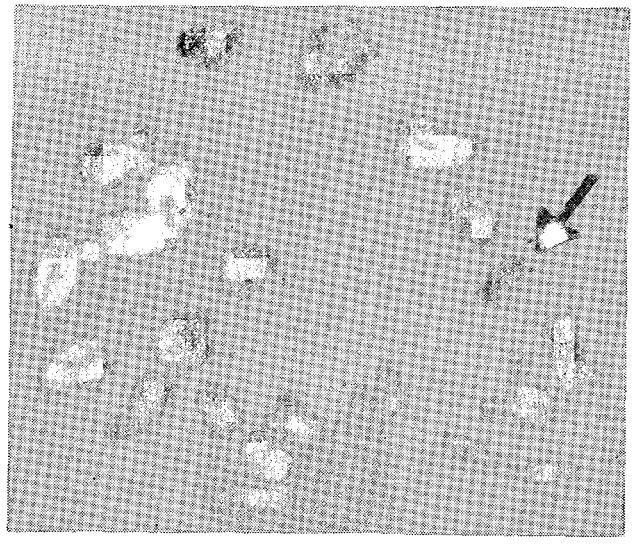
WHEAT INFORMATION SERVICE



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I. Research Notes

An attempt for transferring stem solidity of *T. durum* Desf. to *T. aestivum* L. with the aim of developing new forms of winter common wheat with solid stem, resistant to *Cephus pygmaeus* L.

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Stem solidity present in certain hard wheat varieties, which impart resistance to sawflies of the genus, *Cephide* to them has made many workers to attempt to transfer stem solidity by hybridization to common wheat (Platt and Larson 1944; Larson 1959; Larson and McDonald 1963; McNeal 1961; McKenzie 1965; Tsvetkov 1969, 1971). However, almost all attempts in this respect evoked great difficulties. Yamashita (1937) and later Matsumura (1947) established "e" chromosome of D genome as XX chromosome, classified by Sears in his nomenclature to possess a hollow stem gene, which depresses genes for solid stem in A and B genomes.

For the period 1963~1970 an interspecific hybridization was undertaken at this Institute, with the aim of transferring stem solidity of *T. durum* Desf. to *T. aestivum* L.

We resorted, for this hybridization, to No. 13 and No. 233–II hard wheat varieties with solid stem (*T. durum* Desf.) and to No. 14, No. 11, No. 301 and Bezostaya 1 common wheat varieties with hollow stem (*T. aestivum* L). Reciprocal crossings were made among the individual varieties of both species. Picking out of the forms of common wheat with stem solidity was accomplished only after the disintegration in F_2. Stem solidity of the hybrid material was determined through the use of the technique of Sapegin (1938) and Larson (1959).

Results given in Table 1 show transferring of stem solidity of *T. durum* Desf. to *T. aestivum* L. to be progressed with great difficulty.

In 1966, 1817 hybrid forms of common wheat in F_8 were analysed and only 0.39 per cent of them showed stem solidity in the topmost internode, while 0.17 per cent pos-

Table 1. Number of hybrid forms of common wheat, with solid stem in F_3

Crosses	No. of plants examined	Number (%) of plants with solid stem in :			
		topmost internode only		all internodes	
	1966		%		
No. 14×No. 13	309	4	(1.29)	—	
No. 13×No. 14	157	2	(1.27)	—	
No. 301×No. 13	237	—	—	1	(0.42)
No. 13×No. 301	218	—	—	—	—
Bezostaya 1×No. 13	511	—	—	1	(0.20)
No. 13×Bez. 1	385	1	(0.26)	1	(0.26)
Average	1,817	7	(0.39)	3	(0.17)
	1967				
No. 14×No. 13	39	1	(2.56)	—	—
No. 13×No. 14	88	1	(1.14)	—	—
No. 301×No. 13	99	—	—	—	—
No. 13×No. 301	75	1	(1.33)	—	—
Bez. 1×No. 13	84	—	—	1	(1.19)
No. 13×Bez. 1	71	1	(1.41)	—	—
No. 14×No. 233–II	88	—	—	—	—
No. 283–II×No. 14	38	—	—	—	—
No. 11×No. 233–II	46	6	(13.04)	4	(8.70)
No. 233–II×No. 11	37	—	—	—	—
No. 301×No. 233–II	73	6	(8.22)	2	(2.74)
No. 233–II×No. 301	30	—	—	—	—
Bez. 1×No. 233–II	75	—	—	—	—
No. 233–II×Bez. 1	36	6	(16.67)	1	—
Average	879	22	(2.50)	8	(0.91)

sessed solid stem in all internodes from top to bottom. In 1967 we had the possibility of fulfilling picking out at a wider range of hybrid combinations. Thus of the 879 hybrid forms analysed, 2.50 per cent showed solid stem only at the topmost internodes, and 0.91 per cent possessed a complete stem solidity.

In our research work more significant results were obtained by the crossing of Bezostaya 1 and No. 11 (hollow stem)×No. 13 hard wheat (solid stem) and No. 233–II (solid stem at the topmost internode only); from these crosses, a considerable number of winter common wheats (*T. aestivum* L.) with solid stem were developed.

Data in Table 2 refer to the extent of stem solidity, by internodes, of certain newly selected constant forms of winter common wheat. Results obtained show that according to the extent of solidity of the stem in its topmost internode and in those follow-

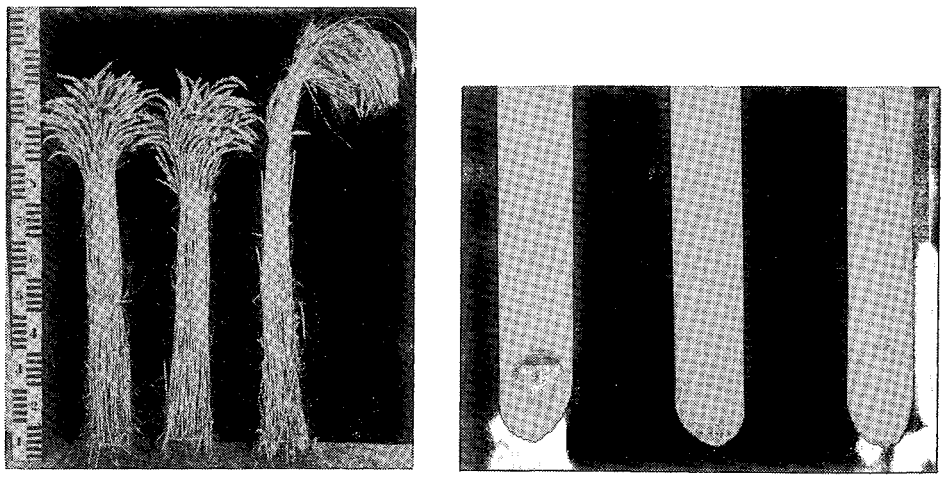
Table 2. Stem solidity by internodes, in certain newly selected forms of winter common wheats in 1972

Parents and hybrids	Stem solidity by internodes						
	topmost internode			internodes following from top to bottom			
	1	2	3	2nd	3rd	4th	5th
Bezostaya 1 (*T. aestivum* L.)	1.2	1.0	1.0	1.0	1.0	1.0	1.9
No. 13 (*T. durum* DESF.)	2.0	3.2	3.0	3.9	4.2	4.3	4.4
Bezostaya 1×No. 13 (*T. aestivum* L.)	2.0	4.9	4.3	5.0	5.0	5.0	4.7
No. 11 (*T. aestivum* L.)	1.0	1.0	1.0	1.0	1.0	1.0	2.0
No. 233-II (*T. durum* DESF.)	2.0	5.0	4.3	1.0	1.0	1.9	2.0
No. 11×No. 233-II (*T. aestivum* L.)	2.0	5.0	5.0	5.0	5.0	5.0	5.0
Bezostaya 1×No. 233-II (*T. aestivum* L.)	2.0	5.0	4.9	5.0	5.0	5.0	5.0

NB : 1=hollow stem (thin walls) ; 2=hollow stem (thick walls) ; 3=intermediate stem solidity ; 4=solid stem with extremely narrow openning ; 5=solid stem.

Table 3. Resistance of the newly selected forms of winter common wheat with solid stem, resistant of to *Cephus pygmaeus* L. in 1972

Varieties and hybrids.	Stem	No. of plants examined	Number (%) of plants damaged by *Cephus pygmaeus* L.
Bezostaya 1 (*T. aestivum* L.)	hollow	134	131 (97.8)
Bezostaya 1×No. 233-II (*T. aestivuu* L.)	solid	238	41 (17.2)



a b c a b c

Fig. 1. Left : Bundles : a. Bezostaya 1 (*T. aestivum* L. with hollow stem) ; b. Bezostaya 1♀×No. 233-II (*T. aestivum* L. with solid stem)♂ ; c. No. 233-II (*T. durum* DESF. with solid topmost internode only.
Right ; Stem cuts : a. Bezostaya 1 (*T. aestivum* with hollow stem) ; b. Bezostaya 1♀×No. 233-II (*T. aestivum* with solid stem)♂ ; c. No. 233-II (*T. durum* with solid topmost internode only).

ing, the hybrid form of Bezostaya 1×No. 13 resembles the paternal parental component, No. 13 (*T. durum* DESF.), with solid stem, and even exceeds it in certain internodes. Of particular interest here are the data obtained with the hybrid lines of common wheat with solid stem, i.e. No. 11×No. 233–II, and Bezostaya 1×No. 233–II. While the maternal parental components, No. 11 and Bezostaya 1 (*T. aestivum* L.), are notable for their hollow stem, and the paternal component, No. 233–II (*T. durum* DESF.), for its solid stem only in the topmost internode, the winter common wheat—No. 11×No. 233–II as also Bezostaya 1×No. 233–II—are notable for their solid stem in all internodes (Table 2, Fig. 1).

The importance of the newly developed winter common wheats with solid stem may best be judged only when solidity is treated on the basis of resistance to *Cephus pygmaeus* L.

Data in Table 3 show that damage caused by *Cephus pygmaeus* L. in Bezostaya 1 winter common wheat with hollow stem goes up to 97.8 per cent, while in the newly developed Bezostaya 1×No. 233–II winter common wheat it runs only to 17.2 per cent.

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"Camara" a tetraploid wheat carrying a 1D disomic substitution for chromosome 1B

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D-genome chromosome substitutions for chromosomes of A and B genomes can be produced in tetraploid wheat (2n=4x=28).

CAMARA, MELLO-SAMPAYO and NORONHA-WAGNER (1966) and MELLO-SAMPAYO and RAMOS (1968) obtained monosomic substitution lines of chromosome 1D for both homoeologous 1A and 1B chromosomes at the tetraploid level.

This was accomplished when both reciprocal nullisomic-tetrasomic lines of chromosomes 1A and 1B of *Triticum aestivum* variety, Chinese Spring, were crossed to *T. durum* variety, Ld 222. The hybrids were then backcrossed to the *durum* wheat parent. Some of the resulting tetraploid plants were double monosomic 1D and 1A or 1B and both showed a $12_{II}+2_{I}$ configuration at meiosis.

It was logically expected that from those plants some individuals carrying 1D disomically substituted for its alternate homoeologous, could be obtained, by selfing. This was true in the case of disomic 1D substitution for 1B which was obtained in 1965. This combination which has only one backcrossing to Ld 222 has been continuously selfed since then and it shows a very stable phenotype. It has been given the name "Camara".

The plant is about 25% shorter than its parent Ld 222, the species being more compact fully fertile and carrying shorter seed and it matures earlier than the durum wheat parent.

"Camara" shows a regular configuration of 14_{II} at metaphase I of meiosis. Both chromosomes 1B were lost when replaced by a pair of 1D chromosomes and the number of nucleolar organizers present in the cells was reduced accordingly. This could be easily detected through the counting of the maximum number of nucleoli shown by somatic cells at telophase-prophase. It was observed that this number which is four in normal tetraploid wheats was reduced to two.

Tests were performed in order to identify both the substituent and substituted chromosomes. Crosses with Chinese Spring ditelosomic lines, 1DL and 1BL, were used for the purpose. When "Camara" was crossed to ditelo 1BL, the telocentric chromosome 1BL remained as univalent in the pentaploid hybrid (meiotic configuration $14_{II}+7_{I}$). On the contrary, when ditelo 1DL was utilized, the 1DL telocentric formed a heteromorphic bivalent. This demonstrated that in the tetraploid complement of "Camara", a pair of chromosomes 1B was replaced by a pair of homoeologous 1D chromosomes.

When "Camara" was crossed to its durum wheat parent, Ld 222, both 1B and 1D chromosomes normally remain as univalents at the metaphase I of F_1 hybrids. However, in some cases it was observed that 1D and 1B chromosomes were paired to each other. It is highly probable that such homoeologous pairing may be considerably increased if the single 1B and 1D chromosomes do not suffer the pairing suppression commanded by chromosome 5B (OKAMOTO 1957 and RILEY 1957). This can be slightly eliminated in tetraploid wheat that carries a pair of homologous translocated 5B.5D chromosomes (MELLO-SAMPAYO 1972). The same is to say of the pairing between 1D and 1A in tetraploid double monosomics for those chromosomes.

Gene transfer of 1D chromosome into tetraploid wheat can be obtained through those translocated chromosomes.

Chromosome 1D may contain genes that are of interest for the improvement of tetraploid wheat (KALTSIKES, EVANS and BUSHUK 1968).

"Camara" can also be tested for the obtention of hexaploid triticales with better bread making properties (LARTER, TSUCHIYA and EVANS 1968).

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(Received August 3, 1973)

Role of chromosome 7D in the expression of seed colour in bread wheat, *Triticum aestivum* L.

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Although mono-, Di- and trigenic inheritance of seed colour in bread wheat has been reported by numerous investigators, precise location of all the genes influencing seed colour is still incomplete. One dominant gene, R_1 was located by SEARS (1944, 1954) on right arm of chromosome 3D. In the present study seed colour was analysed in disomic F_2 and monosomic F_2 populations derived respectively after crossing the variety Cadet and its seventeen monosomic lines with the mexican dwarf wheat variety Sonora 64. Monosomic lines for chromosomes 1D, 6B, 6D and 7B were not ready for investigation.

Both varieties Cadet and Sonora 64 and all the seventeen monosomics of Cadet have red grains. F_2's from disomic and different monosomics of Cadet × Sonora 64 crosses

Table 1. Segregation for seed colour in F_2 populations of di- and monosomic Cadet × Sonora 64

chromosome tested	Red	White	Total	χ^2 (15 : 1)
Cadet	80	—	80	—
Sonora 64	90	—	90	—
F_2 disomic	163	—	163	—
chromosome 1A	113	—	113	—
〃 2A	57	—	57	—
〃 3A	105	—	105	—
〃 4A	74	—	74	—
〃 5A	78	—	78	—
〃 6A	89	—	89	—
〃 7A	80	—	80	—
〃 1B	102	—	102	—
〃 2B	62	—	62	—
〃 3B	37	—	37	—
〃 4B	110	—	110	—
〃 5B	118	—	118	—
〃 2D	66	—	66	—
〃 3D	60	—	60	—
〃 4D	69	—	69	—
〃 5D	148	—	148	—
〃 7D	97	3	100	1.8 ns.

ns : non significant at 5% level.

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were red grained. No segregation was observed in the disomic F_2 and monosomic F_2 populations except F_2 of mono-7D (Table 1). χ^2 test for 15 red grained vs. 1 white grained plants gave a close fit.

F_3 progenies of white grained plants were all white grained. Out of thirty randomly chosen F_2 red grained plants, twenty were homozygous red, and remaining ten again segregated as 15 red vs. 1 white in F_3 generation (Table 2).

Table 2. Segregation for seed colour in F_3 of a cross Cadet mono-6D × Sonora 64

Family	Red	White	Total	χ^2 for 15 : 1
D- 2	54	2	56	0.68 ns
D- 6	56	2	58	0.78 ns
D- 8	31	1	32	0.53 ns
D- 9	64	2	66	1.18 ns
D-15	25	2	27	0.06 ns
D-16	49	1	50	1.55 ns
D-18	72	3	75	0.65 ns
D-19	46	5	51	1.10 ns
D-20	54	6	60	1.44 ns
D-22	42	2	44	0.21 ns

ns : non significant at 5% level.

It should be mentioned that the white grained plants both in F_2 and F_3 populations of the critical cross did not appear to be nullisomics rejecting the notion that the chromosome 7D carries the gene for red kernel colour. However, it is quite apparent that there is a gene(s) on chromosome 7D of the variety Cadet absence of which allows the expression of the other seed colour genes (probably two) in recessive condition.

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Misdivision of five different 3B monosomes in Chinese Spring wheat[1)]

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That isochromosomes and telocentrics originate through misdivision of univalents at meiosis has been well substantiated for wheat (Sears 1946, 1952a, 1952b) since it was first suggested by Upcott (1937) and Darlington (1939, 1940). Sanchez-Monge and Mac Key (1948) believed that the second division of meiosis in their varieties of hexaploid wheat, in which they found about 2% of misdivision of chromosome 5A, was the principal time of origin. In his detailed study Sears (1952) found somewhat more misdivisions at metaphase I than II. In his study chromosome 5A from three different varieties had been introduced into the standard variety Chinese Spring. The frequency for the introduced chromosomes, though lower than for the Chinese 5A (13.7~23.6% vs. 36.0~43.5%), was still considerably higher than that found by Sanchez-Monge and Mac Key.

Telocentrics for the short arm of chromosome 3B, which is conveniently marked with Neatby's virescent gene, are useful for study of the stability of telocentrics (Steinitz-Sears 1966). Data are already available in the publication cited on the frequency with which such telocentrics are obtained through misdivision. It is of interest to learn whether the frequencies of misdivision of 3B are of the magnitude expected, and to compare these frequencies with those of 5A. In addition, chromosomes 3B from other varieties are available in Chinese Spring and can be compared with Chinese Spring 3B for rate of misdivision. Some data on MI misdivision of Chinese Spring 3B were reported by Steinitz-Sears (1966).

Materials and methods

Four varietal substitution lines were supplied by E. R. Sears. These were 'Chinese Spring disomic for chromosome 3B from Thatcher, Timstein, Hope, and Red Egyptian', respectively. Each line was crossed to mono-3B for recovery of off-spring with the substitution chromosome monosomic. For each of the four different 3B chromosomes, several such monosomics were grown, and several fixations were made from each plant. This made it possible to assess the inter-plant variation on one hand, and the day-to-day variation on the other hand.

When a univalent divides at MI, it can divide normally—i.e., into two chromatids,

1) Journal Paper No. 6717 of the Missouri Agricultural Experiment Station. Copied from the Proceedings of the IV Wheat Genetics Symposium by the kind permission of the Editors and Organizing Committee.

each with a long and a short arm. Provided there is enough difference between the two arms, normal division can be easily distinguished from a misdivision resulting in two isochromosomes. Since chromosome 3B was found to have an arm ratio at MI of only 1.4: 1 (as compared to 2.5: 1 for 5A), a misdivision of 3B into two isochromosomes can sometimes be mistakenly recorded as an equal division. In scoring, all doubtful cases of this kind were therefore excluded. Other types of misdivision such as three arms going to one pole and one to the other cannot be mistaken for normal divisions. For this reason when the present results were compared with those Sears obtained for chromosome 5A, special consideration was given to the relative sizes of the 3: 1 classes.

Some misdivisions give rise to chromatids deficient in the centromere region, and these chromatids fail to reach the poles in time for inclusion in the telophase nuclei. In the present study they are only assessed by an increase in the frequency of micronuclei in the tetrads, and this increase is presumably too small to be noticed. The offspring resulting from a monosomic will thus show somewhat fewer isochromosomes and telocentrics than expected from the frequency of misdivision (STEINITZ-SEARS 1966).

Results and discussion

Samples from the same plant taken on different days showed reasonable agreement in frequency of misdivision. The most samples from one plant were five from an individual with a Red Egyptian monosomic. The χ^2 for the misdivision frequencies in these five samples was only 3.04.

The χ^2's for misdivision frequency in different plants with the same monosome all proved to be insignificantly small (below the 5% point). Therefore all the data for each monosome were combined (Table 1). The percentage of misdivision ranged from 14.6 for the Thatcher monosome to 26.9 for Red Egyptian, and χ^2 for the distribution as a whole was a highly significant 23.9.

Table 1. Behavior of monosome 3B at MI

Source of monosome	No. of plants	No. of cells	No. of normal div'ns.	Type and number of misdivisions				
				equ. w. separ. arms	3 : 1	2 isochromosomes	Total misd.	% misd.
Thatcher	5	699	596	62	25	16	103	14.6
Timstein	3	354	292	37	13	12	62	17.5
Hope	4	752	589	94	37	32	163	21.7
Chinese Spring	27	882	693	100	39	50	189	21.4
Red Egyptain	4	569	415	103	19	32	154	26.9

Although the Timstein, Hope, and Chinese chromosomes did not differ significantly among themselves, Thatcher was clearly lower than the other four (beyond the 1% point

of significance), and Red Egyptian was higher (also beyond the 1% point). All the misdivision frequencies were considerably higher than those observed by SANCHEZ-MONGE and MAC KEY (1948) for chromosome 5A but lower than found for 5A by SEARS (1952a).

Detailed comparison of the data for 3B with those of SEARS (1952a, Table 1) for 5A requires that some of Sears' categories be lumped together. His first type of class *a* misdivisions are normal divisions, not misdivisions. The rest of the class *a*'s presumably fit in the "equal with separate arms" class of the present study, while his *b* misdivisions are "2 isochromosomes" and the *c*'s are "3: 1".

If only Chinese Spring is considered, 2 isochromosomes were somewhat more frequent than 3: 1 for 3B (5.7% vs. 4.4%) and also more frequent for 5A (23.0% vs. 13.5%). An even more striking correspondence between 3B and 5A is apparent if all the data are lumped; then 2 isos vs. 3: 1 is 4.1% vs. 4.1% for 3B and 10.7% vs. 12.2% for 5A.

Although there were about three times as many misdivisions of 5A as 3B when either the 3: 1 or 2-iso type was considered, the reverse was approximately true for the "equal with separate arms" class. Here the percentages were 11.3 for 3B vs. 3.2 for 5A (Chinese Spring) and 12.2% for 3B vs. 2.5% for 5A (total). Since the studies of 3B and 5A were made by different investigators, it is possible that differences in standards of scoring could account for some of the differences observed. Sometimes it is a matter of judgment whether the two arms of a univalent passing to a pole are attached to the same centromere or not. Consistent differences might therefore be expected in the results obtained by two investigators scoring the same group of cells. However, the comparatively high values for "equal with separate arms" in the present experiment can scarcely all be attributed to differences in scoring. This is a class that should give rise to telocentric chromosomes, and if, therefore, this class were no larger for 3B than for 5A, we would expect to recover telocentrics and isochromosomes in essentially the same ratio for 3B as for 5A. In fact, however, STEINITZ-SEARS (1966) recovered about four times as many 3B telocentrics as isochromosomes, whereas SEARS (1952a) found only about 50% more 5A telocentrics.

Besides SEARS' (1952) study of misdivision there has been one other report concerned with the misdivision of monosomes, involving chromosomes 5A, 5B, and 5D from different varieties by MORRIS *et al.* (1969). They studied misdivision of the monosomes in hybrids of their various varieties with Chinese Spring monosomics and thus not in a pure Chinese background. The rate of misdivision extended over the range 2.4%~23.6% in this material. Chromosome 5D always misdivided with a lower frequency than chromosomes 5A and 5B.

Micronuclei are formed in the microspores whenever lagging chromosomes fail to be included in the TII nuclei. An important factor determining the frequency of such micronuclei must be the frequency with which univalents divide at MI instead of passing

undivided to one pole or the other. If a univalent does not divide and is included in a TI nucleus, it presumably divides normally at the second division and does not lag. If it divides at MI, its halves not only lag at TI and run a risk of not reaching the poles, but also they lag again at TII and are again uncertain of reaching the poles.

Some types of misdivision result in formation of more than two daughter chromosomes from a single univalent. For example, misdivision at MI can result in one arm going toward one pole, one or two arms toward the other pole, and two or one arms left acentric on the metaphase plate. Also, MII misdivision of the two products of MI division of a univalent results in four separate arms, each of which may fail to reach a pole and will then form a micronucleus. Thus the frequency of tetrads with more than two micronuclei may bear some relation to the frequency of misdivision. Unfortunately, however, there are other events that can lead to more than two micronuclei, especially the failure of two homologues to synapse. Such unsynapsed homologues behave as univalents and are both subject to lagging and possible exclusion from the TII nuclei.

In the present data (Table 2) there were differences in percentage of tetrads with micronuclei, but there was, as expected, no consistent relation to frequency of misdivision. Chinese Spring, rather than Thatcher, had the lowest value, and Hope, not Red Egyptian, had the highest. Nor did the frequency of tetrads with two or more micronuclei prove to be a good indicator of misdivision frequency; instead it varied with the percentage of tetrads having micronuclei, albeit showing a greater range.

Table 2. Micronuclei in tetrads of monosomic 3B

Variety	No. of plants	No. of tetrads with indicated no. of micronuclei				
		0	1	2	more than 2	% tetrods with micronuclei
Thatcher	5	493	194	106	15	38.9
Timstein	2	163	90	67	25	52.7
Hope	4	161	120	71	35	58.2
Chinese Spring	2	239	66	33	4	30.1
Red Egyptian	4	164	79	71	25	51.6

From the MI data in Table 1 and from SEARS' (1952a) experiment, it appears that the same chromosome from different sources may differ in rate of misdivision. Another interpretation is possible, however. The backcrosses by means of which the chromosomes were transferred to Chinese Spring were not enough to eliminate all genes from the other varieties. It is possible, for example, that the genotype of Thatcher conditions a low rate of misdivision, and that one or more genes for this were transferred to the Thatcher-3B substitution line. A desirable comparison would be of Chinese mono-3B, Thatcher mono-3B, Thatcher 3B monosomic in Chinese, and Chinese 3B monosomic in Thatcher.

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A translocation difference between wheat variety HY-11 and Triticale strain ST-69-1

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A Triticale improvement programme was initiated in this laboratory in the year 1971. For this purpose and for some other fundamental projects, crosses were made between wheat variety HY-11 and the Triticale strain ST-69-1. The seed of wheat variety HY-11 was obtained from the wheat specialist, J.N.K.V.V., Power-koeda, and that of Triticale strain ST-69-1 from I.A.R.I. New Delhi. The F_1 individuals were raised in 1972 and these were meiotically analysed. F_1 hybrids showed the formation of a quadrivalent in a large number of pollen mother cells besides variable number of univalents and bivalents in each pollen mother cell. Of the 28 pollen mother cells examined in one F_1 hybrid, 18 cells showed, the presence of a distinct quadrivalent (Fig. 1) in each of them. The F_1 hybrids were selfed. Due to high degree of sterility only few seeds were available. These were raised into plants in 1972～73 and quadrivalent could be observed in some of these F_2 plants also. This confirmed that two nonhomologous chromosomes of A and/or B genomes of wheat variety HY-11 are involved in translocation relative to the A and/or B genomes of Triticale strain ST-69-1.

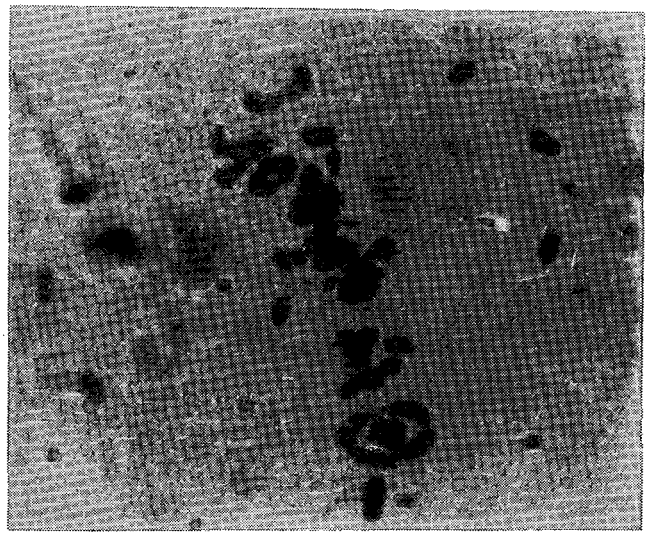

Fig. 1. Metaphase I in a F_1 hybrid (HY-11 × ST-69-1) showing a quadrivalent.

Structural changes in chromosomes of polyploid wheat seem to have played some role in evolution of this group (BAKER & MCINTOSH 1966). There are other reports where reciprocal translocations were reported between different cultivated varieties of wheat. SEARS (1953) described three varieties of wheat which differed from the variety Chinese Spring by a single reciprocal translocation. SEARS (1954) also suggested that Chinese Spring is the primitive variety and that the other varieties were derived due to mutational or structural changes in the chromosomes. Reciprocal translocations between wheat varieties were also described by RILEY and KIMBER (1961) and by BAKER and MCINTOSH (1966).

The present report is perhaps the first where a translocation difference between a wheat variety and a Triticale strain is demonstrated. Since the A and B genome of Triticale come from tetraploid wheat, the translocation difference reported here, is actually a difference between A and B genomes of a tetraploid wheat and hexaploid wheat variety. The sources of the tetraploid wheat and hexaploid wheat variety are not available. It is also difficult to find out whether the translocation difference already existed at the tetraploid level or it resulted after its incroporation into the hexaploid Triticale.

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Methods to improve the gene flow from rye and wheat to Triticale[1)]

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Introduction

The superior potential of the Triticale introductions from the Canadian-Mexican improvement program and from Salinas, Cal., was immediately apparent in the Eastern Orange Free State (JORDAAN *et al.* 1970) and also at Stellenbosch. They, however, lacked general adaptation and failed under adverse conditions. In 1970 it was therefore decided to start a Triticale improvement program at Stellenbosch. The history and potentials of Triticale have been adequartely reviewed by JENKINS (1969).

Crossability with rye

Eighty-two of the better durum introductions and other tetraploid wheats were screened for crossability with the seven best local and introduced rye cultivars. The results summarized in Table 1 were similar to those of KROWLOW (1970). Only 0.6% of the cross-pollinated durum florets yielded viable kernels, but by means of ROMMEL's (1958) embryo-culture technique the yield of seedlings was improved to 1.2% (Table 2).

KNOBLOCH (1968) cited various successful crosses between *Triticum turgidum* ssp. *carthlicum* and rye. Seventeen different crosses between this subspecies and rye were therefore made. Two introductions of ssp. *carthlicum* v. *stramineum*[2)] hybridized readily with the rye cultivars and yielded more than 23 viable kernels per 100 cross-pollinated florets (Table 1). It can, therefore, serve as a very effective bridge for transferring rye genes to the secondary Triticale. The other varieties of *carthlicum*, notably *rubiginosum*, were incompatible with rye.

A *carthlium* hexaploid strain from Sweden hybridized readily with rye to yield very fertile octaploids after colchicine treatment, and were tetraploid. Ten high-quality *T. aestivum* ssp. *vulgare* cultivars were crossed with 7 rye cultivars in order to transfer genes for better adaptation and quality via new primary Triticales to the introduced secondary Triticales. An average of 2.4% of the cross-pollinated florets yielded viable kernels (Table 1). Embryo culture did not significantly improve the yield of seedlings (Table 2).

According to RILEY and CHAPMAN (1967) the wheat cultivars from the East tend to hybridize more readily with rye. Since KNOBLOCH (1968) also cited various successful *T. aestivum* ssp. *sphaerococcum* × *S. cereale* crosses, it was decided to cross 4 *sphaerococcum* introductions with 6 rye cultivars. All *sphaerococcum* varieties, including *echinatum*, *rotundatum* and *rubiginosum*, hybridized with readily rye—on the average 20.7% of florets yielded

1) Copied from the Proceedings of the 4th Wheat Genetics Symposium by the kind permission of the Editors and Organizing Committee.
2) These strains were found to be hexaploid.

Table 1. Seed set and viability from crosses of tetraploid and hexaploid wheats × rye without using the embryo-culture technique

♀parent and no. strains or cultivars	No. rye cvs.	No. of pollinations		No. kernels set		Kernels set (% poll. florets)	Germination %	Viable kernels (% poll. florets)
		spikes	florets (basal)	filled	shrivelled			
4x wheats :								
carthlium (2)	4	9	324	0	136	41.9	0.0	0.0
dicoccoides (3)	2	6	180	0	80	44.4	3.8	1.7
dicoccon (2)	2	3	90	0	22	24.4	0.0	0.0
durum (82)	7	211	7570	0	2577	34.0	1.7	0.6
polonicum (1)	2	3	100	0	40	40.0	0.0	0.0
pyramidale (1)	1	1	38	0	6	15.8	0.0	0.0
turgidum (3)	4	5	150	0	17	11.3	0.0	0.0
dur.-carth. F_1	4	5	214	0	66	30.8	0.0	0.0
6x wheats :								
vulgare (10)	7	59	1933	57	18	3.9	64.0	2.4
sphaerococcum (4)	6	28	860	277	19	34.4	60.1	20.7
vulg.-sphaer. F_1	5	11	376	63	18	21.5	53.1	11.4
sphaer.-vulg. F_1	4	7	226	60	6	29.2	75.8	22.1
sphaer.-dur. F_1	4	13	490	0	0	0.0	0.0	0.0
carthlicum	5	16	444	100	9	24.5	75.2	18.4

viable kernels (Table 1). The *sphaerococcum* × *vulgare* F_1 hybrids when crossed with rye likewise gave a good set of viable kernels (Table 1). *T. aestivum* ssp. *sphaerococcum* must, therefore, be considered an efficient bridge for transferring rye genes via new primary octaploid Triticales to the secondary Triticales.

Sisodia and McGinnis (1970b) recommended that pentaploid wheat hybrids, resulting from Dinkel × Emmer crosses, be hybridized with rye. Our *sphaerococcum* × *durum* F_1 hybrids, when crossed with 4 rye cultivars, did not set any kernels (Table 1).

Triticale crossability

According to Sisodia and McGinnis (1970a, b) the germplasm of 6x wheat, both at the nuclear and cytoplasmic level, is important in the improvement of hexaploid Triticale. Eight Triticale introductions from Salinas, Cal., were therefore crossed as pollen parents with 6 *vulgare* cultivars and 3 *sphaerococcum* strains. Many crosses did not yield any viable kernels and an average set of only 1 viable kernel per 100 cross-pollinated florets was obtained (Table 2). Dissection of the F_1 kernels at 16 days after pollination revealed that the endosperm was a fluid, degenerate mass and that the embryos were underdeveloped—only 1 out of 21 embryo cultures gave rise to a seedling. The methods employed by Kruse (1967, 1969) to overcome incompatibility reactions did not improve the set of viable kernels. In the reciprocal crosses (Triticale × common wheat) 23% of

the cross-pollinated florets yielded viable kernels.

All the durum×Triticale crosses made to date yielded only inviable kernels.

Table 2. Seed set and viability from crosses with rye, making use of the embryo-culture technique

♀parent and no. cultivars	No. rye cvs.	No. of pollinations		Kernels set (16～18 days)		No. kernels dissected	No. embryos trans-planted	Seedlings obtained	
		Spikes	Florets	No.	% poll. florets			% dissected kernels	% poll. florets
4x wheats :									
durum (21)	6	42	1616	600	37.1	325	282	5.8	1.2
6x wheats :									
vulgare (1)	4	5	186	9	4.8	9	9	55.6	2.7
sphaerococcum	1	1	24	13	54.1	10	10	70.0	29.1

Irradiation of Triticale pollen and eggs

BREWBAKER and EMERY (1962) stated that irradiation of mature pollen had been tested with only a minor measure of success in overcoming interspecific incompatibilities. They reported that NISHIYAMA and IZUKA obtained a few viable kernels from two interspecific *Avena* crosses in 1952 when X-irradiated pollen was used. With this result in mind, and also attempting to induce haploidy in common wheat, gamma-irradiated pollen of various species was used to pollinate emasculated wheat spikes. It was found that irradiated *Triticale* pollen resulted in a much improved set of viable F_1 kernels in the common wheat×6x Triticale crosses (Table 3, Fig. 1). When pollination was effected immediately after pollen irradiation by a ^{60}Co source, the best set of viable F_1 kernels was obtained at a gamma-ray dose of 1 kR (15 kR/hr)—at this dose nearly 36% of the cross-pollinated florets yielded viable kernels. Pollination 1 and 3 days after pollen irradiation resulted in peak sets of viable F_1 kernels at gamma-ray doses of 1.5 kR and 2 kR, respectively (Table 3, Fig. 1). Pollination immediately after the pollen received a gamma-ray dose of 3 kR yielded no viable kernels; when the pollination was effected 3 days afterwards, 14.5 per cent of the florets yielded viable kernels.

The most fertile F_1 hybrids resulted from Triticale pollen which received a gamma-ray dose of 0.1～0.5 kR; they yielded as many kernels (±4) per F_1 spike as the F_1 resulting from the control crosses of common wheat×Triticale. Triticale pollen which received a gamma-ray dose of more than 1 kR gave rise to sterile F_1 plants.

In one family of 13 plants, obtained after the Triticale pollen received a gamma-ray dose of 0.05 kR, a single haploid common-wheat plant with 21 somatic chromosomes was found.

In the 6x Triticale×common wheat crosses the production of viable F_1 kernels was not improved by irradiating the Triticale parent. The egg cells of Triticale can tolerate a much higher dose of irradiation than the pollen (*ca.* 7 kR vs. *ca.* 3 kR).

Irradiation of rye pollen

When gamma-irradiated pollen of two rye cultivars was used in crosses with two common-wheat cultivars, a substantial increase of viable F_1 kernels was obtained over

Table 3. The effect of pollen irradiation on the enhancement of viable kernel sets in common wheat × Triticale and common wheat × rye crosses

Dose in kR	When pollinated[1)]	No. cultivars ♀ (wheat)	No. cultivars ♂	No. of pollinations: spikes	No. of pollinations: florets	No. kernels set: filled	No. kernels set: shrivelled	Kernels set (% of pollinated florets)	Germination %	Viable kernels (% poll. florets)
Wheat × Triticale (6x)										
0.0	—	2	selfed	18	570	522	0	91.6	98.6	90.4
0.0	—	6	8	35	1046	15	806	78.5	1.3	1.0
0.1	0–8 hrs.	2	3	3	88	6	48	61.4	5.6	3.4
0.25	do.	3	4	7	216	8	137	67.1	7.6	5.1
0.5	do.	3	4	9	272	34	141	64.3	24.0	15.4
0.75	do.	2	1	4	108	19	66	78.7	17.6	13.9
1.0	do.	3	4	10	304	95	106	66.1	54.2	35.9
1.25	do.	2	1	4	120	37	47	70.0	33.3	23.3
1.5	do.	2	1	5	150	36	73	72.7	23.9	17.3
2.0	do.	3	4	10	308	48	168	70.1	10.2	7.1
2.5	do.	2	1	6	178	5	112	65.7	0.9	0.6
3.0	do.	2	1	4	110	4	76	72.7	0.0	0.0
4.0	do.	1	1	2	52	0	41	78.8	0.0	0.0
0.1	1 day	1	1	1	30	0	28	93.3	0.0	0.0
0.25	do.	2	2	3	88	1	69	79.5	1.4	1.1
0.5	do.	3	2	4	120	12	91	85.8	10.7	9.2
0.75	do.	2	1	2	60	10	35	75.0	15.6	11.7
1.0	do.	3	2	4	130	29	84	86.9	25.7	22.3
1.25	do.	2	1	2	58	21	27	82.8	16.7	13.8
1.5	do.	3	1	4	112	41	52	83.0	37.6	31.3
2.0	do.	3	2	5	150	30	97	84.7	15.7	13.3
2.5	do.	3	1	3	92	14	40	58.7	9.3	5.4
3.0	do.	1	1	1	28	5	21	92.9	3.8	3.6
4.0	do.	1	1	1	28	0	18	64.3	0.0	0.0
0.25	3 days	2	2	3	86	0	69	80.2	1.5	1.2
0.5	do.	2	2	3	80	4	55	73.8	5.1	3.7
0.75	do.	2	1	2	50	5	41	92.0	4.3	4.0
1.0	do.	2	2	4	114	11	56	58.8	23.9	14.0
1.25	do.	2	1	2	56	13	32	80.4	17.8	14.3
1.5	do.	2	2	4	114	36	58	82.5	30.9	25.4
2.0	do.	2	2	4	108	45	36	75.0	38.3	28.7
2.5	do.	2	1	3	84	25	37	73.8	25.8	19.0
3.0	do.	2	2	3	76	14	35	64.5	22.4	14.5
4.0	do.	1	1	1	26	2	19	80.8	0.0	0.0

(Table 3. continued)

Wheat × Rye										
0.0	—	2	selfed	4	164	154	0	93.9	99.4	93.3
0.0	—	2	2	12	401	26	3	7.2	68.9	4.9
0.05	6～10 hrs	2	2	3	103	18	1	18.4	73.7	13.6
0.1	do.	2	2	3	120	15	1	13.3	81.3	10.8
0.2	do.	2	2	3	109	27	1	25.7	75.0	19.3
0.4	do.	2	2	3	96	28	1	30.2	62.1	18.8
0.6	do.	2	2	3	111	24	3	24.3	55.6	13.5
0.8	do.	2	2	3	79	22	0	27.8	63.6	17.7
1.0	do.	2	2	3	105	18	3	20.0	52.4	10.5
1.5	do.	2	2	3	104	8	2	9.6	50.0	4.8
2.0	24 hrs	1	1	2	70	0	9	12.9	11.1	1.4
3.0	...	1	1	1	38	0	0	0.0	0.0	0.0

1) Time after irradiation.

the control crosses (Table 3). The best set of viable F_1 kernels was obtained at gamma-ray doses of 0.05 kR～0.4 kR (15 kR/hr). In contrast to the irradiated Triticale pollen, irradiated rye pollen resulted in an increased kernel set; the germination capacity of these kernels remained constant up to a dose of 0.8 kR.

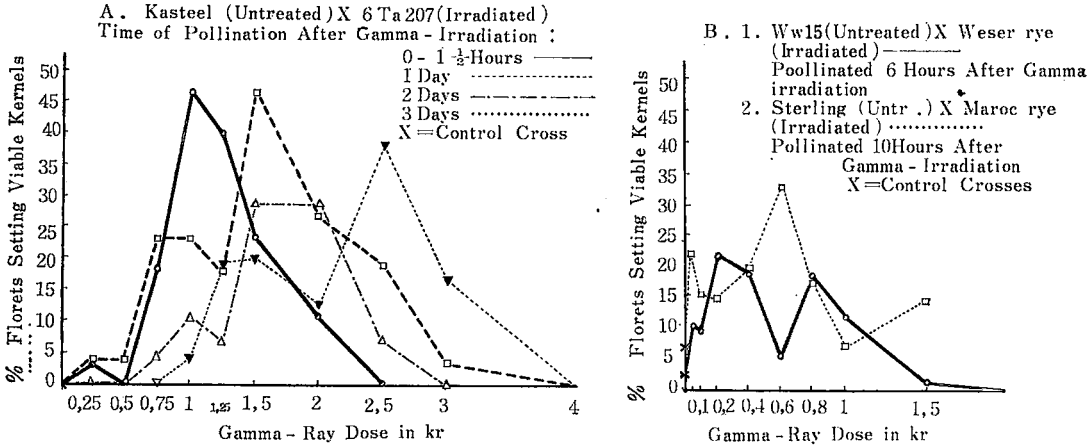

Fig. 1. The effect of gamma-irradiated a) Triticale and b) Rye pollen on crosses with common wheat : viable F_1 kernels as a percentage of the pollinated florets

Conclusion

Irradiation of rye and 6x Triticale pollen effectively facilitates the production of primary octaploid and secondary hexaploid Triticales, respectively.

Acknowledgements

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Meiotic studies of the second substitution backcross to the amphidiploid hybrid, *Triticum durum* DESF. × *Agropyron intermedium* (Host) BEAUV.[1)]

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Individual F_7 and F_8 perennial amphidiploid (AD) plants of *Triticum durum* DESF.

Table 1. Meiotic bivalent, univalent, and total chromosome numbers in 25 SB_1 strains

SB_1 No.	Bivalents			Univalents			Total chrom. No.		No. of PMC's investigated
	avg. no.	range	$S\frac{2}{\bar{X}}$	avg. no.	range	$S\frac{2}{\bar{X}}$	avg.	range	
1	10	5~21	0.51	29	4~42	2.39	49	39~62	24
2	11	3~18	0.47	27	12~45	2.57	49	38~55	27
4	10	0~16	0.67	27	13~47	3.01	47	38~58	27
6	8	0~19	1.61	32	15~47	4.76	48	41~53	19
7	12	6~20	0.96	20	6~37	0.50	44	37~50	14
8	12	6~20	0.79	23	7~35	3.09	47	36~57	21
9	7	4~11	3.11	33	29~40	11.44	47	37~52	3
10	7	5~11	3.44	35	22~44	45.77	49	44~54	3
11	6	0~11	30.25	36	27~45	71.44	48	45~49	3
12b	13	6~18	0.61	22	13~28	26.16	48	34~56	18
13	15	5~25	1.28	18	5~44	22.01	48	33~59	34
14	12	2~25	0.72	21	2~46	22.63	45	16~55	76
15	11	5~17	7.50	30	21~41	20.56	52	49~55	4
17	23	18~26	0.84	8	2~16	1.45	54	47~58	10
18a	8	—	0	16	11~21	2.96	—	—	5
18b	—	—	0	17	16~18	1.00	—	—	2
19	17	14~20	3.11	14	9~22	16.33	48	45~51	3
20a	14	—	0	17	—	0	45	—	1
20b	—	—	0	12	11~13	34.75	—	—	2
22	10	—	0	8	—	0	28	—	1
25	17	13~19	2.25	18	16~22	1.72	52	47~58	4
26	5	—	0	28	—	2.50	38	—	2
30	21	—	0	9	—	0	51	—	1
31	21	—	0	10	—	4.00	52	—	2
33	15	7~21	8.24	23	11~40	33.46	53	51~54	5
	12	0~26		21	2~47		47	16~62	311

1) Contribution of the Montana Agricultural Experiment Station, Bozeman, Montana, U.S.A. Paper No. 428 Journal Series, Montana Agr. Exp. Sta., published with approval of the Director.

2) The term "substitution backcrossing" (SB) has been adopted from KIHARA (1951). It implies that in a series of backcrosses with the male parent to an original interspecific or intergeneric hybrid, the genomes of the male parent can be imbedded into a foreign cytoplasm, namely that of the female parent.

(2n=28)×*Agropyron intermedium* (HOST) BEAUV. (2n=42) were used as parent material in this investigation. *T. durum* was the female parent in these crosses. The original crosses were made by WILLIAM J. SANDO during the period from 1923 to 1935 (U.S.D.A., 1958). We initiated substitution backcrossing[2] to *Ag. intermedium* in 1960. Forty sub-

Table 2. Meiotic bivalent, univalent and total chromosome numbers in 25 SB_2 strains

SB_2 No.	Bivalents			Univalents			Total Chrom. No.		No. of PMC's inves-tigated
	avg. no.	range	$S\frac{2}{X}$	avg. no.	range	$S\frac{2}{X}$	avg.	range	
1– 1	15	5～29	0.46	17	1～37	1.21	47	34～59	67
1– 2	21	17～27	0.14	5	1～13	0.17	47	37～60	36
1– 3	18	10～24	0.47	16	7～27	0.92	52	38～68	30
1– 4	18	10～23	0.67	12	0～21	1.00	48	38～59	30
1– 5	21	20～23	0.01	0	0～ 2	0.00	42	40～46	53
1– 8	19	14～23	0.20	8	2～17	0.42	46	35～51	30
1– 9	19	12～23	0.19	10	6～18	0.25	48	39～55	34
1–11	20	17～25	0.10	9	3～17	0.19	49	40～57	32
1–15	22	19～23	—	0	0～ 2	—	44	40～46	51
1–18	20	18～24	0.06	9	4～14	0.18	49	45～55	30
2–11	19	15～24	0.11	10	4～15	0.18	48	41～52	31
2–13	18	14～22	0.25	6	1～10	0.31	42	35～47	19
2–16	14	4～23	0.95	19	7～39	2.45	47	40～57	30
2–17	17	12～24	0.30	13	5～22	0.61	47	41～60	30
2–21	17	12～23	0.28	16	6～24	0.69	50	42～58	30
2–22	17	12～23	0.23	15	8～26	0.74	49	46～56	30
2–23	16	12～19	0.09	13	8～19	0.21	45	38～53	31
2–27	19	15～23	0.20	2	0～ 9	0.21	40	32～49	30
2–29	21	17～26	0.14	4	2～ 7	0.11	46	39～55	30
2–35	16	13～21	0.85	8	3～11	0.83	40	35～47	9
2–39	21	14～23	0.01	3	0～13	0.03	45	36～47	132
24– 1	21	18～23	0.60	1	0～ 3	0.04	43	39～46	27
24– 2	20	18～21	0.02	1	0～ 3	0.01	41	38～43	29
29– 1	19	16～21	1.56	4	0～ 9	3.13	42	41～44	4
33– 1	19	17～21	0.18	3	0～ 8	0.74	41	40～43	12
	19	4～29		8	0～39		45	32～68	816

Table 3. Number of bivalents, univalents, and total chromosome numbers in SB_1 and SB_2

Generation	Bivalents		Univalents		Total chrom. No.		No. of PMC's investigated
	avg. no.	range	avg. no.	range	avg. no.	range	
SB_1	12	0～26	21	2～47	47	16～62	311
SB_2	19	4～29	8	0～39	45	32～68	816

stitution backcross seeds were obtained from the first backcross attempt. Cytological studies of 25 SB_1 strains have previously been reported (SCHULZ-SCHAEFFER, *et al.* 1971). The average number, range and variance of mean bivalents and univalents and the total number of chromosomes of 25 SB_1 strains are recorded in Table 1.

Second substitution backcrosses (SB_2) were made in 1965. A minimum of two plants of each of 79 vegetatively propagated SB_2 strains was established in the field at Bozeman, Montana. Twenty-five SB_2 strains were investigated cytologically in meiosis. Eighteen of these strains served as parents for the SB_3 generation. The average number, range and variance of bivalents and univalents, and the total number of chromosomes of 25 SB_2 strains are shown in Table 2. A marked decrease in the number of univalents from the SB_1 (21_I) to the SB_2 generation (8_I) was found (Table 3). This suggests a normalization of pairing of *Agropyron* chromosomes and a decrease in the number of *Triticum* chromosomes due to substitution backcrossing. Twenty-one *Agropyron* bivalents and 14 *Triticum* univalents are expected in the SB_1 (SCHULZ-SCHAEFFER 1972, Fig. 1). The average numbers of bivalents (12) and of univalents (21) in the SB_1 differ significantly (P=0.05) from the expected values. The standard heterogeniety χ^2 method was employed to compare the goodness of fit of the SB_1 strains to an expected ratio of 21_{II} and 14_I and the goodness of fit of the SB_2 strains to an expected ratio of 21_{II} and 7_I. The SB_1 strains were heterogeneous and the within strain fit to the expected was poor. Heterogeneity decreased in the SB_2 and the within strain fit of the observed to the expected was markedly improved. This suggests that a second substitution backcross tends to stabilize meiotic behavior. The *Triticum* univalents which decreased from SB_1 to SB_2 apparently have an asynaptic effect on the normal pairing of the *Agropyron* homologues. This phenomenon is supported

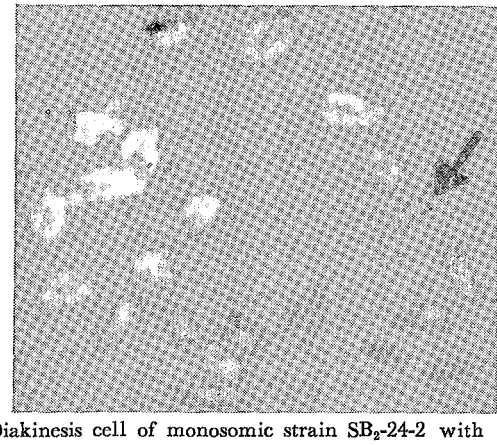

Figure 1. Diakinesis cell of monosomic strain SB_2-24-2 with 20 bivalents and 1 univalent, 2n=41 (magnif. ×1128).
Arrow indicates univalent.

by data of PERSON (1956) who reported partial asynapsis causing excessive univalents in monosomic *Triticum aestivum* L. TSUCHIYA (1959, 1960) ascribed the complete asynapsis of 1% of the sporocytes in single and double primary trisomics of *Hordeum vulgare* L. to the specific effect of the extra No.2 chromosomes. An increase of bivalents from the SB_1 (12_{II}) to the SB_2 (19_{II}) indicates normalization of *Agropyron* bivalent pairing (Table 3).

The stabilizing effect of substitution backcrossing is further supported by changes in averages and variances of numbers of univalents and bivalents (Tables 1 and 2). In general, SB_1 strains are more variable than SB_2 strains. Also, in the SB_1, variances of the mean number of univalents are greater than variances of the mean number of bivalents. This pattern of greater variability in number of univalents than bivalents persists in SB_2, but variances in SB_2 are lower. It should be noted that numbers of observations were less in SB_1 than SB_2.

In at least one case, SB_2–24–2, *Triticum* chromosomes are entirely eliminated. A typical diakinesis cell of this strain is shown in Fig. 1. This strain is monosomic.

We conclude that substitution backcrossing leads rapidly to normalizing meiotic behavior, the elimination of *Triticum* chromosomes, and that bivalents stabilize more readily than univalents.

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Production of male sterility and fertility restorer analogues of Indian wheat varieties involving *Triticum timopheevi*, *Aegilops ovata* and *Ae. caudata* cytoplasms

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Earlier wheat could not be thought to be exploited for heterosis breeding because of an obvious barrier of its floral morphological framework which checks cross pollination. But, KIHARA's discovery of cytoplasmic male sterility in 1951 suggested a mechanism by which cross pollination could be forced in this crop as well. This classical discovery gave an insight to wheat breeders all over the world. Later FUKASAWA's (1959) discovery of male fertility restoration lead to researches on hybrid wheat in many countries. Extensive programmes are in progress to produce male sterile and fertility restorer lines of commercial cultivars.

Success of hybrid wheat will depend upon (i) degree of heterosis (ii) stability of male sterile and fertility restorer lines and (iii) the cost of hybrid seed. Several studies have suggested considerable heterosis in wheat. Success of the male sterile and restorer lines will depend upon their stability and adaptability. Most of such of exotic lines are not quite suited to our conditions. Thus in order to be able to undertake any work on heterosis breeding in wheat we have to develop male sterile and fertility restorer lines in the existing distinct and diverse desirable indigenous wheat strains. With these considerations, in India the work of nucleus substitution to produce male sterile and fertility restorer analogues of local wheat varieties was started by us in October, 1970. Ten promising India wheat cultivars of diverse genetic origin *viz*. C. 306, K. 68, C. 591, N.P. 809, Lerma Rojo, Sonalika, Norteno, Sharbati Sonora, Kalyan Sona and Hira, were selected for the purpose.

Production of male sterile analogues:

Male sterile cytoplasm was transferred into the above mentioned ten wheat varieties from three different sources *viz*. *Triticum timopheevi*, *Aegilops ovata* and *Ae. caudata*. Table 1 shows the sources of male sterile cytoplasm and the Indian wheat cultivars with their important morphological characteristics, in which the male sterile analogues have been produced.

The recipient varieties were used as pollinators to the above mentioned established male sterile lines. The F_1s tested for pollen fertility and selfed seed set showed almost cent percent pollen sterility and no seed set in selfed heads. Subsequent backcrosses were made with the respective recipient varieties and in all the backcross generations data on pollen fertility and selfed seeds set were recorded. Only those plants which showed

Table 1. The male sterile cytoplasm donors and the recipient Indian wheat varieties with their average heights and some yield contributing characters

Cytoplasm donor	Recipient variety	Average height of the plant (cm.)	Spike length (cm.)	1,000 Grain weight (gm.)	Yield per plant (gm.)
T. timopheevi					
(i) m.s. Chris	C.306	120.84	11.21	45.5	39.12
(ii) m.s. Sonora-64	K.68	108.96	11.47	51.0	42.80
Ae. ovata	C.591	125.37	9.05	47.2	52.00
(i) m.s. Norin-26	N.P. 809	157.68	12.62	41.6	24.61
Ae. caudata	Lerma Rojo	107.10	12.96	45.7	36.85
(i) m.s. Cabezorro-2	Sonalika	104.09	11.97	49.4	36.50
	Norteno	90.74	12.37	46.9	17.68*
	Sharbati Sonora	83.47	11.31	43.8	36.80
	Kalyan-Sona	95.79	14.18	40.9	40.26
	Hira	74.09	11.61	42.1	42.65

* Low grain yield due to excessive grain shattering and damage due to birds.

Table 2. Days from showing to flowering and number of effective tillers in ten Indian wheat varieties and their male sterile analogues involving the three cytoplasms

Variety	Normal cytoplasm		*T. timopheevi* cytoplasm		*Ae. ovata* cytoplasm		*Ae. caudata* cytoplasm	
	days to flower	no. of effective tillers/plant	days to flower	no. of effective/ tillers/plant	days to flower	no. of effective tillers/plant	days to flower	no. of effective tillers/plant
C.306	97.7	16.8	*	*	137.0	41.8	—	—
K.68	92.8	17.2	84.0	28.5	136.2	53.0	—	—
C.591	99.3	22.7	107.4	29.8	137.5	42.5	—	—
N.P. 809	102.7	27.6	108.3	36.5	—	—	142.0	72.0
Lerma Rojo	89.5	15.3	91.5	48.9	135.5	55.2	143.0	53.0
Norteno	86.5	8.8	99.8	23.0	135.3	60.6	143.5	62.5
Sonalika	71.8	13.7	90.9	23.1	138.5	42.9	139.3	44.6
Sharbati Sonora	66.7	21.8	87.8	28.1	137.9	34.6	135.0	55.0
Kalyan Sona	90.8	18.2	89.6	27.2	139.3	63.6	—	—
Hira	68.5	19.0	—	—	136.0	32.0	135.0	64.0

* All plants in the F_1 showed necrosis and eventually died.

complete male sterility were used in backcrossing programme. To accelerate the pace of work, two crops were grown every year i.e., one in the normal season and the other as an offseason crop at hills.

Table 2 presents the days to flower and number of effective tillers in recipient wheat varieties and also in the male sterile analogues obtained from the three sources. The

table shows that *Ae. ovata* and *Ae. caudata* cytoplasms, though confer great vigour as exhibited by their profuse tillering capacity, are late in maturity which is an undesirable character under our conditions.

There was a considerable increase in ear length of the *Ae. ovata* analogues. However, *Ae. ovata* and *Ae. caudata* analogues due to their late maturity and with the onset of hot winds at the time of maturity developed highly shrivelled seeds. On the other hand, *T. timopheevi* analogues possessed excellent agronomic and yield abilities without having any undesirable side effect. Keeping in view these facts much emphasis was laid on *T. timopheevi* male sterile and fertility restorer analogues. Thus, male fertility restorer analogues were produced from the *T. timopheevi* source only.

Production of male fertility restorer analogues:

Restorer DIRK (*T. timopheevi*), a promising male fertility restorer line, was crossed with all the above mentioned ten wheat varieties. F_1's were crossed with a male sterile line—M.S. Sonora-64 (*T. timopheevi*) to test whether the F_1's carried R gene(s). Besides, backcrosses were also made with the respective varieties. The tester × the ten F_1's seeds were sown and on selfing it was observed that the F_1's restored to male fertility very effectively. This indicated that R gene (s) have been tranferred. In further backcross generations selection was practiced and only those single plants that carried fertility restoring gene (s) and also resembled morphologically with the recurrent parent variety, were selected and used in advancing the backcross programme.

In addition to the production of male fertility restorer analogues in Indian wheat varieties we also explored the possibility of locating male fertility restoring genes in several wheat varieties *per-se*. Besides three Indian hexaploid wheat varieties i.e., N.P. 839, N.P. 883 and N.P. 880 reported by MIRI, AMAWATE and JAIN (1970) to possess R genes, some twenty four Indian and exotic wheat varieties (N.P. 52, N.P. 165, N.P. 720, N.P. 758, N.P. 761, N.P. 770, N.P. 775, N.P. 792, N.P. 799, N.P. 805, N.P. 818, N.P. 823, N.P. 829, N.P. 852, N.P. 858, N.P. 862, N.P. 865, N.P. 891, NAPO-63, Ciano F-67, GABO, INIA-66 and Norin-59) were crosed with male sterile Sonora-64 (*T. timopheevi*). None of the above mentioned varieties, including those reported by MIRI and his associates could restore the male fertility.

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A chromosomal male-sterility system of producing hybrid wheat[1)]

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It appears reasonable at this point in time to examine in considerable detail the various ways in which hybrid wheat may be produced. Three general methods of obtaining large homogeneous blocks of male-sterile plants are being subjected to examination by various investigators. These three methods involve cytoplasmic male sterility, male gametocides, and chromosomal male sterility, respectively. This paper is concerned with the possible use of chromosomal male sterility in production of hybrid seed.

Proposed system

The system that is being examined involves a recessive male-sterility gene, *ms*, on a wheat chromosome and the corresponding male-fertility gene, *Ms*, on a homoeologous alien chromosome (DRISCOLL, 1972). The three lines involved in the system, which are referred to as the X, Y, and Z lines, are all homozygous *ms* and contain 2, 1, and 0 doses of the alien chromosome, respectively. The *Ms* gene operates on sporophytic tissue such that Y lines produce 21-chromosome gametes and 22-chromosome gametes; however, the former function preferentially because of certation of hyperploid pollen. The X line produces 22-chromosome pollen only and is relatively pure-breeding.

The system in which a pure stand of Z plants is produced involves (i) the production of an original, small amount of Z seed, and (ii) increase of this to required quantities.

Small, initial amount of Z seed

This is obtained from the selfed progeny of a limited number of Y plants, which segregate approximately 25% Y and 75% Z plants, the latter being male-sterile. These Z plants are pollinated by the 21-chromosome, *ms* pollen of the Y plants. The Y plants are removed after pollen has shed, and seed is harvested from the Z plants. This is homogeneous Z seed.

Increase of Z seed

This is achieved by the two steps shown in Table 1. Part of the initial Z seed is used in Step 1. The remainder is used in Step 2 with the Y seed obtained from Step 1. The Z seed obtained from Step 2 can be further increased by recycling through Steps 1 and 2.

The Z seed can then be used as the female block in hybrid seed production. The

1) Copied from the Proceedings of the IV Wheat Genetics Symposium, by the kind permission of the Editors and Organizing Committee.

Table 1. Increase of Z seed

	Pollen Male Block·····→Female Block——→Seed		
Step 1	X	Z	Y
〃 2	Y	Z	Z

male block consists of a normal variety, and the hybrid plants are then heterozygous *Ms ms* on the pertinent wheat chromosome. No alien chromosome is present in the hybrid seed; thus its effect on production characteristics is not a consideration.

Genetic components:

ms on a wheat chromosome

An ideal *ms* mutant would have the following six characteristics:

1. A single recessive gene.
2. No selection against gametes bearing *ms* when in competition with gametes bearing the normal allele.
3. Stability in various varietal backgrounds.
4. Stability in various environments.
5. No pleiotropic effects of the *ms* mutant.
6. A suitable alien homoeologue.

A number of male-sterile mutants of hexaploid wheat that have been reported in the literature are considered in the light of the above characteristics.

PUGSLEY and ORAM (1959) reported male-sterile mutants in an F_1 of Kenya Farmer X_4 bearded Javelin 48. The inheritance was reported as being complex. BRIGGLE (1970) backcrossed this sterility into the variety Chancellor and by appropriate selection obtained a stock that involves a single recessive gene which is transmitted with reasonable rates from heterozygotes. Stability of this sterility is under investigation, and its chromosomal location is unknown.

ATHWAL, PHUL and MINOCHA (1967) reported isolation of a male-sterile type in a complex hybrid. They also reported that the sterility is governed by mutiple factors and is perhaps unstable under various environments.

KRUPNOV (1968) isolated a male-sterile mutant of the variety Saratovskaya-29 which may be controlled by a single gene. It was reported that male-sterile plants are less viable than fertile plants.

FOSSATI and INGOLD (1970) isolated a male-sterile form of the variety Probus after applying 24 kR of X-rays to seed. The sterility was reportedly due to a single recessive gene that is normally inherited. Its chromosome location is unknown. It appears that this mutant may be suitable for the proposed system.

Attempts are currently being made to isolated further *ms* mutants following γ-irradi-

ation of pollen of the variety Pitic 62. The technique involves pollination of monosomics 4A, 4B, 5A, 5B, or 5D with irradiated pollen. Each of these five chromosomes carries a gene or genes for male fertility, and it is known that only one arm of each of these chromosomes is involved (SEARS, personal communication). Thus a deletion including the *Ms* gene(s) would result in a male-sterile mutant. Monosomic F_1's can be scored directly for such deletions.

To date only chromosome 5B has been examined in this way. Although a number of male-sterile F_1 hemizygotes were isolated and pollinated by euploid wheat, no sterile plants have been recovered in progenies derived from 42-chromosome offspring. The genetic basis of this is under investigation. One possible explanation centers on the fact that the male-sterile F_1 plants are hemizygous 5B whereas all plants in later generations are homozygous 5B.

One possible male-sterile mutant has been isolated and maintained following γ-irradiation of monosomic 5A seed (GORMAN and DRISCOLL, unpublished).

Ms on an alien chromosome

At least one alien chromosome is known to belong to each homoeologous group (BIELIG and DRISCOLL, 1973). On the assumption that groups 4 and 5 are the ones of interest, the chromosomes involved are as follows.

Group 4:

An *Agropyron elongatum* (HOST) BEAU. chromosome bearing a gene for blue endosperm (LARSON, personal communication in BIELIG and DRISCOLL, 1971; LARSON and ATKINSON, 1972).

A. elongatum chromosome 4E (DVORAK, SCHELTGEN and KNOTT, 1972).

Preliminary evidence indicates that chromosome D of *Secale cereale* L., variety Imperial, may also be a member of this group (DRISCOLL, unpublished).

Group 5:

The *S. cereale* chromosome 5R, bearing the hairy-neck gene, *Hp* (O'MARA, 1946).

Aegilops umbellulata ZHUK. chromosome C (CHAPMAN and RILEY, 1970).

Information obtained from chromosome substitution lines allows one to conclude that effective *Ms* genes are located on some of these chromosomes. For example, the substitutions of rye chromosome 5R for 5A and for 5D are highly fertile. The selfed seed set of monosomic 5R substituted for 5A and 5D was 70% and 65%, respectively, of that of euploid wheat under the same glasshouse conditions (BIELIG and DRISCOLL, 1970). Compensation for a mutant locus (or short deletion) may be more successful than compensation for loss of the entire wheat chromosome.

It should also be pointed out that alien-addition lines have somewhat different behaviours when they involve homozygous *ms* on a wheat chromosome. Normally disomic

addition lines do not breed true; thus X lines would give rise to some Y and some Z plants. In the scheme proposed such Z lines would be sterile and would not contribute to Step 1 in Table 1. The Y plants would give rise to Z plants in the male block of Step 2 and would fail to contribute to that step. Maintenance of the X line itself is much easier if the 21" decay product is male sterile; however, it may even so require some monitoring.

It is known that some 22-chromosome pollen does compete successfully with 21-chromosome pollen when both are produced from a 43-chromosome plant. This would mean that some Y seed would be produced at the end of stage 2. This would eventually result in a few sterile plants in the commercial crop. These would not be expected to affect the performance of the crop, as they would be pollinated by the abundant pollen present, and they would in any case be presumably present in low numbers.

Comparison of cytoplasm and chromosomal sterility systems:

The chromosomal system is more complicated than the cytoplasmic system, particularly as the stages before the hybrid-seed-production stage are more numerous in the chromosomal system. However, there are comparative advantages in the chromosomal system which may outweigh this disadvantage.

Any deficiency of fertility restoration in the cytoplasmic system affects the commercial crop, whereas in the chromosomal system such deficiencies affect the hybrid-seed-production stage, which is less serious. Also, hybrid-seed production can be carried out in an environment other than those under which the crop is produced.

The male parent utilized in the hybrid-seed production with the cytoplasmic system contains the nuclear, fertility-restoring genes, whereas in the chromosomal system the male parent contains no such special component. It is thus possible to select the male parent on the basis of combining ability and amount of pollen shed.

Hybrids and disease resistance:

Two less obvious advantages of hybrids are as follows. A series of male parents for the hybrid-seed-production stage could be developed which differed by different genes for resistance to a particular pathogen. This would allow for management of these resistances in accordance with their needs as determined by variations in the pathogen.

The development of hybrids would also allow ready use of translocated alien segments bearing disease resistances. If such a translocation is present in one parent only, the hybrid crop not only has a single dose of alien chromatin but it has a dose of the pertinent wheat segment that is missing in pure lines involving the translocation.

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(Received August 20, 1973)

II. News

Announcing an International Symposium on Haploids in Higher Plants

Advances and Potential
June 10~14, 1974
at University of Guelph, Guelph, Ontario, Canada

The Symposium will cover and compare various methods of producing haploids in higher plants and their utilization in research and plant breeding. The program is expected to include invited papers on specific topics, work-shops and perhaps a restricted number of short contributed papers. To ensure the proper coverage of various aspects of haploidy, an International Program Committee has been established and includes: S.S CHASE, G. MELCHERS, S.J. PELOQUIN, R. RILEY, R.F. STETTLER and N. SUNDERLAND. The Symposium will coincide with Centennial Celebrations of the Ontario Agriculture C ollegeof the University of Guelph. To ensure receiving information on mailings, persons may drop a card with their address to the Organizing Chairman, K.J. KASHA, Crop Science Dept., University of Guelph, Guelph, Ontario, Canada.

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III. Editorial Remarks

Announcement for future issues

WIS No. 38 will be planned for publication in March 1974. Manuscripts for this issue are accepted any time, not later than January 31, 1974.

WIS is open to all contributions regarding methods, materials and stocks, ideas and research 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 7×7 cm^2). Lists of stocks are exempted from this page limit. Authors receive 50 reprints of their contributions free of charge. Extra copies are printed by order at cost price. Communications regarding editorial matters should be addressed to:

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

Raise of Membership Fee

Due to the economic situations, the yearly Membership Fee has been raised up to ¥700 for foreign member and ¥500 for Japanese member from the fiscal year beginning April 1973. 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

Diakinesis cell of monosomic strain SB_2-24-2 with 20 bivalents and 1 univalent, 2n=41 (magnif. ×1128). Arrow indicates univalent. (SCHULZ-SCHAEFFER, KIM and CHAPMAN, Fig. 1, p. 23, present issue of WIS).