

HOMOEOLOGIES OF FOUR RYE CHROMOSOMES
WITH THOSE OF WHEAT AND THEIR EFFECT ON
WHEAT-RYE ADDITION AND SUBSTITUTION LINES

BY

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ABSTRACT

The four cytologically identifiable chromosomes of rye (Secale cereale L. var. Dakold), viz. chromosomes I, IV, V and VI (nomenclature after Bhattacharyya and Jenkins, 1960) were successfully substituted for specific chromosomes of common wheat (Triticum aestivum L. var. Kharkov). Varying degrees of genetic compensation (thus chromosome homoeology), as expressed by relative vigor and fertility, were observed in the wheat-rye substitutions obtained. Rye chromosome IV compensated for either wheat chromosomes 6A or 6D, as did rye chromosome VI for 5A. In accordance, chromosomes IV and VI were designated as 6R and 5R respectively. Rye chromosome I compensated satisfactorily for either 3D or 3B and was designated as 3R. The fact that 3R also compensated poorly for wheat chromosomes of group I suggested that it may carry a small translocated segment. Similarly, only partial compensation was observed when rye chromosome V substituted for 4D, which indicated that chromosome V was also a translocated chromosome.

Addition lines for rye chromosomes I, IV, V and VI were also evaluated in the present study. In general, the phenotype and fertility of the recipient wheat parent was

more severely affected when an individual rye chromosome was present in the form of an addition than when it substituted for a specific wheat chromosome.

A comparison of alien addition and substitutions revealed certain genetic effects to be associated with specific wheat and rye chromosomes. Whereas substitution and addition lines involving rye chromosomes I and IV showed an increase in asynapsis relative to the recipient wheat parent, substitution of rye chromosome VI for 5A and the monosomic addition of this chromosome exhibited near normal meiotic behavior. Interestingly, however, disomic addition of the same rye chromosome resulted in a marked breakdown of pairing and increased univalent frequency. Other genes which were shown to be associated with specific chromosomes was one governing normal pollen development, and another controlling the rate of plant development on chromosomes 6B and 6D of Kharkov wheat, respectively.

Comparisons of the winter-hardiness of addition and substitution lines involving all four rye chromosomes were made in 1968-1969 as compared with normal Kharkov wheat. In general, alien substitution lines appeared to be more winter resistant than alien addition lines carrying the same rye chromosome. These observations can only be regarded as preliminary, however, since they represent only one year's data and require further investigation.

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INTRODUCTION

The subtribe Triticinae consists of five genera: Triticum, Aegilops*, Agropyron, Secale, and Haynaldia. It is generally accepted that species in these genera were originally derived from a common diploid progenitor with a basic set of seven chromosomes. Divergent evolution resulting from the accumulation of structural and genic changes gave rise to the diverse genomes which we recognize today. Although certain of the wheat relatives within Triticinae are to some degree interfertile, they form hybrids of low fertility. Such parental species are called alien species and the residual homology exhibited by structurally and genetically related chromosomes of different genomes is termed homoeology.

The existence of wheat-alien chromosome homoeology can be expressed at meiosis either as secondary association (Kempanna and Riley, 1964) or as homoeologous pairing in the absence of wheat chromosome 5B (Sears and Okamoto, 1958; Riley and Chapman, 1958a; Riley and Kimber, 1966; Halloran, 1966; Johnson and Kimber, 1967). Such a relationship is even more clearly manifested, however, by the ability of an alien chromosome to replace and genetically compensate for a homoeologous wheat chromosome. These compensatory properties

* Morris and Sears (1967) suggested the abolishment of this genus as originally proposed by Bowden (1959).

can best be measured by the competitive ability of alien substitution gametes in the presence of normal ones (Smith, 1963), also by the relative vegetative vigor and fertility of mature plants of alien substitution lines in comparison with the normal parental variety. The classical work of Sears (1966) clearly demonstrated the ability of a specific chromosome of one genome to compensate for a specific homoeologue of another in nullisomic-tetrasomic combinations of hexaploid wheat. This study enabled him to classify the 21 wheat chromosomes into seven homoeologous groups, each consisting of a chromosome from the A, B, and D genomes respectively. Genetic compensation was also observed in intergeneric chromosome substitution lines involving wheat and certain alien chromosomes from Aegilops comosa (Riley, Chapman, and Macer, 1966), Agropyron elongatum (Knott, 1964; Johnson, 1966; Quinn and Driscoll, 1967), and Secale cereale (O'Mara, 1947; Riley, 1965). The degree of genetic compensation in these substitutions was a measure of the amount of homology between specific wheat and alien chromosomes.

The interest in intergeneric gene transfers by the production of alien addition ($2n=42W+2A$)* and substitution lines ($2n=40W+2A$) in common wheat began with O'Mara's attempt to introduce certain useful characters from rye (1940, 1947).

* W and A abbreviated for wheat and alien chromosomes respectively.

These methods were designed to overcome the barrier to gene transfers due to failure of wheat and rye chromosomes to pair and to subsequently recombine. Sporadic efforts were made later to incorporate genes controlling disease resistance of Agropyron elongatum (Knott, 1964; Johnson, 1966), and Aegilops comosa (Riley, Chapman and Macer, 1966) into common wheat by the substitution method. In general, the wheat phenotype was adversely affected by the presence of an alien chromosome. Even the transfer of a small alien chromosome segment by induced translocation (Sears, 1956; Knott, 1961; Driscoll and Jensen, 1964) was found to cause gross deleterious effects. A current approach to exploit alien genetic variation has been to induce homoeologous recombination in the absence of chromosome 5B (Riley, Chapman, and Johnson, 1968a, 1968b).

Only limited information on wheat-rye substitutions is available in the reports of O'Mara (1947), Riley (1965), and more recently by Sears (1968). The object of the present investigation was (a) to study the compensatory properties of four rye chromosomes for hexaploid wheat chromosomes, and subsequently determine their homoeologies; (b) to study the effects of individual rye chromosomes in wheat-rye addition and substitution lines.

LITERATURE REVIEW

Following Wilson's successful wheat-rye cross in 1876 many attempts have been made to exploit genetic variation in the genus Secale for the improvement of wheat.

Müntzing (1939) first produced wheat-rye amphiploids (Triticale) in an attempt to combine the two chromosome complements into a stable and fertile species. Chromosome pairing and behavior was found to be irregular in such combinations, at least in unselected material. In an attempt to circumvent this problem, O'Mara (1940, 1951) produced wheat-rye addition lines in which only a single pair of rye chromosomes was added to the normal wheat complement. This he did by backcrossing the wheat variety, Chinese Spring, to a Chinese Spring-rye amphiploid.

Two complete series of wheat-rye addition lines involving different wheat and rye varieties have since been produced by Riley and Kimber (1966) and Evans and Jenkins (1960). In general, these lines were characterized by their low fertility and cytological instability.

Further refinement in chromosome manipulation resulted in the production of alien substitution lines in which a pair of wheat chromosomes was replaced by a pair of alien chromosomes. O'Mara (1947) obtained a line in which a specific rye chromosome governing "hairy neck" was sub-

stituted for wheat chromosome 5A. He observed that this alien substitution line was of good fertility and vigor whereas the alien addition line involving the same rye chromosome produced semi-dwarf plants with some female sterility. He concluded that the effects of an alien chromosome in a substitution line cannot be predicted from its effects as observed in an alien addition line.

A plan to systematically substitute each chromosome of rye for each of the 21 wheat chromosomes was suggested by O'Mara (1953) and extended by Jenkins (1957). The method required the rye chromosome to be karyotypically recognizable so that selection for those plants carrying the alien chromosome could be made following the initial cross between monosomic lines and alien addition lines of the same wheat variety. Sears (1966) demonstrated that genetic compensation observed in nullisomic-tetrasomic combinations within hexaploid wheat is restricted to homoeologous chromosomes. In view of this, it is unlikely that an alien chromosome would substitute for wheat chromosomes of more than one homoeologous group. A possible exception to this general expectation could occur, however, if either the alien or the wheat chromosome was translocated, in which case it would carry segments of two homoeologous groups and conceivably could partially compensate for each.

Riley (1965) and Riley and Kimber (1966) found that

chromosome II of the rye variety King II was able to substitute for all three chromosomes of homoeologous group 6, but for no others. It was concluded that the success of any alien substitution must depend largely upon the genetic relationship between the alien chromosome and the corresponding wheat chromosome. The three substitution lines were vegetatively vigorous, but their fertility was poor. The substitution of the rye chromosome for 6A had the highest fertility (about 50% that of the recipient variety Holdfast), and slightly below that of the corresponding alien addition line. Riley, Kimber and Law (1964) suggested that the rye chromosome should be designated 6R, indicating its homoeology and genome. Similarly Sears (1968) found that rye III (Riley's nomenclature) compensated for wheat chromosomes 2B and 2D, and he designated it as 2R.

Several substitution lines involving alien species other than rye have been produced. Knott (1964) obtained substitutions of an Agropyron elongatum chromosome for wheat chromosome 6A. He noted that the compensating effect of the Agropyron chromosome was very efficient which in turn facilitated selection of plants comparable in yield and quality to the recipient variety Thatcher. Pollen of plants carrying the substitution functioned as efficiently as euploid wheat pollen.

Johnson (1966) attempted to obtain disomic substitution of an Agropyron elongatum chromosome carrying moderate resistance to race 15B of wheat stem rust (Puccinia graminis var. tritici) for all 21 wheat chromosomes. He selfed 21

lines of wheat, each monosomic for both a different wheat chromosome and the alien chromosome. The transmission rate of the alien chromosome was highest in lines monosomic for chromosomes of group 6, and viable disomic substitutions were obtained only for chromosomes 6A and 6D. The genetic relationship of this Agropyron chromosome to homoeologous group 6 was apparent, although its genome relationship was still unknown.

Riley, Chapman and Macer (1966) successfully substituted a chromosome of Aegilops comosa carrying stripe-rust (Puccinia striiformis Westend) resistance for the wheat chromosomes 2A, 2B and 2D. All three substitution lines were fertile and vegetatively vigorous. In the selfed progenies of these plants, each monosomic for a different wheat chromosome and of the constitution $20''+1'+1'Aeg.$, the highest frequency of rust-resistant progeny was obtained when the monosomic involved either 2A, 2B or 2D. Accordingly, the Aegilops chromosome was designated as 2M.

Quinn and Driscoll (1967) confirmed the substitution of an Agropyron chromosome carrying leaf rust (Puccinia recondita) resistance for wheat chromosome 7D. The alien substitution line was of spontaneous origin and was fully fertile and vigorous. The authors concluded that the Agropyron chromosome was homoeologous with wheat chromosomes of group 7.

MATERIALS AND METHODS

A. Plant materials

The materials used for the present investigation were winter rye, Secale cereale L. var. Dakold, and common winter wheat, Triticum aestivum ssp. vulgare var. Kharkov. The initial crosses were already made and resulting progenies were carried to advanced generations by staff of the Rosner Laboratory of the Department of Plant Science, University of Manitoba, prior to the initiation of the present study. Chinese Spring ditelocentric lines (hereafter abbreviated as C.S. ditelos) were originally obtained from Sears, University of Missouri, and used for the verification of presumptive substitution lines.

B. Production and confirmation of substitution lines

The initial crosses involved the 21 Kharkov monosomic lines and four Kharkov-Dakold addition lines. The Kharkov monosomic series was produced by using Kharkov as the male parent in crosses with each of the C.S. monosomics and as recurrent parent in subsequent backcrosses to monosomic F_1 progeny. The Kharkov-Dakold addition lines were produced and identified by Evans and Jenkins (1960) according to the method devised by O'Mara (1940). The rye chromosomes were

designated as I to VII based on a system devised by Bhattacharyya and Jenkins (1960).

The procedure used in the production of substitution lines is depicted in Fig. 1, and two methods were used, viz. the backcross method and the F_2 method.

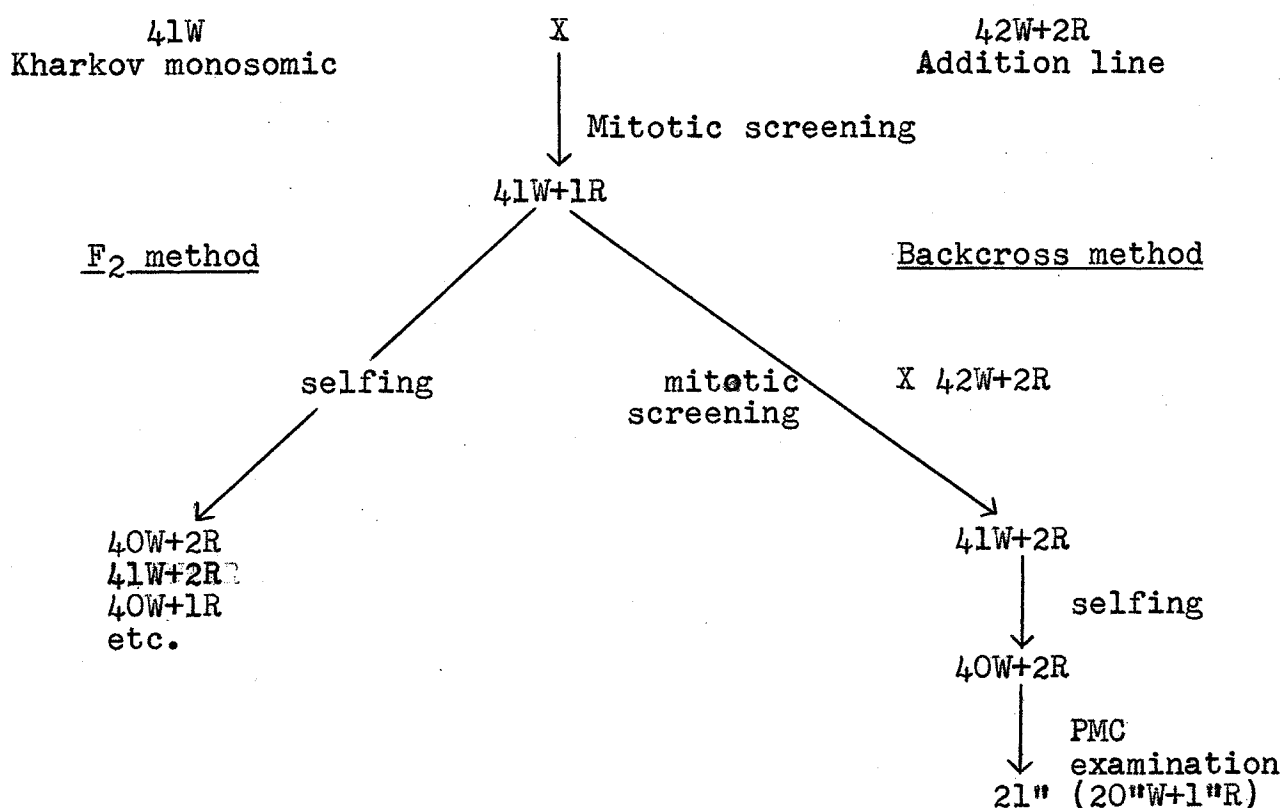


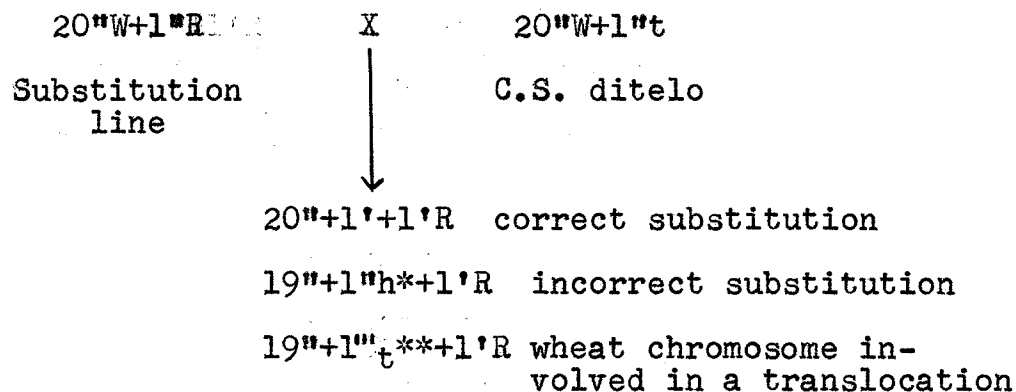
Figure 1: The procedure for the production of wheat-rye substitution lines in which a pair of wheat chromosomes (W) is replaced by a pair of rye chromosomes (R). Two methods are shown: (1) the backcross method, (2) the F_2 method.

The selection of plants with the required chromosome constitution was based on cytological examination of mitotic metaphases. For this reason, only the four rye chromosomes which were distinguishable from wheat chromosomes on the basis of their morphology were involved in the study, viz. chromosomes I, IV, V and VI (after Bhattacharyya and Jenkins, 1960). Their morphological features are described below:

- (1) Chromosome I is relatively large and metacentric, and therefore easily distinguishable from wheat chromosomes (Fig. 3-1).
- (2) Chromosome IV carries a prominent satellite on its short arm and a distinct secondary constriction on its long arm (Fig. 6-1).
- (3) Chromosome V is a long, submedian chromosome characterized by a strong secondary constriction on the long arm.
- (4) Chromosome VI is about the size of the largest wheat chromosome with a submedian centromere. It is heterobrachial with a small terminal satellite on its short arm and an indistinct secondary constriction in its long arm. This chromosome was referred to by O'Mara (1947) as the "hairy neck" chromosome (Fig. 10-1).

Most of the substitution lines were obtained by screening selfed progenies of plants with 41W+2R (W and R abbreviated for wheat and rye chromosome respectively) produced from the use of the backcross method. In comparison, the F_2 method did not provide the same probability as the backcross

approach in obtaining plants of a desired disomic substitution and entailed considerably more cytological work. Once plants with a chromosome constitution of $40W+2R$ were selected, they were examined at meiosis. Those with a meiotic configuration of $2l''$ were crossed with C.S. ditelo specific for the substituted wheat chromosome. Three types of meiotic configurations may be expected in the F_1 of the testcross (Fig. 2). A substitution line was regarded as correctly identified if a meiotic configuration of $20''+l'+l't$ was observed.



C. Comparison of plant characteristics and performance

As both wheat and rye varieties used in this study were of winter habit, all experimental materials were vernalized in a darkroom at 0-2°C for 8-10 weeks before transplanting to clay pots or seedbeds in the greenhouse. Substitution and addition lines, along with the variety Kharkov for control, were grouped on the basis of the rye chromosome involved (Table I). With the exception of group 1, all materials of a group were given identical treatments with respect to vernalization period, fertilizer application, photoperiod and transplanting date. Lines 3B^T/I and 3D/I were grown at a considerably later period relative to all other lines within group 1. The following characteristics were studied:

- (1) Morphological characteristics: height of main culms; number of tillers per plant; spike and leaf morphology.
- (2) Yield potential: percent fertility of lateral florets; number of kernels per spike and per spikelet; weight of 100 kernels.
- (3) Agronomic characteristics: date of heading (50% of spikes emerged); rate of growth; growth habit.

TABLE I

Wheat-rye substitution and addition lines used in the present study

Group 1	Group 2	Group 3	Group 4
Kharkov	Kharkov	Kharkov	Kharkov
RA/I ¹	RA/IV	RA/V	RA/VI
3D/I ²	6A/IV	4D/V	5A/VI
3D ^T /I ³	6D/IV		
3B ^T /I			
1A/I			
Nulli-1A			
1B/I			
Nulli-1B			
1D/I			
Nulli-1D			

1 Rye chromosome I added to wheat complement.

2 Rye chromosome I substituted for wheat chromosome 3D.

3 The substitution involved translocated wheat chromosome 3D.

D. Rye chromosome designations

Since two different systems of nomenclature for Secale chromosomes exist in the literature (Bhattacharyya and Jenkins, 1960; Riley and Chapman, 1958b; Evans and Jenkins, 1960; Riley and Macer, 1966), an attempt was made to reconcile this difference. Wheat-rye addition series were obtained from both sources, viz. Kharkov-Dakold addition lines from Dr. Evans of the Department of Plant Science, University of Manitoba, and Holdfast-King II addition lines from Dr. Riley of the Plant Breeding Institute at Cambridge, England. Lines of these two series were intercrossed and PMCs (pollen mother cells) of the F_1 plants were examined. If 22" were observed, the two rye chromosomes involved as additions were considered homologous.

E. Cytological studies

The selection of plant material with the desired chromosome constitution was based on mitotic examination of root tips pretreated at 0-2°C for 24 hours, fixed in Farmer's solution and squashed in Feulgen. Examination of meiotic cells was carried out using PMCs squashed in aceto-carmin.

F. A study on winter-hardiness

To determine whether there was an effective transfer of winter-hardiness from the winter-hardy rye variety Dakold to

the Kharkov-Dakold addition and substitution lines, material was sown in the field in the fall of 1968 and survival percentages scored the following spring. Included in this test were addition and substitution lines involving rye chromosomes I, IV, V and VI.

EXPERIMENTAL RESULTS

I. Interrelationship of chromosome complements of rye varieties Dakold and King II

On the basis of a cytological study of F_1 hybrids from crosses between addition lines of Kharkov-Dakold and those of Holdfast-King II, it was concluded that rye chromosomes IV, V, and VII, according to Bhattacharyya-Jenkins's designation (Kharkov-Dakold), were the same as chromosomes II, IV and V, respectively, as designated by Riley (Holdfast-King II). Two other pairs of chromosomes were inferred to be common to both varieties on the basis of plant phenotype. Riley's I and Bhattacharyya-Jenkins's VI both produced the "hairy neck" character, while chromosome VII and III as designated by Riley and Bhattacharyya-Jenkins, respectively, resulted in a speltoid-like spike (Table II). These conclusions found support from studies of the morphology of the chromosomes concerned. Two remaining chromosome pairs, viz. Riley's III, VI and Bhattacharyya-Jenkins II, I, respectively, were inferred to be homologous on the basis of chromosome morphology alone, as no distinct phenotypic character could be attributed to the presence of these chromosomes. The Bhattacharyya-Jenkins's system of rye chromosome nomenclature will be used hereafter unless otherwise specified.

TABLE II

The relationship of chromosomes of Secale cereale as previously designated according to two different systems of nomenclature

Bhattacharyya-Jenkins's system	Riley's system	Method of analysis
(Dakold rye)	(King II rye)	
I	VI	chromosome morphology
II	III	" "
III	VII	speltoid spike
IV	II	F ₁ PMC and chromosome morphology
V	IV	F ₁ PMC and chromosome morphology
VI	I	hairy neck
VII	V	F ₁ PMC and chromosome morphology

II. Production of substitution lines

Most of the substitution lines in the present study were either completed or partially completed by Jenkins (1966) but were unconfirmed (Table III). Efforts were therefore directed to completing the substitutions in the more advanced lines and concurrently proceeding to seek verification of the completed lines.

Samples of 30-50 selfed progenies from lines of chromosome constitution $2n=41W+2R$ or $40W+1R$ were cytologically "screened" for plants having $40W+2R$. Of the fourteen lines studied, varying numbers of such plants were found in eleven lines and meiotic studies were made of all the selected plants. Interestingly, selected plants of eight lines were found to have $20''+2'$ instead of the expected $21''$, indicating that two wheat chromosomes were in a monosomic condition, i.e. double monosomics.

Selected plants of two lines were found which produced 21 bivalents at MI. Five such plants of one line, 3D/I, were selected from two parents with $41W+2R$ and were kept separate. In the second line, 6A/IV, five plants of disomic substitution were obtained from 39 selfed progenies of a $40W+1R$ parent. The distribution of the sample with respect to chromosome number is shown in Table IV. In view of the ease with which disomic substitutions were obtained in this line, it was evident that chromosome IV of Dakold rye com-

TABLE III

Production and confirmation of wheat-rye substitution lines
involving recipient wheat variety Kharkov and rye variety
Dakold

Unconfirmed substitutions (Jenkins, 1966)	PMC	F ₁ meiotic configuration (X C.S. ditelo)	Remarks
1A/I	21"	20"+1'+1t	confirmed
1B/I	21"	"	"
1D/I	21"	"	"
2B/I	21"	19"+1" h+2'	unknown substitution
2D/I*	20"+2'	--	double monosomic
3A/I	--	--	lost
3B/I	21"	19"+1C _t +1'	3B translocated
3D/I*	21"	20"+1'+1t	confirmed
	21"	19"+1C _t +1'	3D translocated
4A/I*	--	--	not viable
4D/I*	--	--	" "
5A/I*	--	--	--
5D/I*	--	--	--
6A/I	21"	19"+1" h+2'	unknown substitution
6D/I	20"+2'	--	double monosomic
7B/I*	--	--	--
7D/I*	20"+2'	--	double monosomic
3D/IV*	20"+2'	--	double monosomic
6D/IV	21"	20"+1'+1t	confirmed
7A/IV*	20"+2'	--	double monosomic
1A/V*	20"+2'	--	double monosomic
4B/V	--	--	no rye chromosome
4D/V	21"	20"+1'+1t	confirmed
7B/V	--	--	no rye chromosome
1D/VI	--	--	--
3A/VI*	20"+2'	--	double monosomic
3B/VI	21"	19"+1" h+2'	confirmed to be 5A/VI
5A/VI	21"	20"+1'+1t	confirmed
5D/VI	21"	19"+1" h+2'	confirmed to be 5A/VI
1D/V ⁺	20"+2'	--	double monosomic
3D/V ⁺	20"+2'	--	" "
6A/IV ⁺	21"	20"+1'+1t	confirmed

* Nearing completion. + New substitution. h Heteromorphic.

C_t A chain of three involving the telo. t Telocentric.

pensated efficiently for the deficient wheat chromosome 6A in the alien substitution gamete (20W+1R).

TABLE IV

Chromosome constitution of individual plant progenies of a selfed monosomic substitution plant (40W+1R) of 6A/IV

Chromosome number	Number of plants
40W+2R	5
40W+1R	26
40W+1R+1R _S ^t *	2
40W	1
39W+1R+1R _S ^t	2
Outcross	3
Total	39

* telocentric for the short arm of rye chromosome IV.

III. Alien chromosome addition and substitutions involving chromosome I of Dakold rye

A. Confirmation of substitution and nullisomic lines

The F_1 hybrids from crosses between substitution lines 1A/I, 1B/I, 1D/I and C.S. ditelo 1A, 1B, 1D respectively exhibited a meiotic configuration of $20''+1'+1't$, thus establishing their true identity. However, the testcrosses of presumptive substitution lines 2B/I, 6A/I with C.S. ditelo 2B, 6A, respectively proved these substitutions to be incorrect (Table III). Kharkov nulli-1A, -1B, and -1D lines were also confirmed with the formation of $20''+1't$ in the F_1 of crosses with C.S. ditelo 1A, 1B and 1D respectively.

In the F_1 of the cross between 3B/I and C.S. ditelo 3B, a meiotic configuration of $19''+1'+1'''_t$ (a chain of three involving the telo) was observed, indicating that Kharkov chromosome 3B was a translocated chromosome. The substitution line was therefore designated as $3B^T/I$.

Interestingly, two lines of 3D/I derived from different parents produced different meiotic configurations when crossed with C.S. ditelo 3D. In the first instance, the telo-3D was free in all 59 F_1 PMCs scored, indicating a correct substitution was made involving normal chromosome 3D. However, of 35 F_1 PMCs of the testcross involving a second line, six carried an unassociated telo-3D, four exhibited a heteromorphic bivalent, and 25 carried a triva-

lent including telo-3D (Fig. 3-3). Again, it was indicative that Kharkov chromosome 3D was a translocated chromosome. Accordingly, this line was designated as 3D^T/I to differentiate from the presumably translocation-free line, 3D/I. Attempts to locate the second chromosome involved in the reciprocal translocation with chromosome 3D failed. Hybrids from crosses between 3D^T/I and C.S. ditelo 2A, 2D, 3B, 4A, 4B, 4D, 7A, 7B and 7D, all produced PMCs with a trivalent involving three normal chromosomes and heteromorphic bivalent (Fig. 3-4). The telocentric chromosome was never observed as constituting the third member of a trivalent, which would have furnished the necessary evidence for identifying the interchanged segment.

B. Phenotypic effects produced by the addition and substitution of rye chromosome I

1. Addition line (RA/I). Relative to Kharkov, plants of RA/I were on the average 4.3 cm. shorter in height, they produced relatively weak culms, narrow leaves (Fig. 4-1), short, dense spikes (Fig. 5-1), and flowered two weeks later. The fertility of primary and secondary florets of RA/I was reduced below the level of Kharkov by approximately 24%, and the central florets were highly sterile, as reflected in the number of kernels per spikelet (Table VI). The

Figure 3

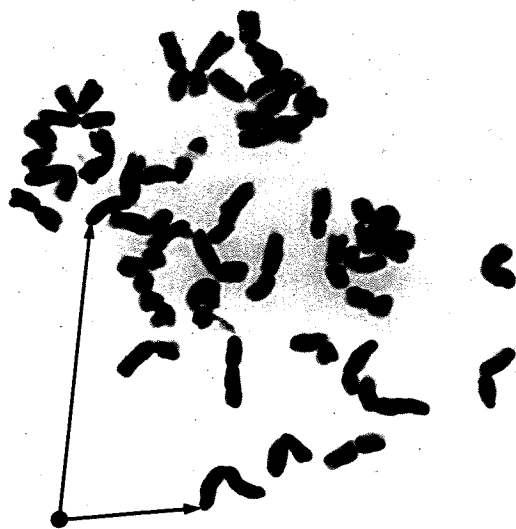
Mitotic and meiotic configurations of lines carrying rye chromosome I.

Fig. 3-1. Rye chromosome I (arrows) in mitotic metaphase of substitution line 1B/I.

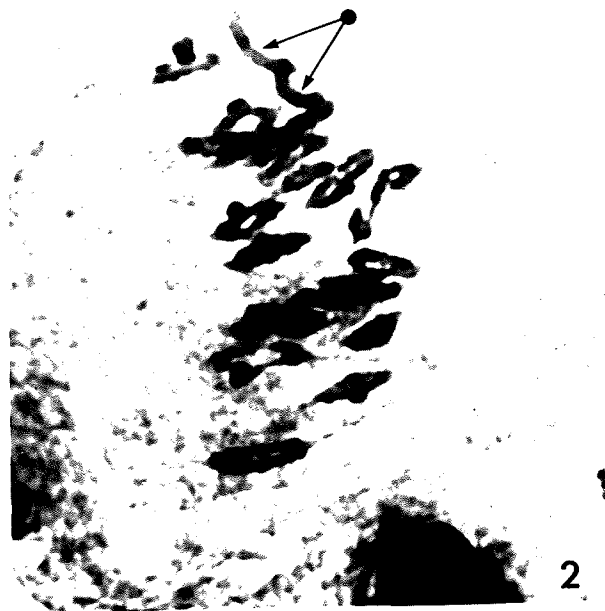
Fig. 3-2. Two univalents of rye chromosome I (arrows) at MI in substitution line $3D^T/I$.

Fig. 3-3. A trivalent (arrow) including telo-3D formed in the F_1 hybrid of $3D^T/I \times C.S.$ ditelo 3D.

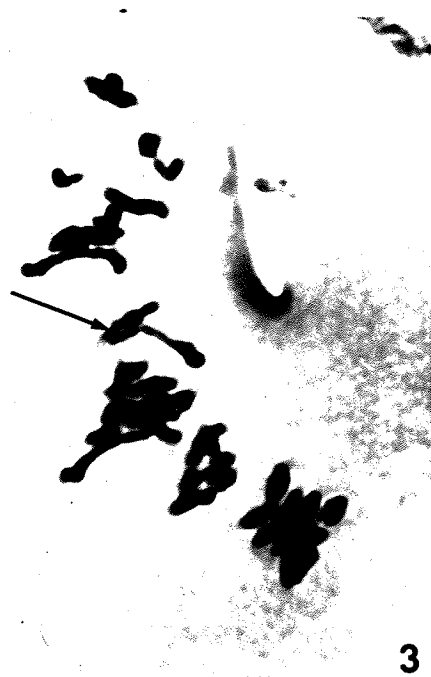
Fig. 3-4. A trivalent (arrow) and a heteromorphic bivalent (above the trivalent) in the F_1 hybrid of $3D^T/I \times C.S.$ ditelo 7A.



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Figure 4

Plant morphology of alien addition and substitution lines carrying rye chromosome I as compared with Kharkov. As shown from left to right:

Fig. 4-1. Kharkov, RA/I, 3B^T/I and 3D^T/I

Fig. 4-2. Nulli-1A, 1A/I, RA/I and Kharkov

Fig. 4-3. Nulli-1B, 1B/I, RA/I and Kharkov

Fig. 4-4. Nulli-1D, 1D/I, RA/I and Kharkov

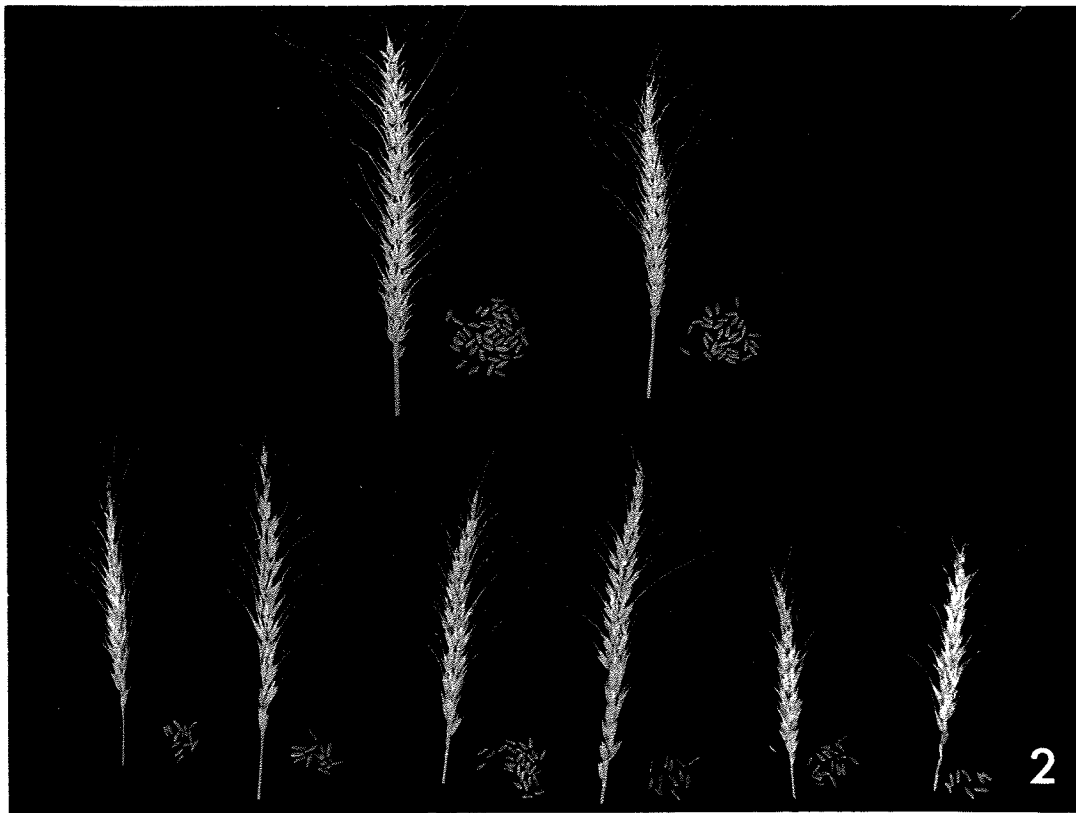


Figure 5

Spikes and kernels of alien addition and substitution lines involving rye chromosome I as compared with Kharkov and nullisomics. As shown from left to right:

Fig. 5-1. Kharkov, RA/I, $3B^T/I$ and $3D^T/I$

Fig. 5-2. Above: Kharkov, RA/I
Below: 1A/I, Nulli-1A, 1B/I,
Nulli-1B, 1D/I, Nulli-1D



kernel size of RA/I was also greatly reduced, with a 100-kernel weight, only 60% that of Kharkov (Fig. 5-1).

TABLE V

The effects of Dakold chromosome I on the morphological and agronomic characters of wheat-rye addition and substitution lines involving Kharkov wheat grown under greenhouse conditions

Line	Height (cm.)	Spikelets/ cm.	Tillers/ plants	Days to heading	Characteristic features
Kharkov	76.6	1.7	3.2	59	
RA/I	72.3	2.3	3.1	73	dense spike, small kernel, weak culm
3D ^T /I	80.8	2.1	2.7	60	dense spike, small kernel, good vigor
3D/I*	101.6	1.9	3.8	--	dense spike, small kernel, good vigor
3B ^T /I*	91.4	1.7	3.5	--	fair vigor and fertility

* Winter planting in 1969, while others were planted in spring of 1968.

TABLE VI

The effects of Dakold chromosome I on the fertility and grain yield of wheat-rye addition and substitution lines involving Kharkov wheat grown under greenhouse conditions

Line	No. Plants	Fertility (%)	Kernels/spikelet	Kernels/spike	Grams/100 kernels
Kharkov	24	90.7	1.9	32.5	3.2
RA/I	39	67.1**	1.4	21.5	1.9
3D ^T /I	21	82.9*	2.0	27.4	2.3
3D/I ⁺	10	83.8*	2.2	35.5	--
3B ^T /I ⁺	18	68.7**	1.4	23.2	--

+ Winter planting in 1969, while others were planted in spring of 1968.

*,** Significantly different from Kharkov at the 5% and 1% levels, respectively.

2. Substitution lines: Dakold chromosome I was successfully substituted for wheat chromosomes of two homoeologous groups, viz. group 3 and group 1.

a. Homoeologous group 3: The ability of Dakold chromosome I to genetically compensate for chromosomes 3B^T, 3D^T, and 3D was very evident, especially for 3D^T and 3D (Table VI). Plants of 3D^T/I approached Kharkov in vegetative vigor and in fertility of lateral florets (91% that of Kharkov), but were taller by an average of 4.2 cm (Fig. 4-1). Kernel weight of plants of this line was approximately

70% that of Kharkov, and their spikes were considerably more dense, as a result of a slightly greater number of spikelets per cm of spike (Fig. 5-1). These features were also present in plants of 3D/I.

In contrast, rye chromosome I exhibited only a fair degree of genetic compensation for wheat chromosome 3B^T. Plants of 3B^T/I had weak culms, narrow leaves (Fig. 4-1) and spikes of moderate density (Fig. 5-1). The fertility of primary and secondary florets was approximately 69%.

During the course of substituting rye chromosome I for wheat chromosomes 3B and 3D, two Kharkov plants nullisomic for 3B and 3D, respectively, were obtained. Both were very weak, with grass-like growth habit. The nulli-3D plant was completely sterile, while the nulli-3B plant produced two seeds.

b. Homoeologous group 1: All three substitution lines in this group were very weak, and were inferior to Kharkov with respect to plant type. Each line was compared with its nullisomic counterpart for a number of morphological and agronomic characters, the results of which are shown in Tables VII and VIII and are summarized as follows:

(i) 1A/I vs. nulli-1A: In comparison with nulli-1A, plants of 1A/I exhibited a lower fertility (63% as compared with 82% in 1A-nulli), an average of 1.2 more tillers

TABLE VII

The effects of Dakold chromosome I on the morphological and agronomic characters of wheat-rye substitution lines 1A/I, 1B/I and 1D/I as compared with both their nullisomic counterparts and to Kharkov wheat

Line	Height (cm)	Spikelets/ cm	Tillers/ plant	Days to heading
Kharkov	76.6	1.7	3.2	59
1A/I	56.6	1.6	2.6	69
Nulli-1A	53.3	1.2	1.5	62
1B/I	59.7	1.7	3.1	65
Nulli-1B	57.9	1.2	1.2	48
1D/I	54.6	1.8	2.6	52
Nulli-1D	56.1	1.3	1.8	58

per plant, longer but weaker culms, a more compact spike with small kernels which were about 61% the kernel weight of those of nulli-1A (Fig. 5-2). In addition, 1A/I was approximately one week later heading than nulli-1A. The growth habit of the lines as compared with Kharkov and RA/I at the juvenile stage is shown in Fig. 4-2.

(ii) 1B/I vs. nulli-1B: Plants of 1B/I produced on the average approximately two tillers per plant more than nulli-1B and developed slightly longer but weaker culms with narrower leaves (Fig. 4-3). Kernels of 1B/I were small, weighing only 70% those of nulli-1B (Fig. 5-2), while its fertility of lateral florets was about equal to that of its nullisomic counterpart (approximately 70%). Date of heading of 1B/I was approximately 17 days later than nulli-1B under the conditions of the present investigation.

(iii) 1D/I vs. nulli-1D: Compared with nulli-1D, plants of 1D/I exhibited an average increase of 30% in fertility although kernel weight was only 76% that of the nullisomic counterpart. No marked improvement in vegetative vigor was observed in 1D/I (Fig. 4-4), although it headed some six days earlier than did nulli-1D.

TABLE VIII

The effects of Dakold chromosome I on the fertility and grain yield of wheat-rye substitution lines 1A/I, 1B/I and 1D/I as compared with both their nullisomic counterparts & with Kharkov wheat

Line	No. of plants	Fertility (%)	Kernels/spikelet	Kernels/spike	Grams/100 kernels
Kharkov	24	90.7	1.9	32.5	3.2
1A/I	40	63.3**	1.3	12.0	1.6
Nulli-1A	32	82.0	2.1	17.7	2.6
1B/I	29	69.2	1.5	14.1	1.8
Nulli-1B	32	70.3	1.9	14.9	2.5
1D/I	35	66.0**	1.2	13.4	1.7
Nulli-1D	24	35.5	0.7	5.8	2.2

** Significantly different from their respective nullisomic counterparts at the 1% level.

C. Meiotic behavior

The presence of Dakold chromosome I in wheat-rye addition and substitution lines caused varying degrees of meiotic irregularity (Table IX). In comparison with Kharkov, a significantly higher percentage of PMCs containing asynaptic univalents was noted in plants carrying rye chromosome I (15-30% as compared with 6% in Kharkov). In 50-75% of these PMCs, the univalents were identified as rye chromosomes

(Fig. 3-1). Rye chromosome I also appeared to contribute to the occurrence of a higher number of open bivalents in both addition and substitution lines. The meiotic behavior of wheat chromosomes appeared to be slightly more irregular in lines carrying the rye chromosome than in normal Kharkov.

The meiotic behavior of $3B^T/I$ appeared to be less stable than RA/I and $3D^T/I$. Approximately 30% of PMCs of $3B^T/I$ carried univalents, which may indicate that $3B^T$ exerted some genetic control over chromosome pairing. This conclusion is supported by the fact that many PMCs in nullisomic-3B plants carried more than 10 univalents.

TABLE IX

The meiotic behavior of wheat-rye addition and substitution lines involving
Dakold chromosome I as compared with the recipient variety Kharkov

Line	No. of plants	No. of cells	Open bivalents/ PMC	Univalent/ PMC	% PMCs			% PMCs showing univalents
					2'	4'	6'	
Kharkov	6	502	1.1	0.1	5.4	0.6	0	6.0
RA/I	4	306	2.2	0.5	20.6	1.6	0	22.2
3B ^T /I	3	332	1.8	0.7	26.8	3.0	0	29.8
3D ^T /I	6	523	1.9	0.3	14.5	0.6	0	15.1

IV. Alien chromosome addition and substitutions involving chromosome IV of Dakold rye

A. Confirmation of substitution lines

Crosses between both substitution lines 6A/IV, 6D/IV and C.S. ditelo 6A, 6D respectively gave a meiotic configuration of $20''+1'+1't$ in F_1 (Fig. 6-3), thus confirming the true identity of the substitutions.

Two plants of monosomic substitution (40W+1R) of the line 6B/IV were obtained. Only one pair of satellited chromosomes (presumably chromosome 1B) was observed, indicating the absence of chromosome 6B, the other large satellited chromosome in a normal wheat complement. Disomic substitution was not obtained due to the occurrence of complete sterility in the monosomic substitution line.

B. Phenotypic effects produced by the addition and substitutions of rye chromosome IV

The presence of rye chromosome IV in addition and substitution lines was easily detected by way of the striking phenotypic expression of plants carrying this chromosome. Such plants developed thick culms, short, semi-erect dark green leaves and were approximately 5-10 cm taller than Kharkov (Table X; Fig. 7-2,3). The intensity of expression of these characters was dependent upon whether the rye chromosome was present in either the monosomic or disomic condition.

Figure 6

Mitotic and meiotic configurations of lines carrying rye chromosome IV.

Fig. 6-1. Rye chromosome IV (arrows) at mitotic metaphase of substitution line 6D/IV.

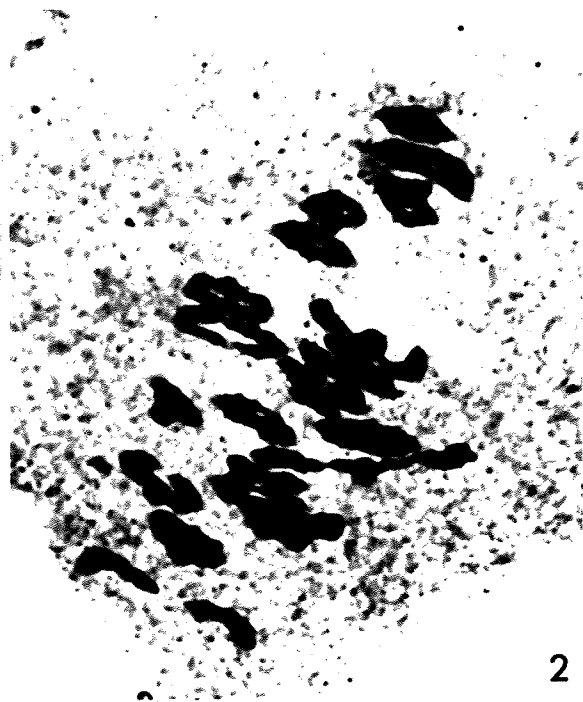
Fig. 6-2. Meiotic metaphase of 6D/IV showing 21 bivalents.

Fig. 6-3. Meiotic configuration in the F_1 hybrid of 6D/IV X C.S. ditelo 6D showing $20''+1'+1't$.

Fig. 6-4. Meiotic configuration showing $20''W$ and one isochromosome of IV^S (short arm of IV) in which chromosome 6A was absent.



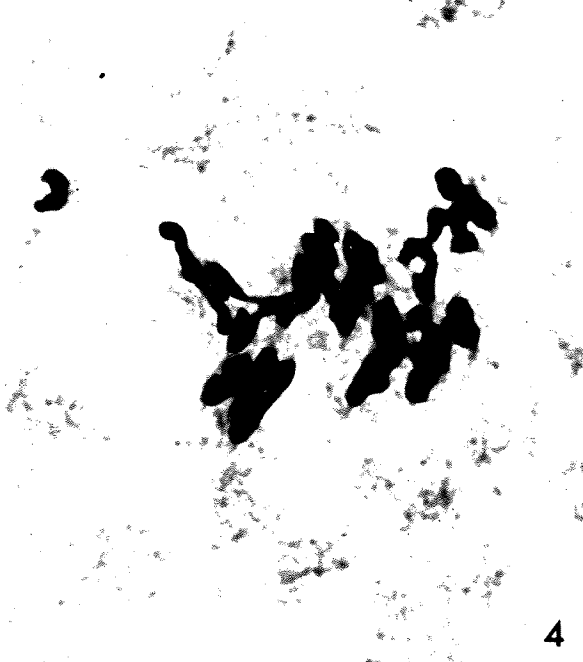
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Figure 7

Spikes, kernels and plant types of alien addition and substitution lines involving rye chromosome IV as compared with Kharkov. As shown from left to right:

Fig. 7-1. Spikes and kernel types: Kharkov, RA/IV, 6A/IV, 6B/IV (monosomic substitution, sterile) and 6D/IV

Fig. 7-2. Plant types at pre-heading stage: Kharkov, RA/IV, 6A/IV and 6D/IV. Note the different rate of growth.

Fig. 7-3. Plant types at post-heading stage: Kharkov, RA/IV, 6A/IV and 6D/IV



Relative to the recipient variety Kharkov, the disomic addition of rye chromosome IV (RA/IV) conferred certain deleterious effects upon the recipient variety, viz. a 23% reduction in fertility of lateral florets, the development of extremely dense spikes with extended apical parts carrying sterile rudimentary florets (Fig. 7-1), a reduction in seed size and a 2-3 week delay in heading time (Tables X & XI). Compared with disomic additions, monosomic addition plants were near-normal in phenotype and the spikes were more typical of the recipient wheat variety, Kharkov.

Many of the adverse effects that were characteristic of the addition line were not present in substitution lines 6A/IV and 6D/IV. The fertility of primary and secondary florets of 6A/IV and 6D/IV were 85% and 92% that of Kharkov, respectively, indicating that genetic compensation of rye chromosome IV for chromosomes 6A and 6D had occurred (Table XI).

A comparison of substitution lines 6A/IV and 6D/IV showed some distinct differences. Relative to 6D/IV, plants of 6A/IV produced slightly larger kernels but were about 6% lower in fertility and exhibited lax spikes (Fig. 7-1). Interestingly, spikes of 6D/IV were relatively compact, bearing on the average 0.4 and 0.2 more spikelets per cm than 6A/IV

and Kharkov, respectively. Another interesting feature of this line was its extremely rapid rate of growth (Fig. 7-2), heading 11 and 15 days earlier than Kharkov and 6A/IV, respectively, during the summer, and 15 and 22 days earlier, respectively, during the winter under greenhouse conditions.

TABLE X

The effects of chromosome IV of Dakold rye on the morphological and agronomic characters of addition and substitution lines of Kharkov wheat

Line	Height cm	Spikelets/ cm	Tillers/ plant	Days to heading		Characteristic features***
				S*	W**	
Kharkov	91.9	1.7	4.1	63	75	
RA/IV	99.4	2.2	1.9	78	96	many late tillers, very dense spikes
6A/IV	102.9	1.5	3.1	67	82	lax spikes, large kernels
6D/IV	96.3	1.9	2.6	52	60	compact spikes

* S summer. ** W winter.

*** All 3 lines were characterized by having red kernels, upright leaves and robust culms.

TABLE XI

The effects of chromosome IV of Dakold rye on the fertility and grain yield of addition and substitution lines of Kharkov wheat

Line	No. of plants	Fertility (%)	Kernels/spikelet	Kernels/spike	Grams/100 kernels
Kharkov	12	90.1	1.8	29.7	3.2
RA/IV	11	69.6**	1.6	25.8	2.8
6A/IV	20	76.9**	1.6	24.9	3.7
6D/IV	19	83.2*	1.9	29.5	3.3

*,** Significantly different from Kharkov at the 5% and 1% levels, respectively.

The two derived plants of monosomic substitution 6B/IV (4OW+1R) were vegetatively vigorous, but were completely male sterile (Fig. 7-1). Their anthers were shrivelled, non-dehiscent and contained only scanty aborted pollen grains.

Monosomic substitutions of rye chromosome IV for wheat chromosome 6A were also obtained. They were slightly weaker than plants of disomic substitutions and produced spikes which were more dense with a 4.6% reduction in fertility (Table XII). Plants carrying chromosome IV^S (short arm of IV) were obtained with relative ease as a result of misdivision of the univalent in plants

TABLE XII

The effects of chromosome IV of Dakold rye in monosomic (4OW+1R) and disomic substitutions (4OW+2R), replacing chromosome 6A of Kharkov wheat

Line	2n	No. of plants	Spikelets/ cm	Fertility (%)	Kernels/ spike	Tillers/ plant
6A/IV 4OW+2R		20	1.5	76.9	24.9	3.1
6A/IV 4OW+1R		10	1.7	72.3*	20.6	2.6

* Significantly different from the disomic substitution at the 5% level.

of 20"W+1'R constitution. Disomic substitution of rye chromosome ditelo-IV^S for 6A (Fig. 6-4) produced very weak plants which were highly sterile. Each plant produced approximately ten seeds, which were pale in color indicating that the gene or genes involved in the expression of red kernel coloration was on the long arm of chromosome IV.

C. Meiotic behavior

It was apparent that the presence of rye chromosome IV in either addition (RA/IV) or substitution lines caused a disturbed meiotic behavior (Table XIII). The frequency of PMCs exhibiting asynaptic univalents was on the average 14.4% in RA/IV compared to only 6.0% in Kharkov.

Open bivalents were also prevalent in this addition line. In comparison, the pairing relationship in the two substitution lines (6A/IV and 6D/IV) was slightly more regular than in the addition line, a condition which was reflected in a higher fertility level. Approximately 10% of the PMCs exhibited incomplete chromosome pairing compared with slightly more than 14% for RA/IV. The number of open bivalents per PMC in the substitution lines was also reduced relative to the addition line.

TABLE XIII

The meiotic behavior of wheat-rye addition and substitution lines involving Dakold chromosome IV as compared with the recipient variety Kharkov

Line	No. of plants	No. of cells	Open bivalents/ PMC	Univalent/ PMC	% PMCs			% PMCs showing univalents
					2'	4'	6'	
Kharkov	6	502	1.1	0.1	5.4	0.6	0	6.0
RA/IV	5	542	3.1	0.3	12.2	2.0	0.2	14.4
6A/IV	4	174	2.8	0.2	9.8	0.6	0	10.3
6D/IV	5	582	2.6	0.2	8.8	0.9	0	9.8*

* One PMC with 8'.

V. Alien chromosome addition and substitution involving chromosome V of Dakold rye

A. Confirmation of substitution lines

Three completed but unconfirmed substitution lines were available at the outset of the present study, viz. 4B/V, 4D/V, and 7B/V. Crosses of these lines with corresponding C.S. ditelos confirmed only the 4D/V substitution (Fig. 8-3).

B. Phenotypic effects produced by the addition and substitution of rye chromosome V

Disomic addition of rye chromosome V to Kharkov reduced plant height by an average of 6.8 cm, also its tillering capacity by almost two tillers per plant (Table XIV). However, plants of this line possess thick, robust culms (Fig. 8-1). Relative to Kharkov, the fertility of primary and secondary florets in RA/V was reduced by approximately 14% but the central florets showed increased fertility as reflected by the high number of kernels developed per spikelet (Table XV). A distinct feature of RA/V was the coarse, large, clavate spikes which was very lax at the base and which became progressively more dense towards the tip (Fig. 8-2). The appearance of a purplish coloration of various plant parts at maturity, especially glumes, peduncle and leaf sheaths, was also distinctive for identification of RA/V. Kernels of this line were very small, 40% of which were completely devoid of endosperm.

TABLE XIV

The effects of chromosome V of Dakold rye on the morphological and agronomic characters of addition and substitution lines of Kharkov wheat

Line	Height (cm)	Spikelets/cm	Tillers/plant	Days to heading	Characteristic features
Kharkov	91.9	1.7	4.1	63	
RA/V	85.0	1.4	2.4	66	coarse-looking, clavate spikes, purplish coloration at maturity
4D/V	76.5	1.3	2.4	70	same as above, but very weak

TABLE XV

The effects of chromosome V of Dakold rye on the fertility and grain yield of addition and substitution lines of Kharkov wheat

Line	No. of plants	Fertility (%)	Kernels/Spikelet	Kernels/spike	Grams/100 kernels
Kharkov	12	90.1	1.8	29.7	3.2
RA/V	18	76.4**	2.0	33.0	1.3
4D/V	16	19.9**	0.4	5.4	1.9

** Significantly different from Kharkov at the 1% level.

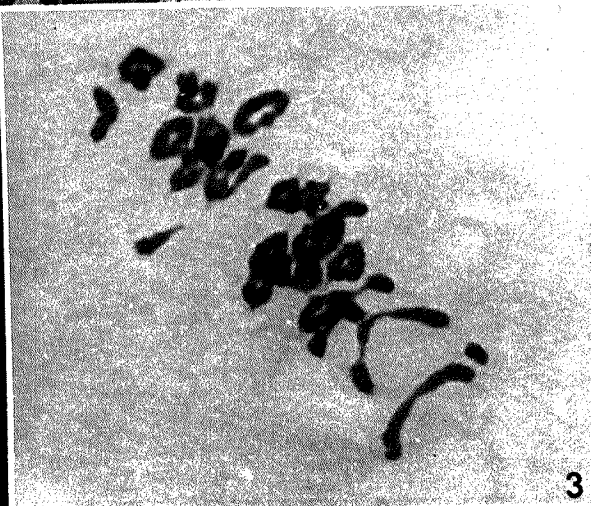
Figure 8

Spikes, plant types and F_1 's meiotic configuration of alien addition and substitution lines involving rye chromosome V. As shown from left to right:

Fig. 8-1. Plant types: Kharkov, RA/V and 4D/V

Fig. 8-2. Spikes and kernel types: Kharkov, RA/V and 4D/V

Fig. 8-3. Meiotic configuration in the F_1 hybrid of 4D/V X C.S. ditelo 4D showing $20''+1'+1't$



Relative to the recipient variety Kharkov, disomic substitution of Dakold chromosome V for chromosome 4D produced weak plants with a reduced number of tillers (Fig. 8-1) and a delayed heading period of about one week (Table XIV). Although endosperm development of seeds from 4D/V was better than from RA/V, the 100-kernel weight of the former was only about 60% that of Kharkov (Table XV). The fertility of 4D/V was low (an average of 20%), with the spikes of late-emerged tillers being completely or nearly completely sterile. Spikes were coarse and clavate-shaped (Fig. 8-2), with a purplish coloration being developed on various plant parts at maturity, an expression similar to that of RA/V.

VI. Alien chromosome addition and substitution involving chromosome VI of Dakold rye

A. Confirmation of substitution lines

Three completed substitution lines for rye chromosome VI, namely 3B/VI, 5A/VI and 5D/VI, were listed by Jenkins (1966). When plants of these lines were grown, all of them produced speltoid spikes with "hairy neck", indicating the absence of wheat chromosome 5A and the presence of Dakold chromosome VI. Crosses of these lines with C.S. ditelo 5A with a subsequent analysis of F_1 PMCs confirmed that they all belonged to the same substitution line, viz. 5A/VI. No multivalents were observed in this material.

B. Phenotypic effects produced by the addition and substitution of rye chromosome VI

Disomic addition of rye chromosome VI to Kharkov (RA/VI) caused certain phenotypic modifications relative to the recipient variety Kharkov. Compared with Kharkov, plants of addition line RA/VI were approximately 12 cm shorter and displayed weak culms (Fig. 9-1). The tillering capacity and fertility of lateral florets were 76% and 80% that of Kharkov respectively under conditions of the present study. The spikes of RA/VI were short and lax; the seeds were small weighing approximately 86% that of Kharkov, while its heading date was five days earlier than Kharkov (Table XVI & XVII; Fig. 9-2). Plants of monosomic addition (42W+1R) grew taller and produced fewer hairs on the peduncle than plants of the disomic addition (42W+2R).

Disomic substitution line 5A/VI compared favorably with Kharkov in vegetative vigor, tillering capacity and earliness. Its kernel weight, however, was 16% less than the 100 kernel weight of Kharkov. The fertility of primary and secondary florets was equal to that of Kharkov (about 80%), but the central florets were more fertile, resulting in the production of an average of 0.4 more kernels per spikelet. However, the actual number of kernels per spike of 5A/VI was 1.2 lower than that of Kharkov because its spikes were very lax and bore fewer spikelets. Two phenotypic expressions

Figure 9

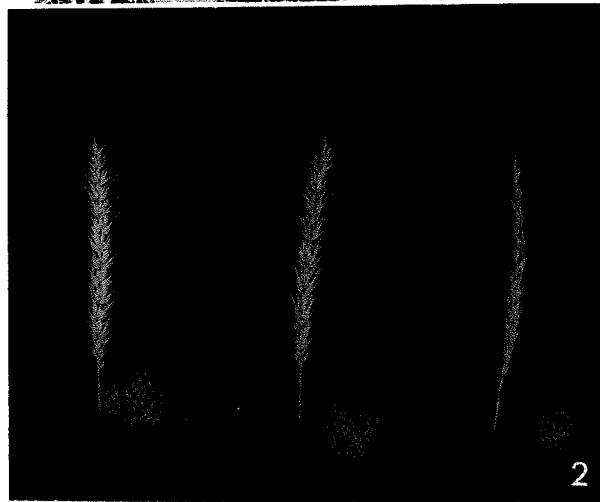
Morphology of plants and spikes of alien addition and substitution lines involving rye chromosome VI as compared with Kharkov. As shown from left to right:

Fig. 9-1. Plant types: Kharkov, RA/VI and 5A/VI

Fig. 9-2. Spikes: Kharkov, RA/VI and 5A/VI



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characteristic of the substitution line 5A/VI were the occurrence of speltoid spikes and "hairy neck".

TABLE XVI

The effects of chromosome VI of Dakold rye on the morphological and agronomic characters of addition and substitution lines of Kharkov wheat

Line	Height (cm)	Spikelets/ cm	Tillers/ plant	Days to heading	Characteristic features
Kharkov	76.6	1.6	3.4	59	
RA/VI	64.7	1.4	2.6	54	semi-dwarf, very lax spike, hairy neck
5A/VI	71.6	1.3	3.4	58	speltoid spike, hairy neck

TABLE XVII

The effects of chromosome VI of Dakold rye on the fertility and grain yield of addition and substitution lines of Kharkov wheat

Line	No. of plants	Fertility (%)	Kernels/ spikelet	Kernels/ spike	Grams/ 100 kernels
Kharkov	12	88.0	1.8	30.1	3.2
RA/VI	12	70.7**	1.5	16.1	2.8
5A/VI	10	88.2	2.2	29.0	2.7

** Significantly different from Kharkov at the 1% level.

C. Meiotic behavior

The addition of rye chromosome VI in the disomic condition disturbed meiotic regularity, resulting in 33.6% of PMCs showing univalents as compared with 6.0% in Kharkov (Table XVIII). Of these cells exhibiting pairing failure, more than 10% carried 4 or more univalents. The number of univalents and open bivalents per PMC in the addition line averaged 1.0 and 4.4, respectively, while Kharkov contained only 0.1 and 1.1 univalents and open bivalents, respectively. In contrast, the meiotic pairing in the monosomic addition line was very regular, with only 3.7% of its PMCs carrying univalents identifiable as those of wheat, and an average of 0.01 univalents and 1.4 open bivalents per PMC. The rye univalents showed a clear constriction at MI and therefore could easily be distinguished from wheat univalents (Fig. 10-2).

The meiotic behavior of the substitution line 5A/VI was highly regular, with only 1.0% of PMCs containing univalents. However, the number of open bivalents per PMC was not proportionately reduced as compared with Kharkov, because of the high incidence of open bivalent formation by the rye chromosome itself. The open and closed bivalents of the rye chromosome very often could be identified by its attenuated condition observable in the region of the secondary constriction (Fig. 10-3, 4).

TABLE XVIII

The meiotic behavior of wheat-rye addition and substitution lines involving rye chromosome VI as compared with the recipient variety Kharkov

Line	No. of plants	No. of cells	Open bivalents/ PMC	Univalent/ PMC	% PMCs			% PMCs showing univalents
					2'	4'	6'	
Kharkov	6	502	1.1	0.1	5.4	0.6	0	6.0
RA/VI(42W+1R)	3	188	1.4	0.01	3.2	0	0.5	3.7*
RA/VI(42W+2R)	2	113	4.4	1.0	20.4	10.6	0.1	33.6**
5A/VI(40W+2R)	3	295	1.0	0.002	1.0	0	0	1.0

* Rye univalent not included.

** Two PMCs with 8' and 10' respectively.

Figure 10

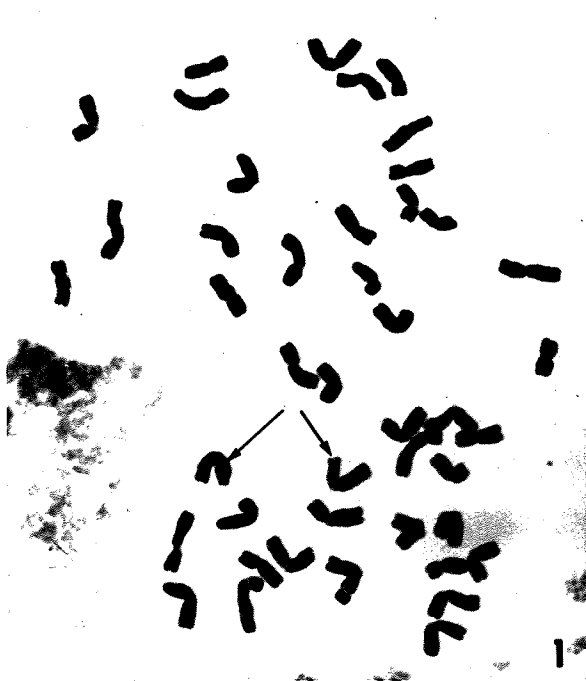
Mitotic and meiotic configurations of alien addition and substitution lines involving rye chromosome VI.

Fig. 10-1. Rye chromosome VI (arrows) in mitotic metaphase of substitution line 5A/VI.

Fig. 10-2. Meiotic configuration showing an univalent of rye chromosome VI (arrow) added to normal Kharkov complement.

Fig. 10-3. An open bivalent of rye chromosome VI (arrow) in 5A/VI showing characteristic stretching.

Fig. 10-4. A closed bivalent of rye chromosome VI (arrow) in 5A/VI.



VII. Winter-hardiness of wheat-rye addition and substitution lines

Preliminary observations on the degree of winter-hardiness of Kharkov-Dakold addition and substitution lines were compared with their parental recipient and donor varieties. The adjusted X^2 values of Kharkov versus all other lines were calculated by using Formula 19.10 of Steel and Torrie (1960) for 2x2 contingency tables (Table XIX).

TABLE XIX

Winter survival of Kharkov-Dakold addition and substitution lines as compared with Kharkov and Dakold (1968-69)

Line	No. of seeds	Survival (%)	X^2 (adjusted)
Kharkov	400	22.5	
Dakold	200	46.0	39.30**
RA/I	300	19.7	0.66
3D ^T /I	300	17.0	2.89
RA/IV	300	10.0	17.99**
6A/IV	400	7.3	35.54**
6D/IV	400	25.1	0.56
RA/V	100	7.0	13.21**
RA/VI	200	8.0	18.29**
5A/VI	200	28.5	2.28

** Highly significant (X^2 values for one degree of freedom are 3.84 and 6.63 at the 0.05 and 0.01 probability levels, respectively).

Comparing the two parental varieties, it was noted that Dakold rye, although exhibiting a winter survival of only 46.0%, significantly exceeded Kharkov by 23.5%. With the exception of RA/I, the four wheat-rye addition lines tested were all significantly more winter susceptible than Kharkov. Two of the four substitution lines, viz. 5A/VI and 6D/IV, were only slightly higher than Kharkov in their winter survival values, although the differences were not statistically significant. Unfortunately, these data can only be regarded as preliminary since they represent only one year's results with small seed samples and do not permit a reliable evaluation.

DISCUSSION AND CONCLUSION

1. Problems relating to the production of alien substitution lines

In the process of alien substitution line production (Fig. 1), it was noted that selected plants carrying $40W + 2R$ formed a meiotic configuration of $20'' + 2'$ at $M\bar{I}$ instead of the expected $21''$. When plants of disomic substitution showing $21''$ were obtained, it was not possible to rule out the possibility that univalent shift had occurred.

It is not unlikely that non-disjunction could occur quite readily in alien addition lines, especially if the addition line used as the male parent was somewhat asynaptic. If compensating alien substitution gametes were produced in the addition line due to meiotic misbehavior, they would generally be more competitive during fertilization than alien addition gametes (Smith, 1963). As a result, substitution lines would be formed in which the rye chromosome substitutes for an unintended wheat chromosome. In a similar manner, plants with $20''W + 1'W + 1''R$ whose wheat univalent is not homoeologous with the rye chromosome could produce compensating alien substitution pollen as a result of univalent shift. The union of such a gamete with a non-compensating alien substitution female gamete would give rise to a double monosomic individual ($20'' + 2'$) with a $40W + 2R$ constitution (Table III).

2. Behavior of Dakold chromosome I in wheat-rye addition and substitutions

The presence of Dakold chromosome I in wheat-rye addition and substitution lines caused characteristic effects on the recipient variety Kharkov. Among the outstanding phenotypic expressions were a reduced kernel size and a significantly higher spike density.

Genetic compensation of Dakold chromosome I for chromosomes $3B^T$, $3D^T$, and $3D$ was very evident. This rye chromosome therefore can be designated $3R$, indicating both its homoeology and its genomic relationship. The translocation involving $3D$ in the substitution line $3D^T/I$ probably occurred during the production of the substitution line, and was not present in the D genome of normal Kharkov. The absence of quadrivalent formation in F_1 hybrids from a Kharkov-Chinese Spring cross supported this hypothesis.

The fertility and vigor of plants of $3D^T/I$ and $3D/I$ approached that of Kharkov. This high level of genetic compensation observed in $3D^T/I$ suggested that the translocated wheat chromosome $3D$ carried a homoeologous segment, possibly from $3A$ or $3B$. The telo- $3B$ was never involved in the formation of a trivalent in crosses between C.S. ditelo $3B$ and $3D^T/I$. Plants of $3B^T/I$ were less vigorous and fertile than plants of either $3D^T/I$ or $3D/I$, indicating that chromo-

some 3B^T may carry a small non-homoeologous segment. Probably because of the small segment involved, multivalents were not detected in Kharkov-Chinese Spring hybrids.

Genetic compensation of Dakold chromosome I for wheat chromosomes of homoeologous group 1 was not clearly evident except for chromosome 1D. Two explanations can account for this situation. Firstly, Kharkov chromosome 1D may carry a small segment of genetic material belonging to homoeologous group 3 with which the rye chromosome showed genetic relationship. This could account for the significant improvement of fertility in 1D/I and not in either 1A/I or 1B/I. Since, however, the D genome of Chinese Spring is thought to represent the most primitive arrangement among the wheats (Riley and Chapman, 1960), moreover since no translocations were detected in F₁'s of Chinese Spring-Kharkov, the possibility of a translocation involving 1D may be ruled out. The other possibility is that in the course of evolution, Dakold chromosome I itself might have been involved in a minor translocation with another rye chromosome. In progenies from crosses between the wild species Secale montanum and Secale cereale var. King II, Riley (1955) detected a minor translocation and two larger ones. In view of the positive improvement in fertility of 1D/I, also in the tillering capacity of 1A/I, 1B/I and 1D/I, it appears that Dakold chromosome I may be the rye chromosome involved in the minor translocation. This agrees with Gupta's (1967) finding that Dakold

chromosome I compensated for both chromosomes 1D and 3D of Kharkov in alien substitution gametes. A study of trivalent formation in F_1 of crosses between either RA/I or 3D/I with S. montanum would be necessary to elucidate this question.

The meiotic regularity of Kharkov was moderately disturbed by the addition and substitution of Dakold chromosome I to its background. It is interesting to note that it was mainly the rye chromosome itself that was contributing to the marked increase in the frequency of asynapsis observed in PMCs from both addition and substitution lines involving rye chromosome I. Plants of $3B^T/I$ showed a significantly higher rate of pairing failure than either Kharkov or $3D^T/I$, thus indicating that some genetic control might be exerted by $3B^T$. It appears that the asynaptic gene found on chromosome 3B of Chinese Spring (Sears, 1954) was also present on Kharkov $3B^T$, and was not compensated for by the rye chromosome.

3. Behavior of Dakold chromosome IV in wheat-rye addition and substitutions

The different phenotypic features expressed in Kharkov-Dakold addition and substitution lines involving Dakold chromosome IV can be classified as parallel and nonparallel. The

parallel characters expressed irrespective of genetic background are attributable to the effects of the rye chromosome. These characters included red kernel color, semi-erect leaves, and robust culms. The non-parallel characters expressed specifically in different lines are attributable to different genetic backgrounds as governed by the presence or absence of a particular wheat chromosome, also the interaction between wheat and rye chromosomes. Thus, the addition line RA/IV in which the full complement of wheat chromosomes is present, produced many late tillers, extremely dense spikes, and matured very late. However, plants of substitution line 6A/IV in which chromosome 6A was absent, produced very lax spikes and large kernels. Plants of 6D/IV, on other hand, produced very dense spikes. The rapid rate of growth and early heading in this line indicated the presence of a gene (s) on Kharkov chromosome 6D which controls rate of development. An analogous genetic factor which controls the same character is located on chromosome 7B of wheat variety Hope (Kuspira and Unrau, 1958). In the present study, monosomic substitution (40W+1R) of the rye chromosome for 6B produced vigorous plants which were completely male sterile. This suggests that Kharkov chromosome 6B was essential for male fertility.

Lines in which Dakold chromosome IV was substituted for Kharkov chromosomes 6A, 6B and 6D expressed a high degree of genetic compensation except for male sterility caused by the deficiency of 6B. It is suggested, therefore, that these 4 homoeologous chromosomes retained much of their genic and structural similarities derived from a common ancestral chromosome.

Riley (1965) studied wheat-rye addition and substitutions involving chromosome II of King II rye (same as Dakold chromosome IV). He noted a higher fertility in the addition line than in any of the three substitution lines. This led him to conclude that alien substitutions can have a more profound effect on the phenotype of the resulting plants than alien additions. However, evidence from the present study indicated that in the Kharkov-Dakold combinations at least, the addition of an alien chromosome caused a much greater imbalance than when it was substituted for a particular wheat chromosome. It appears that a disturbance of genetic balance in an addition line is analogous to the behavior of a wheat tetrasomic and is not apparent, therefore, in compensating alien substitutions.

The narrow range of differences in pairing failure in the addition and substitution lines involving chromosome IV of Dakold indicated the lack of control by this chromosome over meiotic behavior, as it did also for chromosomes 6A

and 6D. It is probable that this rye chromosome was highly asynaptic in Kharkov's cytoplasmic and genetic background as in the case of Dakold chromosome I. In addition, it appears that some degree of asynapsis might result from an interaction between rye and wheat chromosomes. This was evidenced by the occurrence of a much higher number of open bivalents (i.e. reduced chiasmata frequency) per PMC in RA/IV, 6A/IV and 6D/IV as compared with Kharkov and which could not be explained on the basis of the misbehavior of the rye chromosome alone.

4. Behavior of Dakold chromosome V in wheat-rye addition and substitution

The involvement of rye chromosome V either as an addition or a substitution for chromosome 4D of wheat resulted in an overall reduction of viability of the recipient variety Kharkov. The incorporation of chromosome V as an addition was particularly detrimental to kernel development in that a breakdown of endosperm tissue resulted. Disomic substitution of this rye chromosome for chromosome 4D in Kharkov caused marked deleterious effects in that such plants were weak and highly sterile. The fact that nulli-4D in Chinese Spring is known to be completely sterile (Sears, 1954) suggests that rye chromosome V had compensated partially for chromosome 4D of Kharkov. Both the addition and substitution lines involving this rye chromosome produced coarse-looking spikes and purplish coloration on various plant parts at maturity.

Two explanations are possible for the poor compensating ability of rye chromosome V for 4D. Firstly, the Kharkov chromosome could have been involved in a non-homoeologous translocation. However, failure to also substitute Dakold V for wheat chromosomes homoeologous to 4D, viz. 4A and 4B, would suggest that factors other than the proposed translocation were responsible. Furthermore, a trivalent was not observed in F_1 plants of the cross between the substitution line and the ditelo-4D line of Chinese Spring whose D genome is known to have a primitive arrangement (Riley and Chapman, 1960). Therefore, a more logical explanation would be that a translocation involving chromosome V of rye itself might have occurred. Riley (1955) reported that the rye variety King II differed from the primitive species Secale montanum Huss by two large translocations involving three pairs of chromosomes. The variety Dakold may also carry these interchanges and, if so, chromosome V may be one of the three translocated chromosomes. The observation of a trivalent in F_1 's of a cross between S. montanum and the addition line involving chromosome V would support this hypothesis. Some evidence however is available from Gupta's study (1967). In studies of the transmission of alien substitution gametes via the male, he failed to detect any compensating effect of Dakold chromosome V for any of the seven Kharkov wheat chromosomes of the D genome. This finding was indicative of the possible

lethal effect of rye chromosome V on the haploid gametophyte, an effect which could be attributed to the presence of a translocation.

5. Behavior of Dakold chromosome VI in wheat-rye addition and substitutions

O'Mara (1940, 1947) referred to rye chromosome VI as the "hairy neck" chromosome and was the first to study its effect on addition and substitution lines of common wheat. He observed that whereas disomic additions for this rye chromosome caused sterility and semi-dwarfness, disomic substitutions for chromosome 5A produced little or no sterility and no dwarfing effect. The same expressions were observed when Dakold chromosome VI was added and substituted into Kharkov in the present study. It is highly probable that the genetic relationship between this chromosome and wheat chromosome 5A was unaltered by structural changes during the course of their divergent evolution from a common ancestor. This rye chromosome can therefore be designated 5R.

As do the wheat chromosomes of homoeologous group 5, Dakold chromosome VI (5R) also exerted a profound effect on the meiotic behavior of the recipient variety in that it compensated for 5A in promoting synapsis. Interestingly, plants carrying 5R as a monosomic addition also exhibited normal

synapsis of the wheat complement, whereas in a disomic condition, considerable asynapsis occurred. The reason for a reduction in pairing, as brought about by the presence of two homologous alien chromosomes as compared with the presence of only one in a monosomic condition, is difficult to explain. This is particularly true if one considers some preliminary evidence obtained by Feldman (personal communication). He found that neither two nor four doses of $5R^L$ (long arm of 5R) added to the normal chromosome complement of Chinese Spring produced meiotic irregularities. This suggests that a gene(s) which promotes normal pairing may be located on $5R^L$. One can only assume that on $5R^S$ there is present a gene(s) with an opposite effect which in the homozygous condition (disomic addition) exerts a more profound influence than its counterpart on $5R^L$.

6. Conclusions regarding wheat-rye addition and substitution lines

It is evident from the present study that alien substitution lines are generally more fertile and vegetatively vigorous than alien addition lines involving the same rye chromosome. Apparently, genetic imbalance caused by a nullisomic condition of the wheat chromosome complement can effectively be restored by a genetically related rye chromosome

as for example, by 5R and 6R, as shown in the present study, and 2R as found by Sears (1968). It is highly probable that these three rye chromosomes have retained the structural integrity of their respective ancestral chromosomes. Although rye chromosome 3R may have been involved in a minor translocation, it nevertheless compensates fairly efficiently for chromosome 3D.

Rye chromosomes which have undergone chromosomal interchanges during their divergent evolution would show poor compensating ability for specific wheat chromosomes. The partial compensation of Dakold chromosome V for Kharkov chromosome 4D may be an example of such a translocation, although its existence has yet to be demonstrated. Preliminary evidence of the present author indicated that chromosomes V and VII of rye variety King II (or VII and III respectively of the variety Dakold) carried translocated segments. In the F_1 of both crosses between King II-Holdfast addition lines involving the two rye chromosomes and S. montanum, a trivalent was observed quite frequently. It is possible that the aforementioned three rye chromosomes may be responsible for the two large translocations reported by Riley (1955). The effective compensation observed in certain wheat-rye substitution lines reflects the close genetic relationship between wheat and rye genomes--a relationship that

for some homoeologous chromosomes may be partially obscured by the presence of structural changes that have occurred during the course of evolution.

The presence of individual rye chromosomes in Kharkov-Dakold addition and substitution lines generally caused varying degrees of asynapsis, resulting in the occurrence of a higher number of univalents and open bivalents than that found in the recipient wheat variety, Kharkov. Direct observations in the addition and substitution lines involving rye chromosome I indicated that the asynaptic effect was largely attributable to the misbehavior of the rye chromosome per se. This strongly supports the conclusion of Larter, Tsuchiya and Evans (1968) that a high frequency of univalents observed in hexaploid Triticale ($2n=6x=28W+14R$) was due to rye chromosomes. It was also noted that the behavior of wheat chromosomes in addition and substitution lines studied was slightly more asynaptic than in normal Kharkov. An exception to this generalization involved those lines carrying 5R in which the meiotic behavior of wheat chromosomes was very regular in substitution line 5A/VI and monosomic addition line whereas it was highly asynaptic in disomic addition line.

To date, only relatively few substitution lines have been produced in wheat and none has any direct value as an

agricultural variety. The possibility still exists, however, that by substituting an alien chromosome into different genetic backgrounds, a substitution line could be obtained that would be comparable to the recipient variety in yield, and possess special attributes such as disease resistance governed by genes on the alien chromosome. Riley, Chapman and Macer (1966) indicated that work had commenced in the substitution of an Aegilops comosa chromosome (2M) carrying stripe-rust resistance (Puccinia striiformis) into wheat varieties currently grown in Britain.

It is eventually possible by use of the substitution method to compile a chromosome catalogue listing the homoeologues of each genome in the Triticinae. Cytogenetic and genetic comparisons of these homoeologues would provide a greater appreciation of the evolutionary process that has taken place within this subtribe. A partial list of interspecific homoeologues is shown in Table XX, summarizing our current knowledge of this subject.

TABLE XXX

Chromosome homoeologies between wheat and alien species as determined by the alien substitution method

<u>Alien species</u>	<u>Homoeology of alien chromosome</u>	<u>Substituted for wheat chromosome(s)</u>	<u>Authors</u>	<u>Genetic or cytological markers</u>
<u>Agropyron elongatum</u>	3?	3D (Pawnee)	Bakshi & Schlehuber (1959)	leaf rust resistance
	6?	6A (Thatcher) 6D (Thatcher)	Knott (1964) Johnson (1966)	stem rust resistance
	7?	7D	Quinn & Driscoll (1967)	leaf rust resistance
<u>Secale cereale</u>	2R ¹	2B, 2D (Chinese Spring)	Sears (1968)	
	3R ²	3B, 3D (Kharkov)	Lee (1969)	largest of the rye chromosomes & metacentric
	4R ³	4D (Kharkov)	Lee (1969)	strong secondary constriction
	5R	5A (Chinese Spring) 5A (Kharkov) 5B, 5D	O'Mara (1947) Lee (1969) Muramatsu (Sears, 1968)	pubescent peduncle
	6R	6A, 6B, 6D (Holdfast) 6A, 6D (Kharkov)	Riley (1965) Lee (1969)	nucleolar organizer and a satellite
<u>Aegilops comosa</u>	2M	2A, 2B, 2D (Chinese Spring)	Riley, Chapman & Macer (1966)	stripe rust resistance

1 Chromosome III of King II rye (Riley's designation).

2 This chromosome might involve a minor translocation.

3 This chromosome might involve a large translocation.

PROPOSED FUTURE STUDIES

1. Identification of those rye chromosomes with unknown homoeologies

The homoeologous relationship of five rye chromosomes with those of wheat has already been determined by the alien chromosome substitution method (Table XX). The remaining rye chromosomes, chromosomes III and VII, cannot be morphologically or genetically identified from those of wheat, thereby rendering the present method of substitution ineffective. However, a modified approach, using C.S. monotelocentric lines instead of Kharkov monosomic lines (Fig. 11), could be used for this purpose. A proposed procedure is outlined below:

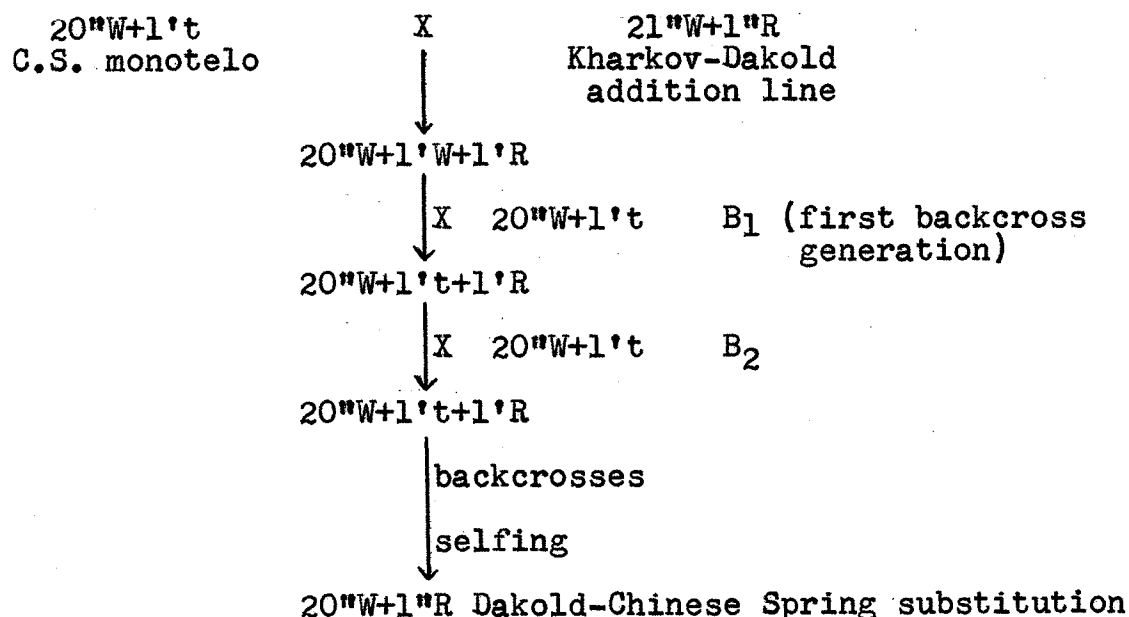


Figure 11: A procedure for the production of alien substitution lines involving rye chromosomes lacking cytological and genetic markers for their identification.

The two Dakold chromosomes would be expected to partially compensate for wheat chromosomes of homoeologous group 1 or 7. Preliminary evidence (Lee, unpublished) indicated that the homologues of these two chromosomes in King II rye were involved in translocations. In such circumstances, the rye chromosome would carry a non-homoeologous segment in place of a homoeologous one, and its compensating ability would not be fully expressed in substitution lines.

2. Study of translocations between *S. cereale* and *S. montanum*

Riley (1955) reported that *S. cereale* L. var. King II differ from *S. Montanum* Huss by two large translocations involving three pairs of chromosomes and another minor translocation involving a fourth pair. Two questions relevant to the present study remain unanswered: (1) do translocations exist between the varieties Dakold and King II, and (2) which of the chromosomes of the variety Dakold are involved in translocations with those of *S. montanum*? Answers to these questions would clarify at least partly the differences in the degree of genetic compensation observed among different Kharkov-Dakold substitution lines. Information of this nature would also add to our present knowledge of the extent of genetic divergence that has occurred between the genomes of wheat and rye. To allucidate these problems, the following crosses involving either Kharkov-Dakold addition or substitution lines and *S. montanum* Huss would have to be made and F_1 PMCs studied:

1. <u>S. cereale</u> var. Dakold	X	<u>S. cereale</u> var. King II
2. RA/I or 3D/I	X	<u>S. montanum</u>
3. RA/II	X	"
4. RA/III	X	"
5. RA/IV, 6A/IV or 6D/IV	X	"
6. RA/V or 4D/V	X	"
7. RA/VI or 5A/VI	X	"
8. RA/VII	X	"
9. Kharkov	X	"

For any particular cross between either an addition or substitution line and S. montanum, the formation of trivalents at a higher frequency than that found in the control cross (Kharkov X S. montanum) would identify the specific rye chromosome as being one of the translocated chromosomes.

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