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A molecular linkage map of rye

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Abstract A genetic map of six chromosomes of rye, (all of the rye chromosomes except for 2R), was constructed using 77 RFLP and 12 RAPD markers. The map was developed using an F_2 population of 54 plants from a cross between two inbred lines. A rye genomic library was constructed as a source of clones for RFLP mapping. Comparisons were made between the rye map and other rye and wheat maps by including additional probes previously mapped in those species. These comparisons allowed (1) chromosome arm orientation to the linkage groups to be given, (2) the corroboration of several evolutionary translocations between rye chromosomes and homoeologous chromosomes of wheat; (3) an increase in the number of available markers for target regions of rye that show colinearity with wheat. Inconsistencies in the location of markers between the wheat and rye maps were mostly detected by multi-copy probes.

Key words Genetic map · RFLP · RAPD · *Secale cereale* · *Triticum aestivum*

Introduction

Rye (*Secale cereale* L.) is a diploid species (2n=2x=14) belonging to the Triticeae tribe of the *Gramineae* family. It shows a range of characteristics that make the study of its genetics of great interest. It is an important crop species grown over wide areas of Europe and North America. The close relationship between rye and wheat and the presence in the rye genome of genes for resistance to several rusts (see Plarre 1985, for a review) have made it a source of alien chromatin appropriate for transferral by homoeologous recombination with wheat. Further, attempts to combine the best characters of wheat and rye led to the production of triticale as a new commercial cereal crop.

Devos et al. (1993a) produced a rye genetic map containing nine biochemical markers and 147 restriction fragment length polymorphisms (RFLPs) detected by genomic and cDNA clones of wheat. Phillip et al. (1994) constructed a map containing 60 loci including 26 RFLPs detected by rye genomic probes, two random amplified polymorphic DNAs (RAPD) and 24 isozyme loci. Using recombinant wheat-rye lines, Rogowski et al. (1993) assigned RFLP markers to regions of chromosome 1R. Maps of chromosome 5R, including molecular markers and agronomically important genes (Plaschke et al. 1993), and of chromosomes 1R, 6R and 7R, integrating cytological and RFLP markers (Wanous and Gustafson 1995; Wanous et al. 1995) have also been produced. In spite of this progress the number of markers mapped in rye is fairly reduced as compared with the mapped in other members of the *Gramineae*.

The integration of the different DNA-based genome maps of a species that have been generated by using different sets of markers and different segregating populations is a goal in the production of progressively more detailed genetic maps. The use of a common set of markers in a single population would facilitate the comparison of different rye maps. Comparisons made between maps of chromosomes 1R, 5R and 7R have shown similarity in the order of most of the common markers, though some small chromosomal rearrangements have been detected (Devos et al. 1993a; Plaschke et al. 1993; Wanous and Gustafson 1995; Wanous et al. 1995). In addition, markers mapped in one species have been used to construct parallel maps in related plant species. In a comparison of rye and wheat, extensive rearrangements in rye relative to wheat were observed (Devos et al. 1993a). Evolutionary translocations involving chromosome arms 2RS, 3RL, 4RL, 6RL, 7RS and 7RL were deduced by RFLP analysis, confirming previous observations from homoeologous pairing of wheat and rye chromosomes (Naranjo et al. 1987; Naranjo and Fernández-Rueda 1991).

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In many cases genomic mapping is directed towards the production of a comprehensive genetic map which covers all chromosomes equally. It has been pointed out that DNA probes from a species may not readily identify markers located throughout the genome of a related species (Devos et al. 1993b; Xu et al. 1994). Therefore, it is advisable to include in a rye map probes derived from its own genome. In this paper a genetic map of six rye chromosomes is presented (all the chromosomes of rye except for 2R) that was produced by using DNA probes from several libraries including clones of rye genomic DNA. Although RAPD markers are probably of little use in comparing different rye maps, they seem to be appropriate for mapping chromosome regions restricted in their number of RFLP markers (Williams et al. 1993). RAPD markers were therefore included in this study.

The map obtained contains 89 markers, 12 of which were previously localized in other rye maps. Of the markers 48 were previously mapped in wheat. The aim of this investigation was to contribute to a better understanding of the rye genome by extending the number of markers mapped and therefore facilitating the construction of a more comprehensive consensus map.

Materials and methods

Plant material

Two rye inbred lines, E and R, kindly supplied by J. Orellana (ETSI Agrónomos, Universidad Politécnica, Madrid, Spain), and 54 F_2 plants from a cross between E and R were used for mapping. The *T. aestivum* cv 'Chinese Spring' – *S. cereale* cv 'Imperial' (Driscoll and Sears 1971) chromosome addition lines were used to determine the chromosomal locations of some RFLPs.

DNA isolation. Southern hybridization

DNA was prepared from young leaves of the parents and F_2 plants as described by Sharp et al. (1988). For wheat-rye addition lines, only plants that had been cytologically verified as containing the additional chromosome were used for DNA extraction. Total DNA samples (15 µg) were digested with *Dra*I, *Eco*RI, *Eco*RV, *Hin*dIII, *Xba*I or *Xho*I. DNA fragments were separated on 0.8% agarose gels (1–2 V/cm) for 16 h and transferred to nylon membranes (Hybond N, Amersham) using 25 mM Na_2HPO_4- NaH_2PO_4, pH 6.5 as the transfer medium. DNA clones from *E. coli* colonies were labeled with Digoxigenin-11dUTP (Boehringer Mannheim) by the polymerase chain reaction (PCR) (Hoisington et al. 1994). Prehybridization and hybridization were carried out in 5SSC, 0.02% SDS, 0.01% sodium lauryl sarcosine and 0.3% blocking reagent (Boehringer Mannheim) at 65°C overnight. The hybridization solution also contained 100 ng/ml of PCR-labeled probe. Membranes were washed twice with 0.15SSC, 1% SDS at room temperature for 5 min, and 3 times at 65°C for 15 min. Detection of hybridization was performed by enzymatic reaction using anti-Digoxigenin-AP and Lumigen-PPD (Boehringer Mannheim) as described by Hoisington et al. (1994). Membranes were exposed to Hyperfilm-ECL (Amersham) for 18–24 h.

DNA probes

A rye genomic library was generated using DNA from the cultivar 'Imperial' digested with the methylation-sensitive enzyme *Pst*I. Fragments were resolved by electrophoresis in a 1% low-melting-point agarose gel. Fragments ranging from 0.7 to 2.0 kb were sliced from the gel and ligated into pUC19 by conventional methods (Sambrook et al. 1989). Colony hybridization was performed using total rye genomic DNA as a probe to select clones that contained single or low-copy-number DNA sequences. These clones were assigned the prefix UAH (for University of Alcalá de Henares) and then given consecutive numbers as they were isolated. Clones were also generously supplied by other laboratories (Table 1). Loci detected by these anonymous clones were designated with the symbol "X" followed by the laboratory designation (uah, psr) or the name of the library (bcd, cdo etc.) and the number assigned to the clone. Loci detected by the same clone were designated with a capital letter following the number of the clone (i.e. *Xuah103A*).

RAPD assays

RAPD reactions were performed following a protocol based on that of Williams et al. (1990). The reaction volume was 25 µl and contained 1×reaction buffer with 1.5 m*M* Mg-Cl_2, 100 µM of each dNTP type, 7.5 ng of primer (10-mer Operon Technology), 0.5 units of *Taq* polymerase (Boehringer Mannheim) and 12.5 ng of genomic DNA. Standard amplifications were carried out for 40 cycles in a Perkin-Elmer thermal cycler. Cycle characteristics were set at 1 min at 94°C, 3 min at 36°C and 2 min at 72°C. Reactions with two different primers were also conducted. A 7.5-ng aliquot of each primer was added to the reaction mixture. Samples were analyzed by electrophoresis on 1.8% agarose gels followed by staining with ethidium bromide. The RAPD markers were designated according to Operon Technology primer designation i.e. *ops10*=primer 10 of Kit S.

Genetic mapping

Linkage analysis was performed on F_2 segregation data using the MAPMAKER V. 3 computer program (Lander et al. 1987). Genetic distances were calculated using the Kosambi function. The chromosomal affiliation of each linkage group was established by the hybridization of selected probes (designated with an asterisk in Fig. 1) to wheat-rye addition lines. Data obtained from previously mapped markers were also used.

Table 1 DNA clones used for genetic mapping of rye

Code	Source laboratory	Type	Reference
BCD	M. Sorrells, Cornell Univ, USA	Barley cDNA	Heun et al. 1991
CDO	D. Hoisington, CIMMYT, Mexico	Oat cDNA	Heun et al. 1991
MWG	A. Jahoor, Technical Univ, Munich	Barley gDNA	Graner et al. 1991
PSR 100–200	M. Gale, IPSR, UK	Wheat leaf cDNA	Devos et al. 1993
PSR >200	M. Gale, IPSR, UK	Wheat gDNA	Devos et al. 1993
UAH	E. Ferrer, Univ Alcalá, Spain	Rye gDN A	This work
WG	D. Hoisington, CIMMYT, Mexico	Wheat gDNA	Heun et al. 1991

Results and discussion

Levels of polymorphism

Genomic DNA of inbred lines E and R was digested with six restriction enzymes (*Dra*I, *Eco*RI, *Eco*RV, *Hin*dIII,*Xba*I and *Xho*I) and probed with 268 clones. The level of polymorphism observed was influenced by the source of the clones. Rye genomic clones detected the largest amount of polymorphism (65.6%) and oat cDNA clones the smallest (31.6%). The remaining clones revealed the following levels of polymorphism: wheat cDNA–40%, wheat genomic DNA–41.2%, and barley cDNA–39.1%. Therefore, the best source of probes for mapping the E×R F_2 population was the rye genomic library. However, only 28% of the rye clones obtained from the *Pst*I library were classified as single or low-copy-number clones.

The level of polymorphism detected by each enzyme was the following: *Dra*I–27.06%, *Hin*dIII–24.9%, *Eco*RI–24.2%, *Eco*RV–20%, *Xba*I–17.06% and *Xho*I–12%. Of the clones which produced polymorphism 72% gave RFLPs with more than one enzyme, indicating that most RFLPs were more probably due to insertions and deletions than to point mutations. The same has been reported elsewhere (Sharp et al. 1988; Heun et al. 1991).

A total of 180 oligonucleotides (10-mers) of arbitrary sequence were used as single primers to amplify DNA from the two inbred lines. While 162 primers produced scorable fragment patterns the number of polymorphic bands (5.5%) was extremely low. Initially, a larger number of fragments was selected as being truly polymorphic, however, some bands were faint or too close to other bands to be reliably scored in the F_2. This stringent selection considerably reduced the number of RAPD loci mapped compared to the number of RFLP loci mapped. In addition, since the electrophoresis conditions were optimized to reveal fragments from 0.5 to 1.5 kb in size a proportion of the rye genome that rendered larger fragments was not surveyed.

Segregation analysis

Seventy-three single and low-copy-number clones from the various libraries were used for mapping. Among these 61.6% were single-copy clones.

Segregation data were analyzed for 104 markers, including 87 RFLP and 17 RAPD markers. Nine clones detected more than 1 polymorphic locus, 5 clones detected duplicated loci, 3 clones detected triplicated loci and 1 clone, CDO786, detected 4 loci. Codominant alleles were scored at 66 RFLP loci (75.8%) and dominant alleles at 21 RFLP loci (24.13%). The higher percentage of null alleles found in this work contrasted with that of barley (14%) (Graner et al. 1991) or *T. tauschii* (16%) (Gill et al. 1991). In the present study, null alleles were more frequently observed for RFLP loci revealed by low-copy-number clones than for RFLP loci detected by single-copy clones, indicating that the comigration of fragments from different loci would lead to the apparent detection of null alleles.

Segregations different to the expected Mendelian ratios, 1:2:1 for codominant alleles and 3:1 for dominant alleles, were observed for 21 loci (20.19%). A significant excess of heterozygotes was observed for 16 markers scored as codominant. Although several of these markers could not be linked to any group, two clusters of loci showing distorted segregation ratios were observed in linkage groups of chromosomes 5R and 6R (Fig. 1). Loci in these clusters showed an excess of heterozygotes. Deviations from the Mendelian ratios have been reported for loci linked to the self-incompatibility loci of rye located on chromosomes 1R and 2R (Wricke and Wehling 1985; Gertz and Wricke 1989). Phillip et al. (1994) reported 34% of loci with distorted segregation preferentially located on chromosomes 1R and 6R. This figure is similar to the 33% detected for chromosomes 1R, 6R and 7R (Wanous et al. 1995). Since rye is an outbreeding species which suffers a strong reduction in viability when inbred, selection operating at any stage of development, from zygote through seedling, may have introduced a bias into the progeny used in this study. On the other hand, given the size of the F_2, chance might be responsible for part of the distortion.

RFLP linkage map

The map generated from the F_2 population derived from the cross between the inbred lines E and R is shown in Fig. 1. The map spans 339.7 cM and contains 77 RFLP and 12 RAPD markers, 4 other loci were linked to markers of some group but they could not be precisely mapped. The markers were distributed within eight linkage groups. Each group was assigned to a specific rye chromosome by the hybridization of markers within the group to Southern blots containing DNA from the 'Imperial' rye – 'Chinese Spring' wheat disomic addition lines (Driscoll and Sears 1971). Problems due to heterozygosity in the 'Imperial' original stock were solved by information provided by markers previously mapped in rye (Rognli et al. 1992; Liu et al. 1992; Devos et al. 1992; 1993 a,b; Rogowsky et al. 1993) and were used to corroborate the assignment of linkage groups to specific rye chromosomes. Homoeology with markers previously mapped in wheat (Nelson et al. 1995 a, b, c; Hohmann et al. 1994; Van Deynze et al. 1995 b; Delaney et al. 1995 a, b; Mickelson-Young et al. 1995) were also used to give a possible orientation of each linkage group with respect to the long and short arms.

Chromosomes 5R and 6R consisted of two unlinked groups. Chromosomes 1R, 3R, 4R and 7R were each within a single linkage group. No linkage group was assigned to chromosome 2R. The proportion of clones used in this work previously located in either rye or wheat chromosomes was not biased towards any particular chromosome. The 11 RFLP markers which showed polymorphism, but remained unlinked, were evenly assigned to different rye chromosomes. Further, a similar number of markers have

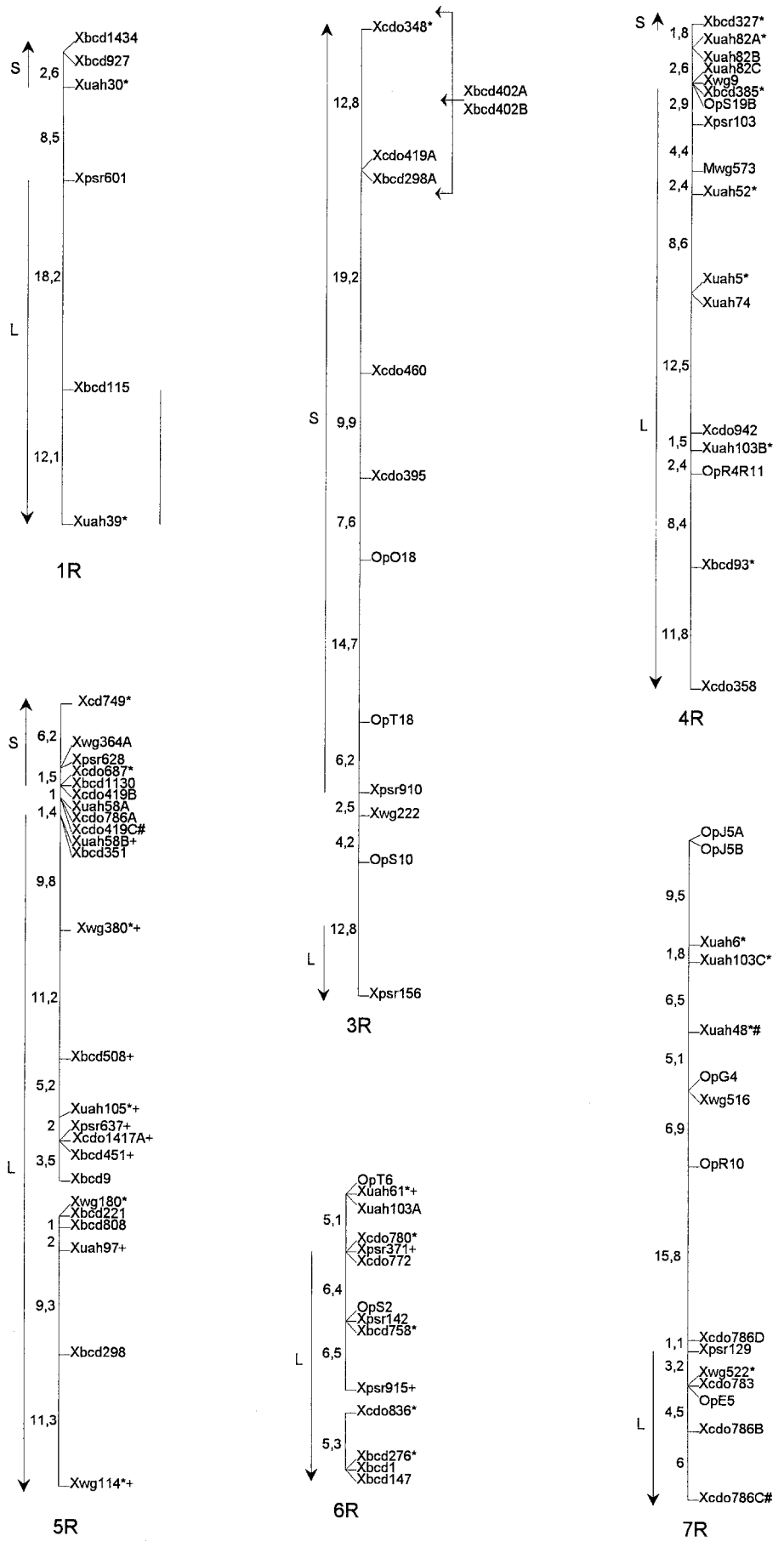

Fig. 1 Genetic maps of six rye chromosomes. Each linkage group has the clone name to the *right* and the distance between markers to the *left*. Markers assigned to a chromosome based on wheat-rye addition line hybridizations are indicated by an *. Codominant markers exhibiting distorted segregation are indicated by a +. Dominant markers exhibiting distorted segregation are indicated by #. *Vertical bars* to the *right* indicate that these marker were linked at LOD<3.5. Ambiguous positions for markers *Xbcd402A* and *Xbcd402B* on chromosome 3R are indicated by *horizontal arrows*. *Vertical arrowed bars* to the *left* indicate groups of markers that can be assigned to the long (*L*) or short (*S*) arm of the chromosome based on the previously known positions of two or more markers of each group

been previously placed on each rye chromosome (Devos et al. 1993a). Therefore, interchromosomal differences in the level of polymorphism between the E and R lines could be responsible for the variation in the number of markers mapped on each linkage group and for the absence of a linkage group for chromosome 2R. A paucity of markers on chromosome 2R was also noted by Phillip et al. (1994), The distribution of markers along the linkage groups was uneven. Most of the linkage groups presented clustering of markers in one or more regions. This was particularly evident in maps of chromosomes 4R, 5R and 6R. Maps for chromosomes 1R and 3R were more evenly distributed. In the linkage maps of Triticeae species a clustering of markers near the centromer has often observed (Devos et al. 1992; Devos et al. 1993 a, b; Kleinhofs et al. 1993).

As a general rule, the source of clones (cDNA and genomic DNA) had no influence on the distribution of markers throughout the linkage groups. Often, clones from different types of library were mapped at the same point or very close by. However, in several cases, markers from genomic libraries (particularly from the rye library) and RAPD markers were able to join to regions that otherwise would have remained unlinked (i.e. *Xuah5* and *Xuah74* in chromosome 4R; *opo18* in 3R or *opr10* in 7R). This would corroborate the assumption that genomic probes generated from the target species would cover regions poorly represented in libraries of related species (Devos et al. 1993 b; Xu et al. 1994). Nevertheless, a larger number of probes from different sources must be mapped before a general conclusion can be reached. In addition, RAPD markers were shown to be associated with chromosomal regions restricted in the number of RFLP markers. This was the only advantage of using RAPD markers in the production of the rye map. RAPD markers were therefore shown to be rather inefficient under the conditions of this investigation.

Comparison with other rye and wheat maps

Only 12 RFLPs mapped in the E×R F_2 population had been previously mapped in other rye segregations. This limited a wide comparative study. Three markers have been previously located on chromosome 1R (Rogowsky et al. 1993; Devos et al. 1993a) and the relative order of these loci was maintained in the present map. With respect to chromosome 5R 2 markers had been previously mapped in rye (Plaschke et al. 1993).

The map positions of markers previously located in wheat allowed the confirmation of several evolutionary translocations that have differentiated rye chromosomes from their homoeologous of wheat (Naranjo et al. 1987; Naranjo and Fernández-Rueda 1991; Devos et al. 1993a), Thus, *Xwg114* was mapped on chromosome 5R. It was located on 4BL, 4DL of hexaploid wheat (Anderson et al. 1992; Nelson et al. 1995 a), and $5A^mL$ of *T. monoccocum* (Ogihara et al. 1994) corroborated the translocation 5L/4L. *Xbcd147* located on group 3L of wheat (Nelson et al. 1995c, Van Deynze et al. 1995b) was mapped on chromosome 6R, confirming the translocation 6L/3L. Several markers, *Xbcd385*, *Xpsr103*, *Xbcd93* and *Xcdo358* mapped on 4R were located on the short arms of wheat group 7 chromosomes (Hohmann et al. 1994; Van Deynze et al. 1995b), consistent with the translocation 4L/7S. Finally, a marker, *Xcdo783*, was located on chromosome 7R and assigned to group 2S of wheat (Delaney et al. 1995a), corroborating the translocation 7L/2S.

Table 2 Clones mapped on rye and showing inconsistencies with previous wheat homoeologous assignation

Clone	Chromosome location in		Reference
	Rye	Wheat	
BCD221	5L	2S	Van Deynze et al. 1995b
BCD402	3S	$5A^mL$	Devos et al. 1995
		4AL-4BS-4DS	Nelson et al. 1995a
BCD808	5L	4AL	Mickelson-Young et al. 1995
CDO348	3S	5BL-5DL	Nelson et al. 1995a
CDO780	6L	4AL-7AS-7DS	Anderson et al. 1992
CDO786	7L	5AL	Ogihara et al. 1994
CDO1417	5L	2S	Van Deynze et al. 1995b
WG180	5L	7S	Nelson et al. 1995a
		7DL	Namuth et al. 1994
WG380	5L	7L	Nelson et al. 1995a
WG516	7L	2DL	Namuth et al. 1994
WG522	7L	7S	Hohmann et al. 1994

Several inconsistencies in the location of markers in rye with the homoeologous group assignments in wheat are listed in Table 2. These observations are similar to those reported by authors in articles dealing with consensus mapping (Van Deynze et al. 1995a,b; Nelson et al. 1995 a, b, c; Delaney et al. 1995 a, b). In the present study, all but two of the clones detecting the inconsistent markers (*Xwg516* and *Xwg522*) revealed more than one fragment in rye. Conversely, it could be possible that the same 2 markers detected multiple loci in wheat. Therefore, the inconsistencies that appeared in the present study could be a consequence of having analyzed fragments in rye which were not orthologous to those of wheat and would map to non-homoeologous chromosomes. However, additional factors such as the occurrence of small chromosome rearrangements within the genomes of the inbred lines used could also be responsible for the discrepancies found.

Maps of chromosomes 3R, 4R and 5R included several markers previously mapped in wheat, and this allowed the comparison of marker order between the maps of both species. For this comparison, maps of wheat that showed different sets of common markers were used. The existence of markers common to these wheat maps allowed the integration of all the markers in a single order. For example, markers *XksuG53-Xcdo460-Xcdo395-Xpsr903* were mapped in this order in the group 3S (Nelson et al. 1995 c). *XksuG53-Xpsr910-Xpsr903-Xpsr156* were located in this order by deletion and genetic mapping in the same group (Delaney et al. 1995 b). Therefore, the order found in rye for the markers *Xcdo460-Xcdo395-Xpsr910-Xpsr156* can be considered to be collinear with that of wheat. In chromosome 4R, 4 markers telomere-*Xcdo358-Xbcd93-*

Xpsr103-Xbcd385-centromere were also linked on the short arm of homoeologous group 7 (Hohmann et al. 1995; Nelson et al. 1995a; Van Deynze et al 1995 b). The order in wheat, telomere-*Xbcd93-Xpsr103-Xbcd385-Xcdo358*-centromere, seemed to indicate the existence of a rearrangement affecting *Xcdo358*. However, since this marker was linked to the map at a LOD score of 3.0 and the remaining markers were ordered at a LOD score of >3.5, a distortion of the rye map cannot be discarded. For chromosome 5R the order of 5 markers, *Xcdo749-Xcdo786-Xbcd508-Xbcd9-Xwg114*, was the same in rye and wheat, as deduced by comparison of the maps of Devos et al. (1995) and Van Deynze et al. (1995b).

The present study has extended the number of markers mapped in rye that are common to different wheat maps. This could facilitate a better integration of the rye map into those of related species such as wheat, barley, rice or maize.

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