The homoeologous relationships of rye chromosomes 4R and 7R with wheat chromosomes

By O. L. KOLLER and F. J. ZELLER

Technische Universität München, Institut für Pflanzenbau und Pflanzenzüchtung, 805 Freising-Weihenstephan, Federal Republic of Germany

SUMMARY

By means of rye chromosome CR from Imperial added to Chinese Spring wheat the alien substitutions 4A/CR, 4A/CR^S, 4B/CR, 4D/CR, 4D/CR^S, 7A/CR^L, 7B/CR, 7B/CR^L, 7D/CR and 7D/CR^L were isolated. Substitutions 4A/CR^S and 4D/CR^S had a better fertility and vegetative vigour than the corresponding substitutions with the complete chromosome CR. In substitutions the entire chromosome CR did not compensate for the absence of wheat chromosomes of group 7, whereas the substitutions 7A/CR^L, 7B/CR^L and 7D/CR^L were more fertile than the corresponding nullisomics 7A, 7B and 7D. It was shown that the short arm of CR is homoeologous to wheat telosomes 4A$^\alpha$, 4B^L and 4D^S, whereas most of the long arm of CR is homoeologous to the wheat arms 7A^S, 7B^S and 7D^S. Rye chromosome CR is designated 4R. Only three substitutions with rye chromosome DR were produced. The fertility of substitutions 7A/DR and 7B/DR were considerably lower than that of nulli-7A and nulli-7B. The 4B/DR substitution was sterile. Rye chromosome DR is believed to be a double interchanged chromosome in comparison to the corresponding *Secale montanum* chromosomes. Rye chromosome DR is designated 7R. On the basis of substitution ability of CR and DR and several homoeologous gene loci on these chromosomes an evolutionary scheme for the derivation of the *Secale cereale* genome from *Secale montanum* is outlined.

1. INTRODUCTION

The genetic relationships of chromosomes within the seven homoeologous groups of hexaploid wheat to specific chromosomes in other species within the subtribe Triticinae are now well established. Homoeologies between wheat chromosomes and those of rye (*Secale cereale*), *Agropyron* ssp. and *Aegilops* ssp. have been reported. Chromosome homoeology studies have been assessed by evaluating the genetic compensation for phenotypic traits, such as vigour and fertility which occur when a pair of specific alien chromosomes is added to a nullisomic line of hexaploid wheat. Homoeologies between five rye chromosomes – 1R, 2R, 3R, 5R and 6R – and corresponding wheat chromosomes have been described (Zeller &

[1] This study is part of a doctoral thesis (Dr.agr.) submitted by the senior author to the Technical University of Munich.

Fischbeck, 1971; Sears, 1968; Acosta, 1961; O'Mara, 1946; Riley, 1965, resp.). Recently Rao (1975) reported that rye chromosome CR of cultivar Imperial compensates partially for the loss of chromosome 4A in Chinese Spring wheat. The purpose of this study was to determine the homoeologous relationships of rye chromosomes 4R and 7R to specific wheat chromosomes.
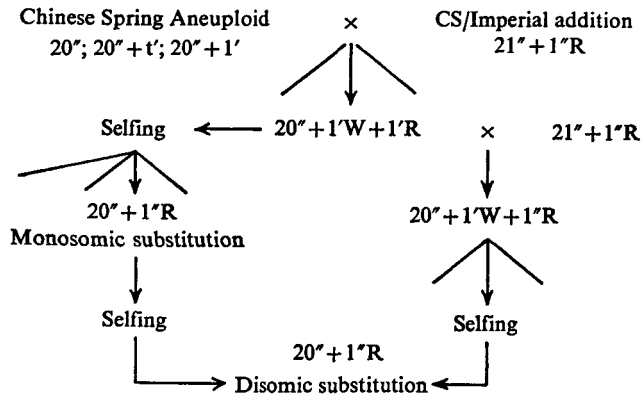

Fig. 1. Scheme for development of wheat–rye substitution lines.

2. MATERIAL AND METHODS

Aneuploid lines used in this work were derivatives of *Triticum aestivum* ($2n = 6x = 42$) variety Chinese Spring. The rye addition lines used were additions of single chromosome pairs of *Secale cereale* cultivar Imperial to Chinese Spring. All these stocks were provided by Dr E. R. Sears, Columbia, U.S.A. Six lines of wheat which were either monosomic, telosomic or nullisomic for chromosomes of groups 4 and 7 were each crossed to Chinese Spring/Imperial disomic addition lines CR and DR. The F_1 plants were either selfed or were backcrossed to the corresponding wheat–rye addition line. The derived material was selfed (see Fig. 1). The 42-chromosome progenies were crossed to corresponding ditelosomic wheat lines. Pairing failure of the wheat telosomic in the hybrids resulting from these crosses was interpreted to mean that the required substitution had been effected. The development of substitution lines is illustrated in Fig. 1.

The degree of compensation was evaluated by comparing, in terms of vigour and fertility, the substitution lines, the corresponding nullisomic lines and euploid Chinese Spring. Several wheat–rye chromosome addition lines of Holdfast/King II and Kharkov/Dakold (supplied, respectively, by Dr R. Riley, Cambridge, and Dr L. E. Evans, Winnipeg) were crossed with the Chinese Spring/Imperial additions CR and DR in order to determine homology between these specific rye chromosomes. Meiosis was studied in Feulgen-stained squashes of pollen mother cells (PMC's) from anthers fixed in acetic-alcohol. Determinations of somatic chromosome constitutions were made from squashes of root-tips previously pretreated in monobromonaphthalene and stained by the Feulgen method. The fertility was

estimated as the proportion of the primary and secondary florets with grains to the total number of florets. The two bottom and the two top spikelets of each spike were omitted from the calculations.

3. RESULTS

(i) *Isolation of substitution lines with rye chromosome* CR

Ten lines were obtained in which the rye chromosome CR, either as a complete chromosome or as a telocentric, substituted disomically for wheat chromosomes of groups 4 or 7. Plants which were monosomic or disomic substitutions of the complete rye chromosome CR, or of its long arm telocentric, had red coleoptiles.

4A/CR. Six monosomic and six disomic 4A/CR substitutions were obtained. Their substitution status was confirmed by meiotic studies of crosses with the corresponding ditelosomic Chinese Spring lines. A metaphase I plate in a PMC of a monosomic 4A/CR substitution (Plate 1, Fig. 2A) shows 20 wheat bivalents and one rye univalent. Nullisomics, telosomics for the short arm, monosomic and disomic substitution lines were isolated by selfing this monosomic substitution. Some preparations of meiotic cells of monosomic and telosomic substitutions showed the complete CR chromosome and its short arm with a small satellite region (Plate 1, Fig. 2B, C). The satellite can also be seen in root-tip cells of plants with the short arm of CR. The disomic substitutions 4A/CR were only two-thirds the height of Chinese Spring and even shorter than nullisomic 4A. The plants had long narrow grains, few tillers and only 4 % fertility (Table 1). However, the ditelosomic substitutions of the short arm of CR were more fertile. Ears of both substitutions are shown in Plate 2, Fig. 3C, D.

4B/CR. Several disomic substitutions were isolated. Culms of these plants were one-third shorter than those of Chinese Spring. The ears were smaller and slightly awned (Plate 2, Fig. 3E; Plate 3, Fig. 4). The fertility was extremely low (1 %) and the date of flowering was 5 days earlier than that of Chinese Spring (Table 1).

4D/CR. Monosomic, disomic and monotelosomic (short and long arm) substitutions were obtained. The 4D/CR^S substitution was taller and had larger tillers than the substitutions of the complete rye chromosomes. The fertility of both 4D/CR and 4D/CR^S substitutions was rather poor (Table 1). Plants with the CR^L telocentric chromosome were sterile. Phenotypically 4A/CR and 4D/CR plants were very similar.

7A/CR. One ditelosomic 7A/CR^L substitution was isolated. This had smaller tillers and was only two-thirds the height of Chinese Spring. Its fertility was considerably better than that of the corresponding nullisomic 7A line (Table 1). The 7A/CR^L ditelosomic substitution is unstable. Thirty to fifty per cent of its progeny usually lose one or both rye telosomics. Plate 3, Fig. 5 shows a metaphase I plate in a PMC of an F$_1$ hybrid between the alien substitutions 7A/CR^L and 4D/CR, forming $19'' + t1'' + 2'$. The heteromorphic rod bivalent consists of CR^L and CR; the two univalents are wheat chromosomes 7A and 4D. Spikes of nullisomics 7A and 7A/CR^L substitutions are seen in Plate 2, Fig. 3J, K.

7*B/CR*. One disomic substitution of the complete rye chromosome and a substitution of a pair of the long-arm telocentrics were obtained. The latter often loses one or both telosomics. The plants of both lines had reduced tillering and the culms were smaller than those of Chinese Spring. The tillering, however, was better than in 7A/CR and 7D/CR (Table 1). The substitution 7B/CR^L was more

Table 1. *Some characteristics of Chinese Spring nullisomic lines and wheat–rye substitution and addition lines*

(The rye chromosomes involved are CR and DR from the cultivar Imperial.)

Lines	Chromosome constitution	No. of plants analysed	No. of spikes per plant	Plant height (cm)	Fertility (%)
Chinese	42W	5	8·9	130	81
nulli-4A	40W	4	12·0	98	0
4A/CR	40W + 2R	5	2·6	88	4
4A/2t^{s}CR	40W + 2t^{s}R	6	7·2	116	19
4B/CR	40W + 2R	8	6·3	80	1
4B/DR	40W + 2R	1	19·0	65	0
nulli-4D	40W	3	9·0	82	0
4D/CR	40W + 2R	7	2·4	78	1
4D/1t^{L}CR	40W + 1t^{L}R	1	5·0	80	0
4D/1t^{s}CR	40W + 1t^{s}R	2	8·5	110	3
nulli-7A	40W	4	8·8	112	2
7A/2t^{L}CR	40W + 2t^{L}R	4	4·2	85	29
7A/DR	40W + 2R	5	8·8	103	1
nulli-7B	40W	5	10·8	101	29
7B/CR	40W + 2R	8	6·0	90	16
7B/2t^{L}CR	40W + 2t^{L}R	3	6·0	89	63
7B/DR	40W + 2R	7	11·0	103	6
nulli-7D	40W	5	7·8	102	28
7D/CR	40W + 2R	5	2·8	69	5
7D/2t^{L}CR	40W + 2t^{L}R	4	3·5	84	56
7D/DR*	40W + 1R	2	—	—	—
CS + 2t^{s}CR*	42W + 2t^{s}R	5	—	—	—
CS + 2t^{L}CR	42W + 2t^{L}R	9	3·0	103	80
CS + 2i^{L}CR	42W + 2i^{L}R	2	2·0	76	65
CS + CR	42W + 2R	4	4·0	96	32
CS + 2t^{s}DR	42W + 2t^{s}R	6	8·7	118	60
CS + 2t^{L}DR	42W + 2t^{L}R	4	10·0	122	38
CS + DR	42W + 2R	4	9·0	107	16

* Plants just growing.

fertile than nulli-7B (Table 1). The complete rye chromosome, however, reduced fertility in the 7B/CR substitutions. Plate 2, Fig. 3M–O show the spikes of nullisomic 7B and of the substitutions 7B/CR and 7B/CR, respectively.

7*D/CR*. The disomic substitutions 7D/CR and 7D/CR^L were two-thirds to half the height of Chinese Spring and had slightly shorter spikes. In plants with the pair of complete rye chromosomes some of the basal spikelets were often replaced by short branches or by supernumerary spikelets. This phenomenon was also
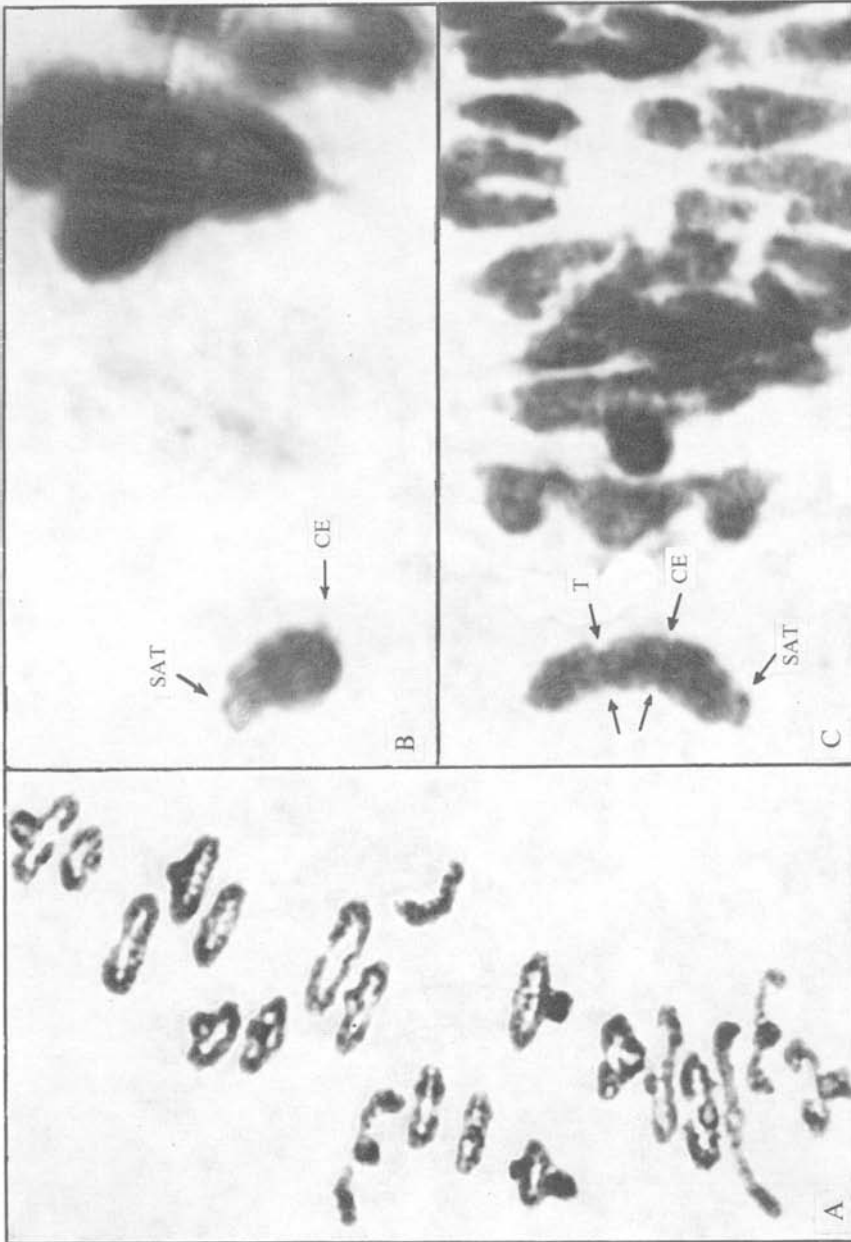
Fig. 2. (2A) First metaphase of meiosis in pollen mother cells of a monosomic substitution 4A/CR with 20″W +1′CR. (2B) shows the satellite region (SAT) of the CR^s-telosome. (2C) The centromere (CE), tertiary constriction (T) and the SAT-region of the complete chromosome CR are arrowed.

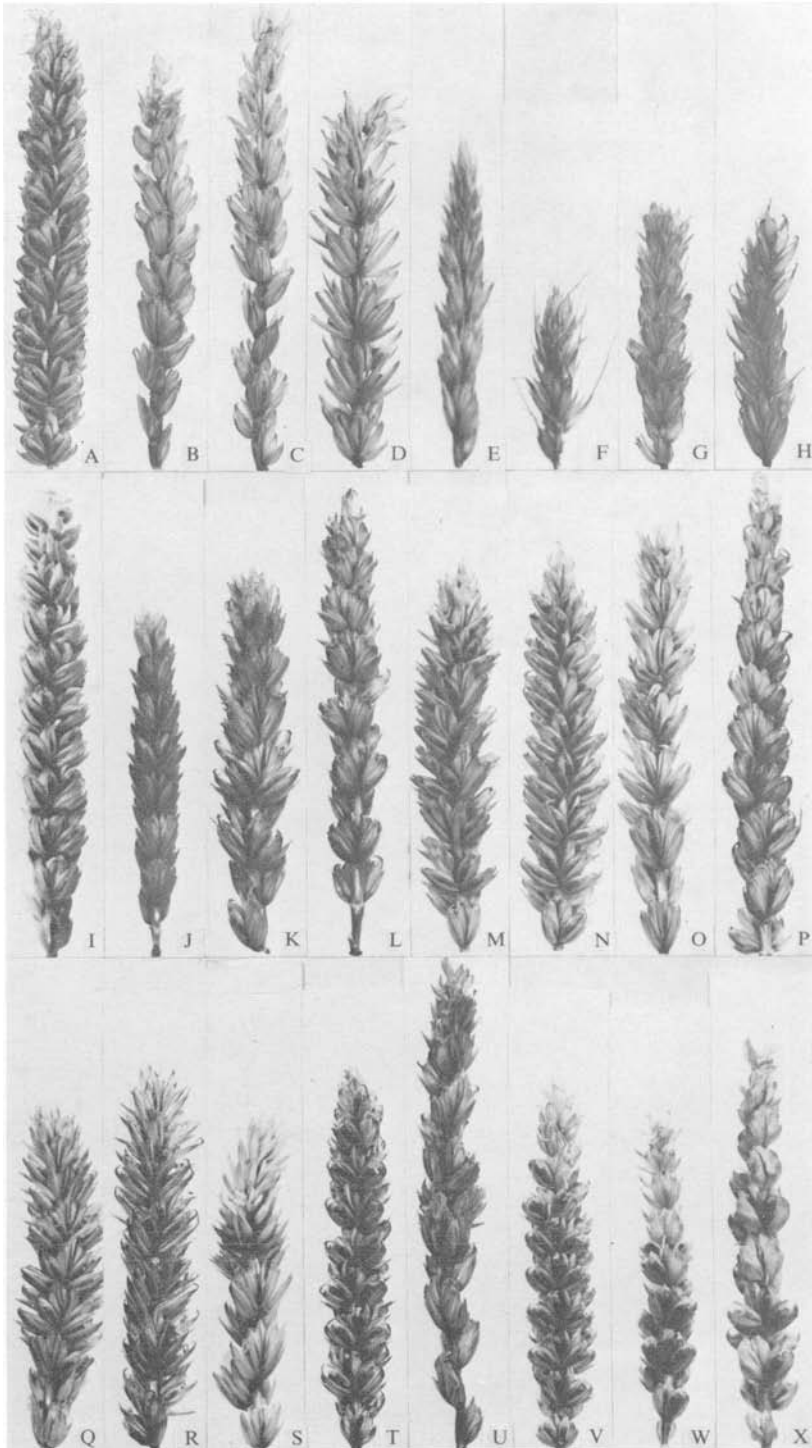O. L. KOLLER AND F. J. ZELLER   (*Facing p.* 180)

Fig. 3

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observed in the disomic addition line CR. In the 7D/CR substitution the fertility was 5 % compared with 28 % in the corresponding nullisomic 7D. In the ditelosomic substitution 7D/CR^L the fertility reached 56 %. In 30–50 % of the plants of its progeny one or both telosomics had been lost. Plate 4, Fig. 6 shows a mitotic cell of a 7D/CR^L substitution with 40W + 2t^L. Due to a tertiary constriction the telo^L-CR chromosome of these plants was not always easily recognizable.

(ii) *Isolation of substitution lines with rye chromosome DR*

4A/DR. No substitution of this constitution was obtained. Only plants with 20″W + 1′4A + 1″DR could be identified. Their progeny mainly had 43 or 44 chromosomes and rarely 42 (41W + 1R).

4B/DR. The somatic chromosome number from approximately 100 seeds was determined in the selfed 20″W + 1′4B + 1″DR. Only seven plants had 42 chromosomes, the rest had 43 or 44 chromosomes. Six of the 42-chromosome plants had the constitution 41W + 1DR. But in the other plant apparently the wheat chromosome pair 4B was replaced by a pair of rye chromosomes DR. This disomic substitution was very short-strawed (Table 1) with good tillering and with extremely narrow leaves which were only one-third the width of those of Chinese Spring. The ears were very small and carried long awns (Plate 2, Fig. 3F; Plate 3, Fig. 4). The plant was completely sterile.

4D/DR. Only one plant with 20″W + 1′4D + t″^{L}DR was isolated. In its progeny there were again plants with 20″W + 1′4D + t″^{L}DR, also some ditelosomic addition lines 21″W + t″^{L}*DR*, but there were no ditelosomic substitutions.

7A/DR. Three disomic substitutions were produced. These plants had good tillering. Their date of flowering like nulli-7A was 5–7 days later than Chinese Spring. They had shorter culms, relatively long ears (Plate 2, Fig. 3L) and narrow, dark-green leaves. The fertility was extremely low (Table 1).

7B/DR. Two disomic substitutions were isolated. Both resembled in phenotype, and date of flowering the 7A/DR substitution and had a fertility of about 6 %. The glumes of the 7A/DR and 7B/DR substitutions were much stiffer than those of Chinese Spring. A spike of the 7B/DR substitution is shown in Plate 2, Fig. 3, P.

7D/DR. Some plants of 20″W + 1′DR are just growing and it is expected that disomic substitutions will be developed in the near future.

Legend to Plate 2

Fig. 3. Spikes illustrating the following genotypes: (A) Chinese Spring; (B) Chinese monotelo- 4Aα; (C) ditelosomic substitution 4A/2t^{8}CR; (D) disomic substitution 4A/CR; (E) disomic substitution 4B/CR; (F) disomic substitution 4B/DR; (G) monotelosomic substitution 4D/1t^{8}CR; (H) disomic substitution 4D/CR; (I) translocation 4A$^\alpha$·DR^8 (4A$^\beta$); (J) Chinese nulli-7A; (K) ditelosomic substitution 7A/2t^{L}CR; (L) disomic substitution 7A/DR; (M) Chinese nulli-7B; (N) ditelosomic substitution 7B/2t^{L}CR; (O) disomic substitution 7B/CR; (P) disomic substitution 7B/DR; (Q) Chinese nulli-7D; (R) ditelosomic substitution 7D/2t^{L}CR; (S) disomic substitution 7D/CR; (T) ditelosomic addition CS + 2t^{L}CR; (U) disomic addition CS + CR; (V) ditelosomic addition CS + 2t^{8}DR; (W) ditelosomic addition CS + 2t^{L}DR; (X) disomic addition CS + DR.

(iii) *Isolation of ditelosomic and di-isosomic wheat-rye addition lines*

Several addition lines with the short and the long arms of chromosomes CR and DR from rye were isolated. The ditelo- additions had better fertility than the additions with the complete rye chromosomes (Table 1; see also Plate 2, Fig. 3T–X). The CR^L telosomic additions were characterized by red coleoptiles, whereas lines with the short arm CR added had green coleoptiles. An addition line of di-iso-CR^L was also obtained. In this the colour of the coleoptile was intensely red and the fertility was considerably higher. A somatic cell in root-tips of a di-iso- addition line with 42 wheat chromosomes and two rye CR^L isochromosomes is shown in Plate 4, Fig. 7A. In the isochromosome a tertiary constriction is clearly visible (Fig. 7B). Plants which carried the long arm telocentric of chromosome DR had narrow leaves. This characteristic was used as a marker in the isolation of DR^L lines. The spikes of the complete addition DR and of the ditelo- addition for the long arm were very similar.

(iv) *Homology of rye chromosomes in wheat–rye addition lines*

Table 2 shows the pairing behaviour of the chromosomes in the F_1 hybrids resulting from crosses between the addition lines (21″W + 1″R) Chinese Spring/Imperial CR, Holdfast/King II, line IV, and Kharkov/Dakold line RA-V. The high frequency of 22 bivalents clearly indicated that rye chromosomes of these additions are homologous. The fact that all three additions possessed red coleoptile, shrivelled kernels, reduced culm length and were able to develop supernumerary spikelets under specific environmental conditions, confirmed the homology of these rye chromosomes.

Meiotic evidence from crosses of the Chinese Spring/Imperial addition DR with Holdfast/King II lines IV, VI, VII and Kharkov/Dakold line RA-V revealed that chromosome DR and King II chromosomes VI and VII in the additions have homologous segments (Table 2). Thus DR is probably completely homologous to VII and partially homologous to chromosome VI of King II. The chromosome configuration of 21″ + 2′ in the F_1 hybrids of the crosses between Chinese Spring/Imperial addition GR and Holdfast/King II, line VI, showed that addition VI is not homologous to GR. Apparently addition line VI from King II has a translocation between two non-homologous rye segments involving part of chromosome VII from King II. Bernard (1976) observed 22 bivalents in F_1 hybrids between wheat–rye addition line B from FEC 28/Petkus and the addition lines VI and VII of Holdfast/King II. These results are further evidence that the rye chromosome in line VI of Holdfast/King II additions has a translocated segment. By means of Giemsa C-banding technique Singh & Röbbelen (1976) concluded that rye chromosomes III and VI of the Holdfast/King II additions each have a deletion on their short arm.

The occurrence of mostly 22 bivalents in the cross Chinese Spring/Imperial addition BR and Holdfast/King II, addition III (Table 2), indicates that these two rye chromosomes are homologous.

Fig. 4. Spikes illustrating decreasing doses of wheat chromosome 4B by the presence of a pair of CR and DR chromosomes, respectively.

Fig. 5. First metaphase of meiosis in pollen mother cells of an F_1 hybrid between $7A/CR^L$ and $4D/CR$, forming $19'' + t1'' + 2'$.
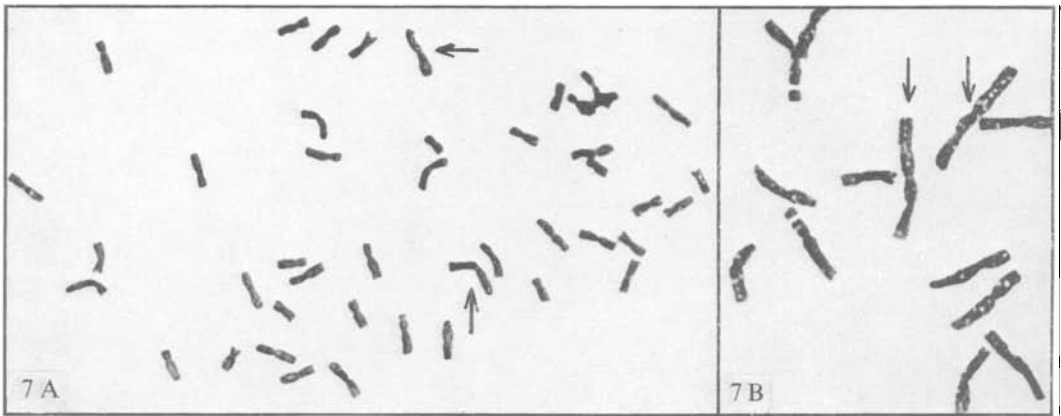
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Fig. 6. Mitotic metaphase in a root-tip squash of a ditelosomic substitution 7D/2t^{L}CR (telosomes are arrowed).

Fig. 7. (A) Mitotic metaphase of a di-iso- addition line CS + iso-CR^L and (B) a pair of iso-CR^L chromosomes showing the tertiary constriction.

Fig. 8. First metaphase of meiosis in pollen mother cells of an F$_1$ hybrid between Kharkov/Dakold addition RA-III and Chinese Spring/Imperial addition DR, forming 18″W + 1^{IV}W + 1″W + 1′DR.

In the F_1 hybrids of the crosses between Kharkov/Dakold addition RA-III and Holdfast/King II additions IV, VII and Chinese Spring/Imperial addition DR the configuration $20'' + 1''' + 1'$ occurred mainly (Table 2). Plate 4, Fig. 8 illustrates a metaphase I of the F_1 hybrid resulting from the cross between RA-III and DR consisting of $18'' + 1^{IV} + 1''' + 1'$. The quadrivalent involves two interchanged wheat chromosomes of Chinese Spring and Kharkov. The selfed RA-III formed a high frequency of $20'' + 1^{IV}$ chromosome configurations (Table 2) and as a consequence it can be concluded that Kharkov/Dakold addition RA-III from Canada is not a disomic wheat–rye addition line. Either it possesses an added pair of a wheat–rye translocated chromosome or – more probably – it is a wheat tetrasomic.

Table 2. *Chromosome configurations of the crosses between wheat–rye addition lines BR, CR, DR and GR from CS/Imperial, III, IV, VI and VII from Holdfast/King II and RA-III and RA-V from Kharkov/Dakold*

Cross	No. of F_1 hybrids	Chromosome configurations				
		$22''$	$21'' + 2'$	Others	$20'' + 1''' + 1'$	$19'' + 1''' + 3'$
CR × IV	9	74	155	56	—	—
CR × RA-V	4	26	78	30	—	—
DR × IV	3	0	46	22	—	—
DR × VI	2	14	39	26	—	—
DR × VII	4	72	122	72	—	—
DR × RA-V	5	0	131	23	—	—
RA-V × IV	5	33	151	39	—	—
RA-V × VII	6	0	136	67	—	—
GR × VI	6	0	144	48	—	—
BR × III	4	35	76	42	—	—
RA-III × IV	3	—	36	8	44	6
RA-III × VII	8	—	33	19	64	21
RA-III × DR	3	—	14	9	23	7
RA-III*	3	20	5	12†	7	—

* Selfed plants. † All of $20'' + 1^{IV}$.

4. DISCUSSION

From the results obtained it may be deduced that rye chromosomes CR, IV and RA-V of the addition lines Chinese Spring/Imperial, Holdfast/King II and Kharkov/Dakold, respectively, are homologous. These chromosomes carry genes for anthocyanin production, reduced tillering and culm length, and supernumerary spikelets as well as shrivelled seeds. These features were also described by Riley and Chapman (1958), Evans & Jenkins (1960), Darvey (1973) and Rao (1975). Genes for red coleoptile, reduced tillering and culm length are located on the long arm of rye chromosome CR. The short arm apparently carries the genetic complex of supernumerary spikelets.

Jenkins (1963) was able to substitute rye chromosome V of Dakold for wheat chromosomes 4B and 4D. Driscoll (1975, personal communication) isolated a

monosomic 4B/CR substitution which was sterile. Rao (1975) substituted rye chromosome CR for wheat chromosome 4A. In the present study the substitutions 4A/CR, 4B/CR and 4D/CR with the complete alien chromosome were characterized by poor fertility and reduced vegetative vigour. The 4D/CR substitution was completely sterile. The substitutions with the short arm of CR in 4A/CR^S and 4D/CR^S were considerably more vigorous and fertile than the corresponding disomic substitutions. This indicates that the short arm of CR exhibits genetic compensation for wheat chromosomes of group 4 and apparently is homoeologous to them.

Jenkins (1963) reported a substitution in which wheat chromosome 7B of Kharkov was replaced by rye chromosome V of Dakold. In the present work the complete alien chromosome did not entirely compensate for the absence of the wheat chromosomes in the disomic substitutions 7B/CR and 7D/CR. In contrast, all three substitutions involving the long arm of CR (7A/CR^L, 7B/CR^L and 7D/CR^L) had better fertility than their nullisomic counterparts. Consequently it seems obvious that the long arm of rye chromosome CR is at least partially homoeologous to wheat chromosomes of group 7.

The experiments have shown that rye chromosome DR of Imperial and chromosome VII of King II are homologous. The genetic factors for narrow leaves and dark-green leaf colour of the long arm of chromosome DR serve as genetic markers for the selection of the substitutions.

For the wheat chromosomes of group 4 only the substitution 4B/DR was isolated. This plant was less vigorous than the corresponding nullisomic line 4B and completely sterile. Apparently the entire chromosome DR is not able to compensate for the deficiency of the wheat chromosomes of homoeologous group 4. By selecting DR substitutions, however, a chromosomal translocation 4A$^\alpha$-DR^S (4A$^\beta$) was obtained (unpublished). This translocation showed better vegetative vigour and seed setting than Chinese Spring ditelo-4A$^\alpha$ (see Plate 2, Fig. 3 I). This suggests a homoeologous relationship between the short arm of DR and 4A$^\beta$ of wheat. The relationship of rye chromosome DR with at least one wheat chromosome of group 4 was confirmed by the isolation of a fertile line which had 20 wheat bivalents, two telosomic chromosomes 4A$^\alpha$, and two telosomic rye chromosomes DR^S. The Chinese Spring lines nulli-4A and ditelo-4A$^\beta$ are completely sterile (Sears, personal communication). It is reasonable to conclude that the short arm of DR, like wheat ditelo-4A$^\beta$, is not able to overcome the sterility caused by the absence of complete wheat chromosome 4A or its α-arm. This might also be the reason why 4A/DR substitutions could not be isolated and why the Chinese Spring lines nulli-4B and ditelo-4B^S are sterile. If DR^S is homoeologous to 4B^S it could not restore fertility in the 4B/DR substitutions.

By zymogram analyses Hart (1973) and Tang & Hart (1975) found structural genes for the production of the enzyme acid phosphatase in Chinese Spring group 4 chromosomes as well as in rye chromosome DR. These findings are consistent with homoeologous relationships between the chromosome arms 4A$^\beta$, 4B^S, 4D^L and DR^S (see also McIntosh, 1973; Joudrier & Cauderon, 1976).

From cytological studies of F_1 hybrids between *Secale cereale* and its presumptive ancestor, *Secale montanum*, it appears that the two species were differentiated by at least two interchanges involving three non-homologous chromosomes (Price, 1955; Riley, 1955). If the evolutionary concept for the origin of chromosomal differences in cultivated rye is correct it would be expected that specific *Secale montanum* chromosomes would substitute for wheat chromosomes of only one homoeologous group. Three (interchanged) chromosomes of *Secale cereale*, however, should be able to compensate at least partially for three different homoeologous groups in wheat.

From the partial substituting ability of chromosome CR for the absence of wheat chromosomes of homoeologous groups 4 and 7 it seems reasonable to expect that CR is involved in one of these rye translocations. Genetic relationships of CR with two homoeologous wheat groups are ascertained by locating genes for anthocyanin production (R_c = red coleoptile) and alcohol dehydrogenase (ADH). Due to the existence of homoeologous genes in the Triticinae one may assume that the locus for anthocyanin production in *Secale montanum* is situated on the short arm of chromosome 7R as is the case in wheat chromosomes $7B^S$ and $7D^S$ (Law, 1966; Rowland & Kerber, 1974). The distance of the locus for purple coleoptile from the centromere in $7D^S$ is approximately 10 crossover units (Rowland & Kerber, 1974). In *Agropyron elongatum* the anthocyanin gene was located in the α-arm of chromosome 7E (Dvořák & Knott, 1974). Homoeologous pairing of chromosome arms showed that the arm $7E\alpha$ corresponds to $7A^S$, $7B^S$ and $7D^S$ of hexaploid wheat (Dvořák, 1976, personal communication). The gene locus for anthocyanin production on the long arm of chromosome CR in *Secale cereale* supports the suggestion that this chromosome is interchanged and that the translocation breakpoint is situated in the long arm of CR (Fig. 9). The location of genes for alcohol dehydrogenase on the wheat telosomes $4A\alpha$, $4B^L$ and $4D^S$ (Hart, 1970; McIntosh, 1973) as well as on the rye chromosomes CR of Imperial, IV of King II and V of Dakold (Irani & Bhatia, 1972; Tang & Hart, 1975) provides further evidence for homoeology of these rye chromosomes with the two groups of wheat chromosomes. On the basis of these findings we conclude that chromosome CR of *Secale cereale* consists of the short arm of *montanum* chromosome 4R, its centromere region plus a segment of *montanum* $7R^S$ including the R_c-locus (Fig. 9). The remaining part of 7R including the centromere apparently fused with a segment of $4R^L$ and has undergone a further translocation involving a segment of the long arm of chromosome 6R. These changes gave rise to a double interchanged chromosome DR in *Secale cereale* (Fig. 9). Chromosome 6R of *Secale cereale* probably consists of the short arm of *montanum* 6R, a part of its long arm and a segment of the long arm of *montanum* chromosome 7R (Fig. 9).

Heemert & Sybenga (1972) found that chromosomes III and V (nomenclature after Sybenga & Wolters, 1972) are involved in the natural translocation complex between *Secale cereale* and *Secale montanum*. By means of Giemsa C banding pattern and phenotypic characteristics in rye trisomics ($2n = 15$) as well as the pairing behaviour in F_1 hybrids between these trisomics and Sybenga's

translocation tester set, chromosomes III and V were identified as DR and 6R, respectively (unpublished).

The notion that chromosome 6R is also involved in the translocation complex between *Secale cereale* and *Secale montanum* is supported by cytological evidence from the papers of Stutz (1957) and Reimann-Philipp & Rhode (1968), who reported that chromosome VI (nomenclature after Lima-de-Faria) is involved in the translocation complex in rye. This chromosome corresponds to 6R (Bhattacharyya & Jenkins, 1960; Heneen, 1962). Riley (1965) described disomic substitution lines in which wheat chromosomes 6A, 6B and 6D were replaced by rye chromosome 6R. The fertility rates of 49, 12 and 22 %, respectively, in these stocks, however, were not very high. In contrast, Brandes (1975) isolated an alien substitution in which rye chromosome 6R of cultivar Petkuser Sommerroggen was able to compensate well for the absence of wheat chromosome 7D. Consequently, this rye chromosome probably exhibits substitution ability for homoeologous groups 6 and 7. The production of substitutions with $6R^L$ for wheat chromosomes 7A, 7B and 7D as well as DR^L for 6A, 6B and 6D has been commenced in order to determine the homoeologous relationships of these rye telosomics.
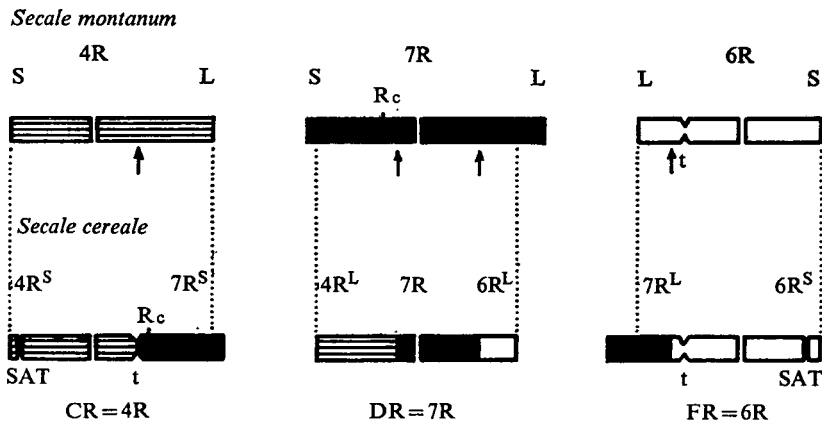

Fig. 9. An evolutionary scheme for the derivation of the *Secale cereale* genome from *Secale montanum* by two interchanges involving three chromosomes. Arrows indicate the probable breakpoints, t means tertiary constriction, R_c = possible position of locus for anthocyanin production.

Due to the homoeologous gene loci for alcohol dehydrogenase production in chromosomes of wheat group 4, rye chromosome CR and its homologues and on the basis of partial genetic compensation of the short arm of CR and the negative effect of the complete chromosome CR in substitutions for chromosomes of wheat group 7 we propose the designation 4R for the rye chromosome CR (Table 3).

The short arm of chromosome DR showed genetic compensation for the loss of the β-arm of wheat chromosome 4A. Assuming that rye chromosome DR is a double translocation, as outlined before, one should expect partial substitution ability for wheat chromosomes of groups 4, 6 and 7. As rye chromosome DR apparently carries the original centromere region from 7R (Fig. 9), it is proposed –

disregarding the structural exchanges – that DR should be designated as 7R. Thus the rye chromosomes in the wheat–rye addition sets Chinese Spring/Imperial, Holdfast/King II and Kharkov/Dakold can be allocated as shown in Table 3.

Table 3. *Allocation of rye chromosomes from cultivars Imperial, King II and Dakold to their homoeologous groups within the Triticinae*

Homoeologous groups	Chinese/ Imperial (Sears)	Holdfast/ King II (Riley)	Kharkov/ Dakold (Bhattacharyya)
1	E	V	VII
2	B	III	II
3	G	VI	I
4	C	IV	V
5	A	I	VI
6	F	II	IV
7	D	VII	III

For a better understanding of the relationships of the rye chromosomes and their homoeologous counterparts in wheat further substitution experiments with rye telosomes $6R^L$ and $7R^L$ are required. Additional homoeologous gene localizations in wheat and rye clarify the genetic relation of chromosomes between these two species of the subtribe Triticinae.

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