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# Rye Chromosome Translocations in Hexaploid Wheat: a Re-evaluation of the Loss of Heterochromatin from Rye Chromosomes

C.E. May
Agricultural Research Institute, Wagga Wagga, NSW (Australia)

R. Appels
Division of Plant Industry, CSIRO, Canberra, ACT (Australia)

**Summary.** Using *in situ* hybridization techniques, we have been able to identify the translocated chromosomes resulting from whole arm interchanges between homoeologous chromosomes of wheat and rye. This was possible because radioactive probes are available which recognize specific sites of highly repeated sequence DNA in either rye or wheat chromosomes. The translocated chromosomes analysed in detail were found in plants from a breeding programme designed to substitute chromosome 2R of rye into commercial wheat cultivars. The distribution of rye highly repeated DNA sequences showed modified chromosomes in which (a) most of the telomeric heterochromatin of the short arm and (b) all of the telomeric heterochromatin of the long arm, had disappeared. Subsequent analyses of these chromosomes assaying for wheat highly repeated DNA sequences showed that in type (a), the entire short arm of 2R had been replaced by the short arm of wheat chromosome 2B and in (b), the long arm of 2R had been replaced by the long arm of 2B. The use of these probes has also allowed us to show that rye heterochromatin has little effect on the pairing of the translocated wheat arm to its wheat homologue during meiosis. We have also characterized the chromosomes resulting from a 1B-1R translocation event.

From these results, we suggest that the observed loss of telomeric heterochromatin from rye chromosomes in wheat is commonly due to wheat-rye chromosome translocations.

**Key words:** Wheat – Rye – Triticale – Highly repeated DNA sequences – Heterochromatin – Translocations

## Introduction

The availability of rye chromosome substitution and translocation lines in hexaploid wheat (collated by Driscoll 1975 et seq.) provides a source of new genetic material for the agronomic improvement of commercial wheats. If the introduction of such chromatin can be shown to confer resistance to pathogens or to introduce other agronomically desirable characters into wheat, it is essential that the rye chromatin remain unchanged after incorporation. Similarly, if triticales (× *Triticosecale* Wittmack) are to be a reliable alternative to wheat, the rye (R) genome chromosomes in these hybrids must be stable when combined with durum (AB) or wheat (ABD) genome chromosomes.

One of the major problems associated with the introduction of rye chromosomes into wheat is that their presence often has deleterious effects on fertility, endosperm development and grain filling (Bennett 1974, 1977; Kaltsikes et al. 1975; Kaltsikes and Roupakias 1975). Bennett et al. (1971, 1975) have suggested that the basis of this problem is the late replicative nature of the rye telomeric heterochromatin (Lima-de-Faria and Jaworska 1972; Ayonoadu and Rees 1973) compounded by unfavourable interactions between the wheat and rye genomes when they are combined into a single nucleus.

It may not be surprising, therefore, that selection for improved triticale phenotypes has occasionally resulted in firstly, the selection of integrated hexaploid triticales in which one or more rye chromosomes have been entirely replaced by their D genome homoeologues (Gustafsson and Zillinsky 1973; Darvey and Gustafsson 1975; Mercker 1975; Gustafsson and Bennett (1976) orsecondly, triticales in which the rye chromosomes have been apparently modified by the loss of their telomeric heterochromatin (Mercker 1976; Roupakias and Kaltsikes 1977). The apparent loss of telomeric heterochromatin has also been observed in addition lines of rye chromosomes to hexaploid wheat (Singh and Röbbelen 1976; Bennett 1977). The fact that rye chromosomes which have lost their telomeric heterochromatin pair more readily at meiosis than those which have not (Thomas and Kaltsikes 1974, 1976;

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Roupakias and Kaltsikes 1977; Kaltsikes et al. 1977) and generate fewer aberrant nuclei in the endosperm (Bennett 1977) has led to the specific suggestion that loss of rye heterochromatin is an essential prerequisite to the genetic stability of such lines. The majority of such studies have relied upon Giemsa C-banding to detect the rye heterochromatin.

We have previously reported the finding of chromosomes which appeared to be the result of a reciprocal translocation between chromosomes 2R of rye and 2B of wheat (May and Appels 1978). This paper proves that these are the translocated chromosomes 2BS/2RL and 2RS/2BL. It is further shown that telomeric heterochromatin loss is due to the loss of entire arms of rye chromosomes with their simultaneous replacement by homoeologous wheat chromosome arms. We suggest that it is the additional wheat euchromatin rather than the loss of rye heterochromatin which explains most instances of modified rye chromosomes behaving more favourably than entire rye chromosomes in wheat germplasms.

## Materials and Methods

The plants investigated were the $BC_1F_3$ progeny of the cross 'Chinese Spring 2R(2B)/Tr535//Timgalen', designated Family 856. (The original 'Chinese Spring'-'Imperial Rye' 2R(2B) substitution line was kindly provided by Dr. E.R. Sears). This cross was instigated to determine the agronomic effects of the replacement of the 2B chromosomes of a commercial wheat by their rye group 2 homoeologues. We were kindly supplied with seed from a plant heterozygous for 1B and a 1BS/1RL translocated chromosome by G.J. Lawrence.

The preparation of mitotic chromosomes from root tip cells for *in situ* hybridization was carried out as previously described (Appels et al. 1978) with the exception that 24 hr ice water treatment of the attached rootlets was preferred to colchicine as the pre-fixative. It was found that if the water was kept at 0°C, particularly good mitotic indices were obtained with good chromosomal morphology. Meiotic preparations of pollen mother cells were made from anthers fixed in 3:1 ethanol:acetic acid and treated as per root tips for *in situ* hybridization.

Chromosomes 1R and 2R and their derivatives were detected using the *in situ* hybridization of $^3$H-cRNA synthesized from rye highly repeated sequence DNA (renatured density in CsCl 1.701 g.ml$^{-1}$) as described by Appels et al. (1978). This radioactive probe hybridizes mainly the telomeric heterochromatin of rye chromosomes with only a minor degree of cross reaction to other sites on rye and wheat chromosomes. Chromosome 1R has approximately six times as much label on the telomeric heterochromatin of the long arm as is present on the short arm and chromosome 2R has approximately four times as much label on the telomeric heterochromatin of the short arm as there is on the long arm.

To assay for the presence or absence of chromosome 2B, we utilized a readily available probe prepared from a highly repeated sequence DNA of *Drosophila melanogaster* (density in CsCl 1.705 g.ml$^{-1}$). This DNA is comprised mainly of the repetitive pentameric nucleotide sequence $\frac{AGAAG}{TCTTC}$ as has been discussed by Appels and Peacock (1978). $^3$H-cRNA synthesized from this DNA can be used to assay wheat highly repeated sequence DNA as this is composed predominantly of the sequence $\frac{GAAGAAGAAGAG}{CTTCTTCTTCTC}$ (Dennis et al. 1979). The major sites of this wheat highly repeated sequence (Gerlach et al. 1978; Dennis et al. 1979) occur on all seven B genome chromosomes of hexaploid wheat (*Triticum aestivum* L. em Thell var 'Chinese Spring') and chromosomes 4 and 7 of the A genome. The *Drosophila* probe gave similar *in situ* hybridization patterns to those reported by Gerlach et al. (1978) although we did find differences in the labelling patterns of a number of these chromosomes as compared to those described for 'Chinese Spring'. Many of these differences could be ascribed to longer autoradiographic exposures. Some, however, could not. For example, chromosome 7A of Family 856 is labelled only on the telomere of the long arm whereas in 'Chinese Spring' it is labelled on the telomeres of both arms. Clearly, qualitative differences such as this indicate that there could well be inter-varietal differences in the sites of labelling of the various chromosomes. We also found that a longer exposure period enhaced the secondary labelling sites on the chromosomes of the remaining A and D genomes (Fig. 1). The so far tentative identification of these chromosomes is based on the position of the centromere, their arm length ratios, and their percentage contribution to the total length of chromosomes present as compared to measurements made in the cultivars 'Chinese Spring' (Sears 1954), 'Cheyenne' (Sasaki et al. 1963) and 'Wichita' (Gill et al. 1963). These identifications have been further investigated using telocentric stocks of 'Chinese Spring' (Dennis et al. 1979).

## Results

### *Detection of Rye Chromosomes in Interphase Nuclei*

The examination of root tips for the presence or absence of rye chromosomes using the rye highly repeated sequence DNA probe is aided by the fact that interphase

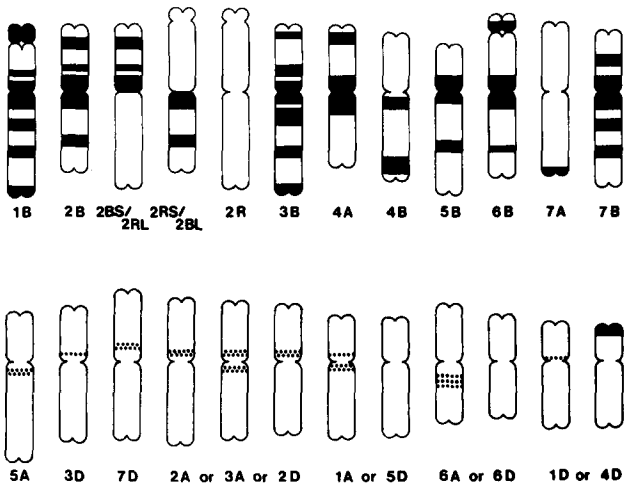


Fig. 1. Diagrammatic representation of mitotic metaphase chromosomes to show the sites of wheat highly repeated sequence DNA assayed by the *in situ* hybridization technique. The shaded areas indicate sites which require relatively long autoradiographic exposures to be reproducibly detected

nuclei can be used to locate plants carrying these chromosomes. Figure 2 demonstrates the ease of this approach in ascertaining the presence or absence of the arms of chromosomes 1R and 2R. For chromosome 2R it is interesting that the intense labelling of the short arm and lesser labelling of the long arm are often in close proximity.

*Identification of Rye Chromosome Arms Using Rye Probe*

The rye probe was applied to the segregating progeny of a plant heterozygous for chromosome 1B and a 1BS/1RL translocated chromosome. This heterozygote had previously been identified by meiotic pairing, chromosome banding and biochemical markers (Lawrence, pers. comm.) and the rey probe was used to confirm the nature of the translocation and to isolate substitution lines disomic for the translocation. A mitotic metaphase from a disomic substitution is shown in Figure 3. The heavy labelling of the telomeric heterochromatin on the long arm of 1R is clearly evident as is the absence of label in the opposite wheat arm.

A similar situation was found in progeny of family 856. Two $BC_1F_3$ plants gave the mitotic labelling patterns shown in Figure 4a,b. From these and other plants, May and Appels (1978) postulated the existence of two translocation chromosomes involving the short and long arms of 2R and suggested that the other chromosome involved was chromosome 2B. In the absence of simple genetic markers for either of these group 2 homoeologues, proof that 2B was the chromosome involved was lacking. We therefore decided to examine these putative 2RS/2BL and 2BS/2RL translocations with a probe specific for wheat chromosomes.

*Identification of the Wheat Arms in the Modified 2R Chromosomes*

To verify the presence or absence of chromosome 2B or its arms in family 856, we assayed for wheat highly repeated sequence DNA in the chromosomes of seedlings which had been demonstrated to carry the putative translocations by assaying with rye highly repeated sequence DNA. Chromosomes 2B and 2R and their derivatives were clearly evident in the $BC_1F_3$ progeny. In plants heterozygous for 2R and the 2RL translocation (progeny of the $BC_1F_2$ plant 856-10-4), chromosome 2R could be identified as the longest chromosome present, sub-metacentric,

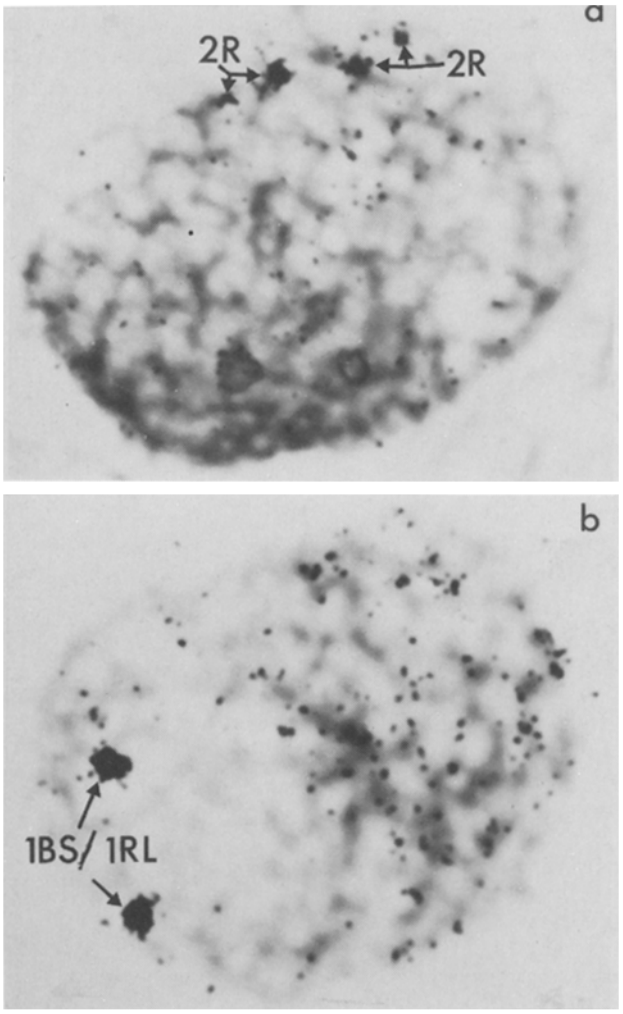


**Fig. 2a and b.** Interphase nuclei labelled with radioactive probe synthesized from rye highly repeated sequence DNA. a 2R(2B) disomic substitution, b 1BS/1RL disomic substitution

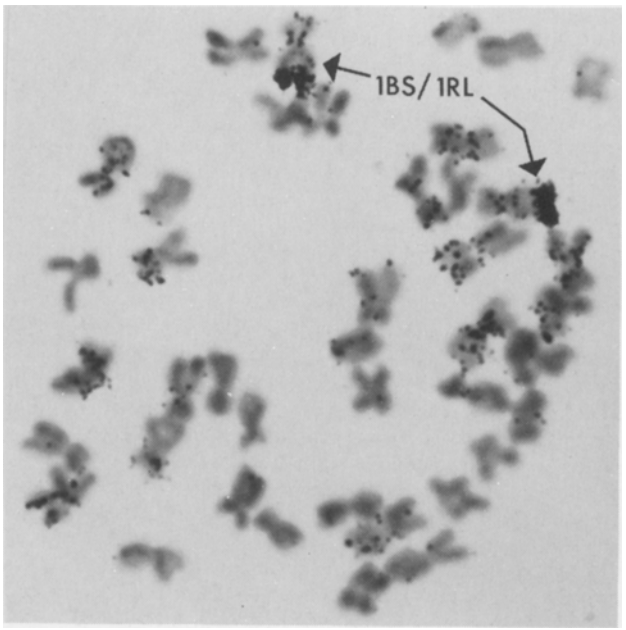


**Fig. 3.** Mitotic metaphase chromosomes from a 1BS/1RL disomic substitution labelled with the radioactive probe synthesized from rye highly repeated sequence DNA

unlabelled and with a sub-terminal constriction on the shorter arm. The translocated chromosome was comprised of an unlabelled long arm and a three-banded short arm identical to 2BS. Furthermore chromosome 2B was absent (Fig. 5). The heterozygous progeny of the $BC_1F_2$ plant 856-1-2 contained the entire five-banded chromosome 2B and the presumptive translocation chromosome comprised of unlabelled 2RS (with its sub-terminal constriction) and two-banded 2BL (Fig. 6). These labelling patterns allowed us to positively identify the translocated chromosomes as being 2BS/2RL and 2RS/2BL respectively. The inserts to Figure 5 show the disomic substitution of 2R and 2BS/2RL in progeny of 856-10-4 and the inserts in Figure 6 show the normal disomic 2B and the 2RS/2BL disomic substitution in progeny from 856-1-2.

*Meiotic Pairing of Chromosomes 2B and 2RS/2BL*

To estimate the effect of rye heterochromatin and/or euchromatin on the meiotic pairing of an adjoining wheat chromosome arm, the pairing behaviour of chromosomes 2B and 2RS/2BL was examined. This translocation was chosen because more than 50% of the chromatin originates from rye and a large block of rye heterochromatin is present. The rye highly repeated sequence DNA probe was used to label the 2RS arm.

In 140 pollen mother cells, 2RS/2BL was identifiable as a univalent in 15 (10.7%) and had formed a rod bivalent with 2B (Fig. 7) in 125. Pairing occurred only between the homologous 2BL arms which was expected since 2R and 2B do not normally pair (Sears 1968). In the same PMC's, one or more of the remaining 20 pairs of chromosomes were found unpaired in 131 instances giving an average frequency of univalency of 4.7%. This relatively high frequency is assumed to be due to either environmental factors or to a lack of homozygosity of the wheat chromosomes in the material examined. The furhter 6% decrease in pairing between 2B and 2RS/2BL is comparable to the pairing of a telocentric to either a second telocentric or to an entire chromosome. In the former case, the pairing frequency is usually some 2% lower (Sallee and Kimber 1978) and in the latter, the frequency of crossing over is reduced (Sears 1972). Although no direct data are available for the telo-2BL and 2B entire combination, it would appear that 2RS has little if any effect on the pairing of the 2BL arm of the 2RS/2BL translocation to the long arm of chromosome 2B entire.

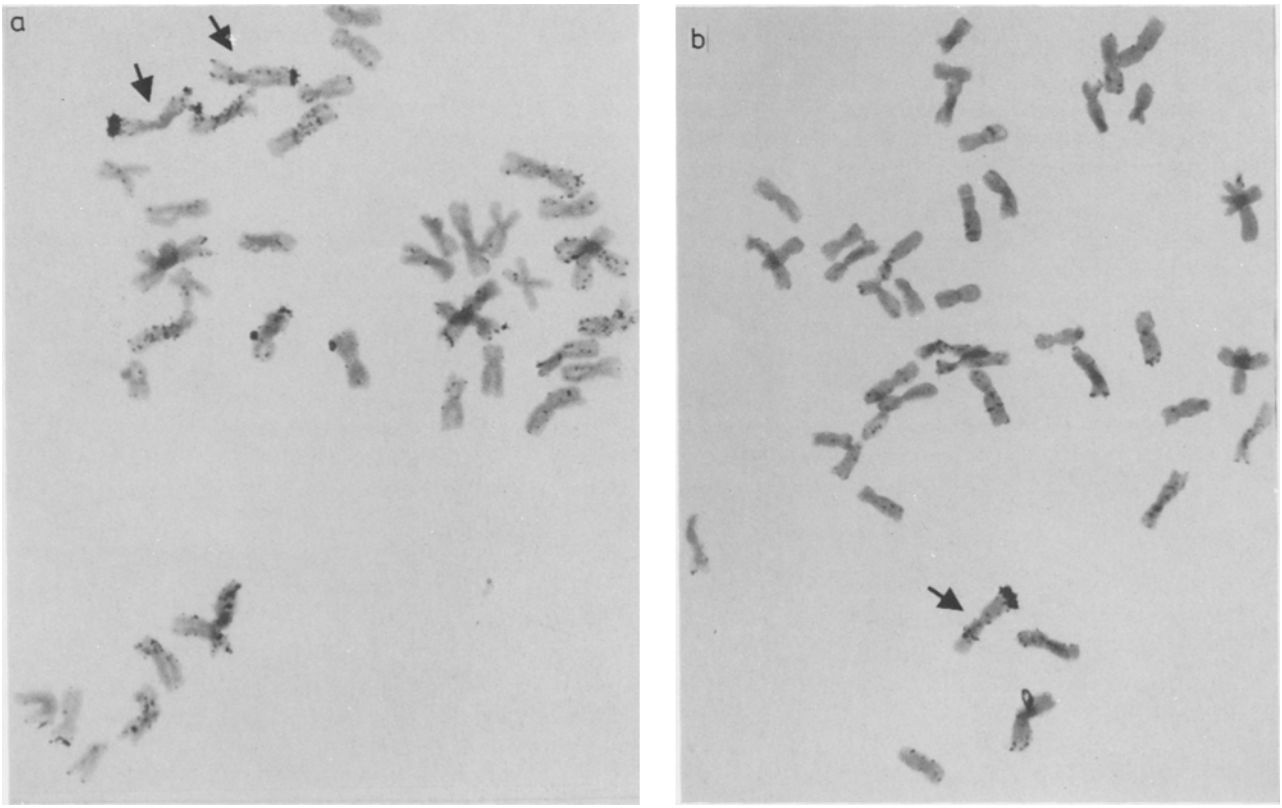


**Fig. 4a and b.** Mitotic metaphase chromosomes labelled with the radioactive probe synthesized from rye highly repeated sequence DNA, from: **a** heterozygous 2R + 2BS/2RL, **b** heterozygous 2B + 2RS/2BL

*Biological Effects of the Translocation Chromosomes*

The chromosomal constitutions of 79 progeny of plant 856-1-2 and 29 progeny of 856-10-4 are presented in Table 1. The data are in agreement with the expected 1:2:1 ratio indicating that pollen containing the translocated chromosomes is of equal viability to pollen containing either 2B or 2R entire.

Germination and subsequent growth of the seed of all karyotypes was normal with the exception of seedlings disomic for the 2RS/2BL translocation. These seedlings died after producing apparently normal primary and sec-

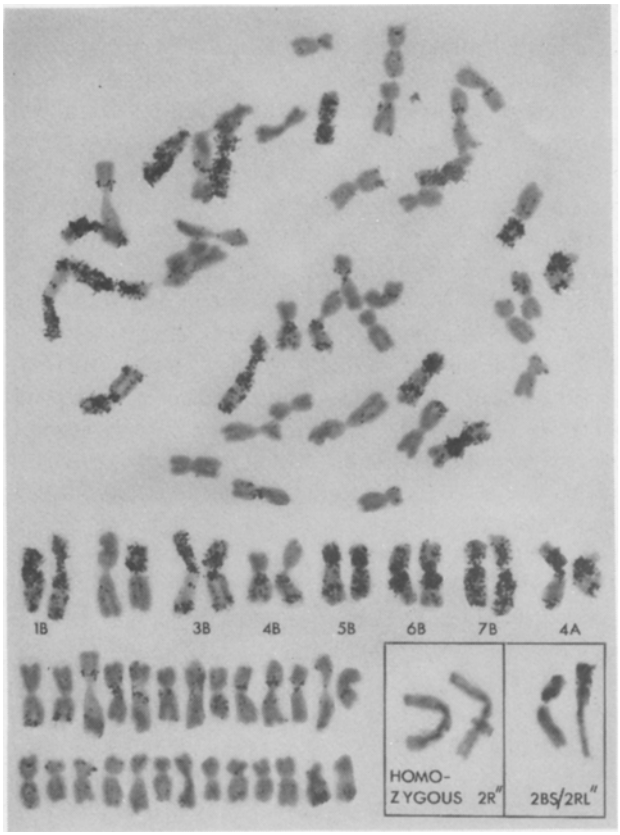


Fig. 5. Mitotic metaphase chromosomes from a heterozygous 2R + 2BS/2RL plant, labelled with radioactive probe specific for wheat highly repeated sequence DNA. The inserts are from plants disomic for 2R and 2BS/2RL

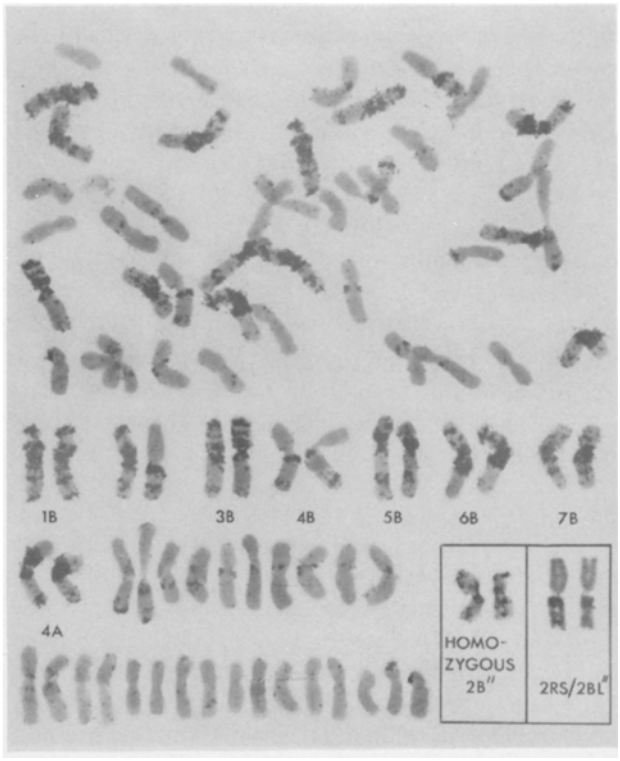


Fig. 6. Mitotic metaphase chromosomes from a heterozygous 2B + 2RS/2BL plant labelled with radioactive probe specific for wheat highly repeated sequence DNA. The inserts are from plants disomic for 2B and 2RS/2BL

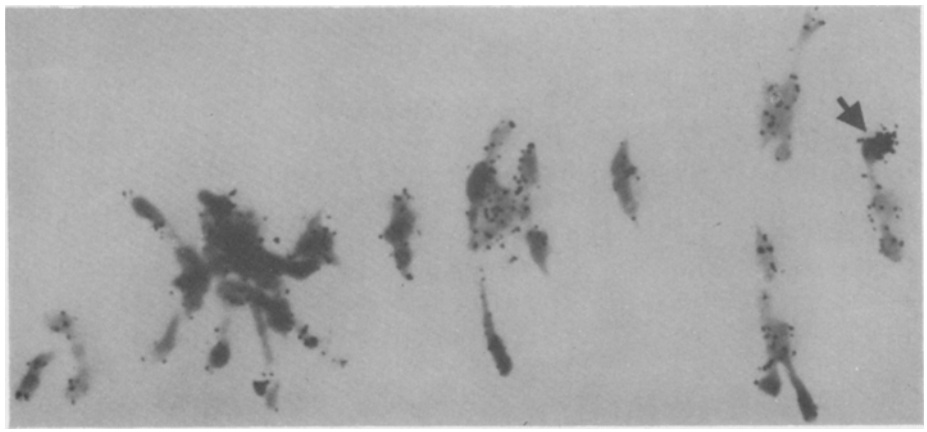

Fig. 7. Meiotic metaphase of a plant heterozygous for 2B + 2RS/2BL labelled with a radioactive probe synthesized from rye highly repeated sequence DNA

Table 1. Segregation of $BC_1F_3$ progeny tested by $\chi^2$ for 1:2:1 distribution

| $BC_1F_2$ parent | 856-1-2 | | | 856-10-4 | | |
|---|---|---|---|---|---|---|
| $BC_1F_3$ karyotypes | 2B" | 2B'+2RS/2BL' | 2RS/2BL" | 2R" | 2R'+2BS/2RL' | 2BS/2RL" |
| n | 18 | 43 | 18 | 8 | 15 | 6 |
| $\chi^2$ | 0.62 | | | 0.31 | | |
| P (d.f.=2) | 0.8 > P > 0.7 | | | 0.9 > P > 0.8 | | |

ondary leaves. Consequently, this translocation can only be maintained in the heterozygous condition. It would appear that these seedlings are unable to survive once the food reserves of the seed are exhausted. This effect could be due to a lethal interaction between the products of genes borne on the 2RS and 2BL arms, an effect which is suppressed if either 2BS or 2RL is present. We are further investigating the seedling leaves of these plants to determine whether or not there are any morphological or anatomical abnormalities which can be correlated to this lethality. Plants disomic for the 2BS/2RL translocation and the 2R(2B) substitution were of normal fertility and appearance.

## Discussion

Translocated chromosomes produced as a result of entire or partial arm exchanges between wheat and rye chromosomes have previously been detected using morphogenetic, disease resistance or biochemical markers (e.g. Sears 1967; Zeller 1973; Shepherd 1973). Unfortunately, there are few such simply inherited genetic markers borne by the homoeologous group 2 chromosomes of wheat and rye. Furthermore, although Giemsa C-banding has been used to identify chromosome 2R of rye (Darvey and Gustafsson 1975), it has been difficult to obtain reproducible results with this technique. Thus, in order to identify chromosomes 2B and 2R and their derivatives in wheat, it was necessary to employ radioactive probes specific for the highly repeated sequence DNA of both rye and wheat, in conjunction with the *in situ* hybridization technique.

With these probes, we have isolated plants in which chromosome 2B has been entirely replaced by 2R and plants in which the short and long arms of chromosome 2B have been replaced by the short and long arms of 2R, respectively, to give the two translocated chromosomes 2BS/2RL and 2RS/2BL. We have analyzed the segregating progeny of a 1B + 1RS/1BL heterozygote. The presence or absence of any of the wheat B genome chromosomes or of 4A and 7A can be determined using the probe specific for wheat highly repeated sequence DNA. In fact we have found that the secondary labelling sites discussed in the Materials and Methods are reproducible and we expect that these will be of use in detecting the replacement of R genome chromosomes by those of the D genome in integrated hexaploid triticales. Karyotype determinations can be routinely effected within three weeks or less, depending upon the concentration of the radioactive probe, allowing the technique to be used in a crossing programme.

In the course of this work, we have gained new data pertaining to the biological effects of rye heterochromatin. When rye chromosomes are introduced into wheat – as has occurred in the synthesis of hexaploid and octoploid triticales – they occur as univalents at meiosis more often than expected (Shkutina and Khvostova 1971; Thomas and Kaltsikes 1972, 1974) and cause other meiotic and developmental irregularities (Kaltsikes et al. 1975; Kaltsikes and Roupakias 1975; Bennett 1977). Such effects have been attributed to the presence of heterochromatin on the rye chromosomes because meiotic pairing is improved when telomeric heterochromatin has apparently been eliminated from the various rye chromosomes (Mercker 1976; Thomas and Kaltsikes 1976; Roupakias and Kaltsikes 1977). Subsequent endosperm and seed development is also improved (Bennett 1977). Indeed, Bennett (1977) has specifically suggested that selection of improved triticales necessitates the incorporation of rye chromosomes which have lost their telomeric heterochromatin.

The possibility that wheat-rye translocations may account for the loss of rye heterochromatin and improved meiotic pairing and subsequent behaviour appears to have been virtually ignored. Even when chromosomes have shown distinct differences in the length of one of their arms to give significantly different arm ratios (Singh and Röbbelen 1976), these have been regarded as being due to terminal deletions of the rye chromosomes. Although Mercker (1975) has suggested that translocations would result in an unbalanced chromosomal constitution, we suggest that such an unbalance would be eliminated upon selection for improved phenotype due to homozygosity of the translocated chromosomes. It is possible that rye-wheat translocations provide a mechanism for the replacement of entire rye chromosomes by D genome chromosomes during the intercrossing of secondary triticales (Darvey and Gustaffson 1975; Mercker 1975). Certainly, translocations can occur fairly commonly as shown by Shepherd (1973) who found that 3 out of 13 putative substitution lines of chromosome 1R for 1D of wheat involved translocations between 1DL and 1S.

We suggest that these and other examples of hetero-

chromatin elimination warrant re-examination to determine whether it is the acquisition of wheat chromatin by a rye chromosome rather than the loss of rye heterochromatin alone that improves the overall biological performance of these chromosomes in wheat cytoplasm. As far as we have been able to ascertain for chromosomes 1R and 2R, the heterochromatin is a stable part of the chromosome arm on which it is found, and the heterochromatin on the short arm of 2R has no significant effect on the pairing behaviour of the 2RS/2BL chromosomes with chromosome 2B entire.

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Dr. C.E. May
NSW Department of Agriculture
Agricultural Research Institute
Wagga Wagga, NSW 2650 (Australia)

Dr. R. Appels
CSIRO, Division of Plant Industry
P.O. Box 1600
Canberra, ACT 2601 (Australia)