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Structural Variation in the Heterochromatin of Rye Chromosomes in Triticales

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Summary. Although Giemsa C-banding techniques have been used extensively for assaying cereal heterochromatin, a more specific technique for analyzing cereal heterochromatin has been developed recently with the isolation of DNA sequences present in heterochromatin and their employment in in situ hybridization to cereal chromosomes. A number of triticales were examined for the occurrence of modified rye chromosomes using the in situ hybridization technique. With a heterogeneous sequence probe the amount of rye heterochromatin appears to be relatively constant in wheat backgrounds but when a specific sequence probe was employed variation was observed. Whether this variation reflects polymorphism in rye or whether it is a result of adaption of the rye genome to coexistence with the wheat genome in triticales is discussed. – The triticale Rosner was examined in detail and it was established that the rye chromosome 2R had been replaced by the wheat chromosome 2D.

Key words: Rye – Heterochromatin – Variation – Triticales

Introduction

The development of triticale (× *Triticosecale* Wittmack) (for review see Gustafson 1976, 1982) and in particular identification of rye (*Secale cereale* L.) chromosomes present (Darvey and Gustafson 1975; Merker 1975) has raised the issue of the stability of rye chromatin in wheat backgrounds. Rye chromosomes can be substituted by D-genome chromosomes (Gustafson and Zillinsky 1973, 1978; Merker 1975; Gustafson et al. 1980), and wheat-rye translocations have been observed when rye chromosomes were transferred into commercial wheat varieties (Mettin et al. 1973; Shepherd 1973; Zeller 1973; Blüthner and Mettin 1977; May and Appels 1980). These modifications to the triticale chromosomes can result in the reduction of specific regions of rye chromatin which may be associated with aberrant endosperm development (Bennett 1977; Gustafson and Bennett 1982; Bennett and Gustafson 1982) or with seedling lethality (May and Appels 1980). Bennett et al. (1977) suggested that rye heterochromatin may be specifically implicated and that its elimination reduces these deleterious effects. While in several instances elimination of rye heterochromatin was postulated to explain experimental observations (Merker 1976; Roupakias and Kaltsikes 1977) recent data has shown that, qualitatively, heterochromatin DNA sequences are stable in wheat (Bedbrook et al. 1980; Appels et al. 1981). We therefore examined twenty four triticales to determine if major structural changes in rye chromosomes could be detected.

Materials and Methods

Triticales

Twenty triticales from an Australian interstate yield nursery conducted by the Waite Agricultural Institute, Glen Osmond, South Australia (C. Driscoll, M. McLean, D. Jewel, manuscript in preparation) were examined. In addition the triticales "Rosner", "Siskiyou", 6A530 and their respective F1 hybrids (obtained from the University of Manitoba) and the triticale 6TA876 (from the Australian wheat collection) were also examined. Further details of the triticales are given where relevant in the text.

Chromosome Analyses

The procedures for collecting root-tip metaphase chromosomes and their treatment for visualizing C-bands have been described (Bennett et al. 1977). The in situ hybridization analyses used probes for detecting rye and wheat repeated DNA sequences (Appels et al. 1978; May and Appels 1980; Appels et al. 1981).

Staining of autoradiograms with Giemsa was found to be more reliable using the following procedure. Developed slides were stained in a 10% Giemsa solution (v/v) containing 0.01 M sodium phosphate pH 6.8 for approximately

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60 min after which excess stain was removed with tap water. Slides were then air dried and generally left for several hours before destaining. To destain, a layer of water was deposited on the slide followed by brief immersion in absolute ethanol and then washing in water. This procedure was repeated until the desired level of destaining was attained; the advantages of the protocol are that the emulsion is cleared of stain before chromosomal material destains and that it minimizes the chance of destaining the chromosomal material too much. Karyotypes were usually constructed from complete metaphase spreads. Confirmatory karyotypes were also constructed from incomplete metaphase spreads where no more than one chromosome was absent. Pairing of wheat chromosomes in the karyotypes was usually on the basis of maximum similarity in morphology since the radioactive probes used were mostly specific for rye chromosomes.

Results and Discussion

Probes for the Detection of Cereal Heterochromatin

The diagrammatic karyotypes of rye and wheat chromosomes shown in Fig. 1 summarize the various probes, and their chromosomal distribution utilized in this paper.

Identification of Rye Chromosomes Present in Rosner

The triticale Rosner was of particular interest in this study since it had been suggested that chromosome 2R was modified and no telomeric heterochromatin re-

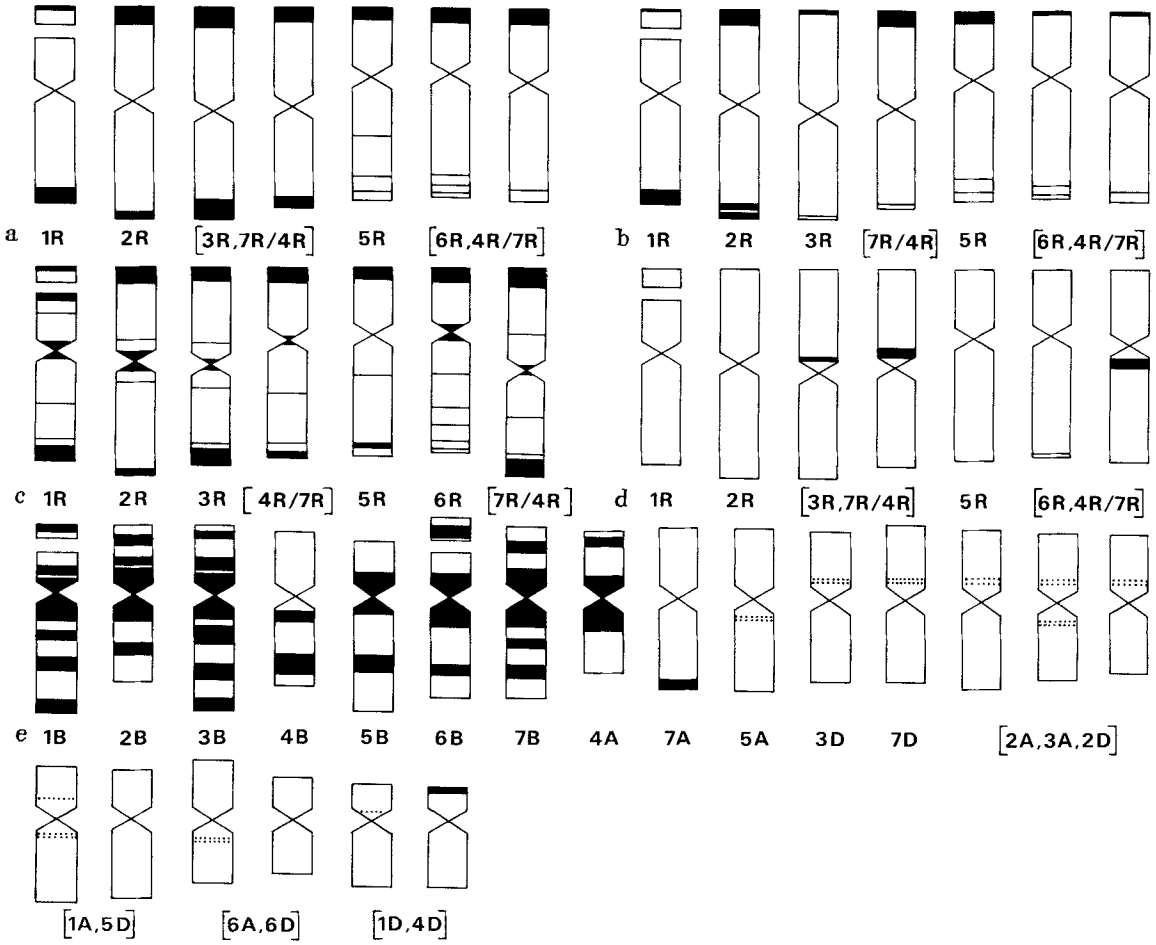

Fig. 1a–e. Diagrammatic maps of the heterochromatic regions of rye and wheat chromosomes. **a** Rye chromosomes (from *Secale cereale* cv. Imperial) showing the distribution of the major sequences present in a heterogeneous probe isolated as a rapidly renaturing (Cot 0.01 – 0.02) fraction of DNA. ^{3}H-cRNA synthesized from the DNA is hybridized to chromosomes in situ and autoradiography used to determine the distribution of the sequences (Appels et al. 1978). **b** Rye chromosmes (from *Secale cereale* cv. Imperial) showing the chromosomal distribution of the major sequence present in a rapidly renaturing fraction of DNA. The sequence was purified using cloning techniques (Appels et al. 1981) and is carried in a plasmid pSc7235. **c** Rye chromosomes stained by the C-banding technique, based on descriptions by Bennett et al. (1977). **d** Rye chomosomes (from *Secale cereale* cv. Imperial) showing the chromosomal distribution of a repeated sequence which is related to the simple *Drosophila melanogaster* satellite DNA sequence ... AGAAG/TCTTC ... (Appels et al. 1978). **e** Wheat chromosomes (from *Triticum aestivum* cv. Chinese Spring) showing the chromosomal distribution of the repeated DNA sequences assayed in **d** (May and Appels 1980; Dennis et al. 1980). Chromosomes 4R/7R and 7R/4R are also referred to as CR and DR respectively. At a rye cytogenetics workshop in Wageningen, March, 1982 (organized by J. Sybenga) it was agreed to refer to these chromosomes as 4R and 7R, respectively

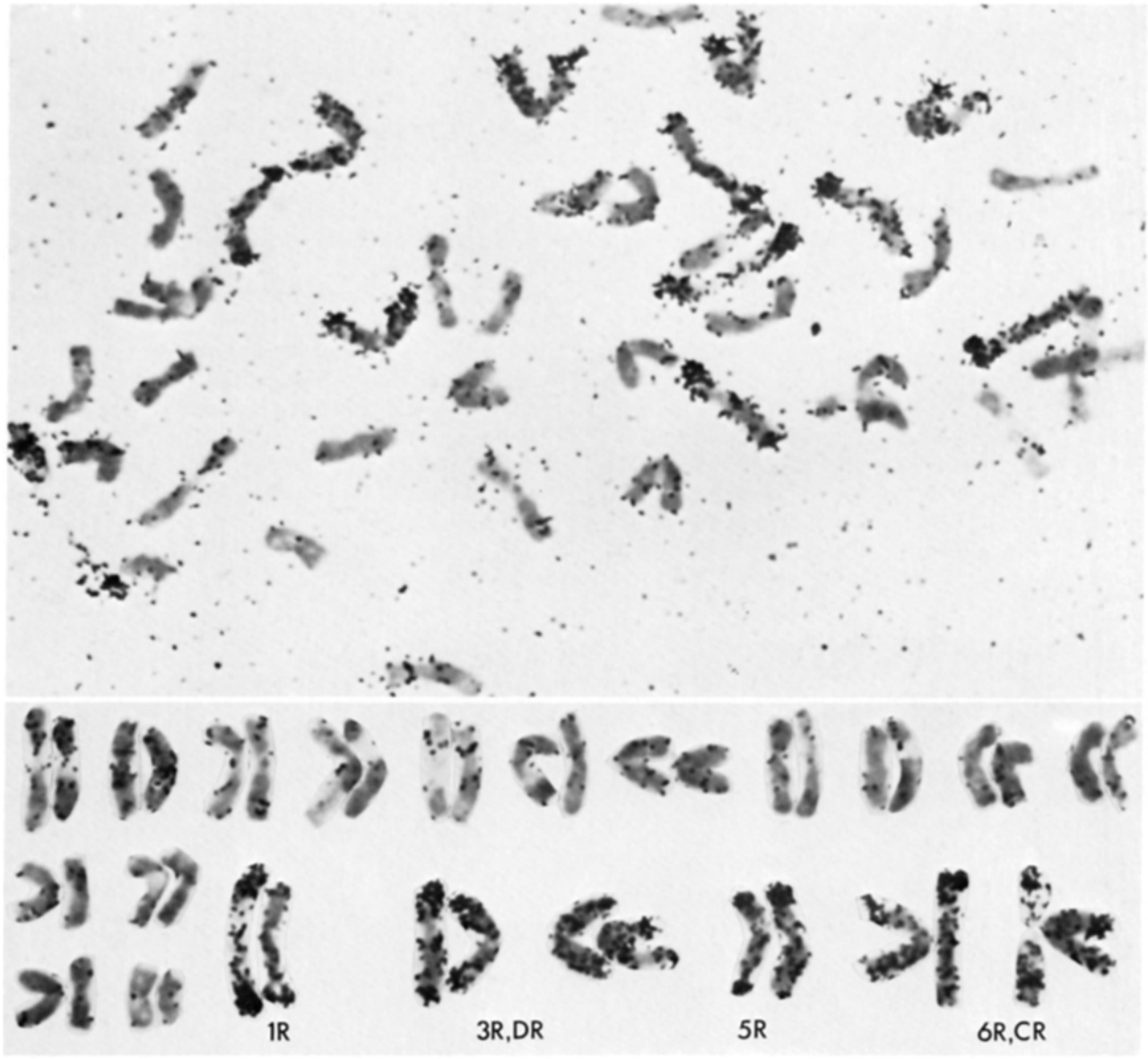

Fig. 2. The chromosomes of Rosner showing the distribution of DNA sequences present in a heterogeneous probe isolated as a rapidly renaturing fraction of rye DNA. (Fig. 1a for further details of the probe)

mained (P. J. Kaltsikes pers. comm.; for a critical discussion see Gustafson 1976). The heterogeneous probe for rye heterochromatin (Fig. 1a) was useful because, in addition to detecting the major regions of telomeric heterochromatin, some sequences present in the probe were distributed throughout the rye chromosomes in higher density than on the wheat chromosomes (Fig. 2). This allowed the detection of rye chromosomes lacking the terminal heterochromatic regions. Six pairs of rye chromosomes could be readily identified in Rosner, and these did not include chromosome 2R (Fig. 2), consistent with earlier observations by Merker (1975). Two further pairs of chromosomes were evident wich showed above average labelling (first two pairs in karyotype shown, Fig. 2). However, these chromosomes are often seen among wheat chromosomes labelled with the probe (Fig. 3 in May and Appels 1980) and rather than being modified rye chromosomes are wheat chromosomes containing sequences showing cross-hybridization with the rye probe. A further examination of Rosner was undertaken by crossing it to 6A530 and Siskiyou, which are known to contain seven pairs of banded rye chromosomes; Siskiyou contains a 2R with a large interstitial band, using C-banding, in the middle of the long arm (Gustafson, unpubl. data).

A total of 184 PMC's from 9 F_1 plants of the Rosner/6A530 cross were analyzed and not one PMC contained 21 bivalents. Only 10.32% of the cells con-

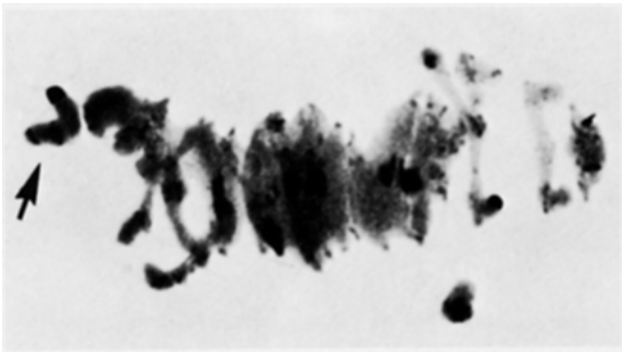

Fig. 3. Giemsa banded pollen mother cell from a Rosner/Siskiyou F_1 plant. The arrow indicates the 2R chromosome present as a univalent

tained 20 bivalents (average number of bivalents per PMC = 17.16) and 27 cells (14.67%) contained multivalents. The C-banding technique was used to analyze the PMC's from 3 plants and indicated that 6 chromosomes in Rosner paired with 6 of the 7 normally banded rye chromosomes in 6A530 (data not shown). The more easily identifiable 2R in Siskiyou allowed an unambiguous analysis of PMC's from the Rosner/Siskiyou F1 hybrid. The PMC's were subjected to the C-banding technique and 72 metaphase I cells were examined. In all cells the rye chromosome 2R from Siskiyou was present as a univalent (Fig. 3), consistent with the meiotic analysis of the Rosner/6A530 PMC's. Further, analysis of the cross Rosner/Holdfast-King II $2R^{resis}$ (containing the telocentric chromosome 2RL) established that no heteromorphic bivalent was present (50 PMC's examined).

The root tip chromosome karyotype, after in situ hybridization with the probe for rye repeated DNA sequences, clearly indicated only one rye chromosome 2R was present in the F1 progeny of the Rosner/Siskiyou and Rosner/6A530 crosses (Fig. 4). Since rye chromosome 2R was readily identifiable in Siskiyou and 6A530 and not in Rosner (Fig. 2), the rye chromosome 2R in the F1's was derived from Siskiyou and

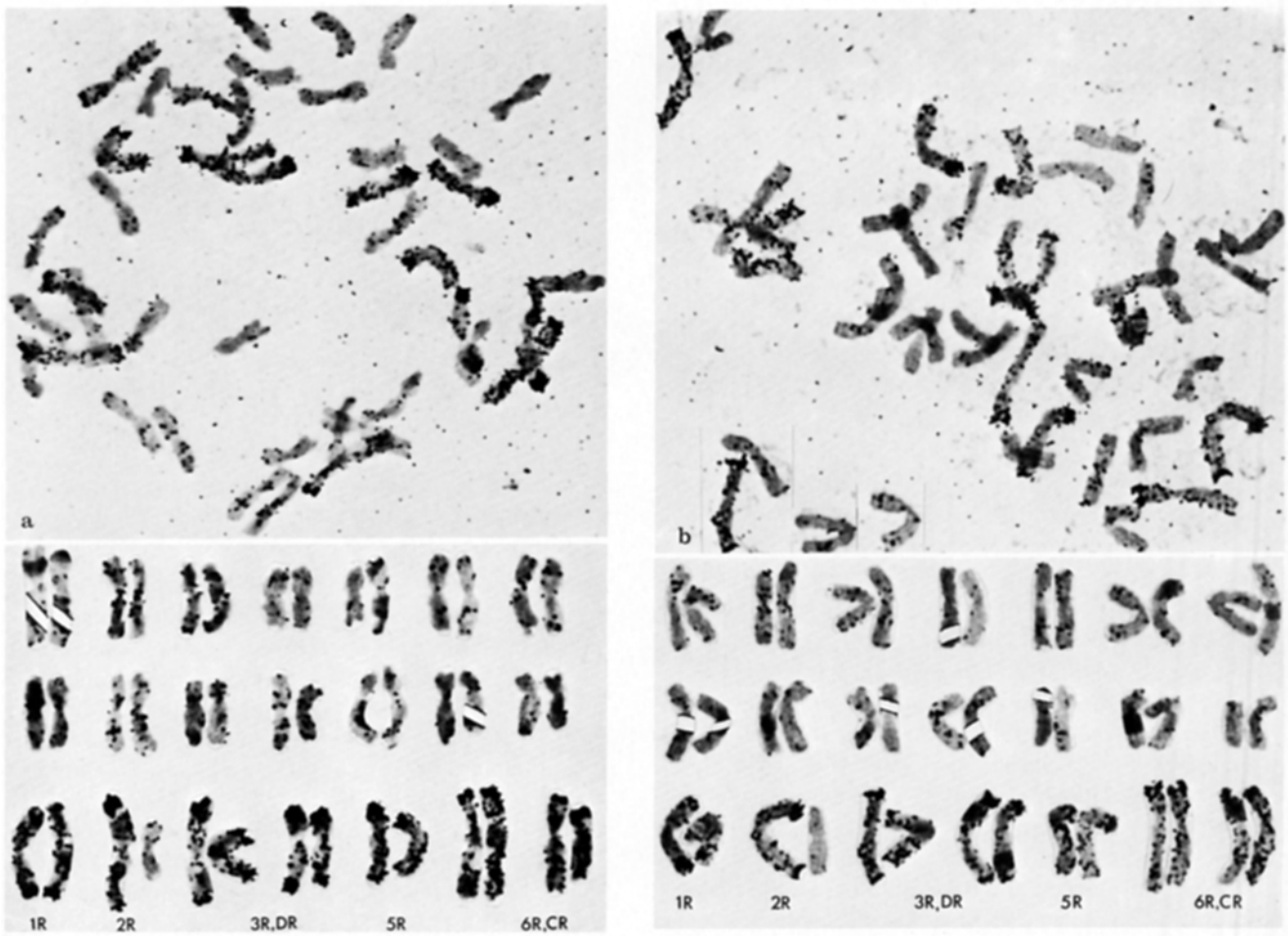

Fig. 4a and b. The chromosomes of the F_1 progeny of Rosner × Siskiyou (**a**) and Rosner × 6A530 (**b**) crosses analyzed as described in Fig. 2

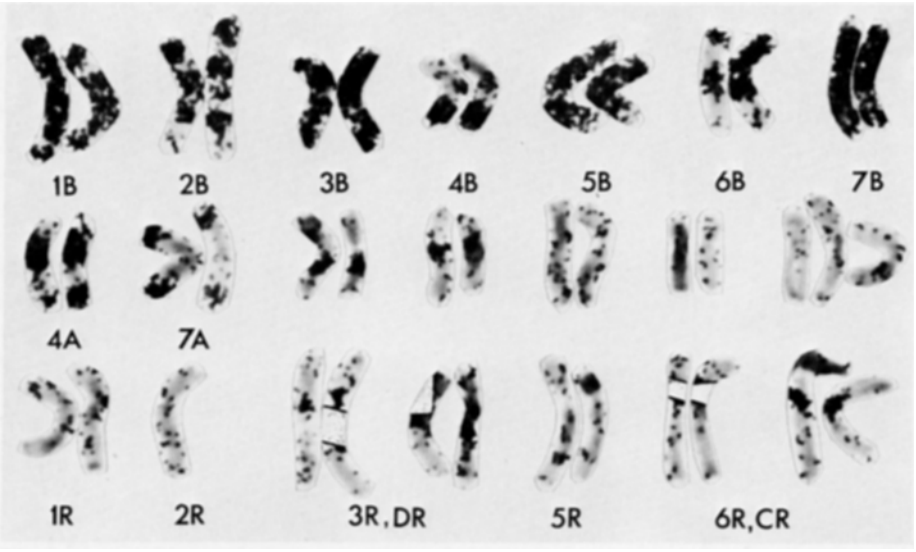

Fig. 5. The chromosomes of a Rosner×6A530 plant showing the in situ distribution of sequences related to the repetitive sequence . . . AGAAG/TCTTC . . . (Fig. 1d, e for further details of the probe)

from 6A530, respectively. Examination failed to find any modified rye chromosome 2R in Rosner; such a modified chromosome would necessarily be present without a partner in the karyotypes shown in Fig. 4.

The absence of 2R from Rosner suggested that it had been substituted by a wheat chromosome. Karyotype analysis of chromosomes from the Rosner/6A530 cross using a probe for detecting wheat heterochromatic sequences (Fig. 5) did not allow unequivocal identification of the wheat chromosome involved; the analysis did show that extra 2B chromosomes were not present. Both 2A and 2B of wheat are unlikely to be present in a tetrasomic state in Rosner per se since high frequencies of trivalents and quadrivalents are not observed. Chromosome 2D is the most likely chromosome to replace 2R, and this was confirmed by crossing Rosner to a ditelosomic 2DS line of wheat; the 2D telosome was always paired (2 plants, 100 cells examined). Thus Rosner is analogous to the triticale "Armadillo" in having 2R replaced by 2D (Gustafson and Zillinsky 1973).

The Rye Chromosomes Present in Other Triticales

All the triticales examined in this study showed no major reductions of rye heterochromatin (compared with Imperial rye chromosomes) as assayed by the heterogeneous rye probe summarized in Figure 1a (Figure 4 shows this for Rosner, Siskiyou, and 6A530). Furthermore no rye-wheat translocations were evident. Against this background of apparent uniformity of rye chromosomes in the triticales examined with the heterogeneous probe, it was surprising to find a great deal of variation when rye chromosomes were assayed with a probe which had been purified, by cloning, from the heterogeneous rye heterochromatic sequences. The

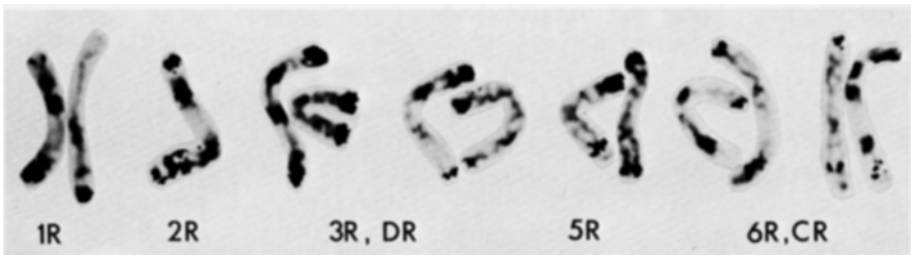

Fig. 6. The rye chromosomes of a Rosner×Siskiyou F_1 plant showing the distribution of the cloned heterochromatic DNA sequence carried in the plasmid pSc7235. See Fig. 1b for further details of the probe. Note the polymorphism of grain number in the lower heterochromatic block in the 3R chromosome

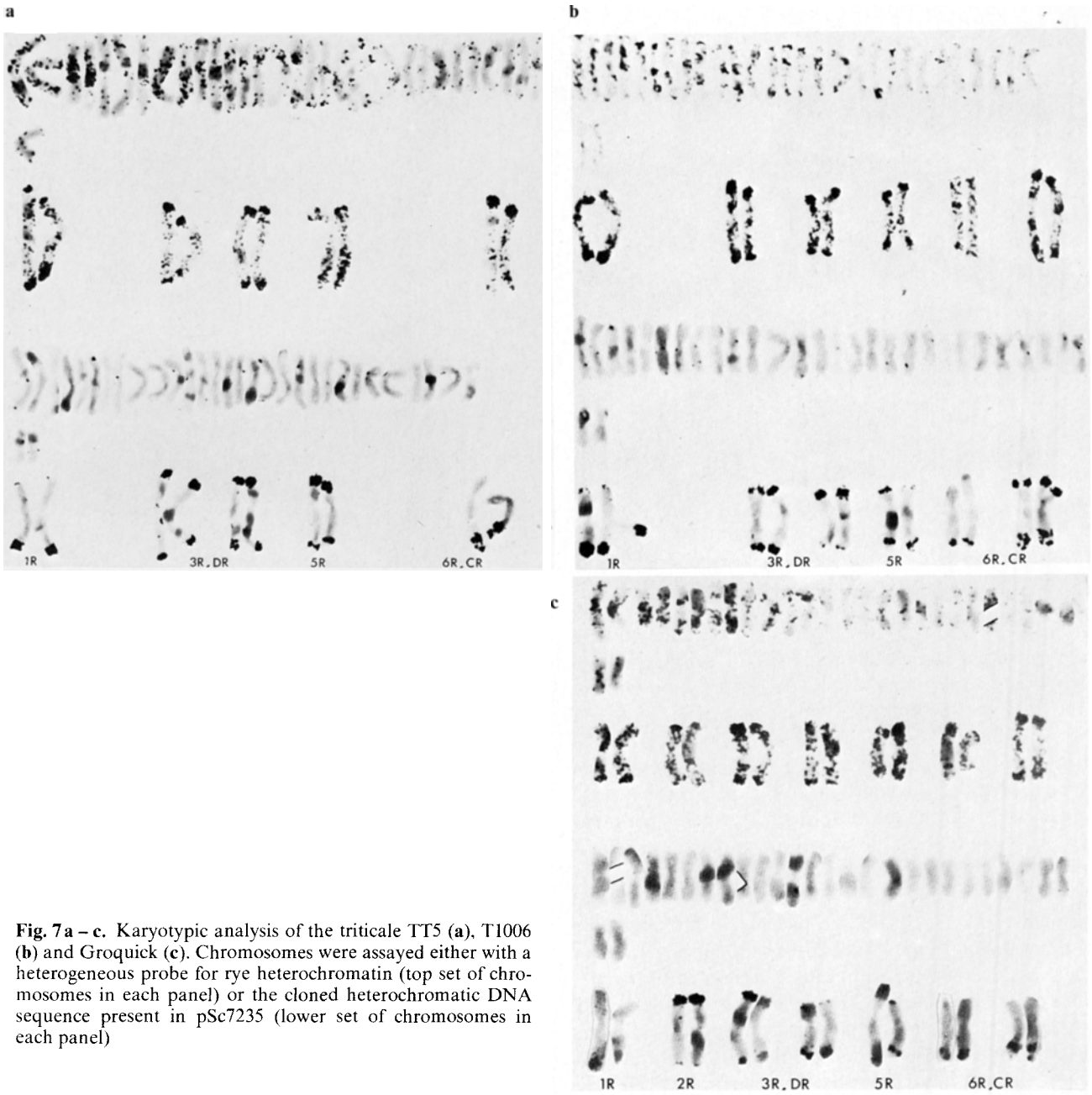

Fig. 7 a – c. Karyotypic analysis of the triticale TT5 (**a**), T1006 (**b**) and Groquick (**c**). Chromosomes were assayed either with a heterogeneous probe for rye heterochromatin (top set of chromosomes in each panel) or the cloned heterochromatic DNA sequence present in pSc7235 (lower set of chromosomes in each panel)

chromosomal distribution of this cloned probe in *Secale cereale* cv. "Imperial" is summarized in Fig. 1 b.

The karyotype of the Rosner × Siskiyou F_1 illustrated some of the variation observed using the cloned probe (Fig. 6). The studies carried out on the 20 triticale varieties assessed in Australia-wide trials provided further information on the nature of this variation. With the cloned probe the chromosome tentatively assigned as being the 4R/7R (CR) chromosome of the triticale T1006 has a characteristic pair of labelled regions on the long arm and heavy labelling on the telomeric region of the short arm. In contrast, triticales TT5 and Groquick carried a chromosome which has a similar labelling on the long arm but no label on the short arm. However, using the heterogeneous probe for rye heterochromatin it became clear that the short arm of the presumptive 4R/7R (CR) chromosome in TT5 and Groquick still contained some heterochromatic DNA sequences (Fig. 7). In addition, variation was observed with the presumptive 3R and 7R/4R (DR) chromosomes in lines T1006 and TT5; the difference observed appeared similar to the polymorphism for 3R, with respect to the content of the cloned probe, observed between different rye cultivars (Appels et al.

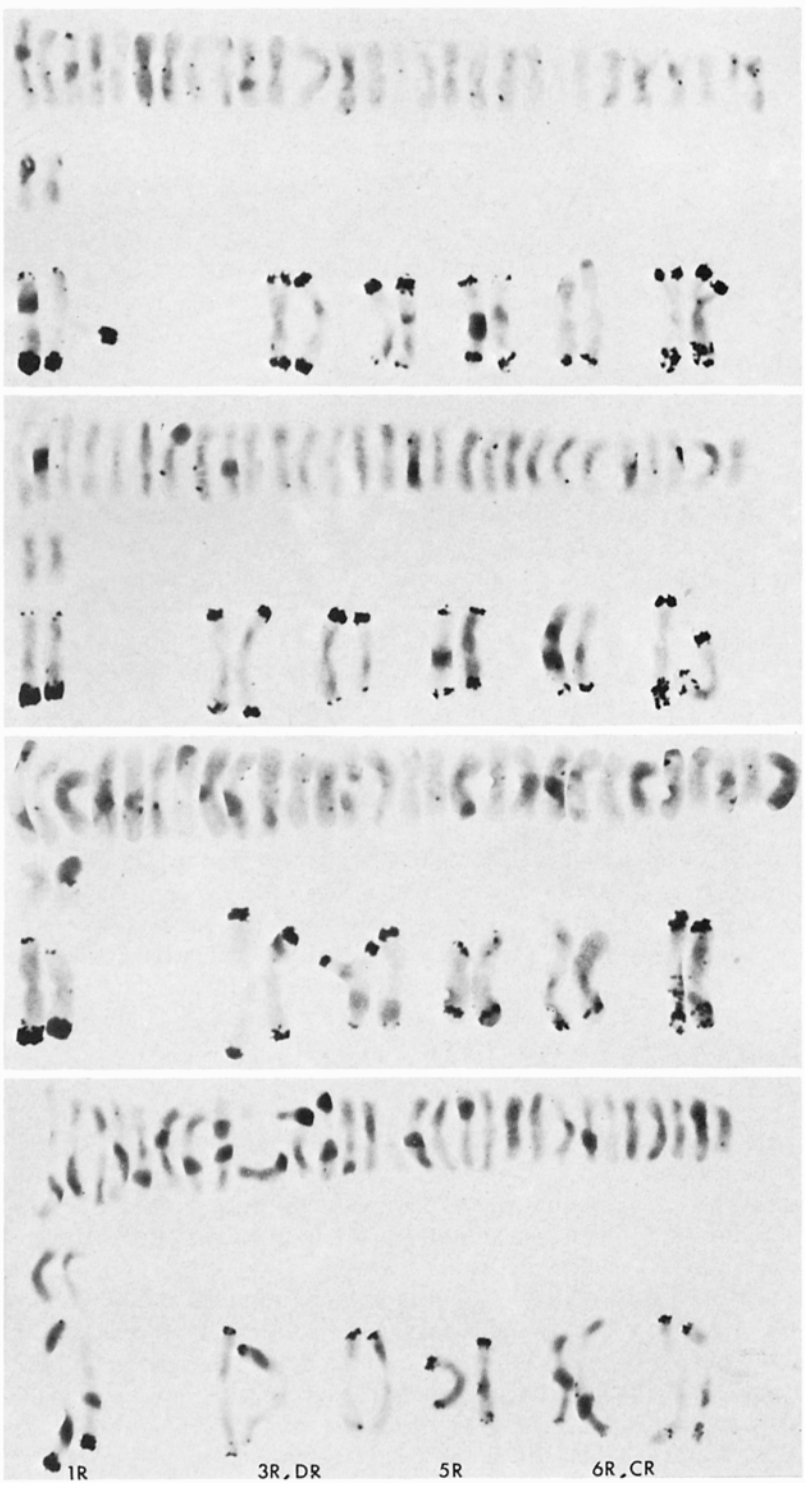

Fig. 8. Karyotypic analysis of the triticales Tyalla, T1245, T1006 and Mapache after hybridization to detect the cloned heterochromatic DNA sequence present in pSc7235. The pedigrees on the right-hand side indicate the CIMMYT history of the material. The numbers and letters indicate the specific plant from which the seed came in each generation (numbers) and the location (M = Mexico City; N = Navajoa, Sonora; Y = Yaqui Valley (Obregon, Sonora)). Arm "S" is the CIMMYT triticale Armadillo selection, and Maya II is an octoploid triticale with the parentage of Inia (wheat) × rye (unknown)

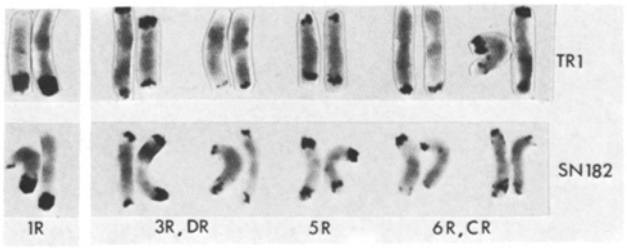

Fig. 9. Comparison of the rye chromosomes in the triticales SN182 and TR1 after in situ hybridization with a probe to detect the distribution of pSc7235 sequences

1981). It can be concluded that the relative composition of certain heterochromatic DNA sequences in the telomeric regions of some rye chromosomes varies from line to line.

The changes in heterochromatic DNA sequence composition observed when the distribution of the cloned probe is compared to the heterogeneous probe can be accounted for on the basis of the molecular composition of telomeric heterochromatin. Several different sequences are known to be located within the heterochromatic regions (Bedbrook et al. 1980; Appels et al. 1981), and thus a heterogeneous probe would show a positive hybridisation pattern even if, for example, two out of four sequences were missing from the region under examination. In contrast the cloned probe is specific enough so that if its homologous sequence is absent, no hybridisation is observed.

The rye chromosome variation associated with one triticale did not agree with is presumptive pedigree. The CIMMYT cross Maya II×Arm "S" (X2802) gave rise to four triticales in the group of 20 examined (Fig. 8). The rye chromosomes in Tyalla, T1245 and T1006 were identical whereas the chromosomes assigned as 5R and 4R/7R (CR) in Mapache were clearly different from those in the other three triticales. This suggested that the structure of the rye chromosomes in these triticales may have altered after their introduction into wheat. However, when the pedigrees are examined in detail, it becomes clear that Mapache was grown separate from the others in the F2 and subsequent generations (Fig. 8). Tyalla, T1245 and T1006, in contrast, were selected from the same 5th generation plant and only then differentiated with respect to the environments in which they were selected. It seems plausible that outcrossing of Mapache to another triticale during its selection could have led to its altered rye chromosome complement. Consistent with this observation was the fact that the TR1 triticale has the putative 4R/7R (CR) chromosome found in Mapache (i.e., predominant labelling of short arm) together with the 5R chromosome present in Tyalla (label on short arm approximates that of the sub-terminal band on the long arm). (Fig. 9). Alternatively, triticale SN182 had the putative 4R/7R (CR) chromosome found in Tyalla where the label on the short arm approximated that in the bands of the long arm together with the 5R chromosome seen in Mapache (label on short arm is 2–3 times that of the sub-terminal band on the long arm, Fig. 9). The differences between the rye chromosomes may have arisen after placement into a wheat background, however outcrossing between triticales could contribute to the various combinations of rye variants observed.

Conclusions

The rye chromosomes present in 24 triticales were examined in detail using the in situ hybridization of various radioactive probes (Fig. 1). The analysis of Rosner established that chromosome 2R was not present in any modified or translocated form and that it had been replaced by a wheat chromosome. We note that while the absence of 2R is common among the triticales examined, it is clearly not a prerequisite for a successful triticale since many varieties in the present study (namely Siskiyou, Groquick, Venus, DRIRA, 6A530, 6TA876) and from around the world contain seven pairs of rye chromosomes (see also Gustafson 1982; Lukaszewski and Apolinarska 1981). No translocations between wheat and rye chromosomes were found in any of the triticales examined. Variation among rye chromosomes for the content and composition of specific DNA sequences in the telomeric heterochromatic regions was readily found, and these variants could possibly determine whether C-banding techniques show modified rye chromosomes or not.

It seems likely, from the present study and the work of others (Weimark 1975; Lelley et al. 1978; Giraldez et al. 1979; Naranjo and Lacadena 1980; Miller et al. 1980; Appels et al. 1981), that heterochromatin variation among rye chromosomes prior to their introduction into triticales is a major source of variation of heterochromatin between triticale rye chromosomes. The levels of polymorphisms observed and particularly the variation in composition of DNA sequences within heterochromatin are of considerable interest from an evolutionary point of view. Many of the available parameters such as those from morphological studies (Bell 1965), nuclear DNA (Bendich and McCarthy 1970; Flavell et al. 1977) and chloroplast/mitochondrial DNA studies (Vedel et al. 1980) indicate that rye and wheat are closely related. However, the rye and wheat chromosomes have been differentiated in an almost absolute manner with respect to some of the DNA sequences in heterochromatin. Since the rye heterochromatic sequences analyzed here are difficult to detect in *Secale silvestre* (Bedbrook et al. 1980),

Aegilops species (Hutchinson et al. 1980) and *Hordeum* (Appels, unpubl. data) it seems possible that they are of relatively recent origin in the amplified form in which they are found in *S. cereale* chromosomes. The observed polymorphisms in rye heterochromatin may reflect the fact that rye chromosome structure is still evolving rapidly (Bennett et al. 1977) and that one particular set of heterochromatic sequences in combination with the rest of the genome has not had a sufficient advantage over other combinations to be fixed in the time available, and/or that its selective advantage varies under different conditions.

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