportunity to recombine in a single cross. This is of importance since chromosomes from this genome can replace rye chromosomes in substitutions.

In crosses between octoploid and hexaploid triticale, and in crosses between hexaploid triticale and bread wheat the F_1 and the early generations have an unbalanced chromosome composition resulting in meiotic disturbances and aneuploid chromosome numbers. This causes an increased frequency of inferior and more or less sterile plants. By natural selection and by increasing homozygosity in later generations chromosomal balance is restored. This means that a bulk propagation in earlier generations and selection of individual plants in later generations is the most suitable breeding method for this type of crosses.

In intercrosses between hexaploid triticales the F_1 also has an unbalanced chromosome constitution if the crossed lines have differences in their chromosome composition. This results in chromosomal disturbances, however not as severe as in the crosses discussed earlier. In this case it should be possible to rely on single crosses and make selections in early generations.

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Identification of a wheat-*Agropyron* and a wheat-rye chromosome substitution

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Introduction

There are several examples of alien substitution lines in hexaploid wheat in which the alien chromosome has been derived from related genera of the sub-tribe Triticinae (see for ref. ZELLER and FISCHBECK 1974). In 1958 KNOTT described a wheat strain with a chromosome from *Agropyron elongatum* (HOST) BEAUV. carrying a genetic factor for blue aleurone colour. Most of the already identified wheat-*Agropyron* substitution lines are substitutions for eliminated chromosomes of the wheat D-genome (BAKSHI and SCHLEHUBER 1959, QUINN and DRISCOLL 1967, KNOTT 1958, LARSON and ATKINSON 1970). From these results it was inferred that the aforementioned wheat-*Agropyron* line is a substitution for a chromosome of the wheat D-genome.

Wheat strain 205~70 is characterized by a pubescent peduncle. Since rye chromosome 5R bears the gene for hairy neck, the transfer of hairy neck to wheat must have occurred either by a translocation or by a substitution involving 5R and a wheat chromosome. O'MARA (1946), DRISCOLL and SEARS (1965), SEARS (1967), BIELIG and DRISCOLL (1970b), and ZELLER and BAIER (1973) have shown that rye chromosome 5R is genetically related to wheat chromosomes of the homoeologous groups 4 and 5. Therefore one of these wheat chromosomes was suspected of being involved in the wheat-rye chromosome substitution of strain 205~70.

Material and Methods

A wheat strain (F_4) called 'Blue Dark' from a cross between Thatcher and 'Blue A' was kindly supplied by Dr. D.R. KNOTT (Canada). Blue A was developed from the backcross Rescue (2n=42) × *Agropyron elongatum* (2n=70) × Rescue (KNOTT 1958). The Chinese Spring lines MT (monotelosomic)-1D, MT-3D, mono-4D, MT-5D and mono-6D were crossed with Blue Dark. Then the chromosomes of the F_1 hybrids were counted in root-tip meristem cells and the chromosome pairing analyzed in PMC's of the first meiotic metaphase. The somatic chromosomes were pretreated in monobromonaphthalene. Root tips and anthers were hydrolyzed in 1*N* HCl and stained in basic fuchsin.

The strain 205~70, kindly provided by Dr. KISS of Hungary, was derived from a hybrid (F_7) of *Triticale* Hadmers-leben (2n=56, Prof. VETTEL) and Ottawa wheat (KISS, pers. communication). This strain was observed mitotically in the somatic cells and then crossed with disomic Chinese Spring, disomic Kolibri and the aneuploid Chinese Spring lines mono-4A, MT-4B, mono-4D, MT-5A, MT-5B and MT-5D. The pairing configurations of the disomic and monosomic F_1 hybrids were analyzed cytologically.

Results and Discussion

The pairing configurations of the meiotic metaphase chromosomes in the monosomic F_1 hybrids between five Chinese Spring aneuploids and the strain Blue Dark are summarized in Table 1. In the mono-1D, 3D, 5D and 6D hybrids most frequently PMC's with chromosomes forming 19 bivalents and three univalents were observed. The commonest chromosome configuration in the mono-4D cross, however, was 20 bivalents and one univalent (Table 1). From these configurations it may be concluded that wheat chromosome 4D in Blue Dark has been eliminated and replaced by a specific chromosome from *Agropyron elongatum*.

LARSON and ATKINSON (1973), using a wheat-*Agopyron* triple-alien-substitution line that was derived like Blue Dark from a hybrid between *Triticum aestivum* L. var. Rescue and *Agropyron elongatum* (2n=70), obtained similar results. In an attempt to select the corresponding three single disomic substitutions from the triple substitution line LARSON and ATKINSON (1970) found that the 4D disomic substitution is characterized by seeds with blue aleurone.

It is of interest to know that ZELLER and BAIER (1973) recently described a wheat-rye chromosome substitution line in which wheat chromosome 4A was replaced by rye chromosome 5R. This substitution (Blaukorn) also is characterized by blue aleurone and additionally by pubescent peduncle. It is, however, not yet certain whether the segment with the gene for blue aleurone is carried by the hairy neck chromosome or attached to a wheat chromosome by a translocation. We intend to locate the blue-kernel-colour gene after backcrossing 'Blaukorn' to Chinese Spring for several generations. Linkage of pubescent peduncle and blue aleurone, however, would support the assumption that both loci are carried by the 5R rye chromosome.

Table 1. Chromosome pairing in monosomic F_1 plants of five different Chinese Spring monosomics with 'Blue Dark', a wheat-*Agropyron* substitution line

Pairing	Monosomic				
	1D	3D	4D	5D	6D
$20''+1'$	—	—	177	—	—
$19''+3'$	94	107	97	63	74
$18''+5'$	14	13	11	3	10
$18''+1^{IV}+1'$	—	—	7	—	—
$18''+1''+'2'$	—	—	1	1	—
$17''+7'$	—	2	—	2	—
$17''+1^{IV}3'$	5	5	4	—	2
$17''+1'''+4'$	—	2	2	—	—
$16''+1^{IV}+5'$	1	2	—	—	—
$16''+1'''+6'$	1	—	—	—	—
No. of plants	3	2	5	1	4

The cytological analysis of the somatic chromosomes of the Hungarian strain 205~70 revealed that the genome is comprised of 40 complete chromosomes and two long telocentric chromosomes. In crosses of the strain with disomic Chinese Spring and Kolibri, resp. 20 bivalents and two univalents occurred in the PMC's. Furthermore the strain 205~70 was crossed with each of the six monosomic Chinese Spring lines of the homoeologous groups 4 and 5. Table 2 demonstrates that in the F_1 hybrids of monosomic lines 4A, 4B, 4D, 5B and 5D, 19 bivalents and three univalents usually were formed. In the monosomic plants of the cross between Chinese Spring monotelocentric 5A and the Hungarian strain, 20 bivalents and one univalent most frequently occurred (Figure 1). The unpaired chromosome of the critical cross most probably is the long arm of rye chromosome 5R. This arm is characterized by a large constriction visible in most of the PMC's. This phenomenon has also been reported by BIELIG and DRISCOLL (1970a, b) and is typical for the complete chromosome 5R, too, if present as a univalent (KATTERMANN 1937, O'MARA 1951, ZELLER and BAIER 1973).

Different authors reported several instances of substitutions and translocations of wheat chromosomes belonging to homoeologous groups 4 and 5 by rye chromosome 5R (see ZELLER and FISCHBECK 1974). Spontaneous chromosome substitutions and translocations may serve as evidence for the homoeology of rye chromosome 5R. The present case of a substitution of the wheat chromosome pair 5A by a telo-$5R^L$ pair supports the assumption that at least this arm of the hairy neck chromosome is homoeologous to wheat group 5.

Recently we reported in numerous spontaneous chromosome substitutions and translocations of different origin the preferred tendency of a specific rye chromosome (1R) to replace the complete wheat chromosome 1B or a part of it. We proposed to designate this behaviour of chromosomes of the sub-tribe Triticinae preferential substituting ability (ZELLER 1973). It appears likely that strain 205~70 is a further example of this phenomenon. More instances of identified 5R substitution and translcoation lines, however,

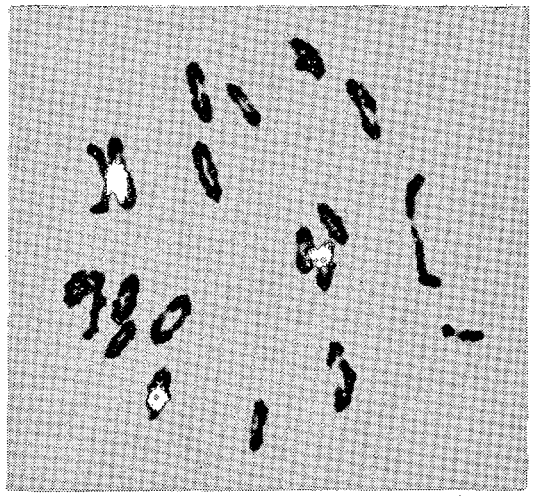

Figure 1. First metaphase of meiosis in a monotelocentric F_1 hybrid between Chinese Spring MT-5A and strain 205~70, showing 20 bivalents and one telo-5R^L univalent with tertiary constriction

Table 2. Chromosome pairing in monosomic F_1 plants of six different Chinese Spring monosomics with wheat strain 205~70

Pairing	Monosomic					
	4A	4B	4D	5A	5B	5D
$20''+1'$	—	—	—	450	—	—
$19''+3'$	151	147	200	116	240	275
$18''+5'$	47	18	21	8	8	29
$18''+1^{IV}+1'$	—	—	—	3	—	—
$17''+7'$	5	1	3	1	1	1
$17''+1^{IV}+3'$	1	—	—	—	1	4
$17''+1'''+4'$	1	—	—	—	—	—
$16''+1^{IV}+5'$	3	—	—	—	—	—
No. of plants	3	3	4	6	3	5

must be known to be able to state that rye chromosome 5R is homoeologous to group 4, 5 or both groups. Possibly chromosome 5R is one of the three interchanged chromosomes which differentiate *Secale cereale* L. from *Secale montanum* Guss., the presumptive ancestor of cultivated rye (see Riley 1955).

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Effect of sodium azide and N-nitroso-N-methylurea on M_1 and M_2 generations of hexaploid Triticale (× Triticosecale)[1)]

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In recent years chemical mutagens have been used extensively in cereal grains to create genetic variability for desirable traits and as a source of new germ plasm material (BROCK 1971, KONZAK 1973). Genetic variability has been shown to increase considerably with increasing concentrations of mutagens (VAGERA 1969 and 1971; KONZAK *et al.* 1964). The limited variability in existing triticales offers an excellent opportunity to generate new genotypes in a relatively short time by mutation breeding. To date, only very few studies have been reported on the use of chemical mutagens in this new cereal crop. The objective of this study was to examine the effect of varying concentrations of sodium azide (NaN_3) and N-nitroso-N-methylurea (MNH) on seedling establihsment and other plant characteristics of hexaploid triticale in the M_1 and M_2 generations.

Materials and Methods

Seeds of hexaploid triticale cultivar 6TA 131 were presoaked in water for two hours at 30°C. The mutagen solutions were freshly prepared in 0.05M phosphate buffer at pH 3.0 for NaN_3 and at pH 7.0 for MNH. Seeds were soaked in three concentrations of NaN_3 (1.0, 1.5, 2.0 g/l) and MNH (0.20mM, 0.25mM, 0.30mM) for 4 hours at 30°C. After treatment, they were rinsed in distilled water for two hours and air dried for three days (procedure suggested by C.F. KONZAK, Personal Communication). One hundred seeds were space-planted in a four-meter single-row-plot with four replications in a randomized complete block design for both M_1 and M_2 generations in October of 1972 and 1973, respectively. Seedling establishment was recorded four weeks after each planting date. Plant height, length of first internode below peduncle, length of spike, seed set and 1000

1) The work reported is upported by the U.S. Department of Agriculture, Cooperative State Research Service Grant Nos. CSRS 416–15–07 and CSRS 316–15–27.

kernel weight were determined on ten randomly-selected plants per plot in both M_1 and M_2 generations.

Results and Discussion

In the M_1 generation, increases in concentration of sodium azide reduced the seedling establishment from 60% in control to below 20%, but no differences due to treatments were found in the M_2 generation. Concentrations of MNH did not affect stand establishment in either generation (Fig. 1). VAGERA (1969) reported strong depression of germination at similar concentrations, particularly at 0.3mM concentration of MNH in einkorn wheat seeds. Sodium azide treatments caused about 35cm reduction of plant height in M_1 generation when compared with the control but no significant differences were observed between concentrations (Fig. 1). However, M_2 plants were as tall as the control, indicating that the height depression in M_1 plants was probably a reduced vigor caused by mutagen treatment instead of being a genetically expressed change observed in later generations. Mean plant height was not affected by MNH treatment in either M_1 or M_2 generation.

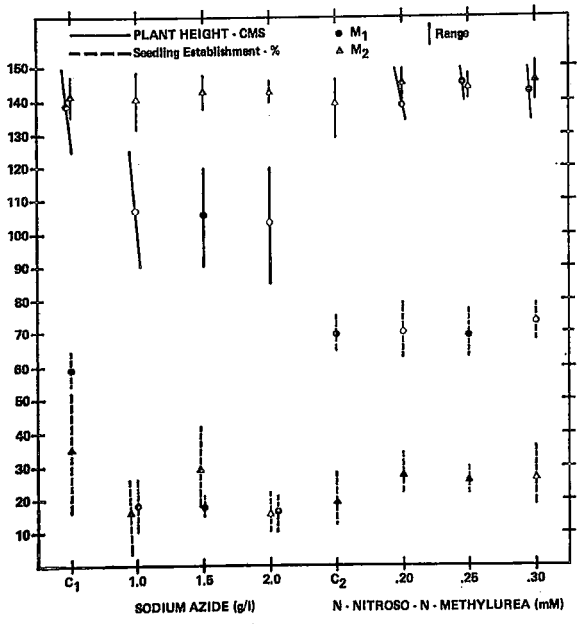

Figure 1. Effect of sodium azide (NaN_3) and N-nitroso-N-methylurea on plant height and seedling establishment in M_1 and M_2 generation of hexaploid triticale.

Means of spike length and of the first internode below the peduncle showed no significant differences between concentrations of NaN_3 or MNH, except that NaN_3 treatments reduced internode length in M_1 plants by 3cms (mean internode length for control 31cm and 27, 28, and 27cm for 1.0, 1.5 and 2.0 g/1, respectively). With increasing concentrations of NaN_3, a reduction in both seed set and kernel weight occurred in M_1 plants

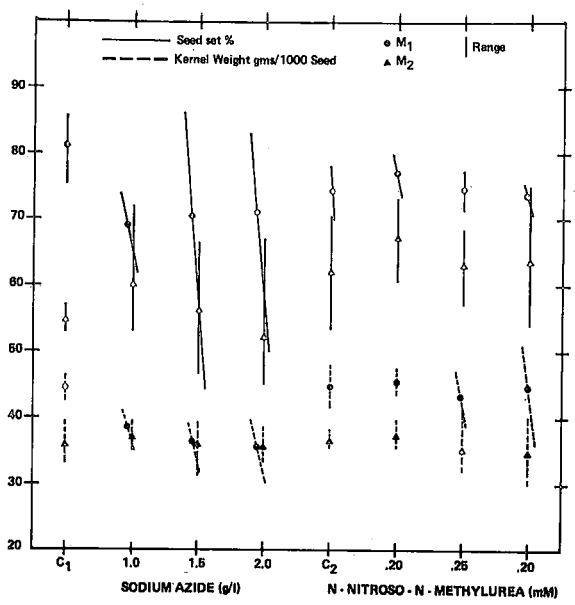

Figure 2. Effect of sodium azide (NaN_3) and N-nitroso-N-methylurea on seed set and kernel weight in M_1 and M_2 generation of hexaploid triticale.

but no differences were found between concentrations of MNH for either character in M_1 or M_2 generations (Fig. 2). In general, seed set and kernel weight showed the greatest range of variability in the M_1 generation due to different concentrations of NaN_3.

This study showed that MNH was an ineffective chemical for inducing genetic variability in triticale at these concentrations. Sodium azide had a depressing effect on all characters studied in the M_1 generation but M_2 plant character means were generally similar to the controls. However, two important yield components (seed set and seed weight) showed reduced mean values from each set of NaN_3 treatments in the M_2 generation with seed set suffering the most. The much larger variation for seed set caused by the NaN_3 treatments in both generations than that occurring in the controls, indicates that selection for higher fertility might be feasible, especially in light of the narrow range and smaller effect on kernel weights. In most treatments, NaN_3 did increase the genetic variability in the M_3 generation as many individual plants of less than 100cms in height have since been selected. Because triticale is an allopolyploid, it may be that full expression of genetic variability is delayed until M_3 or later generations. In this study, we did not observe any chlorophyll mutations in either M_1 or M_2 generation which were reported to be numerous in NaN_3 treated barley seeds (NILAN *et al.* 1973).

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The technique of giemsa staining of cereal chromosomes

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Recently developed staining techniques that result in differential banding of somatic metaphase chromosomes permit the identification of individual chromosomes and have considerably enhanced cytogenetic studies in mammals. With these methods all of the chromosomes have been identified in man, mouse, and many other animal genera; further, in mouse almost all the linkage groups have been correlated with specific chromosomes and chromosome arms. Unfortunately, the application of these techniques to plant chromosomes has not been particularly successful. One of the differential staining techniques, Giemsa C-banding (C=constitutive heterochromatin), which was first applied to animal chromosomes, involves denaturation-reassociation of DNA, with the highly repetitive DNA reassociating faster and appearing as dark bands. Attempts have been made to identify individual plant chromosomes with conventional staining methods, but the interpretation of the results is difficult. In this communication we report a Giemsa staining procedure on grass chromosomes that can be routinely used and by which the individual chromosomes can be easily identified.

Technique:

1. Germination of seeds:

A. Place seeds on damp filter paper in Petri dish for 24 hours at 25°C, 24 hours at 2°C, and then 24 hours at 25°C.

2. Root tip treatment:

A. Collect root tips when 0.5 to 1.5 centimeters long.

B. Place the detached root tips in a freshly prepared saturated solution of monobromonapthalene in tap water. This solution can be made by placing one or two milliliters of monobromonapthalene in 250 ml. of water and violently agitating. The time of treatment at room temperature (72°F) varies from three hours for diploid species to three and a half for polyploid species. Too long a treatment will cause over-contraction and obscure faint bands.

C. Fix in glacial acetic acid overnight (twelve hours minimum, three days maximum) in refrigerator (2°C).

3. Enzyme softening:

A. Wash roots in distilled water and transfer to tubes filled with enzyme solution.

B. Leave root tips in enzyme for one to one-and-a-half hours at room temperature.

4. Root squashing (put 100cc of 2× SSC and dish in oven to begin warming to 60°C):

A. Transfer root tip to distilled water for washing.

B. Place two or three tips on slide and cut off meristematic portion of the tip. Wipe off excess water and the elongated portion of the root.

C. Add small drop of 45% acetic acid and macerate completely.

D. Place cover slip on slide and tap vigorously.

E. Heat slide till warm to touch and press under filter paper.

F. Remove cover slip:

Freeze the macerated material under the coverslip by either placing the slide in contact with solid carbon dioxide or spraying it from below with liquid CO_2. Pry off the cover slip before the frozen material melts.

5. Dehydration:

A. Place slide in fresh 95% ethyl alcohol (see discussion).

B. Remove slide and air dry.

6. Barium hydroxide denaturation:

A. Place slide in barium hydroxide solution for five minutes. (Keep dish covered to prevent carbonation.)

B. Rinse slide in distilled water for ten minutes, changing the water three times.

C. Air dry.

(Start filtering Giemsa stock solution)

7. 2x SSC renaturation:

A. If slide has a film of barium hydroxide on it, place in cold SSC for four minutes.

B. Place in hot (60°C) 2x SSC for one hour.

C. Wash in distilled water for ten minutes and change water three times.

D. Air dry. (During the drying prepare the staining solution and remove the scum from the surface.)

8. Giemsa staining:

A. Stain in Giemsa for appropriate time.

B. Wash in distilled water. If it is not stained enough, restain. If it is overstained, decolorize in 95% ethyl alcohol.

C. Air dry. Place in xylene overnight. Mount with Canada balsam.

Solutions

Enzyme Solution

1. The enzyme solution is made up by adding 500mg of pectinase and 500mg of cellulase to 10cc of distilled water to which six drops of 1N hydrochloric acid are added. This solution should not be used for 24 hours after being made, but it will keep for one to two months in the refrigerator. Tubes containing the enzyme may be reused but should be kept corked and at about 2°C when not in use.

Barium Hydroxide:

1. 100cc distilled water+about 5 gm. barium hydroxide till solution is saturated. Shake vigorously while preparing.
2. Use fresh solution every time.
3. Keep bottle well stoppered.

2x SSC (saline sodium citrate):

1. 8.716gm sodium chloride + 4.410gm sodium citrate + 6 drops 1N hydrochloric acid+500cc distilled water.
2. Heat to 60°C before using.
3. Stock solution keeps about two weeks at 2°C.

Giemsa Stock Solution:

1. 1 gm Giemsa powder + 66cc glycerin + 66cc methanol.
2. Dissolve Giemsa powder in the glycerin at 60°C for one hour with constant stirring.
3. Add methanol and continue stirring at 60°C for one day (24 hours).
4. Keep refrigerated when not in use.
5. Stock solution will keep one or two months.

Citrate Buffer:

1. 2.1gm citric acid +100cc distilled water=A. 14.2gm sodium phosphate + 500cc distilled water=B.
2. Mix 4.55cc of A with 15.45cc of B to prepare stock citrate buffer.

Giemsa Staining Solution:

1. 5cc filtered Giemsa stock solution + 1.5cc methanol + 1.5cc stock citrate buffer + 60cc distilled water.
2. Before using skim the top of the staining solution.

Sources of Chemicals:

1. Cellulase (2000 units/gm.) – E. Merck, catalog number 2329.
2. Pectinase (1.1 units/gm., polygalacturonase) – Sigma Chemical Company, catalog number P–4625.
3. Giemsa powder – Fisher Chemical Company, catalog number G–146.
4. The soruce of all other chemicals did not prove to be critical.

Discussion

This technique has been used to investigate a range of grass chromosomes. Giemsa stained karyotypes have been produced for *Secale*, *Triticum* and some of its diploid and tetraploid relatives, and banding has been observed in *Fescue*, *Agropyron*, *Elumus*, *Hordeum*, and *Avena*.

Several aspects of the technique require greater attention than do others. The length of time in the mono-bromonapthalene solution is important. During this phase of the technique the spindle is inhibited, and the chromosomes contract. Too long a treatment will result in overly contracted chromosomes and will obscure faint bands. Too short a treatment will not allow the easy recognition of individual chromosomes. The treatment is temperature sensitive and appears to be accomplished best at about 70°–72°F.

The time in alcohol (stage 5B) has optimum values for different species, with a degradation of the staining occurring with divergence from the best time. The best time for wheat is between 1 1/4 and 1 1/2 hours, and rye requires 2 1/2 hours.

The length of the Giemsa staining also should be adjusted so that alcohol decolorization is generally not required. The times used have ranged from as little as fifteen seconds to as long as one and a half minutes.

As with all techniques used in identifying individual chromosomes, there are limitations to the relability of the data obtained. If it is possible to identify the chromosomes by other techniques, then the banding pattern can be assigned with certainty to that chromosome. For example, the satellited chromosomes are conspicuous in any case and thus their banding pattern is easily identified. It is better to construct karyotypes of species from single, whole cells rather than from assembling a number of individual chromosomes. By using a complete cells, each chromosome can be identified disomically and the possibility of confusion between similarly banded chromosomes is reduced.

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II Genetic Stocks

Necrosis genes in common wheat varieties from the South Europe

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We have undertaken further investigations on the geographical distribution of necrosis and chlorosis genes, using 280 common wheat varieties (or strains) from Portugal (32 varieties), Spain(116), Italy(61), Yugoslavia(17), Rumania(10), Hungary(5), Bulgaria (27) and Greece (12). Those varieties were crossed to three testers, Jones Fife (*ne*1*Ne*2*ch*1*Ch*2), Prelude (*Ne*1*ne*2*ch*1*Ch*2) and Macha (*Ne*1*ne*2*Ch*1*ch*2), and their F_1 phenotypes were observed as to necrosis and chlorosis. Based on this observation, their genotype was determined as shown in the following table.

Table. Phenotypes with respect to necrosis and chlorosis of F_1 hybrids between three testers and 280 varieties (or strains) obtained from the various countries of the South Europe

GLKU No.	Country	Species	Variety name (or Collection site)	Growth habit	Awnedness	Glume hair	Tester			Necrosis genotype	Place of collection
							× J.F.	× Prelude	× Macha		
3003	Portugal	V	Candeal de Barbadillo	W	+	−	+	+	c	*ne*1*ne*2*ch*1*Ch*2	Elvas
3011	〃	〃	Cieza Numero 2	S	+	−	+	+	c	〃 〃	〃
3012	〃	〃	Barbilla Tenerfe	W	+	?	+	+	c	〃 〃	〃
3013	〃	〃	Colorado de Soria	S	±	−	+	n	c	*ne*1*Ne*2*ch*1*Ch*2	〃
3015	〃	〃	Corriente de Jaca	W	+	−	n	+	c	*Ne*1*ne*2*ch*1*Ch*2	〃
3016	〃	〃	Catalan de Monte Duro de Casterogeriz	I	+	−	+	+	+	*ne*1*ne*2*ch*1*ch*2	〃
3021	〃	〃	Barbilla de Badajoz	S	+	−	n	+	c	*Ne*1*ne*2*ch*1*Ch*2	〃
3023	〃	〃	Candeal Basto de Paredes	〃	+	−	?	+	c	? *ne*2*ch*1*Ch*2	〃
3026	〃	〃	Jeja de Leganiel	W	+	−	+	+	c	*ne*1*ne*2*ch*1*Ch*2	〃
3033	〃	〃	Jeja Parda de Ricote	〃	+	−	+	+	c	〃 〃	〃
3039	〃	〃	Negrete de Belmonte	〃	+	−	+	+	c	〃 〃	〃
3041	〃	〃	Hembrilla Catalana de la Vega	I	+	−	+	+	c	〃 〃	〃
3050	〃	〃	Secano de Alfaro	S	+	−	+	+	c	〃 〃	〃
3059	〃	〃	Nuria	W	+	−	+	n	c, n	*ne*1*Ne*2*ch*1*Ch*2	〃
3106	〃	〃	Negrillo de Madrigal	〃	+	+	+	+	c	*ne*1*ne*2*ch*1*Ch*2	〃
3111	〃	〃	Negrillo Raspinegro de Molina de Aragon	〃	±	−	+	n	c	*ne*1*Ne*2*ch*1*Ch*2	〃
3114	〃	〃	Jeja de Belmonte	〃	+	+	+	+	c	*ne*1*ne*2*ch*1*Ch*2	〃
3123	〃	〃	Cabdeal del Centro	S	−	−	+	+	c	〃 〃	〃

Table (Continued)

GLKU No.	Country	Species	Variety name (or collection site)	Growth habit	Awnedness	Glume hair	Tester			Necrosis genotype	Place of collection
							J.F. ×	Prelude ×	Macha ×		
3128	Portugal	V	Candeal de Tresjuncos	W	+	−	?	?	c, n	*ne1Ne2ch1Ch2*	Elvas
3135	〃	〃	Ricote	S	+	−	n	+	c	*Ne1ne2ch1Ch2*	〃
3143	〃	〃	Guipuzcoa (Zona Alta)	〃	+	−	+	+	c	*ne1ne2ch1Ch2*	〃
3148	〃	〃	Isla de Fverteventura	W	+	−	?	n	c	*ne1Ne2ch1Ch2*	〃
3150	〃	〃	Raspinegro de Secano de "El Bonillo"	〃	+	−	+	+	c	*ne1ne2ch1Ch2*	〃
3165	〃	〃	Jeja de Albacete	〃	+	−	n	+	c	*Ne1ne2ch1Ch2*	〃
3168	〃	〃	Canivano de Torre del Mar	S	+	−	+	+	c	*ne1ne2ch1Ch2*	〃
3178	〃	〃	Soria 1	〃	+	−	+	+	c	〃 〃	〃
3180	〃	〃	Catalan de Monte (Alfajarin)	W	+	−	+	+	c	〃 〃	〃
3184	〃	〃	Barbilla Colorada de Estepona	S	+	−	n	+	c	*Ne1ne2ch1Ch2*	〃
3191	〃	〃	Jeja de Monte el Bonillo	〃	+	−	+	+	c	*ne1ne2ch1Ch2*	〃
3197	〃	〃	Menudillo de Aragon (Hembrilla)	I	+	−	+	+	c	〃 〃	〃
3203	〃	〃	Cañivano de Malaga	S	+	−	+	+	c	〃 〃	〃
3213	〃	〃	Hembrilla de Jaca	I	±	−	n	+	c	*Ne1ne2ch1Ch2*	〃
3001	Spain	〃	Barilla de la Laguna	S	+	−	+	+	c	*ne1ne2ch1Ch2*	Canarias
3002	〃	〃	Geja Colorada de Villarrobleds	〃	+	−	+	+	c	〃 〃	Albacete
3004	〃	〃	Jeja del Villar de Domingo Garcia	W	+	−	+	+	c	〃 〃	Cuenca
3005	〃	〃	Jeja de Barcelona	〃	+	−	+	+	c	〃 〃	INIA
3006	〃	〃	Rojo de Carcedo	〃	+	−	+	+	+	*ne1ne2ch1ch2*	〃
3008	〃	〃	Jeja de Tarragona	S	+	−	+	+	c	*ne1ne2ch1Ch2*	〃
3014	〃	〃	Hembrilla de Alfaro	W	−	−	n	+	c	*Ne1ne2ch1Ch2*	〃
3017	〃	〃	Molino de Plata	〃	+	−	+	+	c	*ne1ne2ch1Ch2*	Zaragoza
3019	〃	〃	Rojo de Burgos	〃	+	−	+	+	c	〃 〃	INIA
3027	〃	〃	Caravaca 6	S	±	−	+	+	c	〃 〃	〃
3028	〃	〃	Catalan de Sahagun	W	+	−	+	+	c	〃 〃	〃
3029	〃	〃	Aragon 03	〃	+	−	+	+	c	〃 〃	Zaragoza
3030	〃	〃	Rojo de Villacarralon	〃	+	−	+	+	c	〃 〃	INIA
3031	〃	〃	Hembrilla	S	−	−	+	+	c	〃 〃	Zaragoza
3034	〃	〃	Candeal Basto de Calera	I	+	−	+	+	c	〃 〃	INIA
3036	〃	〃	Jeja de Torrecilla	W	+	−	n	+	c	*Ne1ne2ch1Ch2*	Cuenca
3037	〃	〃	Jeja Colorada Barrox	S	+	−	+	+	c	*ne1ne2ch1Ch2*	Albacete
3040	〃	〃	Monte Aragon	W	+	−	+	+	c	〃 〃	Teruel
3043	〃	〃	Jeja Monte del Pozuelo	〃	+	−	+	+	c	〃 〃	Albacete
3044	〃	〃	Monte de Albacete	〃	+	−	+	+	c	〃 〃	〃
3047	〃	〃	Marceno de Pontevedra	I	+	−	+	+	c	〃 〃	INIA
3048	〃	〃	Cabezon de Gõni	W	+	−	n	+	c	*Ne1ne2ch1Ch2*	Navarra
3056	〃	〃	Cabezon de Valdegoni	〃	+	−	n	+	c	〃 〃	INIA
3058	〃	〃	Aragon de Huerta	〃	+	−	+	+	c	*ne1ne2chCh2*	Teruel
3060	〃	〃	Rojo Sabando	〃	+	−	+	+	c	〃 〃	Alava
3061	〃	〃	Xexa de Allcante	〃	+	−	n	+	c	*Ne1ne2ch1Ch2*	INIA
3063	〃	C	Las Palmas Num. 10	S	+	−	+	+	c	*ne1ne2ch1Ch2*	LasPalmas

Table (Continued)

GLKU No.	Country	Species	Variety name (or Collection site)	Growth habit	Awnedness	Glume hair	Tester			Necrosis genotype	Place of collection
							J. F. ×	Prelude ×	Macha ×		
3069	Spain	V	Bonito de Caceres	I	+	−	+	+	c	*ne1ne2ch1Ch2*	INIA
3072	〃	〃	Candeal de Munogrande	?	+	−	+	+	c	〃 〃	Barcelona
3073	〃	〃	Cana Ruesa	W	+	−	+	+	c	〃 〃	INIA
3076	〃	〃	Quaderna	S	+	−	+	+	c	〃 〃	Jerez
3078	〃	〃	Libero (Littorio)	〃	+	−	+	+	c	〃 〃	INIA
3079	〃	〃	Albimonte	〃	+	−	+	+	c	〃 〃	Barcelona
3080	〃	〃	Ardito	W	+	−	+	+	c	〃 〃	INIA
3081	〃	〃	Vitoria 9	S	±	+	+	+	c	〃 〃	Alava
3082	〃	〃	Involcable de Alave	?	+	+	+	+	c	〃 〃	INIA
3084	〃	〃	Rapon de Asturias	W	+	−	n	+	c	*Ne1ne2ch1Ch2*	〃
3086	〃	〃	E.M.V. Numero 1	〃	−	−	+	+	c	*ne1ne2ch1Ch2*	Alava
3087	〃	〃	Mocho Blanco	〃	−	−	n	+	c	*Ne1ne2ch1Ch2*	〃
3088	〃	〃	Blanquillo de Badajoz	S	−	−	+	+	c	*ne1ne2ch1Ch2*	INIA
3090	〃	〃	Durango	I	−	−	+	+	c	〃 〃	Vizcaya
3091	〃	〃	Mocho Africano	W	+	−	+	+	c	〃 〃	Navarra
3092	〃	〃	Inovolcable Navarro 101	〃	±	−	+	+	?	*ne1ne2* ?	INIA
3094	〃	〃	Toseta de Navascues	〃	±	−	+	+	c	*ne1ne2ch1Ch2*	Navarra
3096	〃	〃	Mocho Ruiz de Arroniz	I	−	−	+	n	c	*ne1Ne2ch1Ch2*	INIA
3101	〃	〃	Blanco de Liebana	W	−	−	+	+	c	*ne1ne2ch1Ch2*	Santander
3102	〃	〃	Blanquillo de Almaden	〃	±	−	+	+	c	〃 〃	INIA
3103	〃	〃	Mocho o Palon de Caceres	I	±	−	+	+	+	〃 〃	〃
3105	〃	〃	Negrillo de Guadalajara	W	+	+	+	+	c	〃 〃	Barcelona
3109	〃	〃	Negrete de Priego	S	+	+	n	+	c	*Ne1ne2ch1ch2*	Cuenca
3113	〃	〃	Ideal	〃	+	+	+	+	c	*ne1ne2ch1Ch2*	Ejea
3117	〃	〃	Candeal de Soria	I	+	−	+	+	c	〃 〃	INIA
3118	〃	〃	Blando de Talandauded	S	+	−	+	+	c	〃 〃	Tetuan
3119	〃	〃	Candeal de la Sagra	W	+	−	+	+	c	? *ne2ch1Ch2*	INIA
3120	〃	〃	Candeal de Arevalo	〃	+	−	?	+	c	*ne1ne2ch1Ch2*	〃
3122	〃	〃	Candeal Argelino	S	+	−	+	+	c	〃 〃	Navarra
3125	〃	〃	Candeal de Ciudad Real	I	+	−	+	+	c	〃 〃	INIA
3126	〃	〃	Candeal de Villanueva de la Canada	W	+	−	+	+	c	〃 〃	Madrid
3133	〃	〃	Bergantinos	S	+	−	+	+	c	〃 〃	INIA
3136	〃	〃	Del Pais (Tetuan)	〃	+	−	+	+	c	〃 〃	Tetuan
3137	〃	〃	Terminillo	?	?	−	+	+	c	〃 〃	Bologna
3141	〃	〃	Jeja de Conesa	W	+	−	+	+	c	〃 〃	Tarragona
3142	〃	〃	Rieti	〃	+	−	+	+	c	〃 〃	INIA
3144	〃	〃	Jeja de Almendros	〃	+	−	+	+	c	〃 〃	Cuenca
3145	〃	〃	Monte o del Pais	〃	+	−	n	+	c	*Ne1ne2ch1Ch2*	INIA
3146	〃	〃	Cabegon Alto	〃	+	−	+	+	c	*ne1ne2ch1Ch2*	Navarro
3147	〃	〃	Montearagon	〃	+	−	+	+	+	*ne1ne2ch1ch2*	INIA
3149	〃	〃	Villaverde de Trucios	〃	+	−	+	n	c	*ne1Ne2ch1Ch2*	Santander
3155	〃	〃	Mentana	S	+	−	+	+	c	*ne1ne2ch1Ch2*	Jerez
3159	〃	〃	Ruso Con Raspa	〃	+	−	+	+	c	〃 〃	Ona (Burgos)
3161	〃	〃	Jeja de Monte Barrox	W	+	−	n	+	c	*Ne1ne2ch1Ch2*	Albacete
3164	〃	〃	Rojo de Humanes	〃	+	−	n	+	c	〃 〃	INIA

Table (Continued)

GLKU No.	Country	Species	Variety name (or Collection site)	Growth habit	Awnedness	Glume hair	Tester			Necrosis genotype		Place of collection
							× J.F.	× Prelude	× Macha			
3166	Spain	V	Montjuich del Pais	W	+	−	+	+	c	*ne1ne2ch1Ch2*		Tarragona
3167	〃	〃	Sierra Nevada	S	+	−	+	+	c	〃	〃	INIA
3169	〃	〃	Caspino	W/S	+	−	+	+	+	〃	〃	Zaragoza
3170	〃	〃	Rojo de Eslava	S	+	−	+	+	c	〃	〃	INIA
3172	〃	〃	Rojo de Pamplona	W	+	−	+	+	c	〃	〃	〃
3173	〃	〃	Jeja de Cuenca	〃	+	−	+	+	c	〃	〃	〃
3174	〃	〃	Santa Marta	S	+	−	+	+	c	〃	〃	〃
3176	〃	〃	Vimbodi	〃	+	−	+	+	c	〃	〃	Tarragona
3177	〃	〃	Castilla 1	〃	+	−	+	+	c	〃	〃	INIA
3179	〃	〃	Pirineos	I	−	−	+	n	c	*ne1Ne2ch1Ch2*		〃
3181	〃	〃	Cabeza Negra	W	+	−	+	+	c	*ne1ne2ch1Ch2*		〃
3182	〃	〃	Jeja de Castellon	S	+	−	+	+	c	〃	〃	〃
3186	〃	〃	Monbuey	W	+	−	+	+	c	〃	〃	〃
3187	〃	〃	Catalon	〃	+	−	+	+	c	〃	〃	Zaragoza
3188	〃	〃	Grandal	S	+	−	+	+	c	〃	〃	INIA
3189	〃	〃	Montjuich	〃	+	−	+	+	c	〃	〃	〃
3190	〃	〃	Barbilla de Seirlla	〃	+	−	+	+	c	〃	〃	Barcelona
3194	〃	〃	Zona Media de Guipuzcoa	〃	+	−	+	+	c	〃	〃	INIA
3196	〃	〃	Jeja de Manzanares	〃	+	−	+	+	c	〃	〃	〃
3199	〃	〃	Hembrilla de Navarra	W	+	−	+	+	c	〃	〃	Albacete
3200	〃	〃	Catalan de Monte	〃	+	−	+	+	c	〃	〃	INIA
3201	〃	〃	Aragon	〃	+	−	+	+	c	〃	〃	Madrid
3204	〃	〃	Tremesino de Olivenza	S	+	−	+	+	c	〃	〃	INIA
3205	〃	〃	Huerta de Montblanch	〃	+	−	+	+	c	〃	〃	Tarragona
3206	〃	〃	Coruche	〃	+	−	+	+	c	〃	〃	INIA
3207	〃	〃	Grandal de Mondonedo	〃	+	+,−	+	+	c	〃	〃	Lugo
3210	〃	〃	Vitoria 1	W	±	−	+	+	c	〃	〃	INIA
3211	〃	〃	Fluvia	S	±	−	?	+	c	? *ne2ch1Ch2*		Barcelona
3212	〃	C	Pane 247	〃	±	−	+	n	c	*ne1Ne2ch1Ch2*		Lérida
3215	〃	V	Chamorro de Villar de Canas	W	±	−	n	+	c	*Ne1ne2ch1Ch2*		Cuenca
3218	〃	〃	Toseta de Soria	〃	±	−	+	+	c	*ne1ne2ch1Ch2*		INIA
3219	〃	〃	Toseta de Huesca	I	±	−	+	+	c	〃	〃	〃
3220	〃	〃	Marceno de Lerida	S	±	−	+	+	c	〃	〃	〃
3221	〃	〃	Marzal de Gerona	〃	−	−	+	+	c	〃	〃	〃
3222	〃	〃	Mocho de Rioja	W	±	−	+	n	c	*ne1Ne2ch1Ch2*		〃
3223	〃	〃	Mocho o Rapinvde las	I	−	−	+	+	c	*ne1ne2ch1Ch2*		〃
3224	〃	〃	San Rafael Regueras	W	±	−	+	+	c	〃	〃	〃
3225	〃	〃	Marrnecos o Mocho	I	±	−	+	n	c	*ne1Ne2ch1Ch2*		〃
3226	〃	〃	Roma	W	±	−	?	+	c	? *ne2ch1Ch2*		〃
3227	〃	〃	Mocho Rajo Alto	〃	±	−	+	+	c	*ne1ne2ch1Ch2*		Navarra
3228	〃	〃	Pelado de Altojona	〃	−	−	+	n	c	*ne1Ne2ch1Ch2*		〃
3229	〃	〃	Toseta de Jaca	〃	±	−	+	n	c	〃	〃	INIA
3230	〃	〃	Cabezorro de Caceres	S	−	−	+	n	c	〃	〃	〃
3231	〃	〃	L-4	W	±	−	+	n	c	〃	〃	Zaragoza
3702	Italy	C	Italian No. 2	〃	+	−	+	+	c	*ne1ne2ch1Ch2*		
3703	〃	V	No. 3	〃	+	−	+	+	c	〃	〃	
3704	〃	S	No. 4	〃	−	−	+	+	c	〃	〃	
3705	〃	V	No. 5	〃	−	−	+	n	c	*ne1Ne2ch1Ch2*		

Table (Continued)

GLKU No.	Country	Species	Variety name (or Collection site)	Growth habit	Awnedness	Glume hair	Tester			Necrosis genotype	Place of collection
							× J. F.	× Prelude	× Macha		
3706	Italy	V	Italian No. 6	S	+	−	+	+	c	*ne1ne2ch1Ch2*	
3707	〃	〃	〃 No. 7	〃	+	−	+	+	+	*ne1ne2ch1ch2*	
3708	〃	〃	〃 No. 8	〃	−	−	+	+	c	*ne1ne2ch1Ch2*	
3709	〃	〃	〃 No. 9	〃	+	−	+	+	c	〃 〃	
3710	〃	〃	〃 No. 11	W	−	−	+	n	c	*ne1Ne2ch1Ch2*	
3711	〃	〃	〃 No. 22	〃	+	−	+	+	c	*ne1ne2ch1Ch2*	
3712	〃	〃	〃 No. 32	〃	+	+	+	n	c	*ne1Ne2ch1Ch2*	
3713	〃	〃	〃 No. 50	S	+	−	+	n	c	〃 〃	
3714	〃	〃	〃 No. 51	〃	+	−	+	n	c	〃 〃	
3716	〃	S	〃 No. 61	〃	+	−	+	n	c	〃 〃	
3717	〃	V	〃 No. 64	〃	+	−	+	+	c	*ne1ne2ch1Ch2*	
3718	〃	C	〃 No. 66	〃	+	−	n	+	c	*Ne1ne2ch1Ch2*	
3719	〃	〃	〃 No. 67	〃	−	−	+	+	c	*ne1ne2ch1Ch2*	
3720	〃	〃	〃 No. 68	〃	−	−	+	+	c	〃 〃	
3721	〃	V	〃 No. 69	〃	−	−	+	+	c	〃 〃	
3722	〃	C	〃 No. 70	〃	+	−	+	+	c	〃 〃	
3723	〃	〃	〃 No. 71	〃	−	−	+	+	c	〃 〃	
3724	〃	〃	〃 No. 72	〃	+	−	+	+	c	〃 〃	
3725	〃	〃	〃 No. 73	〃	−	−	+	+	+	*ne1ne2ch1ch2*	
3726	〃	V	〃 No. 74	〃	+	−	+	+	c	*ne1ne2ch1Ch2*	
3727	〃	〃	〃 No. 75	〃	−	−	+	+	c	〃 〃	
3728	〃	〃	〃 No. 76	〃	+	−	?	+	c	? *ne2ch1Ch2*	
3729	〃	C	〃 No. 77	〃	−	−	n	+	c	*Ne1ne2ch1Ch2*	
3747	〃	V	Inalettabile	W	−	−	+	+	c	*ne1ne2ch1Ch2*	
3748	〃	〃	Rieti	〃	−	−	+	+	c	〃 〃	
3749	〃	〃	Rieti II	〃	+	−	n	+	c	*Ne1ne2ch1Ch2*	
3750	〃	〃	Riertifamiglie	〃	+	−	+	+	c	*ne1ne2ch1Ch2*	
3751	〃	〃	Ancona	S	+	−	n	+	c	*Ne1ne2ch1Ch2*	
3752	〃	〃	Ardito	〃	+	−	+	+	c	*ne1ne2ch1Ch2*	
3753	〃	〃	Bologna Veneta	W	+	−	+	+	c	〃 〃	
3754	〃	〃	Bologna Veneta famil gia 12	〃	+	−	+	+	c	〃 〃	
3755	〃	〃	Bresica	〃	+	−	+	+	c	〃 〃	
3756	〃	C	Cremana	S	−	−	+	+	c	〃 〃	
3757	〃	〃	Damiana chiesa	〃	−	−	+	+	c	〃 〃	
3758	〃	V	Frassineto 405	〃	−	−	+	+	c	〃 〃	
3759	〃	〃	Gentile rosso No. 1	W	−	−	n	+	c	*Ne1ne2ch1Ch2*	
3760	〃	〃	〃 No. 2	〃	−	+	+	n	c	*ne1Ne2ch1Ch2*	
3761	〃	〃	〃 fam 58	〃	−	−	?	+	c	? *ne2ch1Ch2*	
3762	〃	〃	Inalettabile fam 210	〃	+	−	+	+	c	*ne1ne2ch1Ch2*	
3763	〃	〃	Land Wheat	〃	−	+	+	+	c	〃 〃	
4764	〃	〃	Littorio	I	+	−	+	+	c	〃 〃	
3765	〃	〃	Mentana	S	+	−	+	+	c	〃 〃	
3766	〃	〃	Neopol	W	−	−	+	n	c	*ne1Ne2ch1Ch2*	
3767	〃	〃	Pieve	S	±	−	+	+	c	*ne1ne2ch1Ch2*	
3768	〃	〃	Pisa	〃	+	−	+	n	c	*ne1Ne2ch2Ch2*	
3769	〃	〃	Quaderna	〃	+	−	n	+	c	*Ne1ne2ch1Ch2*	
3770	〃	〃	Reno	W	−	−	+	+	c	*ne1ne2ch1Ch2*	
3771	〃	〃	Riale	S	±	−	+	+	+	*ne1ne2ch1ch2*	
3772	〃	〃	Rieti	〃	−	−	+	+	c	*ne1ne2ch1Ch2*	

Table (Continued)

GLKU No.	Country	Species	Variety name (or Collection site)	Growth habit	Awnedness	Glume hair	Tester			Necrosis genotype	Place of collection
							J.F. ×	Prelude ×	Macha ×		
3773	Italy	C	Roma	W	±	–	+	+	c	*ne1ne2ch1Ch2*	
3774	〃	〃	Sangiargio	〃	±	–	+	+	c	〃 〃	
3775	〃	〃	Sun Wheat	〃	–	–	+	?	c	*ne1* ? *ch1Ch2*	
3776	〃	V	Trento	〃	–	–	+	+	c	*ne1ne2ch1Ch2*	
3778	〃	〃	Virgilio	〃	–	–	+	?	c	*ne1* ? *ch1Ch2*	
4328	〃	S	(name unknown)	S	–	–	+	+	c	*ne1ne2ch1Ch2*	
4332	〃	〃	〃	〃	+	–	+	n	c	*ne1Ne2ch1Ch2*	
4333	〃	〃	〃	〃	+	–	+	n	c	〃 〃	
3981	Yugoslavia	V	Novosadska 1439	W	+	–	+	+	c	*ne1ne2ch1Ch2*	
3982	〃	〃	〃 143913	〃	+	–	+	+	c	〃 〃	
3983	〃	〃	〃 1446	〃	+	–	+	+	?	*ne1ne2ch1* ?	
3984	〃	〃	〃 1910	〃	+	–	+	+	c	*ne1ne2ch1Ch2*	
3985	〃	〃	Krusevacka 22	S	+	–	+	+	c	〃 〃	
3986	〃	〃	〃 2217	〃	+	–	+	?	c	*ne1* ? *ch1Ch2*	
3987	〃	〃	〃 9083	W	+	–	+	+	c	*ne1ne2ch1Ch2*	
3988	〃	〃	U 1	〃	–	–	+	+	c	〃 〃	
3989	〃	〃	U 143	〃	–	–	+	?	c	*ne1* ? *ch1Ch2*	
3990	〃	〃	Bolacel	〃	+	–	+	+	c	*ne1ne2ch1Ch2*	
3991	〃	〃	Stara banatska populacia	〃	+	–	+	+	c	〃 〃	
3992	〃	〃	Rumska Crvenka	〃	+	–	+	+	c	〃 〃	
3993	〃	〃	Rumunska Crevenka	〃	+	–	+	+	c	〃 〃	
3994		〃	Leganj bez osja	〃	–	–	+	+	c	〃 〃	
3995	〃	〃	Leganj sa osjem	〃	+	–	+	+	c	〃 〃	
3996	〃	〃	Fakultetska 30	〃	+	–	+	+	c	〃 〃	
3997	〃	〃	Topciderska 0136	〃	+	–	+	+	c	〃 〃	
4022	Rumania	〃	Cenad Albina	〃	+	–	+	?	c	*ne1* ? *ch1Ch2*	
4023	〃	〃	Cenad Vesenooa	〃	+	–	+	+	c	*ne1ne2ch1Ch2*	
4024	〃	〃	Cenad Tohodia	〃	+	–	+	+	c	〃 〃	
4025	〃	〃	Cenad 117	〃	+	–	+	+	c	〃 〃	
4026	〃	〃	Odvas 241	〃	+	–	+	+	c	〃 〃	
4027	〃	〃	Suceava A-Urziceni	〃	+	–	+	+	+	*ne1ne2ch1ch2*	
4028	〃	〃	Suceava M-Chelam	〃	+	–	+	+	c	*ne1ne2ch1Ch2*	
4029	〃	〃	Purcari × Hostianum	〃	+	+	+	+	c	〃 〃	
4030	〃	〃	Tiganesti 909	〃	+	–	+	?	c	*ne1* ? *ch1Ch2*	
4322	〃	C	(name unknown)	W	–	–	+	+	c	*ne1ne2ch1Ch2*	
4983	Hungary	V	Besostaya 1				+	+	c	〃 〃	
4984	〃	〃	Skorospelka 3b				+	n	c	*ne1Ne2ch1Ch2*	
4328	〃	S	(name unknown)	S	–	–	+	+	c	*ne1ne2ch1Ch2*	
4332	〃	〃	〃	〃	+	–	+	n	c	*ne2Ne2ch1Ch2*	
4333	〃	〃	〃	〃	+	–	+	n	c	〃 〃	
4301	Bulgaria	V	No. 11	W	+	–	+	+	c	*ne1ne2ch1Ch2*	
4302	〃	〃	No. 100–10	I	+	–	+	+	c	〃 〃	
4303	〃	〃	No. 134	W	+	–	+	+	c	〃 〃	
4304	〃	〃	No. 159	〃	+	–	+	+	c	〃 〃	
4305	〃	〃	No. 301	〃	+	–	+	+	c	〃 〃	
4306	〃	〃	No. 1616	〃	+	–	+	+	c	〃 〃	
4307	〃	〃	Ubileina II	S	+	–	+	+	c	〃 〃	
4308	〃	〃	〃 III	W	+	–	+	n	c	*ne1Ne2ch1Ch2*	
4309	〃	〃	〃 I	S	+	–	+	+	c	*ne1ne2ch1Ch2*	

Table (Continued)

GLKU No.	Country	Species	Variety name (or Collection site)	Growth habit	Awnedness	Glume hair	Tester			Necrosis genotype	Place of collection
							× J.F.	× Prelude	× Macha		
4310	Bulgaria	V	No. 14	W	+	−	+	+	c	*ne1ne2ch1Ch2*	
4311	〃	〃	No. 165	〃	+	−	+	+	c	〃 〃	
4312	〃	〃	Okerman 17	S	+	−	+	+	c	〃 〃	
4314	〃	〃	Sadovska ransoreika 4	〃	+	−	+	+	c	〃 〃	
4316	〃	C	Herisson sans barbes	〃	+	−	+	+	c	〃 〃	
4317	〃	〃	Ble de Kilkis	〃	+	−	+	+	c	〃 〃	
4321	〃	〃	Ideal Winterweizen	W	+	−	+	+	c	〃 〃	
4323	〃	〃	Kamtschtka mestonaia	S	+	+	n	+	c	*Ne1ne2ch1Ch2*	
4324	〃	〃	Binke	W	−	−	+	+	c	*ne1ne2ch1Ch2*	
4326	〃	S	White spelta	S	−	−	+	+	c	〃 〃	
4327	〃	〃	(no name)	〃	−	−	+	n	c	*ne1Ne2ch1Ch2*	
4331	〃	〃	Weisser Grannenspelz	〃	+	−	+	n	c	〃 〃	
4336	〃	〃	Anatolien	W	−	−	+	n	c	〃 〃	
4337	〃	〃	Kipperhaus roter Spelz	〃	−	−	+	n	c	〃 〃	
4338	〃	〃	Schworzer Bartspelz	S	+	−	+	+	+	*ne1ne2ch1ch2*	
4340	〃	〃	Tola	W	+	+	?	+	c	? *ne2ch1Ch2*	
4341	〃	〃	Brauner Winteri Grannen aus Nordlingen	W	+	−	+	+	c	*ne1ne2ch1Ch2*	
4375	〃	V	(no neme)	〃	+	−	+	+	c	〃 〃	
3005	Greece	〃	Kiosses Thrakis	I	−	−	+	+	c	〃 〃	
4007	〃	〃	Geinias Patzon	W	+	−	+	+	c	〃 〃	
4008	〃	〃	Sozokondz glli zis Patzon	S	+	−	+	+	c	〃 〃	
4010	〃	〃	Meliggitsi Sezzon	W	+	−	+	n	c	*ne1Ne2ch1Ch2*	
4012	〃	〃	Afnalaso Phiotiches	S	+	−	+	+	c	*ne1ne2ch1Ch2*	
4013	〃	〃	Sidizostozo maloka Kzitis	〃	+	−	+	+	c	〃 〃	
4014	〃	〃	Coatroulostazo Rethymnis	W	+	−	+	+	c	〃 〃	
4015	〃	〃	Kentazadi Ahaias	S	+	−	+	+	c	〃 〃	
4016	〃	〃	Zouta Asuestopetzas	W	−	−	+	+	c	〃 〃	
4239	〃	〃	(BMUK 3865)	S	+	+	+	+	c	〃 〃	
4240	〃	〃	(〃 3867)	〃	+	+	+	+	c	〃 〃	
4242	〃	〃	(〃 3869)	〃	+	+	+	+	c	〃 〃	

The materials used were kindly provided by Dr. C. DASKALOFF of the Institute for Crop and Plant Introduction, Sofia, Bulgaria; Dr. H. OOHATA of the Central Agricultural Experiment Station, Konosu, Japan; Dr. S. RAJKI of the Agricultural Research Institute, Hungary; and Dr. E. SANCHEZ-MONGE of INIA, Spain. We wish to express deepest appreciation to all of them.

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III. Gene Symbols

Catalogue of Gene Symbols for Wheat
(Cf. WIS No. 39 p. 31)

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Reprints of the Catalogue are available on request. Annual Supplementary Lists will not be available in reprint form as they shall appear in Cereal Research Communications, Wheat Information Service and Wheat Newsletter.

1975 Supplement - Catalogue of Symbols

Crossability with Rye

Kr_1. 5BL (133A). s: CS*/Hope 5B (133A)

Height/Semidwarfness

A committee led by Dr. Rosalind Morris is deciding a new format for this section and a section relating to Gibberellin Sensitivity.

Response to Photoperiod

ppd_1 2D (314A). v: Lancer ppd_2 (110); Warrior ppd_2 (110).

ppd_2. 2B (314A). v: Lancer ppd_1 (110); warrior ppd_1 (110).

Ppd_1 Ppd_2 v: Sonora 64 (110).

Response to Vernalization

Vrn_5 (135). $e_1{}^H$ (137). 7BS (137). s: CS*6/Hope 7B Vrn_3 (134). v: Hope.

Reaction to *Erysiphe graminis*

Pm_5 (137A Replaces 33)

Pm_7 By agreement of a committee following a request for allocation. Chromosome 4Aβ.

Reaction to *Puccinia graminis*

Sr_9f (141A). v: Chinese Spring (141A). Not present in the near isogenic I Sr_9a–Ra (141A).

Sr_{22} See also 111A.

Sr_{23} v: Etoile de Choisy (169B).

By agreement of a committee of wheat stem rust workers, the following allocations have been made:–

Sr_{24} 3DL. v: Agent, Blueboy II, Cloud, Fox, Sage, Sears 3D/Ag translocations. Completely linked in coupling with Lr_{24}.

Sr_{25} 7DL. v: Agatha, Sears' 7D/Ag translocations. Completely linked in coupling with Lr_{19}.

Sr_{26} 6Aβ. v: Eagle (Australian cultivar), Kite, Knott's 6A/Ag translocation.

Sr_{27} 3A. v: WRT (wheat-rye translocation), available in CS, Thatcher and Pembina backgrounds. Translocated from Imperial Rye by Acosta.

Sr_{28} 2BL. v: Kota Sr_7b Sr_{18}.

Reaction to *Puccinia recondita*

Lr_{23} (169A). *LrG* (170A). 2BS (169A). i: Lee FL310/6 *Thatcher (169A). s: CS*/Timstein 2B (169A); CS*7/Kenya Farmer 2B (169A). v: Gabo (307); Gamenya (307); Lee (307); Kenya Farmer (307); Timstein (307).

Lr_{24} *LrAg* (38B). 3Dα (262B). v: Agent (38B); Preska (222A); Timpaw (222A); Wanken (222A). Fox Lr_{10} (38B). Blueboy II Lr_1 Lr_{10} (38B).

Lr_{25}. 4Aβ (54A, 54B). v: Fedsec (54C); Transec (55A).

Genetic Linkages

Chromosome 4A		
$Lr_{25} - Pm_7$	No. recombination	54B
Lr_{25}/Pm_7 – centromere	1%	
Chromosome 5B		
Kr_1 – centromere	11.45±3.0%	133A
Chromosome 7B		
Pm_5–Vrn_5	39±6%	137
Pc–Vrn_5	26±5%	137

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IV. Anddendum to WIS No. 40, 1975

The following paragraphs should be added to the article "Genetic control of factors regulating the phenol reaction of wheat and rye grain" by Colin W. Wrigley, WIS., No. 40, pages 6 to 10.

In view of the lack of biochemical knowledge about the phenol reaction, it is suggested that any gene symbol adopted should not refer to an enzymic reaction possibly involved, but that it should refer to the actual test used – the phenol reaction. Indeed, the consideration of a genetic symbol(s) should be delayed until the availability of further inheritance data involving hexaploid wheats.

However, it is clear that chromosomes 2A, 2D and 2R are important in controlling the synthesis of factors responsible for the phenol reaction. No support has yet been found for the suggestion of ZEVEN (1972) that a homoeologous locus will be found on chromosom 2B.

V. Editional Remarks

Announcement for future issues

WIS No. 43 will be planned for publication in October 1976. Manuscripts for this issue are accepted any time, not later than September 30, 1976.

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

Kosuke YAMASHITA
Wheat Information Service
Kihara Institute for Biological Research
Misima 411, Japan

Membership Fee

Due to the economic situations, the yearly Membership Fee has been raised up to ¥ 1,000 for foreign member and ¥ 700 for Japanese member from the fiscal year beginning April 1975. The money should be paid by the Foreign Postal Money Order, othersiwe considerable loss is caused due to the bank charges. Back numbers are available.

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The Managing Editor

Explanation of the Figure on the Cover

Spikes of normal CS, F_1 pentaploid hybrids with CS, *durum*, *squarrosa*, *cylindrica* and *crassa* cytoplasms, and *T. durum* var. *melanopus* (from left to right).
(M. MURATA and S. TSUJI, Fig. 1, p. 3, present issue of WIS).

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