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Detection and characterization of 1B/1R translocations in hexaploid wheat

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Total genomic DNA from rye was labelled with biotin and used as a probe for *in situ* hybridization to show the sizes and translocation points of the rye chromosome segments in five wheat varieties which carry a translocation between wheat chromosome 1B and the short arm of rye chromosome 1R (1B/1R). All the translocation breakpoints were at, or very near to, the centromere. Using genomic DNA to block some cross-hybridization, little signal from hybridization between the rye probe and wheat chromosomes was observed despite the 78 per cent sequence homology between the species. The translocation was identified in cells at all stages of the cell cycle. Total genomic rye DNA used as a probe was also able to distinguish rye, triticale and wheat varieties carrying the translocation, by Southern hybridization. The techniques using genomic probes are useful for detecting, characterizing and following alien chromosomes or chromosome segments through breeding programmes, by both *in situ* and Southern hybridization.

INTRODUCTION

Hexaploid ($2n = 6x = 42$) wheats which contain a segment of the rye chromosome 1R translocated onto the long arm of the 1B chromosome of wheat (1B/1R) are widely used in agriculture. For example, the variety Hornet, bred by IPSR (formerly Plant Breeding Institute), contains the translocation and gives exceptionally high yields in fertile and high input situations, with good disease resistance characteristics (NIAB, 1987). However, the presence of the translocation is associated with poor breadmaking quality (Zeller *et al.*, 1982); all the current European varieties carrying the translocation are classified as feed or biscuit wheats. Because of the possible correlation between the presence of the translocation and increased disease resistance or yield, it is desirable to detect its presence in early breeding lines, when a yield advantage of a few per cent may be statistically undetectable. It is also important to examine a range of breeding lines and varieties to see if there is variation in the size of the rye translocation which might enable any association between higher yield and poorer quality to be broken.

A wide range of cytogenetical methods has been applied to identify the 1B/1R translocation. The 1R chromosome arm can be distinguished from all other chromosome arms in Giemsa stained root-tip metaphase cells of hexaploid wheats carrying the translocation by the presence of a nucleolar organizing region (NOR) and a telomeric band. However, because of the limited number of C-bands in the cereals, it is only possible to state that the wheat–rye translocation chromosomes contain the major part of the short arm of chromosome 1R (1RS; Bennett and Smith, 1975). Appels *et al.* (1986) suggested the use of a cloned rye rDNA spacer 2·4 kb long to show the presence of the rye NOR, but this probe gives no information about the size of the translocation. Koebner and Shepherd (1986) and Koebner *et al.* (1986) made novel 1R-wheat recombinant lines, which were characterized by restriction fragment length polymorphisms (RFLPs) and zymograms. A further method which has been used to identify the presence of the translocation is *in situ* hybridization. Rayburn and Gill (1985) used a cloned, rye specific probe to look at rye chromosomes in triticale (wheat × rye hybrids), while Lapitan *et al.* (1986) looked at wheat-rye translocations, but the isolation of dispersed, genome-specific probes has, in general, proved difficult, and their specificity is dependent on hybridization stringency and detection systems.

Hybridization with total genomic DNA can be used to distinguish chromosomes and chromosome segments originating from different genomes in

barley × rye species hybrids (Heslop-Harrison *et al.*, 1988; Schwarzacher *et al.*, 1989) and in triticale (wheat × rye) and 1B/1R wheats (Le *et al.*, 1989). The genomic probing method potentially allows accurate determination of chromosome breakpoints. In the present work, we describe (1) a Southern hybridization method using labelled total genomic rye DNA as a probe to identify the presence of a rye chromosome segment in a wheat background; (2) results from *in situ* hybridization showing the size and translocation point of the rye chromosome segments in five wheat varieties carrying the 1B/1R translocation; and (3) the appearance of the translocated arm throughout the cell cycle.

MATERIALS AND METHODS

Plant materials

The plant species and varieties which were used are described in table 1, and the pedigrees of the wheat varieties carrying the 1B/1R translocation are shown in fig. 1.

DNA extraction, digestion and transfer

Methods for DNA extraction, restriction enzyme digestion, agarose gel electrophoresis and alkaline "Southern" transfer of DNA to nylon membranes were as described by Sharp *et al.* (1988) with minor modifications, such as the use of Hybond N+ (Amersham) charged membranes and lambda *Hin*dIII digests as a size marker. Other techniques followed standard protocols (Sambrook *et al.*, 1989). Total genomic DNA was cut to completion using *Eco*R1 and *Dra*1 restriction endonucleases (BRL) and size separated on 0.8 per cent agarose gels loaded with 1 μg/track. The wheat ribosomal DNA clone pTa71 containing spacer and coding sequences (Gerlach and Bedbrook, 1979) was kindly provided by R. B. Flavell and M. O'Dell (IPSR, Norwich) after recloning in pUC19.

Southern hybridization

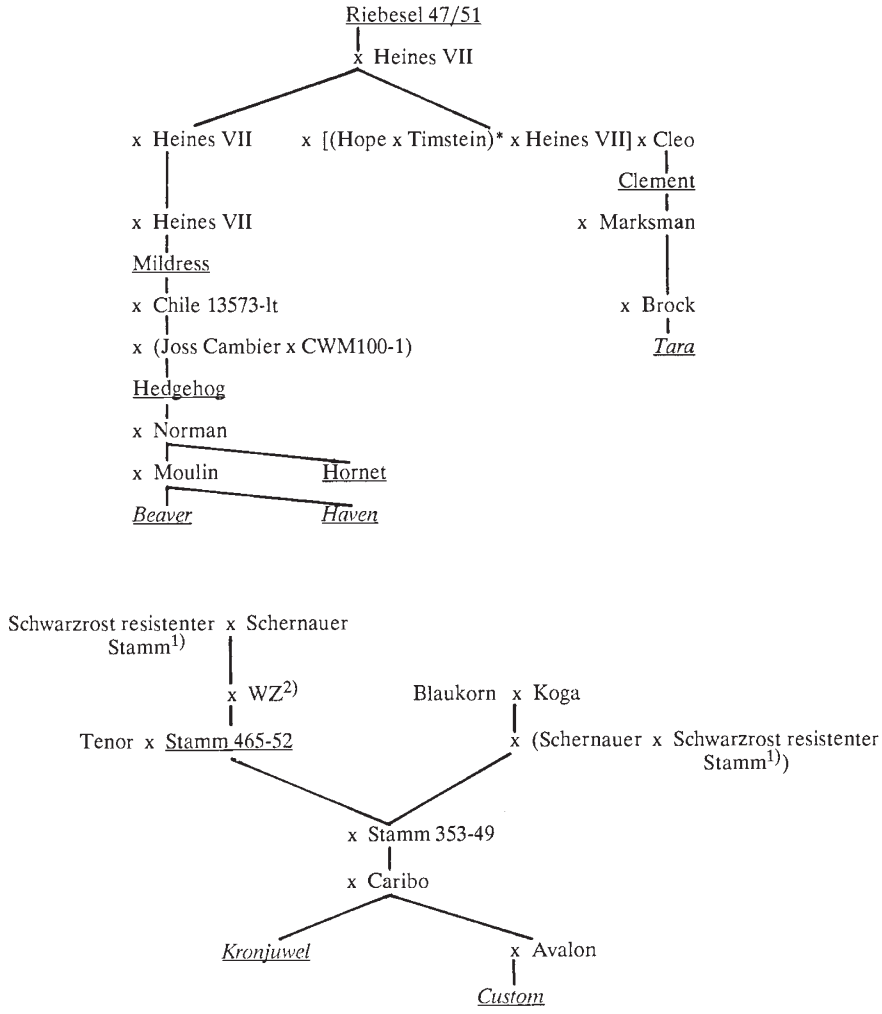
The non-radioactive chemiluminescent method, ECL (Amersham), was used for probe labelling, hybridization and detection of hybridization sites, following modified manufacturer's instructions. Total genomic DNA from rye was mechanically sheared to 10–12 kb and pTa71 was digested with *Eco*R1 to cut the insert from the vector. Following denaturation by placing in boiling water for 5–7 min, the DNAs were labelled by cross-linking to horseradish peroxidase with glutaraldehyde. The transfer membrane was incubated for at least 15 min at 42°C in ECL hybridization buffer containing 6 M urea with addition of 0·1 M NaCl, giving a stringency of 90 per cent. The labelled probe (10 $ngml^{-1}$) and lambda DNA (4 $ngml^{-1}$) were added and hybridized overnight. After post-hybridization washes (stringency 97 per cent), hybridization sites were detected on film by the enzyme-catalysed emission of light by oxidation of luminol to give the luminographs shown in the results.

Quantification of hybridization

The amount of probe hybridization to the Southern membranes was measured semi-quantitatively with a microcomputer-based image digitizing system. Luminographs with short exposure times (where the most intense areas on the film were not quite black) were digitized, and the average grey level

Table 1 The species and varieties of cereals used in the work

Genomic constitution	English name	Species name	Variety
R	Rye	*Secale cereale* L.	*cv.* Petkus Spring
ABR	Triticale	*Triticosecale* Wittmark	*cv.* Lasko
AB	Durum wheat	*Triticum durum* Desf.	
A	Diploid wheat	*Triticum monococcum* L.	
ABD	Hexaploid wheat	*Triticum aestivum* L.	
		without rye chromosome segment	*cv.* Chinese Spring
		carrying 1B/1R translocation	*cv.* Beaver
			cv. Custom
			cv. Glennson
			cv. Haven
			cv. Kronjuwel
			cv. Tara



1) stem rust resistant line
2) octoploid triticale from the collection of G. Kattermann

Figure 1 The pedigree of some wheat varieties known to carry the short arm of rye chromosome 1R translocated to wheat chromosome 1B (1B/1R; underlined). Varieties examined by *in situ* hybridization in the present study are in *italics*. Riebesel 47/51, (sometimes referred to as Riebesel 57/41) arose from crosses made by Riebesel in the 1930's in eastern Germany between octoploid triticales and wheats. * This cross was more probably made with the variety Lee which is (Hope × Thatcher) and not (Hope × Timstein) (R. Johnson, personal communication). *Sources*: NIAB (1987, 1989); Zeller (1973); Mettin *et al.* (1973); G. Zimmermann (personal communication).

of each track was calculated. The background level from an unhybridized track was subtracted from the level of each track, and relative amounts of signal calculated.

In situ *hybridization*

In situ hybridization followed the techniques of Schwarzacher *et al.* (1989) and Leitch *et al.* (1990) with various modifications. Spread preparations of chromosomes were made from seedling root tips of wheat varieties carrying a 1B/1R translocation after a 24 h treatment with ice water or 0·05 per cent colchicine at 4°C to accumulate and synchronize metaphases. Total genomic DNA (5–10 μg/ml) from rye was mechanically sheared to 10–12 kb and labelled with biotin-14-dATP or biotin-11-dUTP by nick translation. Autoclaved DNA from tetraploid ($2n = 4x = 28$) durum wheat (100–200 base pairs long; used as the block) and the

labelled DNA were then added to the hybridization mixture of 50–60 per cent formamide, 10 per cent dextran sulphate and 0·1–0.5 per cent SDS in 2×SSC and placed over the root tip preparation on a slide. Block DNA was used at 10 to 30 times the probe concentration. Probe, block and root-tip chromosome DNA were then denatured before hybridization overnight at 37°C. Washing was carried out in 50 per cent formamide in 2SSC at 40–42°C (estimated 85 per cent stringency). The sites of hybridization of biotinylated probe were detected using avidin linked to Texas red, which fluoresces red when excited with green light. Chromosomes were simultaneously stained with DAPI (4′,6-diamidino-2-phenylindole) which fluoresces blue when excited with UV light.

RESULTS

Southern hybridization with total genomic DNA

Fig. 2 shows a luminograph of *Dra*1 digested genomic DNA after probing with total genomic DNA from rye (10 ngml^{-1}). The rye track showed the strongest hybridization signal. Amounts of hybridization in other tracks were measured as a proportion of the hybridization to this track (100 per cent). Triticale showed 55 per cent of the rye signal, while the wheats containing the 1RS chromosome arm showed 14 per cent (*cv.* Glennson) and 20 per cent (*cv.* Beaver) of the rye signal. All the tracks carrying the rye chromosome segment showed strong hybridization in the high molecular weight region. The remaining two wheats, carrying no rye chromatin (*cv.* Chinese Spring hexaploid wheat and the diploid wheat *T. monococcum*), showed only 6 per cent of the hybridization to rye, with little detectable hybridization to fragments larger than 9kb.

Fig. 3 shows the same membrane as fig. 2 probed with the rDNA clone, pTa71. The hexaploid and diploid wheats, and triticale tracks have a labelled restriction fragment of about 9 kb. The tracks from wheat genotypes carrying the short arm from rye chromosome 1R, triticale and rye have two labelled restriction fragments of about 4 and 4·5 kb.

In situ *hybridization*

Fig. 4(a) shows a complete DAPI-stained metaphase from the hexaploid wheat variety Beaver which carries the 1B/1R chromosome translocation. Sites of hybridization of the labelled genomic DNA from rye were revealed by Texas red fluorescence (fig. 4(b)). The two chromosome arms of rye

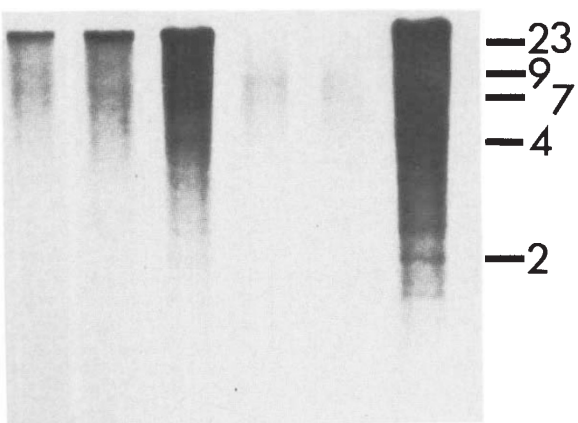


Figure 2 A luminograph showing sites of hybridization of labelled total genomic rye DNA to a Southern membrane of *Dra*1 digested genomic DNA from triticale, rye, three varieties of hexaploid wheat and a diploid wheat. The four tracks with the strongest hybridization signal include chromatin of rye origin, while the two weakly hybridized tracks (4 and 5 from left) do not include chromatin of rye origin. 10 min exposure. Tracks, left to right, *T. aestivum* (wheat) *cv.* Glennson; *T. aestivum cv.* Beaver; triticale *cv.* Lasko; *T. aestivum cv.* Chinese Spring; *T. moncoccum*; *S. cereale* (rye) *cv.* Petkus Spring; Lambda *Hin*dIII size markers (in kb).

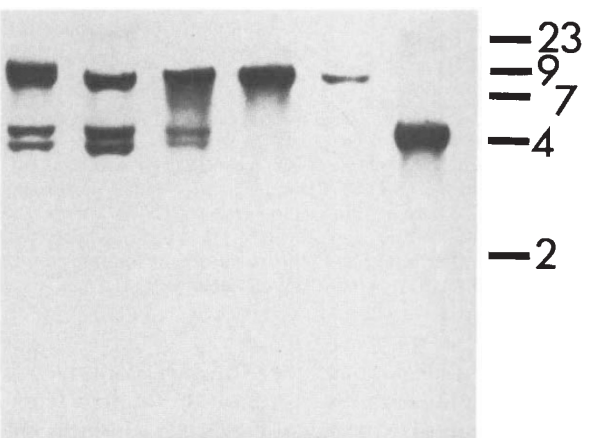


Figure 3 A luminograph of the same membrane as fig. 2 after hybridization of the rDNA clone pTa71. The hexaploid and diploid wheat tracks and the triticale track showed a restriction fragment of about 9 kb, while the rye, triticale, and wheats carrying a 1B/1R translocation, have two other bands about 4 and 4·5 kb. ECL detection of Southern hybridization; Tracks as fig. 2; 5 min exposure.

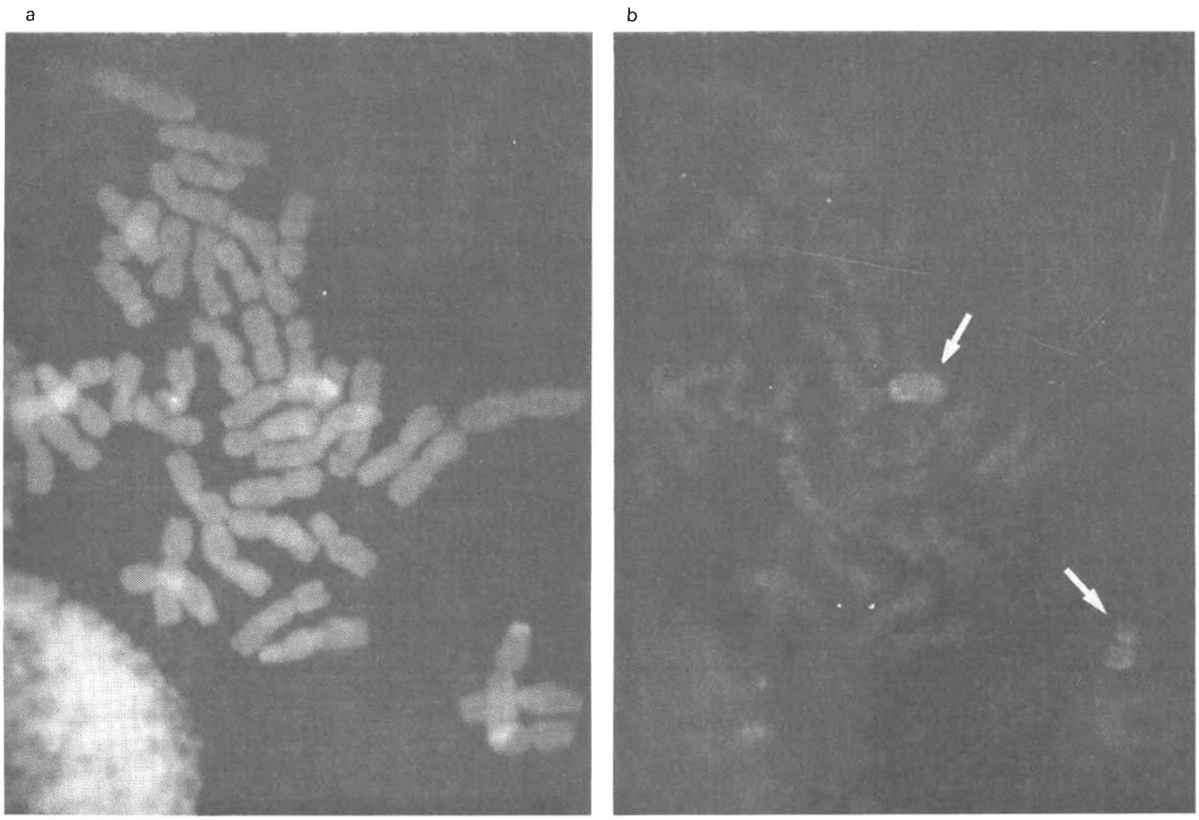


Figure 4 A root tip metaphase from the hexaploid ($2n = 6x = 42$) wheat variety Beaver seen (a) after DAPI staining for DNA and (b) after blocked genomic *in situ* hybridization using biotinylated total genomic DNA from rye as a probe, and a fluorescence detection system. The variety carries a translocation between chromosome 1B and the short arm of rye chromosome 1R, which is seen after *in situ* hybridization as the two brightly fluorescing chromosome arms (arrows). Magnification ×1500.

origin fluoresced brightly, while other chromosome arms showed little fluorescence. A dark gap marked the secondary constrictions (NOR) in the otherwise uniformly fluorescing rye arms. Under DAPI fluorescence, the terminal heterochromatic region on the 1RS arm was visible.

Fig. 5 shows individual chromosomes with the 1B/1R translocation from metaphases of the wheat varieties Custom, Haven, Tara and Kronjuwel. The sites of rye probe hybridization are shown by Texas red fluorescence in fig. 5(a), and the whole chromosomes are shown by DAPI fluorescence in fig. 5(b).

At interphase and prophase all the chromatin shows DAPI fluorescence, but no individual chromosome arms could be distinguished (fig. 6(a), (c)). After genomic *in situ* hybridization the 1RS arm could be identified by Texas red fluorescence (fig. 6(b), (d)). At interphase (fig. 6(b)) the rye chromosome segments remained discrete, as two strands with alternating high and low fluorescence intensities. At prophase the rye translocation chromosomes showed helical folding (fig. 6(d)), although no such folding pattern could be seen at metaphase (fig. 4(b)) or interphase (fig. 6(b)).

Similar hybridization to that shown in figs. 4(b), 5(a), 6(b) and 6(d) occurred in about two-thirds of the nuclei and chromosomes on every slide. The remainder were obscured by cytoplasm and cellular debris or were distorted, scratched or otherwise damaged during the process of *in situ* hybridization. This is expected for any cytological technique involving many steps.

DISCUSSION

Genomic probing of Southern transfers

Size separated restriction fragment digests of the various genomic DNAs were probed with labelled total genomic rye DNA. The tracks of DNA including rye genomes or rye chromosome arms showed much stronger hybridization than the tracks from

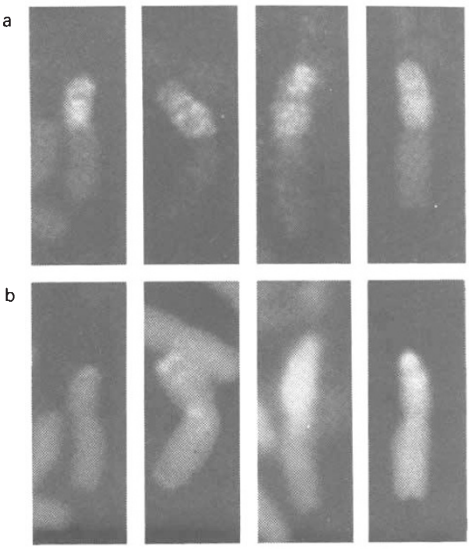


Figure 5 Single 1B/1R translocation chromosomes from metaphases of the varieties (left to right) Custom, Haven, Kronjuwel and Tara. (a) Following detection of the sites of hybridization with labelled genomic rye DNA. (b) DAPI fluorescence; the terminal end of the rye chromosome arm shows a heterochromatic, brightly staining, region in Custom, Haven and Tara. In all four varieties, the rye translocation has occurred at or very close to the centromere. Magnification ×2100.

wheat species without the 1RS arm (fig. 2). The difference was not accounted for by restriction fragments from the rDNA locus, since no major bands are in common between the two probings of the membrane (figs 2, 3), and much of the probed DNA of rye origin is cut infrequently by *Dra*1 (fig. 2). Schwarzacher *et al.* (1989) have shown that *Hordeum* and *Secale* can be distinguished using genomic probes in dot-blot filter hybridizations. The present results extend this work to show that total genomic DNA can be used to detect the presence of single chromosome arms in species which are evolutionarily close and share 78 per cent of DNA sequences (Flavell *et al.*, 1977; 1981).

1RS chromosome arms detected by in situ *hybridization in a wheat background*

The labelled total genomic rye probe hybridized strongly to the rye chromosome arms in the wheat metaphase cell spreads (figs. 4 and 5). No other chromosome arms showed such strong hybridization in any of the varieties investigated. The specificity of probing was increased by blocking DNA because the wheat blocking DNA cross-hybridized with sequences common to both the wheat and rye genome. In the present work, blocking DNA was used at 10–30 times the probe concentration (Heslop-Harrison *et al.*, 1988), while Le *et al.*, (1989) used equal amounts of probe and blocking DNA. On Southern hybridizations, Anamathawat-Jónsson *et al.* (1990) used up to 500-fold concentrations of blocking DNA. The block presumably hybridizes to the probe in solution and to sequences on the chromosomes which prevents subsequent binding of labelled probe. The effect of blocking may be enhanced by steric hindrance to probe hybridization after blocking DNA has hybridized to adjacent DNA sequences. The use of high ratios of block to probe improved the specificity of hybridization, but may also increase the background signal on chromosome spread preparations.

The pedigree of the plants (fig. 1) shows that the lines analysed arose from two distinct crosses between wheat and rye (Zeller, 1973 and G. Zimmermann, personal communication). The variety Kavkaz (analysed by Le *et al.*, 1989) probably includes the same rye segment as Riebesel 47/51 (see fig. 1; Zeller, 1973; Zeller and Sastrosumarjo, 1972). In all the wheat varieties carrying a 1B/1R translocation which have been examined, the translocation is at, or very close to, the centromere of the translocated chromosome (figs 4 and 5; Le *et al.*, 1989; Lapitan *et al.*, 1986, in variety Bobwhite). Thus, there is apparently no variation in the size of the translocated arm which would give a different combination of wheat and rye genes in the variety. The absence of the *Ph*1 (homoeologous pairing repression) gene would be required to generate such variability.

The sub-telomeric heterochromatin of the rye chromosome segment was visible under DAPI fluorescence as a bright band (fig. 5), although no increased hybridization of the probe was evident. Indeed, the strength of hybridization was uniform along the 1RS chromosome arm. The 1RS arm has several families of repeated sequences including the sub-telomeric repeat sequences, many of which have been cloned and characterised (Bedbrook *et al.*, 1980); the tandem repeats of rDNA (Gerlach and Bedbrook, 1979); and interspersed repeated sequences. It is perhaps surprising that no differentiation between these regions (except for a gap at the NOR, which was also visible in DAPI fluorescence) was detected by differential strengths of hybridization. The detection of hybridization may not be sensitive enough to reveal changes in repetitive DNA composition, as the signal may be saturated along the full length of the chromosome arm. The absolute amount of probe hybridization

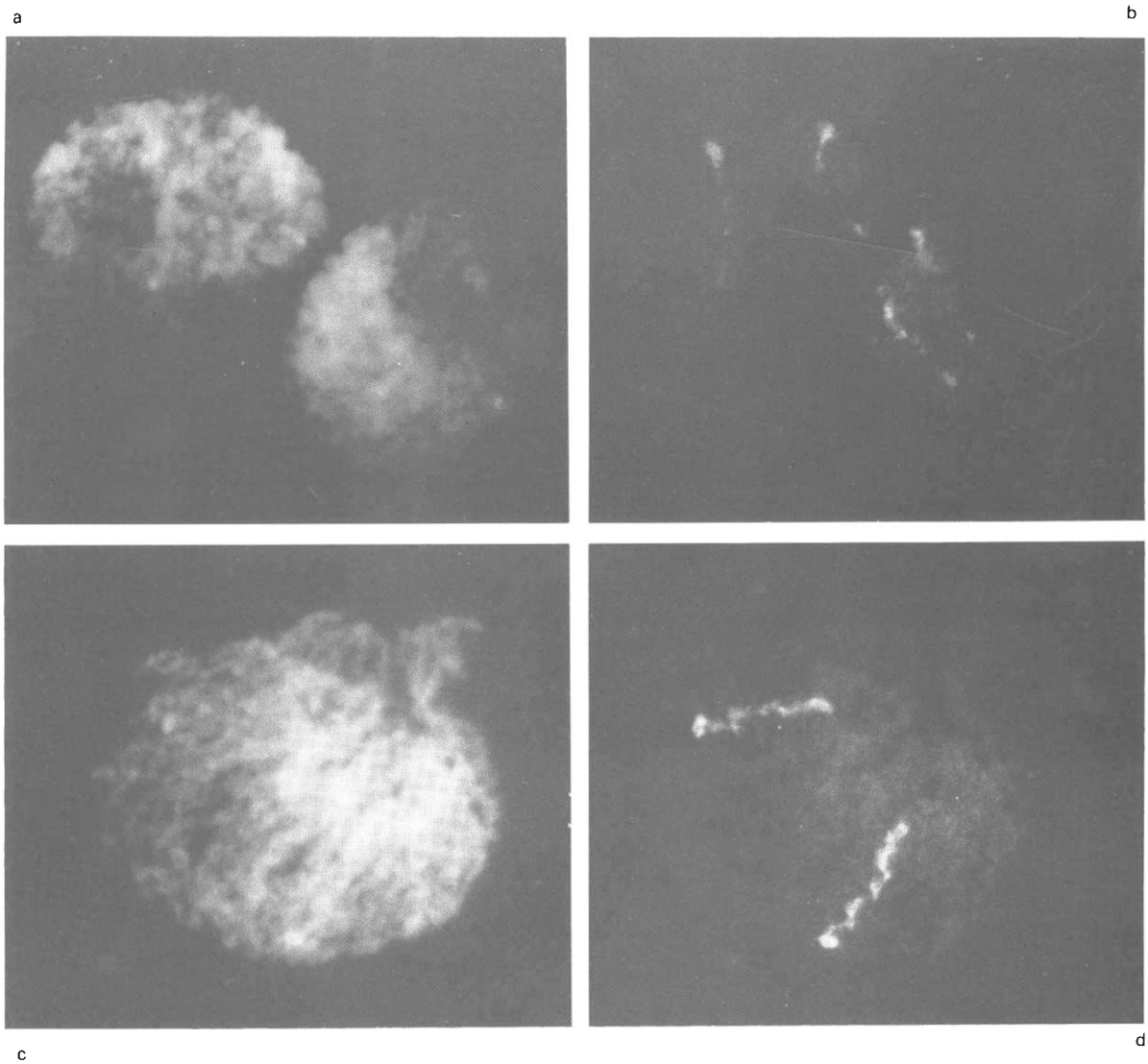


Figure 6 Root tip chromosome spreads of the wheat variety Beaver seen (a), (c) after DAPI staining for DNA and (b), (d) after blocked genomic *in situ* hybridization using biotinylated total genomic DNA from rye as a probe and a fluorescence detection system. The 1B/1R translocation is seen in both interphase (b) and prophase (d) as brightly fluorescing chromosome arms. Magnification ×1500

to any region of the chromosome may be limited although then the specificity of the genomic probe would be more surprising given the many sequences in common between wheat and rye (Flavell *et al.*, 1977; 1981).

The 1RS translocation was visible as a discrete entity throughout the cell cycle. The hybridized segments in interphase cells probably represent highly repeated condensed chromatin and the non-fluorescing regions of the translocation regions of decondensed or low copy sequences where signal strength was too low to be detected. During prophase the chromosomes condense and a strong helical folding pattern is seen in the translocated arm (fig. 6(d)). The pattern is similar to that previously reported in human metaphase cells (Boy de la Tour and Laemmli, 1988), although the chromatid with opposite helical handedness was not seen. The two chromatids of the arm were not resolved in interphase or prophase cell spreads suggesting that the chromatids tended to remain together.

Using human genomic DNA as a probe, Manuelidis (1985) has shown that individual

human chromosomes in human × hamster fusion-hybrid nuclei tend to lie in domains and do not intermix with the other chromosomes in the nucleus. In sexual wide hybrids between different cereal genera, Leitch *et al.* (1990) have shown that the two parental sets of chromosomes occupy separate domains many cell cycles after fertilization. The present work shows that the 1RS chromosome arm tends to remain in an isolated domain within the cereal nucleus.

CONCLUSIONS

The techniques using genomic probes are of potentially wider application for detecting and following alien chromosomes or chromosome segments through breeding programmes, by both *in situ* and Southern hybridization. Genomic probes may be particularly useful for examining alien introductions when genome-specific sequences have not been cloned. Finally, genomic probing has a unique potential to detect changes in the physical size of an alien chromosome segment.

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