

THE SYSTEMATIC SUBSTITUTION OF TWO RYE CHROMOSOMES  
IN WINTER WHEAT

by

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A Thesis

Submitted to the Committee on Graduate Studies  
in Partial Fulfilment of the Degree of  
Doctor of Philosophy

The University of Manitoba

August 1962

## ABSTRACT

An attempt was made to systematically substitute Dakold winter rye chromosomes V and VI for each of the Kharkov winter wheat chromosomes. The varieties Kharkov and Dakold were chosen because of the practical possibility of obtaining a substitution line or lines with the combined hardness of wheat and rye. The rye chromosomes chosen for study were V and VI: V because it is easy to identify and VI because it is associated with the expression of the hairy-neck character.

Three methods were utilised to obtain the disomic substitutions: selfing plants with the chromosome formula (a)  $20^{II}W + 1W + 1R$ , (b)  $20^{II}W + 1R$  and (c)  $20^{II}W + 1W + 1^{II}R$ . Of the three methods, the third one appears to be most promising in that it has yielded the largest number of substitution lines. To date, only 8 of the 42 possible substitution lines have been obtained. They are lines 4B (VIII), 7B (VII), 4D (XV) and 7D (XXI) of Kharkov by chromosome V of rye and 5A (IX), 3B (III), 1D (XVII) and 5D (XVIII) by chromosome VI of Dakold. It is expected that most if not all 42 of the possible substitutions will be obtained by selfing plants with the chromosome formula  $20^{II}W + 1W + 1^{II}R$ .

It was observed that both chromosomes took on a slightly different morphological behaviour when substituted into wheat. Chromosome V shows a very short terminal satellite in the short arm and VI shows a submedian secondary constriction in the long arm which is very pronounced at metaphase I. It was also observed that the

very short terminal satellite in chromosome VI is typically less densely stained than the remaining portion of the same chromosome and sometimes appears as a fine faintly stained thread-like body. The meiotic behaviour of disomic substitutions studied appears to be quite normal with only a few cells showing the rye pair as two univalents. Mitotic and meiotic studies of their progenies indicate that the disomic substitutions are more stable than the addition lines for the same rye chromosomes.

Morphological studies of the disomic substitutions showed that when a pair of rye chromosome VI was substituted for chromosomes 5A (IX), 3B (III), 1D (XVII) and 5D (XVIII) of Kharkov nearly normal tall plants were obtained, whereas when the rye pair was simply added to the entire wheat complement, the reduction of plant height was very pronounced. Plants seem to deviate considerably from normal when rye chromosome V is substituted for any of Kharkov chromosomes studied thus far.

This study corroborates previous findings that the gene or gene-complex controlling the hairy-neck character of rye is located in the long arm of chromosome VI. Disomic substitutions for lines 5A (IX), 3B (III) and 5D (XVIII) show dense hairiness on the neck, but the substitution for 1D (XVII) shows no hairiness on the neck. The degree of hairiness was seen to vary with the same dose of rye chromosome VI against the background of different wheat chromosomes. There would appear to be some interaction between wheat and rye chromosomes in the degree of expression of hairiness, rather than a dosage effect.

A number of generalizations appear to be possible on the results to date. While the transmission of rye chromosome VI is higher than that of V on the female side, in general owing to misdivision, rye chromosome VI is lost in a greater frequency. There is no relationship between the frequency of transmission of the rye chromosomes and the side of transmission (male or female), but the frequency of transmission seems to depend on the particular wheat chromosome involved. For example, chromosome 3B (III) was substituted for much more frequently than either 3A (XII) or 3D (XVI). There is also evidence that certation is exerted on both the male and female sides in the transmission of rye chromosomes. The absence of Kharkov chromosome 7B (VII) was associated with the misdivision of rye chromosome V. A small amount of asynapsis in the wheat chromosomes was observed to cause a few unexpected types in some of the lines.

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## ACKNOWLEDGMENTS

The writer wishes to express his appreciation to Dr. B. C. Jenkins for his advice and assistance during the entire course of this study.

Thanks are also extended to Professor L. H. Shebeski, Dr. R. C. McGinnis and technicians for their assistance at various times during the term of this project.

Grants in aid of research from the National Research Council of Canada made this project possible and these grants are hereby gratefully acknowledged.

## INTRODUCTION

Evidence indicates that certain genes of winter rye would be very valuable in wheat since wheat lacks some characters which are present in rye. Many attempts have been made to combine in one strain the quality and uniformity of wheat and the desired characters of rye.

Wilson in 1876 first described a sterile wheat-rye hybrid, while Triticale, its fertile allopolyploid derivative, was first described by Rimpau in 1891. Their reports were based on the crossing of common wheat and rye and selection for the desired recombinations in subsequent self-pollinated or backcross progeny. The lack of homology among the parental chromosomes prevents natural recombination and results in chromosome additions or substitutions rather than chromosome rearrangement (38). Melnyk and Unrau (11) and Riley, Chapman and Kimber (33) indicate that a certain amount of pairing between the chromosomes of rye and those of some species of Aegilops and Triticum can occur, but the chance of suitable recombination is still remote. To overcome these difficulties different techniques or approaches have been made such as chromosome doubling, addition of individual pairs of rye chromosomes to the common wheat complement and substitution of a pair of chromosomes from rye (Secale cereale) to common wheat.

The present study of the systematic substitution of alien chromosomes in common wheat has been limited to the substitution of Dakold winter rye chromosomes V and VI (2) for each of the Kharkov

winter wheat chromosomes. The varieties Kharkov and Dakold were chosen for the purpose of obtaining a substitution line or lines with the combined hardiness of wheat and rye. Rye chromosomes V and VI were chosen because it is easy to identify both of them cytologically by their length and other morphology. Aside from the practical aspect of increasing the hardiness of winter wheat, the primary purpose of this project was to study the cytological and phylogenetic significance of the behaviour of two specific rye chromosomes when substituted into winter wheat. It was for both practical and theoretical reasons, therefore, that the present studies on the substitution of individual chromosomes from rye to wheat were undertaken.

## LITERATURE REVIEW

Many attempts have been made to produce fertile and true-breeding hybrids between wheat and rye. Wilson (46) was the first one who produced a wheat-rye hybrid, but it was sterile. Its fertile allopolyploid was first produced by Rimpau in 1891. Since then, many varieties of both wheat and rye have been used for the production of "Triticale" (12) but none have suitable quality and fertility.

The hybrid between Triticum durum Desf. and Secale cereale L. was reported by Aase in 1930, and the desired allopolyploid by O'Mara (27). The hybrid between T. monococcum L. and S. cereale L. has not been reported. The hybrid between T. timopheevi Zhukov. and S. cereale has been described by Kostoff (10). In addition hybridization has also been done between T. compactum, T. spelta and T. sphaerococcum and Secale by Kagawa and Chizaki (8), and Nakajima (14, 15, 16, 17, 18, 19, 20, 21, 22). Nakajima (23) tried to obtain four hybrids between T. macha and each of 4 species of Secale, namely, cereale, vavilovii, africanum and montanum and studied the F<sub>1</sub> plants only. Sears (38) and O'Mara (31) pointed out that the sterile F<sub>1</sub> hybrids have shown the occurrence of limited pairing all of which is believed to be autosyndetic involving only wheat chromosomes and results in chromosome additions or substitutions rather than the gene transfer from rye to wheat.

Many different methods have been used to reach the ultimate goal of combining wheat and rye into one. One of the methods is

to produce the fertile amphiploid by doubling the chromosomes in  $F_1$  hybrids. Müntzing (12, 13) and Sanchez-Monge (36, 37) have reviewed the results of this method to date including the production and performance of 42, 56 and 70 chromosomes "Triticales" and concluded that none has suitable agronomic qualities.

As an alternative means of overcoming these difficulties O'Mara (25) proposed a procedure by which individual pairs of rye chromosomes could be added to the wheat complement. To obtain addition lines he crossed the wheat-rye amphiploid with wheat and the derivatives were allowed to self for one or more generations. Following this method, O'Mara (25, 30) successfully obtained a few monosomic additions and three different disomic additions of individual rye chromosomes to Chinese Spring. Subsequently Chapman and Riley (4) and Riley and Chapman (32) have obtained the disomic additions of rye chromosomes of the variety "King II" individually to the common wheat variety Holdfast. By using different techniques Hyde (42) added a chromosome of Aegilops umbellulata to common wheat, Gerstel (6) made chromosome transfers between species of Nicotiana and Sadanaga (35) described rye chromosome additions to T. durum. A more recent report is the addition of seven chromosomes of "Dakold" winter rye individually to the winter wheat variety "Kharkov" (5). Riley and Chapman (32) indicated that each chromosome pair of the donor species can be isolated from the rest of the complement and examined separately against the graphic background of the recipient species. It may thus be possible to determine the linkage groups of genes, the expressions of which are epistatic to

those of the recipient species, or which interact with genes of the recipient species.

Another promising avenue for this type of study is the substitution of rye chromosomes individually in common wheat. Although different methods of the substitution of alien chromosomes into common wheat have been outlined (41), no systematic substitution program has been attempted. The number of possible substitutions is much greater than that of additions. If only whole chromosome substitutions be considered there are 147 possible whole chromosome substitutions - seven rye chromosomes for each of the twenty-one wheat chromosomes.

At present only one known substitution has been determined. O'Mara (26) reported the substitution of a pair of rye chromosome I for chromosome 5A (IX) of wheat. This occurred in the progeny of a slightly asynaptic disomic addition line. The effect of this substitution of chromosome 5A (IX) of wheat by rye chromosome I in comparison to the corresponding addition line was to restore male fertility, greatly increase female fertility, increase meiotic stability and improve plant vigor to normal; whereas adding the bivalent to normal T. vulgare resulted in semi-dwarf partially female-sterile plants. These observations indicate that the effects of substitution cannot be wholly predicted from additions.

The present study is mainly concerned with the systematic substitution of rye chromosomes V and VI (2) to the winter wheat variety Kharkov. Following is the detailed review of their behaviour in addition lines, their morphology and other important characters in relation to these two rye chromosomes.

O'Mara (30), Chapman and Riley (4) and Riley and Chapman (32) utilized the morphology of the added chromosomes during meiosis in order to identify lines possessing different rye chromosomes but have not related this directly to the karyotype of the rye parent. Recently Bhattacharyya and Jenkins (2) reported on the karyotype of "Dakold" winter rye and pointed out that all the seven rye chromosomes can be differentiated individually by their size, arm index, secondary constrictions and the location of satellites. The morphology of these rye chromosomes at mitotic metaphase was used by Evans and Jenkins (5) as a means of identifying wheat-rye addition lines. The identification of rye chromosomes at mitotic metaphase in substitution lines was also based on the morphology described by Bhattacharyya and Jenkins (2).

Chromosome V of Dakold rye is a long chromosome (average length 10.39 ) with a submedian primary constriction and a secondary constriction in a submedian position in the long arm (2). The average arm index is 1.50. This pair differs from Chromosome IV in having no satellite at the end of the short arm. In addition, its short arm is always longer than that of Chromosome IV. Chromosome VI of Dakold rye is comparatively short (average length 9.74 ) with submedian primary constriction and a very short terminal satellite on the short arm (2). The long arm is almost double the length of the short arm. The average arm index is 1.82. As an addition to the wheat complement, this rye chromosome governs the morphological expression of the hairy-neck character in the plants.

Following is the summary of the phenotypic expressions of

plants with the addition of rye chromosomes V and VI. In the case of Chromosome V, the major phenotypic effect is to reduce plant height and spike density (5). Disomic plants of this group frequently have supernumerary spikelets but the expressivity of this character is variable. The major phenotypic effect in the case of Chromosome VI addition is the production of pubescent peduncles, the reduction of plant height (about two-thirds of normal) and spike density (5). The effects of this chromosome were much more pronounced when it was in the disomic condition. The following table, taken from the paper by Evans and Jenkins (5), on "Individual Secale cereale Chromosome additions to Triticum aestivum", (page 212), shows some comparisons.

Line	No. of plants	Height inches	Density Spikes/cm	Fertility seeds/spikelets	Tillering capacity
Kharkov	10	50.5	1.60	2.87	40.8
V monosomic	9	50.1	1.47	2.25	41.8
V disomic	10	45.2	1.37	2.08	26.7
VI monosomic	9	45.6	1.56	1.50	47.6
VI disomic	11	36.8	1.47	0.75	32.8

As to the numbering of chromosomes, in relation to those given by previous workers, the chromosome I designated by O'Mara (29) and Riley and Chapman (32) correlates with chromosome VI of the present study. This correlation was made by Bhattacharyya and Jenkins (2), but no correlation was pointed out for chromosome V.

The amphiploid between wheat and rye has been made several times and its cytology has been thoroughly investigated by Müntzing

(12). All the amphiploids reported thus far have been asynaptic to some degree, showing univalents at metaphase I. No triticales strain has been reported with a perfectly regular meiosis. O'Mara (25) stated that the rye chromosome, when disomic, did not always form a bivalent but was present in a small percentage of cells as two univalents, and when present as a bivalent, often separated when the wheat chromosomes were at anaphase. O'Mara (30) also pointed out that plants which are disomic or monosomic addition for the rye chromosome are partially asynaptic. As a result of this irregularity, variations could be observed in the chromosome numbers of the gametes and of the progenies. From the meiotic studies in the addition lines obtained in the Department of Plant Science, University of Manitoba, it was observed that the addition lines for rye chromosome VI showed a greater percentage of cells with two univalents than that for chromosome V and the percentage of progenies with 44-chromosomes was about 62% in the case of rye chromosome VI whereas in V over 90% (Evans, private communication).

In connection with the variability of the rye chromosome morphology in the addition lines, the following interesting observations were made by Bhattacharyya, Evans and Jenkins (5). They point out that the morphology of rye chromosomes V and VII change when they are present with the wheat complement. The total length of chromosome V remained constant but the average arm index changed from 1.50 in the parental species to 1.29 in the disomic addition line. Bhattacharyya, Evans and Jenkins (3) concluded from these observations that this change in the relative length of the two arms

is possibly due to the effect of the new combination of wheat and rye chromosomes. Chromosome VII did not show any change in length and arm index but the secondary constriction in the short arm (2) became almost inconspicuous in the addition line and when visible appeared to have shifted close to the centromere producing a larger terminal satellite. Navashin (24) also pointed out that the satellite of one species disappears in the interspecific crosses of the genus Crepis. He explained this fact as due to the fusion of the satellite with the proximal end of the satellited chromosome. This change was reversible and the satellited chromosomes recovered their normal shape as soon as the original chromosome complement was extracted from the hybrid by means of segregation.

There is a considerable amount of information in the literature in relation to the behaviour of rye chromosome VI (previously designated as chromosome I by O'Mara (29)). Since some interesting observations come out in the present study of systematic substitution of rye chromosome VI in wheat, a review of these works will be helpful for evaluating the behaviour of this chromosome.

O'Mara (29), Kattermann (9) found two kinds of chromosome VI, since both the chromosomes were producing the same effect in the phenotype (hairy-neck) of the wheat plant. O'Mara (29, 30) pointed out that one had a median constriction which was very clear, leaving the two chromosome halves (isobrachial) connected by a small isthmus or thread and the other chromosome, which had an indistinguishable phenotype, had a submedian constriction which seemed identical in the degree to which it constricted the chromosome (heterobrachial). O'Mara

(30) assumed that the sub-median type was derived from the median type by the loss of a part of the chromosome, or secondly that median chromosome was derived from the submedian type by the loss of the short arm and duplication of the long arm in misdivision. O'Mara (29, 30) and Riley and Chapman (32) concluded that the very strong constriction in this chromosome is not the kinetochore constriction, but is a secondary constriction of a very pronounced type. This secondary constriction is a very pronounced at metaphase I. The two types which produce the same phenotype when added to the wheat are: (1) the normal rye chromosome, which has a subterminal kinetochere and a very pronounced median and secondary constriction; and (2) the long arm of this chromosome, which carries the same constriction in a sub-median position and a terminal kinetochere at the end of the shorter arm.

Chromosome VI of rye is marked with the characteristic expression of hairy-neck in wheat plant possessing it. The gene for pubescence was found in the long arm (30, 32). Sears (43) pointed out that the hairy-neck gene must be near the centromere of the rye chromosome. Besides the pubescence character, the long arm also carries some other characters as shortening or compressing of the internodes which is the character of addition lines. The short arm seemed to have little or no detectable effect in one or two doses. The long arm when present twice had all the obvious effects of two whole chromosomes (30, 31).

The following review was made from O'Mara's paper in 1940. Those plants which were monosomic for chromosome VI were slightly

shorter than normal wheat plants and had heads with broader and coarser spikelets. When the chromosome was disomic, the plants were approximately two-thirds the height of normal wheat, and had coarser, broader spikelets than the plants monosomic for the chromosome. A comparison of the amounts of pubescence on the necks of plants monosomic and disomic addition for the rye chromosome and on the neck of the amphiploid is interesting. It shows that the amphiploid has the least pubescence although it has the rye chromosome present in two doses. Nakajima (23) crossed Triticum macha and each of 4 species of Secale (cereale, vavilovii, africanum and montanum) and studied several F<sub>1</sub> plants from the four combinations. He indicated that the F<sub>1</sub> plants did not show the hairy-neck character which was expected in the F<sub>1</sub> plants between Triticum-Secale hybrids. These observations indicate that the expression of hairy-neck in wheat plants is not simple.

O'Mara (29, 30) obtained the five different types of additions arising from the misdivision of rye chromosome VI. They are: 1. the normal univalent, 2. the tetocentric chromosome representing the long arm, 3. the isochromosome representing duplication of the long arm, 4. the telocentric chromosome representing the short arm, and 5. the isochromosome representing duplication of the short arm. Some of these were unstable, like the univalent derivatives in wheat (39). Since the rye chromosome often occurs in the univalent condition in addition lines, even when it is present as two homologues, stable additions of the rye chromosome to wheat would seem to be difficult (31). O'Mara (29) studied the effect of chromosome substitution on

competition between gametes. He crossed common wheat with the chromosome formula  $20^{II}W + 1W + 1R$  (obtained by crossing  $20^{II}W + 1^{II}R$  with common wheat). The male gametes produced by these individuals with two non-homologous univalent chromosomes will be of four types, if the products of misdivision are excluded: nullisomic gametes (i.e.  $20W$ ), those in which either the Triticum or the Secale chromosome present ( $20W + 1W$  or  $20W + 1R$ ) and those in which both are present (i.e.  $20W + 1W + 1R$ ). If pollen from these plants is placed on the stigmas of normal Triticum plants, the resultant progeny should indicate the relative success of the different classes of gametes in competition. The percentage of successful gametes was 60% for normal gametes, 26% for substitution gametes, 8% for gametes with both chromosomes and 6% for nullisomic gametes. The data indicated that the normal gametes did not have an extreme advantage in competition and the substitution gametes effected fertilization once for each 2.3 normal gametes. No reports were available of the reciprocal cross.

## MATERIALS AND METHODS

### Materials

For this study, the winter wheat variety Kharkov-MC22 was chosen to receive the rye chromosomes from the winter rye variety Dakold 23. Kharkov-MC22 is one of the hardiest winter varieties in commercial use in Canada and is most popular in southern Alberta where the majority of this class of wheat is grown. The Canada department of Agricultural Research Station at Lethbridge, Alberta is responsible for maintaining foundation stock of this variety. The winter rye variety, Dakold 23 was chosen as the contributor of rye chromosomes largely because it is also one of the hardiest varieties available. Stock of this variety is maintained by the Crop Science Department, University of Saskatchewan, Saskatoon, Saskatchewan.

### Methods

The following pre-requisites are necessary for the systematic substitution of Dakold rye chromosomes in winter wheat Kharkov. They are (a) to establish the monosomic series in Kharkov wheat and (b) to establish the disomic addition lines of wheat (Kharkov) and rye (Dakold).

The establishment of a monosomic series in Kharkov wheat was being carried as a departmental project, in the department of Plant Science by separately crossing this variety with each of the twenty-one monosomics of the variety Chinese Spring obtained from Dr. E. R. Sears. The selected monosomics in  $F_1$ 's were backcrossed to Kharkov

six or seven times to reconstitute the Kharkov germplasm with the respective chromosome deficiencies. With the exception of chromosome line 6D (XIX), all monosomics in Kharkov were considered to be sufficiently reconstituted.

The wheat-rye addition lines had been produced by using the following methods. Kharkov wheat was crossed with Dakold rye and the sterile hybrid was treated with colchicine to produce an amphiploid which proved to be reasonably fertile. These plants were crossed with Kharkov and the resulting plants have twenty-one pairs of wheat chromosomes, plus the seven rye chromosomes occurring singly. These plants were either backcrossed to wheat again or self to produce the seven possible addition lines.

Five of these have been obtained in the disomic condition, but the two lines (II and III) in the monosomic condition (5). For the present study, only the disomic addition lines for the rye chromosomes V and VI were used.

#### Methods used to obtain disomic substitutions

The following three methods have been used for obtaining the disomic substitution lines. The necessary steps are described below for each of the methods.

##### A. Method suggested by O'Mara (26) and Sears (41):

(1) Select the plants with the chromosome formula  $41W + 1R$  by checking mitotic divisions in the root tips of plants obtained from each of the 21 Kharkov monosomics crossed with each of two Kharkov-Dakold addition lines (as male parent) namely V and VI.

(2) Check the meiosis of each plant to be sure that there are 20 bivalents and 2 univalents (one of wheat and one of rye).

(3) Self these plants ( $20^{II} + 2^I$ ).

(4) Check the root tips of progenies obtained from respective lines to select the plants with the chromosome formula  $40W + 2R$ .

(5) Check the plants with  $40W + 2R$  meiotically to make sure that there are 21 bivalents of which 20 bivalents are from wheat and one pair from rye.

B. Method not previously suggested:

(1) Cross the monosomics of Kharkov with the chromosome formula  $20^{II}W + 1W + 1R$  (obtained as in A).

(2) Check the root tips to select the plants with  $40W + 1R$  from these crosses and also from the progenies obtained by selfing the plants with the chromosome formula  $20^{II}W + 1W + 1R$ .

(3) Check the meiosis of every plant to be sure that there are 20 bivalents and one univalent.

(4) Self these plants ( $20^{II}W + 1R$ ).

(5) Check the progenies obtained from the respective lines to find the plants with  $40W + 2R$ .

(6) Check the plants with  $40W + 2R$  meiotically to make sure that there are 21 bivalents.

C. Outlined by Sears (41):

(1) Cross the  $F_1$  plants with the chromosome formula  $20^{II}W + 1W + 1R$  as female parent, to the addition lines which are disomic for rye chromosomes V and VI.

(2) Select the individuals which are monosomic for the wheat

chromosome and disomic for the rye chromosome, i.e.  $20^{IIW} + 1W + 1^{III}R$ .

(3) Self these plants; following selfing, these monosomic-disomic plants should produce some nullisomic-disomic offspring, i.e.  $20^{IIW} + 1^{III}R$  by the loss of wheat univalents during division.

(4) Check the progenies to find the plants with  $40W + 2R$ .

(5) Check meiosis to make sure that there are 21 bivalents.

#### Identification of rye chromosomes

Both the rye chromosomes V and VI can be identified cytologically by their morphology. Chromosome V has a submedian primary constriction and secondary constriction in a submedian position in the long arm (2). Chromosome VI has a submedian primary constriction and a very short terminal satellite on the short arm (2). Its morphology is very distinct due to the length of the long arm which is nearly double the length of the short arm. Presence of chromosome VI can also be recognized by the expression of the hairy-neck character in addition lines.

#### Cytological Techniques

Mitotic metaphase studies were made on root tips pretreated in tap water at  $0 - 2^{\circ}C$ . for 24 hours and fixed in acetic-alcohol (1:3) as outlined by Tsunewaki and Jenkins (45). Squashes were made using the standard Feulgen technique. Meiosis was studied in pollen mother cells fixed and stored in Carnoy's solution (6:3:1 of ethyl alcohol, chloroform and glacial acetic acid), by the acetocarmine smear technique as outlined by Smith (44).

Abbreviations

The following abbreviations are being used in this thesis:

K - refers to the winter wheat variety Kharkov

W - wheat

R - rye.

## RESULTS AND DISCUSSION

MORPHOLOGY OF RYE CHROMOSOMESA. Chromosome V

Bhattacharyya and Jenkins (2) described chromosome V of Dakold rye which had a submedian primary constriction and a secondary constriction in the submedian position in the long arm. It is interesting to note that when this chromosome is substituted in wheat, a small distinct terminal satellite appears in the short arm. The following results indicate a possible explanation of the change.

Navashin (24) observed that the satellite in interspecific crosses of Crepis disappeared. He explained this as due to the fusion of the satellite with the proximal end of the satellited chromosome. This change was reversible and the satellited chromosomes recovered their normal shape as soon as the original chromosome complement was extracted from the hybrid by means of segregation. Battacharyya, Evans and Jenkins (3) pointed out that the secondary constriction in the short arm of chromosome VII is almost inconspicuous in the addition lines. They explained that in the presence of nucleolar chromosomes of wheat the nuclear function of rye chromosome VII is not necessary and as a result, the secondary constriction region is not completely expressed.

The present study shows that when rye chromosome V replaces any one of the 21 wheat chromosomes (in plants with the chromosome formula  $20^{IIW} + 1W + 1R$ ), the terminal satellite is expressed. A

similar situation is also observed when a pair of wheat chromosome 4D (XV) is substituted. This indicates that it is probably not due to the effect of any specific wheat chromosome, but a change in the genomic construction may cause the change of morphology of the alien chromosome. The change of morphology may not be expected in all the alien chromosomes.

### B. Chromosome VI

Chromosome VI has a submedian primary constriction and a very short terminal satellite on the short arm (2). Another type of chromosome VI was described by Kattermann (9) and O'Mara (30), in which they mentioned that this chromosome had also a median constriction which lies in the long arm. Both types were associated with the expression of the hairy-neck character. O'Mara (30) proposed two assumptions for the two types of chromosome VI, one that the submedian type was derived from the median type by the loss of a part of the chromosome, or two, that the median chromosome was derived from the submedian type by the loss of the short arm and duplication of the long arm in misdivision.

The present study also shows the presence of both types. The second type has a secondary constriction in the long arm, but this is not distinct in all the metaphase plates of mitosis. It has been observed that this secondary constriction lies in the submedian position of the long arm (Fig. 1) instead of the median position. The change in the morphology is probably due to the background in which the alien chromosome is incorporated. It indicates that there is only one type of rye chromosome VI present, which can be changed

into the second type.

O'Mara (30) and Riley and Chapman (32) indicated that this chromosome showed a very strong median constriction at first metaphase of meiosis in the form of an isthmus separating equal arms, but this constriction is not the kinetochore constriction. A similar observation was also made in the present study. This constriction is very distinct in all the metaphase plates of meiosis and it is easy to distinguish this chromosome from the other wheat chromosomes by its characteristic appearance (Fig. 2). Therefore, it appears that the secondary constriction in the submedian position of the long arm which is not always distinct at metaphase of mitosis, becomes distinct in all the metaphase plates of meiosis. This characteristic seems to be helpful in distinguishing rye chromosome VI from the others in meiosis.

Aside from the secondary constriction in the long arm, another interesting observation was made during mitotic metaphase in connection with the terminal satellite in the short arm. This satellite takes comparatively less stain than the remaining part of the same chromosome and sometimes appears as a fine faintly stained thread-like body (Fig. 3). It may be due to the effect of the unnatural background for the rye chromosome. This characteristic can also be used for the identification of chromosome VI from wheat chromosomes at mitosis.

#### EVALUATION OF METHODS

In order to obtain the disomic substitutions, three methods were used. They are based on selfing the plants with the following

chromosome formula (a)  $20^{II}W + 1W + 1R$ , (b)  $20^{II}W + 1R$ , and (c)  $20^{II}W + 1W + 1^{II}R$ . The success of each method depends on transmission of the rye chromosome, production of functional gametes, pairing affinity of the gametes and certation. In the present study, both rye chromosomes V and VI are taken into consideration and discussed separately.

A. Selfing of plants with the chromosome formula  $20^{II}W + 1W + 1R$

Plants with the chromosome formula  $20^{II}W + 1W + 1R$  produce four types of gametes, i.e.  $20W$ ,  $21W$ ,  $20W + 1R$  and  $21W + 1R$  and nine types of progenies with the chromosome formula  $40W$ ,  $40W + 1R$ ,  $40W + 2R$ ,  $41W$ ,  $41W + 1R$ ,  $41W + 2R$ ,  $42W$ ,  $42W + 1R$ ,  $42W + 2R$  are expected.

(a) Rye chromosome V

Frequency results for each type of progeny in different lines are presented in Table I. It may be seen that progenies with  $2n = 41W$ ,  $42W$  were obtained in the greatest frequency and that the next most frequent type was  $2n = 41W + 1R$ . There are very few progenies with  $2n = 40W$ ,  $40W + 1R$ ,  $41W + 2R$ ,  $42W + 1R$  and  $42W + 2R$  whereas the type  $2n = 40W + 2R$  is almost non-existent and completely absent in most of the lines.

(b) Rye chromosome VI

Frequency results for each type of progeny in different lines are presented in Table II. These results also indicate a similar situation as in the case of rye chromosome V.

Results from both tables indicate that gametes with  $20W$  or  $21W$  have a greater chance of pairing with each other. A low fre-

Table I. Chromosome distribution in the progenies of Kharkov aneuploids with the chromosome formula  $20^{II}W + 1W + 1R$  when rye chromosome V is involved.

Chromosome Line	Progeny type and frequency									Total
	40W +1R	40W +2R	41W	41W +1R	41W +2R	42W	42W +1R	42W +2R	Total	
K2A (XIII)			2	4		20	8		34	
K3A (XII)		1	17	7		7	2		34	
K4A (IV)	4	3	12	4	1	5			29	
K5A (IX)		4	21	7		10	2		44	
K6A (VI)	3	1	26	13	1	13	3		60	
K7A (XI)	3	4	24	7		3	3		44	
K1B (I)	1		39	11	1	12	4		68	
K2B (II)	3	2	19	5		12	2		43	
K3B (III)			1	4		8	2		15	
K4B (VIII)		1	20	6		8	1		36	
K6B (X)	2		19	6		10	8		45	
K7B (VII)		3	16	10	3	11			43	
K1D (XVII)	3	2	37	7	1	6	2		58	
K2D (XX)	1		29	4		8	1		43	
K3D (XVI)		1	23	8		7			39	
K4D (XV)		1	1	3	2		1		8	
K5D (XVIII)			3	6	1	27	5		42	
K7D (XXI)	2	2	19	10		22	3		58	
Total	22	25	1	330	121	8	190	46	0	743

Table II. Chromosome distribution in the progenies of Kharkov aneuploids with the chromosome formula  $20IIW + 1W + 1R$  where rye chromosome VI is involved.

Chromosome Line	Progeny type and frequency									Total
	40W	40W +1R	40W +2R	41W	41W +1R	41W +2R	42W	42W +1R	42W +2R	
K2A (XIII)		1		2			4			7
K3A (XII)				13	2		7	2		24
K4A (IV)	2	1		10	3		3			19
K5A (IX)		3	1	14	1		4			23
K6A (VI)		2		27	8		15	4		56
K7A (XI)	1			4			17	2		24
K1B (I)		4		10	5		9			28
K2B (II)	2			35	5		13	1		56
K3B (III)		1		1	2		4			8
K4B (VIII)	2	1		7	3		11	2		26
K6B (X)	5			12			4	1		22
K7B (VII)		1		15	3	1	31	3		54
K1D (XVII)	9	4		8	3	1	1	1		27
K2D (XX)	4	3		20	2		23	2		54
K3D (XVI)		1		3	5			1		10
K4D (XV)		1		28	6		14	2		51
K5D (XVIII)	1		2	11	5		4	1		24
K7D (XXI)				2	6		21	5	4	38
Total	26	23	3	222	59	2	185	27	4	551

quency of nullisomics indicates that gametes with 20W are able to function but the union of 21W with 21W is much more frequent. It seems that the gametes with only wheat chromosomes have an extreme advantage in competition over the gametes with a rye chromosome. A low frequency of progenies with  $2n = 41W + 2R$  and  $42W + 2R$  indicates that the fertilization of gametes with rye chromosome from both the male and female sides does not occur frequently. Few or no progenies with  $2n = 40W + 2R$  indicates that the gamete with  $20W + 1R$  does not frequently unite with a similar type of gamete. Therefore, it seems that this procedure may not be a very successful one to obtain the disomic substitution, i.e.  $20^{II}W + 1^{II}R$ .

B. Selfing of plants with the chromosome formula  $20^{II}W + 1R$

Two types of gametes e.g. 20W and  $20W + 1R$  could be expected from plants with the chromosome formula  $20^{II}W + 1R$  and following selfing, three possible types of progenies, i.e. 40W,  $40W + 1R$  and  $40W + 2R$  could be expected.

(a) Rye chromosome V

Frequencies of the different types of progenies obtained from selfing this type are presented in Table III. Following selfing, different types of progenies i.e.  $2n = 40W$ , 41W, 42W,  $40W + 1R$ ,  $40W + 2R$ ,  $41W + 1R$ ,  ~~$42W + 2R$~~ ,  ~~$41 + 2R$~~  and  $39W + 2R$  were obtained, whereas only the three types  $40W$ ,  $40W + 1R$  and  $40W + 2R$  were expected. This may be due to the asynaptic condition of some of the wheat chromosomes which causes the formation of irregular types of gametes resulting in unexpected progenies. Table III shows

Table III. Chromosome distribution in the progenies of Kharkov aneuploids with the chromosome formula  $20^{II}W + 1R$  where rye chromosome V is involved.

Chromosome Line	Progeny type and frequency								Total
	40W	41W	42W	40W +1R	40W +2R	41W +1R	39W +2R	Total	
K3A (XII)	1	5	1					7	
K4A (IV)	15	39	4	1		1*		60	
K5A (IX)	3	19		1*				23	
K7A (XI)	3	20		1*				24	
K2B (II)		7	1					8	
K4B (VIII)		2	7					9	
K7B (VII)	7	12	3	6*	6*	2*	4*	40	
K1D (XVII)	4	23	7	1	1*	4*		40	
K2D (XX)		1	1					2	
K3D (XVI)		4	6					10	
K5D (XVIII)		3						3	
K6D (XIX)	1	29	3			2		35	
K7D (XXI)	1	30	21	2	2	8		64	
Total	35	194	54	12	9	17	4	325	

\* Normal wheat + rye fragment

that the frequency of progenies with 40W, 41W and 42W is greater than for the other types observed. This is an indication that the gametes with wheat chromosomes only have an extreme advantage in competition over the gametes with a rye chromosome. Thus there is a greater frequency of progenies with only wheat chromosomes.

(b) Rye chromosome VI

Data obtained from selfing the plants where rye chromosome VI was involved are given in Table IV. Here the types of progenies are more or less restricted to 40W, 41W and 42W, and there is not as great a range of types as in the case of rye chromosome V. The greater frequency of progenies with  $2n = 40W, 41W$  and  $42W$  also indicates that gametes with only wheat chromosomes unite more frequently with similar gametes rather than those with the rye chromosome. In this case, the transmission of the rye chromosome through the male or female side seems to be very low, whereas with rye chromosome V it was greater.

C. Selfing of plants with the chromosome formula  $20^{II}W + 1R + 1^{II}R$

Only four types of gametes, namely 20W, 21W,  $20W + 1R$  and  $21W + 1R$  can be obtained from plants with the chromosome formula  $20^{II}W + 1W + 1^{II}R$ . Following selfing, nine types of progenies i.e.  $2n = 40W, 40W + 1R, 40W + 2R, 41W, 41W + 1R, 41W + 2R, 42W, 42W + 1R$  and  $42W + 2R$  are expected.

(a) Rye chromosome V

The frequencies of different types of progenies obtained from selfing this type are given in Table V. Here the frequency of plants with the rye chromosome is greater than for plants with only

Table IV. Chromosome distribution in the progenies of Kharkov aneuploids with the chromosome formula  $20^{II}W + 1R$  where rye chromosome VI is involved.

Chromosome Line	Progeny type and frequency						Total
	40W	41W	42W	40W +1R	40W +2R	41W +1R	Total
K4A (VI)	5	10	4				19
K1B (I)	1	13	4				18
K3B (III)	1	6	10				17
K4B (VIII)	1	17	2				20
K1D (XVII)		17	2				19
K2D (XX)	9	9		1*			19
K3D (XVI)		13	1				14
Total	17	85	23	1	0	0	126

\* Normal wheat + rye fragment

Table V. Chromosome distribution in the progenies of Kharkov aneuploids with the chromosome formula 20IIW + IW + 1IR where rye chromosome V is involved.

Chromosome Line	Progeny type and frequency										Total	
	40W	40W +1R	40W +2R	41W	41W +1R	41W +2R	42W	42W +1R	42W +2R	43W#		44W#
K3A (XII)			1	3	17**	17**	1	2**	1	4	3	39
K2B (II)		1		1		13**	1	2**	4	2	1	25
K4B (VIII)			1			35		2	6			44
K7B (VII)			2*	2	4*	1	1*			3		33
K3D (XVI)		1			37	1	2	2	2	2		45
Total	0	2	24	6	17	96	4	9	13	11	4	186

# Unexpected types  
 \*\* Normal wheat + rye isochromosome  
 \* Normal wheat + rye fragment

wheat chromosomes. Very few plants have 40W, 41W and 42W. Plants with  $2n = 41W + 2R$  are most frequent, indicating that the combination of gametes with  $20W + 1R$  and  $21W + 1R$  is more frequent than others. The number of plants with  $40W + 2R$  is appreciably greater than was obtained with the two methods already described. The data indicate that the rye chromosome is frequently transmitted through both the male and female sides. This is probably due to the fact that the rye chromosome is present as a pair rather than a univalent as before. Here simply because gametes with the rye chromosome occur in a much greater frequency they have an advantage over gametes with only wheat chromosomes.

It is interesting to notice here that the disomic substitution for wheat chromosome 7B (VII) occurred in the highest frequency, whereas 4B (VIII) gave one out of 44 progenies and 3A (XII), one out of 39 progenies. This indicates that the function of gametes with  $20W + 1R$  differs from line to line.

A few unexpected types of plants with  $2n = 43W$  and  $44W$  were obtained. This is probably due to the slight asynaptic nature of the wheat chromosomes which may cause irregular types of gametes resulting in unexpected types of progenies.

(b) Rye chromosome VI

The frequencies of the different types of the progenies are presented in Table VI. Here also the frequency of plants with only wheat chromosomes is less than the plants with rye chromosomes. A frequent occurrence of progenies with  $2n = 41W + 2R$  indicates the more frequent union of gametes with  $20W + 1R$  and  $21W + 1R$ . Pro-

Table VI. Chromosome distribution in the progenies of Kharkov aneuploids with the chromosome formula  $20^{IIW} + 1W + 1^{II}R$  where rye chromosome VI is involved.

Chromosome Line	Progeny type and frequency											Total		
	40W	40W +1R	40W +2R	41W	41W +1R	41W +2R	42W	42W +1R	42W +2R	43W	44W		43W +1R	39W +2R
K2A (XIII)			2?	1	2	1*	1	2	2	1	1	43W +1R	39W +2R	12
K4A (IV)			2	1	5*	13*	3	4	1	6	2			37
K7A (XI)			5	1	3	20**	2	4	5	7	5			52
K3B (III)			28		1	7	1						3	40
K4B (VIII)						4		1	1					6
K6B (X)				1	1*	7*		7*	22*		5	3		46
Total	0	0	37	4	12	52	7	18	29	15	13	3	3	193

# Unexpected types

\*\* Normal wheat + rye isochromosome

\* Normal wheat + rye fragment

genies with disomic substitutions are also obtained in a reasonable frequency, but the number in line 3B (III) is much greater than for the other lines. About 70% of the progenies are disomic substitutions in line 3B (III). A lower frequency of progenies with  $2n = 40W$ ,  $41W$  and  $42W$ , indicates that gametes with the wheat chromosomes only have less opportunity to unite with similar gametes. Also the occurrence of a few unexpected types of progenies with  $2n = 43W$ ,  $44W$ ,  $43W + 1R$ ,  $39W + 2R$  may be due to the slight asynaptic condition in the wheat chromosomes causing formation of irregular gametes and thus resulting in these types of progenies.

#### Discussion of methods

The end results of each of the three methods described in the foregoing is to obtain as many as possible of the disomic substitutions. From the first one, it was found that plants with  $40W + 2R$  (i.e. disomic substitution) are very rare and most of the lines do not produce any at all. A similar situation was also found in the case of progenies from parents with the chromosome formula  $20^{II}W + 1R$ . This indicates that for the rye chromosomes under study the transmission is extremely rare when each is present in the univalent condition. This is probably due to great loss of the rye chromosome during divisional stages.

The third method, selfing plants with the chromosome formula  $20^{II}W + 1W + 1^{II}R$ , seems to be better than the other two. In this case, progenies with rye chromosomes occur more frequently than those with wheat chromosomes alone. This indicates that the transmission of rye chromosomes from both male and female sides is most frequent

and also that union of gametes with rye chromosomes has an advantage over the gametes with only wheat chromosomes. The high rate of transmission of rye chromosomes is probably due to the presence of the rye chromosome as a pair, thus permitting a more normal distribution in meiosis. The frequency of progenies with  $40W + 2R$  (i.e. disomic substitution) is sufficient to make this method reasonably successful.

Therefore, it seems that the method of selfing plants with the chromosome formula  $20^{II}W + 1W + 1^{III}R$  and selecting disomic substitutions from the progenies is the best one of the three methods. By following this method it may be possible to obtain disomic substitutions in most if not all of the lines.

#### RYE CHROMOSOME TRANSMISSION STUDIES

##### A. Wheat monosomics x wheat-rye additions

###### (a) Rye Chromosome V.

This type of cross was made to obtain the plants with the chromosome formula  $20^{II}W + 1W + 1R$  which can be produced by the union of gametes with  $20W$  and  $21W + 1R$  from the male side. Progenies from each of the 21 lines (except line 1A, <sup>5B</sup> and 6D) were cytologically checked and the type of progenies obtained are recorded in Table VII. From the table it appears that plants with  $20^{II}W + 1W + 1R$  are quite numerous in most of the lines. Plants with  $2n = 41W$  and  $42W$  can only be produced when the rye chromosome is lost from the male side. Therefore, the presence of progenies with  $41W$  and  $42W$  indicates that a certain percentage of the rye chromosome is lost from the male side.

Table VII. Chromosome distribution in the progenies from the cross between Kharkov aneuploids and wheat-rye addition line where rye chromosome V is involved.

Chromosome Line	Progeny type and frequency				Total
	41W+1R	42W+1R	41W*	42W*	
K2A (XIII)	4	-	-	1	5
K3A (XII)	6	4	-	-	10
K4A (IV)	6	2	-	-	8
K5A (IX)	6	1	2	-	9
K6A (VI)	7	2	1	1	10
K7A (XI)	3	1	1	1	6
K1B (I)	7	2	-	-	9
K2B (II)	5	2	1	-	8
K3B (III)	3	4	1	2	10
K4B (VIII)	6	1	-	-	7
K6B (X)	5	-	1	1	6
K7B (VII)	7	-	-	3	10
K1D (XVII)	7	-	-	2	9
K2D (XX)	4	1	1	4	10
K3D (XVI)	7	-	1	2	10
K4D (XV)	6	-	1	1	8
K5D (XVIII)	4	3	1	-	8
K7D (XXI)	5	5	-	-	10
Total	98	28	9	18	153

\* Rye chromosome lost

This loss of the rye chromosome is due to a slight asynapsis for this chromosome during the divisional stages of meiosis and results in gametes without a rye chromosome. From these data, it is also possible to calculate the frequency of gametes with  $20W$  and  $21W$  from the female side in Kharkov, and these calculations will be presented later.

(b) Rye Chromosome VI

A similar situation exists for this cross as for the one involving the wheat-rye addition line V. Data are presented in Table VIII. From the table it appears that the frequency of plants with  $2n = 41W$  and  $42W$  is greater than for rye chromosome V. This indicates that the rate of loss of rye chromosome VI is greater than for chromosome V, because progenies with  $41W$  and  $42W$  can only be produced when the rye chromosome is lost.

B.  $F_1$  type, i.e.  $20^{II}W + 1W + 1R$  x wheat-rye additions

(a) Rye Chromosome V

This type of cross is made with the object of obtaining plants with the chromosome formula  $20^{II}W + 1W + 1^{II}R$ . They can be produced if gametes with  $20W + 1R$  combine with those of  $21W + 1R$  from the male side. The progenies obtained from this cross were studied and the frequency of different types of progenies is presented in Table IX. From this cross, only four types of progenies, namely  $2n = 41W + 1R$ ,  $41W + 2R$ ,  $42W + 1R$  and  $42W + 2R$  can be expected, but if no rye chromosome is transmitted from the male side, two more types namely  $2n = 41W$  and  $42W$  can also be expected.

The presence of a small number of plants with  $41W$  and  $42W$

Table VIII. Chromosome distribution in the progenies from the cross between Kharkov aneuploids and wheat-rye addition line where rye chromosome VI is involved.

Chromosome Line	Progeny type and frequency				Total
	41W+1R	42W+1R	41W*	42W*	
K2A (XIII)	4	4	1	1	9
K3A (XII)	1	-	3	1	5
K4A (IV)	-	-	5	2	7
K5A (IX)	3	-	2	3	8
K6A (VI)	4	-	-	4	8
K7A (XI)	6	-	2	2	10
K1B (I)	4	-	3	2	9
K2B (II)	5	1	1	-	7
K3B (III)	3	3	1	2	9
K4B (VIII)	5	1	2	-	8
K6B (X)	2	4	1	2	9
K7B (VII)	3	1	1	1	6
K1D (XVII)	3	-	2	3	8
K2D (XX)	2	-	2	4	8
K3D (XVI)	3	3	2	1	9
K4D (XV)	1	-	4	1	6
K5D (XVIII)	2	3	-	4	9
K7D (XXI)	1	1	2	1	5
<b>Total</b>	<b>52</b>	<b>21</b>	<b>33</b>	<b>34</b>	<b>140</b>

\* Rye chromosome lost.

Table IX. Chromosome distribution in the progenies from the cross between Kharkov aneuploids with the chromosome formula  $20^{11}W + 1W + 1R$  and wheat-rye addition line where rye chromosome V is involved.

Chromosome Line	Progeny type and frequency									Total
	41W	41W +1R	41W +2R	42W	42W +1R	42W +2R	40W* +1R	40W*	43W* +1R	
K1A (XIV)		12	1	1	1					15
K2A (XIII)		6				4				10
K3A (XII)	3	10	1		8		1			23
K4A (IV)		4		3	5				1	13
K5A (IX)		14	1		1					16
K6A (VI)	3	15		2	3					23
K7A (XI)	3	1			1					5
K1B (I)	2	6		1	1					10
K2B (II)		11	5				2			18
K3B (III)		1			3					4
K4B (VIII)	4	13	4	1	4			1		27
K6B (X)	3	10		1	5		1			20
K7B (VII)	1	3			1					5
K1D (XVII)		6			1					7
K2D (XX)	4	12		2	1		25	2		<del>44</del> 46
K3D (XVI)	3	15	1		5		12			36
K5D (XVIII)	1	10		1	5					17
K6D (XIX)		7		1	1	1				10
K7D (XXI)		1			1					2
Total	27	157	13	13	51	3	39	3	1	307

\* Unexpected types

indicates that in some situations rye chromosome V is lost. The frequency of plants with  $41W + 2R$  and  $42W + 2R$  is less than for the other types. This indicates that the transmission of a rye chromosome on the female side is very low. A few unexpected types of plants with  $2n = 40W + 1R$ ,  $40W$  and  $43W + 1R$  were obtained. This may be due to the slight degree of asynapsis which causes irregularity in certain gametes.

(b) Rye Chromosome VI

Data for this cross are given in Table X. With the exception of a few differences, the situation is similar here to the one in the case of chromosome V. The greater frequency of plants with  $2n = 41W$  and  $42W$  indicates the greater loss of rye chromosome VI. The frequent occurrence of progenies with  $41W + 2R$  and  $42W + 2R$  indicates that the transmission of rye chromosome VI through the female side is higher than that for V. The highest frequency of plants with  $41W + 2R$  in line 3B (III) indicates that gametes with  $20W + 1R$  on the female side unite most frequently with the gamete  $21W + 1R$  from the male side. On the other hand, it also indicates that the transmission of rye chromosomes on the female side is higher. A few unexpected types of plants with  $40W + 1R$  and  $40W$  were obtained. This is probably due to a slight degree of asynapsis. It is quite clear from Table X that though 3B (III), 3A (XII) and 3D (XVI) belong to the same homoeologous group 3, they differ in the frequency of plants with  $2n = 41W + 2R$ . It would seem therefore that this is the effect of certain individual wheat chromosomes.

Table X. Chromosome distribution in the progenies from the cross between Kharkov aneuploids with the chromosome formula  $20^{\text{IV}}\text{W} + 1\text{W} + 1\text{R}$  and wheat-rye addition line where rye chromosome VI is involved

Chromosome Line	Progeny type and frequency								Total
	41W	41W +1R	41W +2R	42W	42W +1R	42W +2R	40W* +1R	40W*	
K1A (XIV)	7	1		2	1				11
K2A (XIII)	5	18	2	2	3				40
K3A (XII)	10	14	1	8	3		1	2	39
K4A (IV)	1	8	1	1	1		1		13
K6A (VI)	1	4		1		1			7
K7A (XI)	6	11	3	4		1			25
K1B (I)	3	4	1	8	7	4			27
K2B (II)	2	5		1	1	1		1	11
K3B (III)		5	11	1	2	4			23
K4B (VIII)	1	10		1	4				16
K6B (X)	2	10	2		1	1			16
K7B (VII)	8	2		4			1		15
K2D (XX)	3	4							7
K3D (XVI)	8	17	2	1	8	1	1	1	39
K7D (XXI)	2	2							4
Total	59	115	23	34	31	13	4	4	283

\* Unexpected types

### Discussion

Results indicate that a certain percentage of rye chromosomes V and VI are lost in the addition lines during the divisional stages and this results in progenies of the crosses with only wheat chromosomes namely  $2n = 41W$  and  $42W$ . The frequency of loss seems to be higher in the case of rye chromosome VI than for V. A lower frequency of progenies with  $41W + 2R$  and  $42W + 2R$  (from Table IX), in the case of rye chromosome V, indicates the low transmission of a rye chromosome through the female side, but in the case of rye chromosome VI the frequency is greater (Table X). From the data it is seen that rye chromosome VI is accepted more frequently in line 3B (III) than for lines 3A (XII) and 3D (XVI) despite the fact that they belong to the same homoeologous group 3. This seems to indicate that individual wheat chromosomes have different effects. In some of the lines, no plants with  $41W + 2R$  were found which is probably due to the low acceptance of the rye chromosome and a very low transmission of the rye chromosome through the female side.

It may be possible to overcome this difficulty of obtaining plants with  $41W + 2R$  by increasing the population size so that there will be more chance of the union between gametes with  $20W + 1R$  and  $21W + 1R$ . From Tables VII and VIII, it may be observed that the frequency of different types of progenies differs from line to line. This may be explained on the basis of differential acceptance of the rye chromosome by the different wheat chromosomes. Few unexpected progenies were obtained. This is probably due to a slight degree of asynapsis in wheat chromosomes causing irregular types of gametes and resulting in unexpected types of progenies.

TRANSMISSION STUDIES WITH RYE CHROMOSOME VI

To study the transmission frequency of rye chromosome VI and the formation of different types of gametes, the reciprocal crosses with normal Kharkov were made. One parent was normal Kharkov and the other the  $F_1$  type i.e.  $20^{IIW} + 1W + 1R$ . The male or female gametes produced by these individuals with two non-homologous univalent chromosomes would be of four types - nullisomic gametes, those in which either the wheat or the rye chromosome is present, and those in which both are present; and the normal Kharkov should produce only normal gametes. In the cross normal Kharkov x  $F_1$  type (male), the resultant progenies should indicate the relative success of each type of gamete in competition on the male side and similarly the reciprocal cross should show the success of each type of gamete on the female side.

A. Normal Kharkov x  $F_1$  type, i.e.  $20^{IIW} + 1W + 1R$

Root tips of plants from this cross were checked cytologically and frequency results for some of the different types of the progenies appear in Table XI. From the percentages, one can estimate the frequency of function for the four types of gametes which are formed by the  $F_1$  plants.

In all lines, the percentage of nullisomic gametes is low, ranging from 0 to 12.50. The percentage of normal gametes ranges from 65.62 to 93.75; substitution gametes from 0 to 32.81 and addition gametes from 1.56 to 9.61. O'Mara (29) calculated the percentage of different types of gametes in line 5A (IX), and showed the

Table XI. Chromosome distribution in the progenies of the cross between normal Kharkov and plants with the chromosome formula  $20^{II}W + 1W + 1R$  in different Kharkov aneuploid lines where rye chromosome VI is involved.

Chromosome Line	Progeny type and frequency				Total
	41W	42W	41W+1R	42W+1R	
K6A (VI)	6 11.53%	39 75%	2 2 3.84%	5 9.61%	52
K1B (I)	3 6.81%	36 81.81%	1 2.27%	4 9.09%	44
K2B (II)	2 12.50%	13 81.25%	0	1 6.25%	16
K7B (VII)	1 3.12%	30 93.75%	0	1 3.12%	32
K1D (XVII)	1 1.66%	48 80%	4 6.66%	7 11.66%	60
K4D (XV)	2 4.34%	36 78.26%	4 8.69%	4 8.69%	46
K5D (XVIII)	0	42 65.62%	21 32.81%	1 1.56%	64
Total	15 4.77%	244 77.71%	32 10.19%	23 7.32%	314



following gametic frequencies: nullisomic 6%, normal 60%, substitution 26% and addition 8%. From Table XI, it appears that normal gametes have a great advantage in competition with the other gametes on the male side. The variation in percentage of the substitution gametes in the different lines indicates that the degree of compensation for the missing wheat chromosome depends upon the type of wheat chromosome which is missing. Chromosome 5D (XVIII) of wheat can be replaced by a rye chromosome in the greatest frequency, whereas 2B (II) and 7B (VII) are difficult to replace. These differences may not be so great with a larger population size.

B. F<sub>1</sub> type i.e. 20<sup>II</sup>W + 1W + 1R x Normal Kharkov

Results for this cross are given in Table XII. It is clear from the table that nullisomic gametes are produced more frequently than other types in all the lines. The percentage of normal gametes ranges from 9.38 to 50, nullisomic gametes from 27.58 to 81.25, substitution gametes from 0 to 24.13 and addition gametes from 0 to 17.85.

Discussion

It is quite clear from the results that there is a characteristic variation in the percentage of different types of gametes in the different lines. This may be due to the effect of the different wheat chromosomes and the degree of compensation may depend upon the type of wheat chromosome involved. The frequency of nullisomic gametes is lower than for normal gametes on the male side, but higher on the female side. This indicates that the transmission of univalents through the female side is extremely low. In other words,

Table XII. Chromosome distribution in the progenies of the cross between plants with the chromosome formula  $20^{II}W + 1W + 1R$  indifferent Kharkov aneuploid lines where rye chromosome VI is involved and normal Kharkov.

Chromosome Line	Progeny type and frequency					Total
	41W	42W	41W +1R	42W +1R	40W +1R	
K3A (XII)	28 73.68%	5 13.15%	3 7.89%	2 5.26%	-	38
K6A (VI)	15 75%	3 15%	0 0%	2 10%	-	20
K1B (I)	8 28.57%	14 50%	1 3.57%	5 17.85%	-	28
K2B (II)	21 50%	9 20.93%	10 23.25%	3 6.97%	-	43
K7B (VII)	23 74.19%	8 25.81%	0	0	-	31
K1D (XVII)	8 27.58%	0	7 24.13%	0	14 48.27%	29
K3D (XVI)	23 74.19%	3 9.67%	3 9.67%	2 6.45%	-	31
K4D (XV)	31 75.61%	10 24.39%	0	0	-	41
K5D (XVIII)	52 81.25%	6 9.38%	5 7.81%	0	1 1.56%	64
Total	209 64.31%	58 17.85%	29 8.92%	14 4.31%	15 4.62%	325

nullisomic gametes have an extreme advantage through the female side whereas normal gametes have the advantage through the male side. This evidence points out that some sort of certation effect, i.e. the differential competition among different types of gametes, is present in both the male and female sides.

From Table XIII, it may be seen that there is variation in the percentage of substitution gametes as between male and female sides in the same line. For example, on the male side of line 2B (II), no substitution gametes were obtained whereas on the female side there were 23.25%. In line 4D (XV), 8.69% were obtained on the male side, whereas none was obtained on the female side. From this, it is quite clear that the degree of substitution by a rye chromosome is independent of whether it passes through the male or female side. It also indicates that there is a certain degree of certation in both male and female sides. In line 7B (VII), no substitution gametes were obtained from either the male or female sides, possibly due to the small population involved. The variation in percentage of the substitution gametes from line to line may be due to the effect of different wheat chromosomes. In the disomic substitution column of Table XIII, it may be seen that the range of disomic substitution lines is from 0 to 2.56%. More complete results with additional lines might reveal a greater frequency of substitutions. The percentage of disomic substitutions can probably be increased by increasing the population size, but it may be difficult to obtain disomic substitutions in some of the lines.

Table XIII. Expected percentage of disomic substitutions in different chromosome lines where rye chromosome VI is involved.

Chromosome Line	Expected percentage of disomic substitution		
	Male Side $n = 20W+1R$ %	Female Side $n = 20W+1R$ %	
K6A (VI)	3.84	0.00	0.00
K1B (I)	2.27	3.67	0.08
K2B (II)	0.00	23.25	0.00
K7B (VII)	0.00	0.00	0.00
K1D (XVII)	6.66	24.13	1.61
K4D (XV)	8.69	0.00	0.00
K5D (XVIII)	32.81	7.81	2.56
Average	7.75	8.35	0.64

### MISDIVISION OF RYE CHROMOSOMES V AND VI

Quite often fragments, telocentrics and isochromosomes were observed in the present study. The isochromosomes for the short arm of rye chromosome VI (Fig. 4) and that of the long arm of rye chromosome V were most commonly found. The telocentrics for the long and short arms of chromosome VI and the short arm of chromosome V were also quite common in some lines. The results indicate that the transmission of the telocentric or centric fragment for the short arm of chromosomes V and VI are more frequent than for the isochromosome of the same arm. From the cytological results reported in Table III, it appears that wheat chromosome 7B (VII) probably has stabilizing influence on rye chromosome V. It has been observed that whenever chromosome 7B (VII) is absent, rye chromosome V frequently shows misdivision, producing fragments, isochromosomes and telocentrics in higher frequency than in other lines.

### GAMETIC FREQUENCIES IN KHARKOV MONOSOMICS

Since the monosomics of Kharkov were used in the present study, it was possible to accumulate the results on nullisomic and normal gametic frequency from both the male and female sides. The results are presented in Table XIV. Percentage of gametes with 20W and 21W chromosomes from both the male and female sides deviates slightly from the results presented by Sears (40) for Chinese Spring. This deviation may be due to varietal differences.

Table XIV. Percentage of different types of gametes from both male and female sides of Kharkov monosomics.

Type of gamete (n)	No. of gametes		Percentage of gametes	
	Female side	Male side	Female side	Male side
20	430	47	71.31	14.97
21	173	267	28.69	85.03
Total	603	314		

STABILITY OBSERVATIONS ON DISOMIC SUBSTITUTIONS

About 40 progenies from each of the disomic substitution lines 4D (XV) by rye chromosome V (Fig. 5) and 5A (IX), 1D (XVII) and 5D (XVIII) by rye chromosome VI (Fig. 6) were checked cytologically and found to be completely stable. On the other hand, a cytological check of disomic addition lines for rye chromosomes V and VI revealed that, owing to a loss of the rye chromosome, not all of the progenies were of the addition type. Since there was no variation of chromosome number in the progenies of disomic substitutions, it is quite clear that the rye chromosome is not similarly lost during divisional stages. It appears that the disomic substitutions for rye chromosomes V and VI will probably be more stable than the disomic addition lines for the same rye chromosomes.

DISOMIC SUBSTITUTIONS

Number obtained

To date the following disomic substitutions have been obtained from the sources indicated:

Chromosome line	Rye Chromosome	Source (obtained by selfing plants with the chromosome formula)
K 4B (VIII)	V	$20^{II}W + 1W + 1^{II}R$
K 7B (VII)	V	$20^{II}W + 1W + 1^{II}R$
K 4D (XV)	V	$20^{II}W + 1W + 1R$
K 7D (XXI)	V	$20^{II}W + 1R$
K 5A (IX)	VI	$20^{II}W + 1W + 1R$
K 3B (III)	VI	$20^{II}W + 1W + 1^{II}R$
K 1D (XVII)	VI	$20^{II}W + 1W + 1^{II}R$
K 5D (XVIII)	VI	$20^{II}W + 1W + 1R$

### Meiotic behaviour

The pairing for rye chromosomes V and VI is quite normal (Fig. 7 and Fig. 8), except in a very small percentage of cells which show two univalents (Fig. 9). A similar observation was made by O'Mara (25). The failure of rye chromosomes to pair as regularly as wheat chromosomes is difficult to explain. It may represent some inability of rye chromosomes to operate normally in a cell which is predominantly wheat.

### Morphological characters of the disomic substitutions

#### A. Rye Chromosome V

Morphological characters of the disomic substitutions in different lines for rye chromosome V may be categorised as follows:

(1) Plants with the substitution for wheat chromosome 4D (XV) look very weak in the growing stage and are shorter than Kharkov and the disomic addition. The flag leaves generally become curly and fall downward, the tillering capacity is reduced and the plants are later than Kharkov. Spikes are more lax and seed fertility is lower than either Kharkov or the disomic addition. (Fig. 10)

(2) Disomic substitutions for 4B (VIII), 7B (VII) and 7D (XXI) seem to be more vigorous than the substitution for 4D (XV), but plants with 4OW + 2 fr. (substitution for 7B) are of a bushy type. Complete results are not available at present. A few plants representing the disomic substitution of rye chromosome V for wheat chromosome K 4D (XV) were compared to Kharkov and the disomic addition on the basis of plant height, spike density and fertility. These results are presented in Table XV. No comparative data are

available for disomic substitutions of rye chromosome V for wheat chromosomes K 4B (VIII), K 7B (VII) and K 7D (XXI), because they have just been obtained and there has not been sufficient time to make comparisons.

Table XV. Data from morphological comparisons of disomic substitutions for rye chromosome V with the disomic addition and Kharkov.

Line	No. of Plants	Height inches	Density spikes/cm.	Fertility seeds/spikelets
Kharkov	5	43.7	1.73	2.87
Disomic addition	5	40.5	1.41	2.43
K 4D (XV)	5	36.5	1.33	2.30

#### B. Rye chromosome VI

Morphological characters of the disomic substitutions in different lines for rye chromosome VI may be categorised as follows:

(1) Plants with disomic substitution of rye chromosome VI for 5A (IX), and 5D (XVIII) are taller than disomic additions where the reduction of plant height is very pronounced. Spikes are more lax than Kharkov and the disomic addition and the seed fertility is very high. Spikes are of the speltoid-type and the peduncle is densely pubescence. (Fig. 11)

(2) The disomic substitution for 3B (III) is a very new one and it is not possible to give a detailed description. Plants seem to be taller than the disomic addition and are vigorous. The spikes

appear to be similar to the substitution for 5D (XVIII). The peduncle is densely pubescent. Spikes are more lax than for all other lines obtained to date.

(3) The disomic substitution for 1D (XVII) gives plants that are taller than those for the disomic addition. The spikes are more dense and fertility is greater than for the disomic addition and thus they are similar to Kharkov. The complete absence of pubescence on the peduncle is the most unusual character of this substitution line.

A small population of each disomic substitution for rye chromosome VI was compared to Kharkov and the disomic addition on the basis of plant height, spike density and fertility. These data are presented in Table XVI. Line K 3B (III) was recently obtained and consequently it is not possible to describe it in detail.

#### Discussion

Plant morphology indicates that when a pair of rye chromosome VI is substituted for chromosomes 5A (IX), 3B (III), 1D (XVII) and 5D (XVIII) of wheat, much more normal tall plants with high fertility were obtained whereas when a pair of rye chromosomes VI was simply added to the entire wheat complement, the reduction of plant height is very pronounced. Plants with a pair of rye chromosome V substituted for any pair of wheat chromosomes studied thus far deviate considerably from normal Kharkov. They are all similar to Kharkov in susceptibility to leaf and stem rust.

It has been observed that the disomic substitutions for 5A

Table XVI. Data from morphological comparisons of disomic substitutions for rye chromosome VI with the disomic addition and Kharkov.

Line	No. of Plants	Height inches	Density spikes/ cm.	Fertility seeds/ spikelets
Kharkov	5	43.7	1.73	2.87
Disomic addition	5	32.0	1.44	1.06
K5A (IX)	5	42.7	1.23	3.36
K3B (III)	5	-	1.11	-
K1D (XVII)	5	36.8	1.75	2.67
K5D (XVIII)	5	41.5	1.38	2.71

(IX), 3B (III) and 5D (XVIII) show dense pubescence on the peduncle, but the substitution for 1D (XVII) shows no pubescence. It would appear that there is some interaction between wheat and rye chromosomes which alters the degree of expression of pubescence.

### Hairy-neck Character

#### A. Rye chromosome VI

It was already pointed out that rye chromosome VI carries a gene or gene complex for the hairy-neck character. This entity is located in the long arm (30, 32). Sears (43) observed that the hairy-neck gene must lie near the centromere of rye chromosome VI. In the present study, it has also been observed that the hairy-neck gene lies in the long arm. It is also found that the short arm has no detectable effect in one or two doses. Similar observations were also made by O'Mara (31).

#### B. Percentage of hairy-neck plants

Plants with the chromosome formula  $20^{II}W + 1W + 1R$  (VI) for eighteen of the twenty-one lines were selfed and progenies grown. The percentage of plants with hairy-neck in relation to the total number of plants for each line was recorded. Results are given in Table XVII.

From the table it appears that the percentage of hairy-neck plants varies from line to line and also within the same homoeologous group. Six different chromosome formulae, namely  $40W + 1R$ ,  $40W + 2R$ ,  $41W + 1R$ ,  $41W + 2R$ ,  $42W + 1R$  and  $42W + 2R$  are represented in the progenies. The percentages of hairy-neck plants in different lines

Table XVII. Incidence of hairy-neck plants obtained following selfing of plants with the chromosome formula  $20^{II}W + 1W + 1R$  where rye chromosome VI is involved.

Chromosome Line	Total no. of plants	No. of plants with hairy-neck	Percentage of hairy-neck plants
K2A (XIII)	311	41	13.18
K3A (XII)	339	34	10.02
K4A (IV)	107	11	10.28
K5A (IX)	349	128	36.67
K6A (VI)	114	25	21.92
K7A (XI)	246	24	9.75
K1B (I)	160	30	18.75
K2B (II)	74	10	13.51
K3B (III)	56	3	5.35
K4B (VIII)	57	14	24.56
K6B (X)	331	51	15.41
K7B (VII)	78	16	20.51
K1D (XVII)	125	24	19.20
K2D (XX)	217	38	17.51
K3D (XVI)	24	4	16.66
K4D (XV)	40	2	5.00
K5D (XVIII)	20	10	50.00
K7D (XXI)	362	51	14.08

will indicate the variation in the rate of transmission of rye chromosome VI. While peduncle pubescence is not expressed in all lines, the overwhelming majority have this characteristic.

### C. Effect of hairy-neck character

It is already well established that rye chromosome VI carries a gene or gene complex in the long arm near the centromere which is responsible for the hairy-neck character (30, 31, 32, 43). It was assumed that this expression was invariable and that the presence of this rye chromosome can always be detected by the phenotype. However, results in this study do not support this assumption.

A comparison of the amount of pubescence on the necks of plants monosomic and disomic for the rye chromosome and on the neck of the amphidiploid is interesting, in that such a comparison shows that the amphidiploid has the least pubescence (Fig. 12), although it has the rye chromosome present in two doses. A similar observation was made by O'Mara (25). In the present study, it has been observed that the amount of pubescence on the neck of plants with the chromosome formula  $20IIW + 1W + 1R$  (i.e. monosomic for the wheat and rye chromosome) is less than for plants with the monosomic addition of rye chromosome VI, although they have the rye chromosome present in one dose (Fig. 13). A few cases were observed in the present study where the pubescence is completely absent on peduncles, despite the fact that the rye chromosome is present in a single or double dose (Fig. 14). Peduncle pubescence is not expressed in some cases when the plant is nullisomic for wheat chromosomes and mono- or disomic for the substitution of this rye chromosome. Examples may be found

in the mono- and di-somic substitution for wheat chromosome 1D (XVII), mono-substitution for 3A (XII), and possibly in others not yet observed. Nakajima (23) studied the F<sub>1</sub> hybrids between T. macha and 4 species of Secale namely cereale, vavilovii, africanum and montanum and reported that none had a hairy-neck.

Taking Nakajima's results along with the information obtained in the present study, it may be assumed that there is a mechanism interacting between certain wheat chromosomes and chromosome VI of rye which regulates the degree of expression of peduncle pubescence. The postulation of a simple dosage effect of the rye chromosome does not seem to fit the present results. Nakajima has indicated that T. macha represents a case where the entire complement inhibits pubescence and it may be assumed that in the evolution of common wheat there would be gradation from this extreme to that of the complete expression of pubescence.

## SUGGESTIONS FOR FUTURE STUDY

(1) To obtain disomic substitutions, it is suggested that the  $F_1$  ( $20IIW + 1W + 1R$ ) be backcrossed to the wheat-rye addition line and  $B_1$  individuals selected which are monosomic for the wheat chromosome and disomic for the alien chromosome. Following selfing, disomic substitutions can be obtained by the loss of the wheat univalent during divisional stages. By this method, it might be possible to obtain the disomic substitution within a reasonably small population.

(2) All the disomic substitutions should be compared to Kharkov with respect to winter hardiness, quality, yield, disease resistance, etc. Such studies should produce information indicating which substitution lines have the greatest practical value.

(3) The transmission rate of the rye chromosomes via male and female gametes should be studied further to determine whether different wheat chromosomes have different effects on the transmission. It would thus be possible to calculate the percentage of disomic substitutions in different lines and to detect differences within the same homoeologous group.

(4) Progenies obtained from monosomic substitution parents i.e.,  $20IIW + 1R$ , should be studied cytologically to determine why the majority have  $41W$  and  $42W$  instead of  $40W + 1R$  and  $40W + 2R$  as expected.

(5) The hairy-neck character associated with chromosome VI in rye should be studied in all the possible disomic substitution

lines.

(6) Disomic substitution lines which do not show the hairy-neck character should be backcrossed to normal Kharkov to produce the  $F_1$  type i.e.  $20^{II}W + 1W + 1R$  which must show the hairy-neck.

PLATE I.

Significant characteristics of rye chromosome VI

(Arrows indicate the rye chromosome)

- Fig. 1. The secondary constriction in the submedian position of the long arm.
- Fig. 2. The very strong median constriction at metaphase I.
- Fig. 3. The fine faintly stained thread-like body in the short arm.
- Fig. 4. The isochromosome of short arm.

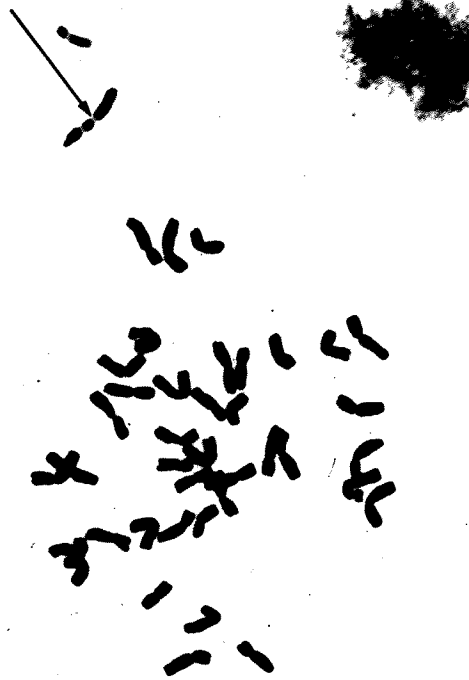


Fig.1.



Fig.2

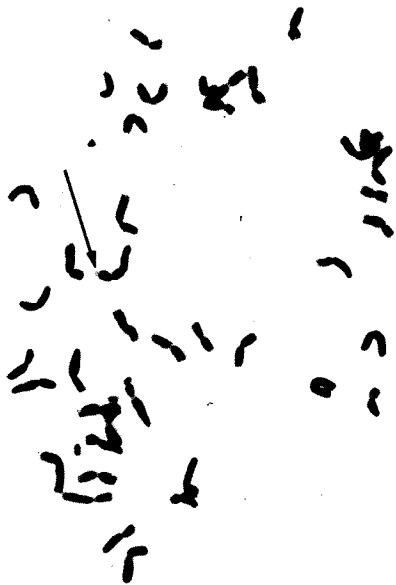


Fig.3

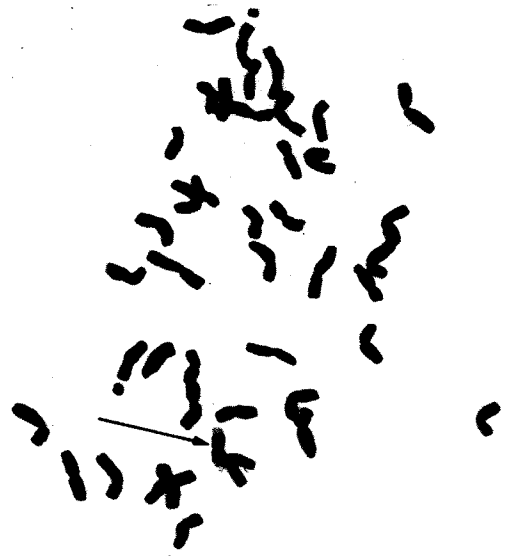


Fig.4

PLATE II.

Mitotic metaphase from disomic substitutions having  
20 pairs of wheat and one pair of rye chromosome.  
(Arrows indicate the rye chromosomes)

Fig. 5. Disomic substitution for rye chromosome V.

Fig. 6. Disomic substitution for rye chromosome VI.

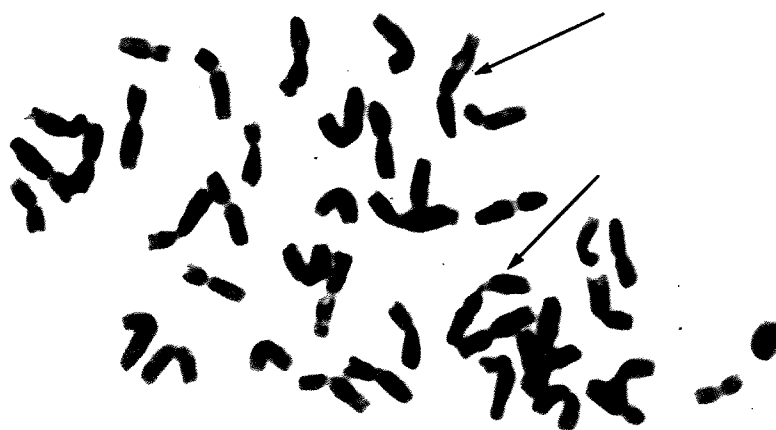


Fig.5

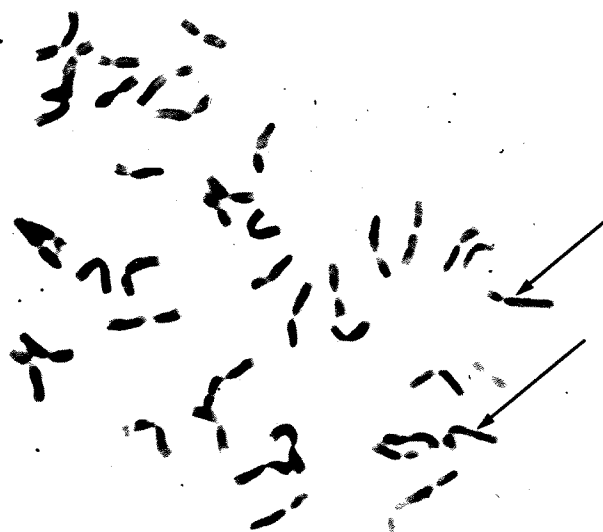


Fig.6

PLATE III.

Meiotic metaphase I of disomic substitutions.

(Arrows indicate the rye chromosomes)

Fig. 7. Disomic substitution for rye chromosome V.

Fig. 8. Disomic substitution for rye chromosome VI.

Fig. 9. Disomic substitution, showing two univalents of rye chromosome VI.

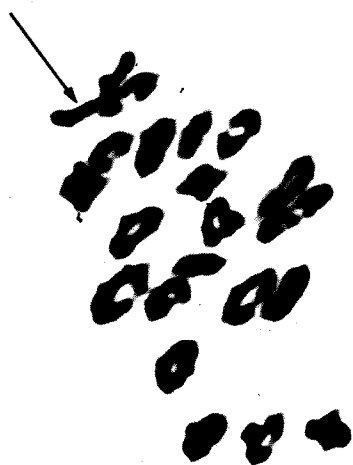


Fig.7

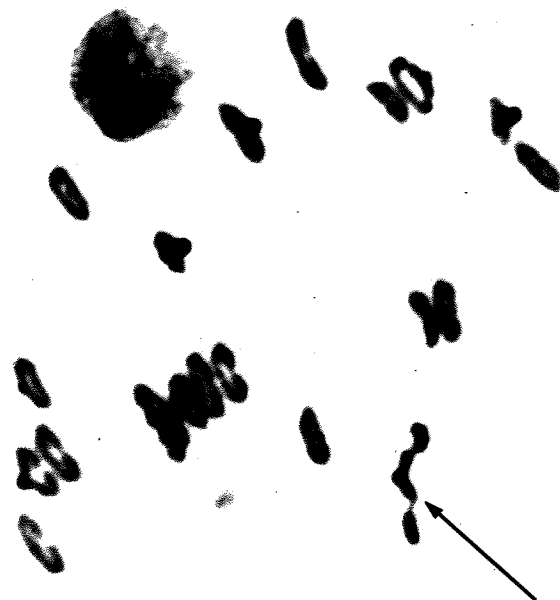


Fig.8

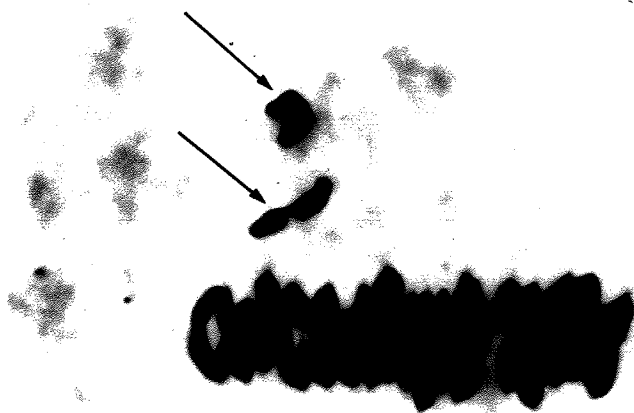


Fig.9

PLATE IV.

Typical spikes of Kharkov and Disomic substitutions  
for rye chromosomes V and VI.

Fig. 10. Kharkov (left) and disomic substitution for rye  
chromosome V.

Fig. 11. Kharkov (left)  
a, b, c, & d - disomic substitutions for the wheat  
chromosomes 5A (IX), 3B (III),  
1D (XVII) and 5D (XVIII) by rye  
chromosome VI respectively.



Fig.10



Fig.11

PLATE V.

Illustrations showing the variation in peduncle pubescence for plants with different genotypic backgrounds involving rye chromosome VI (magnified about three times).

Fig. 12. Amphiploid (left) and the disomic addition.

Fig. 13.  $F_1$  type, monosomic for the wheat and the rye chromosome (left) and the monosomic addition.

Fig. 14. Disomic substitution for wheat chromosome 1D (XVII) (left) and disomic substitution for wheat chromosome 5A (IX).



Fig.12

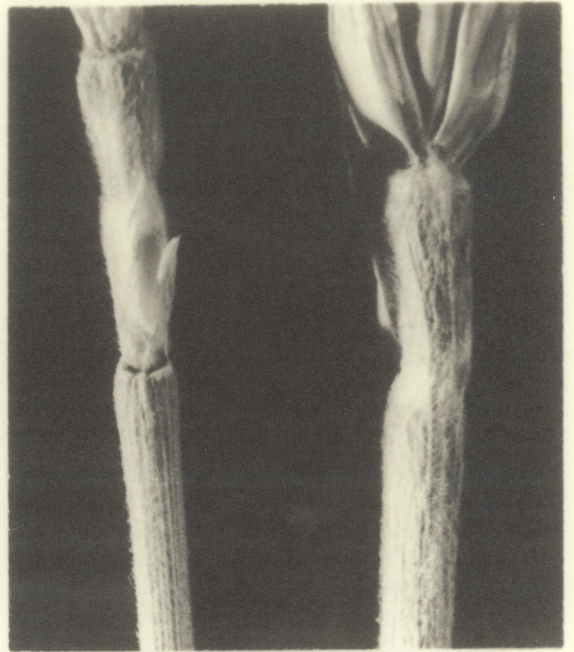


Fig.13

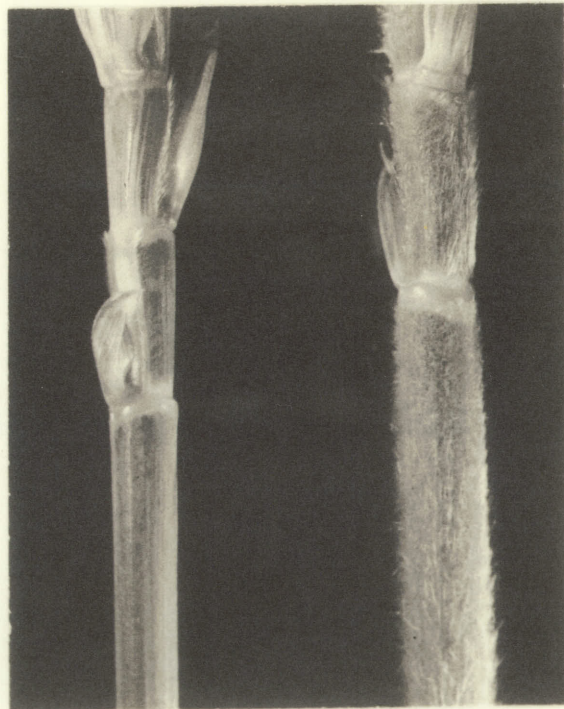


Fig.14

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