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Genetic mapping of cytological and isozyme markers on chromosomes 1R, 3R, 4R and 6R of rye

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Abstract Cytogenetic maps involving chromosomes 1R, 3R, 4R and 6R have been developed from the analysis of offspring of crosses between multiple heterozygous rye plants. The maps include isozyme loci *Gpi-R1*, *Mdh-R1* and *Pgd2* (located in chromosome 1R), *Mdh-R2* (located in chromosome 3R), *Pgm-R1* (located in chromosome 4R) and *Aco-R1* (located in chromosome 6R). Various telomeric and interstitial C-bands of these four chromosomes, the centromere split of chromosome 3R, and translocation *TR01* were used as cytological markers. By means of electron microscope analysis of spread pachytene synaptonemal complexes, the breakpoint of *TR01* was physically mapped in chromosome arms 4RS and 6RL. From the linkage data, conclusions were derived concerning the cytological locations of the isozyme loci and the physical extent of the evolutive translocations involving chromosome arm 6RL.

Key words Rye · C-heterochromatin bands · Isozymes · Translocation · Genetic mapping

Introduction

The existence of a wide number of evolutionary translocations in the chromosomes of rye that are absent in wheat (for references see Devos et al. 1993) has enhanced interest in developing physical (or cytogenetic) rye maps in order to improve the possibility of wheat-rye transfers by homoeologous recombination with a positive effect on wheat breeding. The main cytological markers that have been used in assembling these maps have been telocentric (centromere split) chromosomes, translocations and polymorphic C- bands (de Vries 1983; de Vries and Sybenga 1984; Figueiras et al. 1985, 1989, 1991a, 1991b; Singh et al. 1990; Sybenga et al. 1990, 1991; Lukaszewski 1992; Alonso-Blanco et al. 1993a, b; Orellana et al. 1993). Telocentric chromosomes mark the centromere, the cytological points defined by C-bands can be distinguished after the analysis of C-banded mitotic chromosomes and the position of the breakpoint of a translocation can be accurately determined by electron microscope analysis of spread synaptonemal complexes of heterozygous plants.

In the investigation described in this paper, six isozyme loci located in chromosomes 1R, 3R, 4R and 6R were mapped relative to nine different C-bands located in these chromosomes, the centromere split of chromosome 3R and translocation *TR01*, which involves chromosomes 4R and 6R.

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Materials and methods

Plant material

Two multiple heterozygous plants (3-2 and 3-3) for several C-bands located in chromosomes 4R and 6R, for isozyme loci *Pgm-R1* and *Aco-R1* and for translocation *TR01* involving these two chromosomes (Goicoechea et al. 1991) were obtained from different crosses between plants of rye (*Secale cereale* L.) derived from cvs 'Ailés' and 'Raña'. These 2 plants were crossed with 1 plant (6-2) derived from different crosses involving cvs, 'Ailés' and 'Merced', inbred line E (Giraldez et al. 1979) and a line double ditelocentric for chromosome 3R (obtained from J. Sybenga). Plant 6-2 was also multiple heterozygous for several C-bands located on chromosomes 1R and 3R, for isozyme loci *Gpi-R1*, *Mdh-R1*, *Mdh-R2* and *Pgd2* and for the centromere split (ditelocentric) of chromosome 3R. The segregation analysis was made in 159 plants of the progeny from the crosses 3-2 × 6-2 and 3-3 × 6-2.

Isozyme assay

Isozyme analyses were carried out on extracts of 12-day-old leaves from plants obtained by germination of half-grains containing the embryo. Five isozymatic systems, phosphoglucose mutase (PGM, EC 2.7.5.1), glucosephosphate isomerase (GPI, EC 5.3.1.9), malate dehy-

drogenase (MDH, EC 1.1.1.37) phosphogluconate dehydrogenase (PGD, EC 1.1.1.44) and aconitase (ACO, EC 4.2.1.3), were assayed after horizontal 12% starch gel electrophoresis using the buffers and staining methods described by Figueiras et al. (1985) and Chenicek and Hart (1987). The electrophoretic patterns of the isozyme alternatives present in the plants analyzed have been described previously (Alonso-Blanco et al. 1993a).

Karyotype and C-banding analysis

Excised root tips were immersed in tap water at 0 °C for 24 h to shorten the chromosomes and then fixed in acetic acid: alcohol 1:3. The fixed material was maintained in the fixative for 1–4 months at 3–4 °C. It was then squashed and stained following the Giemsa C-banding technique described by Giraldez et al. (1979).

Synaptonemal complex analysis

The pachytene synaptonemal complexes (SCs) of a plant heterozygous for translocation *TR01*, ditelocentric for chromosome 1R and ditelocentric for chromosome 3R were analyzed following the spreading and staining procedures of de Jong et al. (1989) as modified by Naranjo et al. (1989). The SCs were studied in the electron microscope, photographed and printed at final magnification of 7000. The lengths of the SCs were measured on the photographic prints by means of a digitizing tablet connected to a computer.

Statistical analysis

Recombination frequencies and their standard errors were calculated using the method of maximum likelihood. Jensen and Jorgensen's (1975) application of the Kosambi (1944) function was used to convert recombination fractions to map distances in centiMorgans (cM).

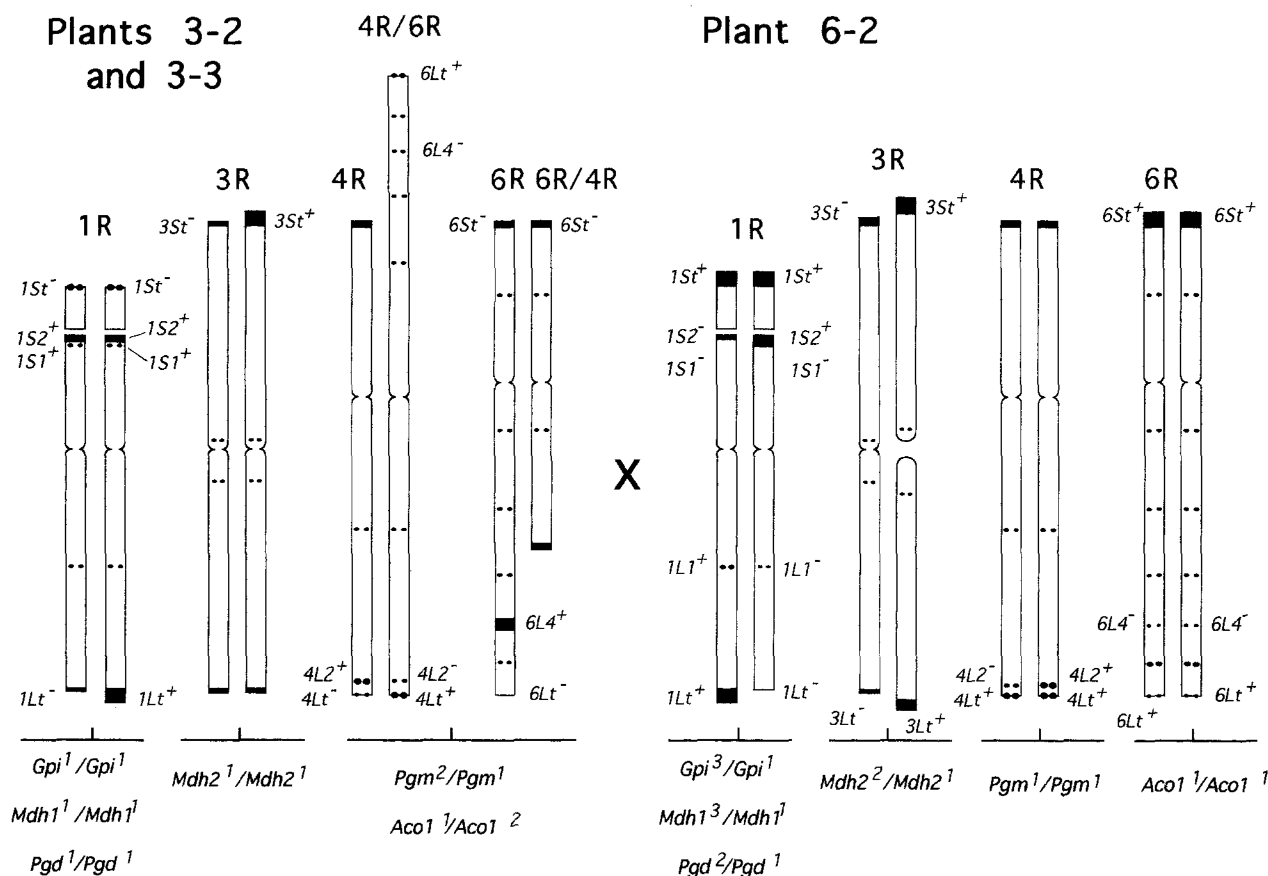
Results and discussion

Figure 1 shows a diagram of the cytological constitution of chromosomes 1R, 3R, 4R and 6R of the plants used as parents as well as their genetic constitution with respect to the isozyme loci analyzed. In the analyzed progenies of crosses 6-2 × 3-2 and 6-2 × 3-3, the segregation of markers located in chromosomes 1R and 3R is due to heterozygosity for these markers in plant 6-2, whereas that of markers located in chromosomes 4R and 6R is due to the heterozygosity of plants 3-2 and 3-3.

Chromosome 1R

Plant 6-2 was homozygous for a large telomere C-band in the short arm of chromosome 1R and heterozygous for the amount of C-heterochromatin in the telomere C-band of the long arm (*1Lt*; alternatives *1Lt*$^+$ and

Fig. 1 Diagram of the constitution of chromosomes 1R, 3R, 4R and 6R of the rye plants used as parents, showing the structural changes, C-heterochromatin bands and isozyme loci segregating in the progenies analyzed



1Lt^{-}), in the C-band adjacent to the nucleolar organizer region (*1S2*; alternatives *1S2*$^{+}$ and *1S2*$^{-}$) and in the C-band located in the middle of the long arm (*1L1*; alternatives *1L1*$^{+}$ and *1L1*$^{-}$). This plant was also heterozygous for three isozyme loci located in chromosome 1R: *Gpi-R1* (alleles GPi^1 and Gpi^3), *Mdh-R1* (alleles Mdh^1 and Mdh^3) and *Pgd2* (alleles Pgd^1 and Pgd^2).

Plant 3-2 and 3-3 were homozygous for these three isozymes (alleles Gpi^1, Mdh^1 and Pgd^1) and for a small telomere C-band in the short arm of chromosome 1R. The difference in C-banding pattern concerning the telomere C-band of 1RS between these plants and plant 6-2 (Fig. 2) allowed the unequivocal identification of the C-banding pattern of the segregating chromosomes coming from plant 6-2 in the crosses 6-2 × 3-2 or 6-2 × 3-3.

The joint segregations and the recombination percentages for the most relevant pairs of markers of chromosome 1R are shown in Table 1. The inheritance of each individual marker fitted the expected 1:1 segregation. A comparison between the physical and the genetic maps of this chromosome is shown in Fig. 4. Both the order of markers determined from these results (*Gpi-R1*...*1S2*...*Mdh-R1*...*1L1*...*Pgd2*...*1Lt*) and the relative restriction of chiasmata to the distal regions of the chromosome agree with previous observations (Alonso-Blanco et al. 1993a, b).

Chromosome 3R

Plant 6-2 was heterozygous for a centromere split of chromosome 3R (marker *Cen3*, alternatives $Cen3^{N}$ and $Cen3^{DT}$), the normal chromosome carrying two telomere C-bands (*3St*$^{-}$ and *3Lt*$^{-}$) smaller than the corresponding ones present in the two telosomics (*3St*$^{+}$ and *3Lt*$^{+}$). This plant was also heterozygous for isozyme locus *Mdh-R2* (alleles $Mdh^1$and Mdh^2) located in chromosome 3R.

Plants 3-2 and 3-3 were homozygous for *Mdh-R2* (allele Mdh^1), had structurally normal 3R chromosomes and were heterozygous for both telomere C-bands of this chromosome. The *Mdh-R2* and *Cen3* constitution

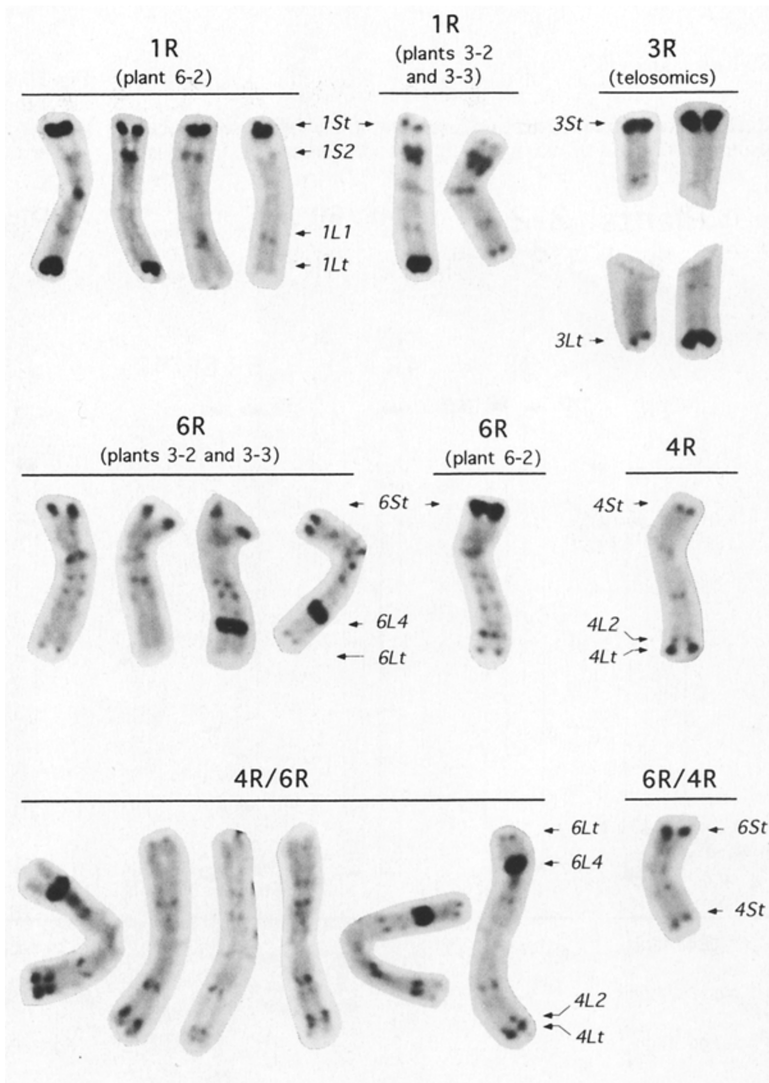


Fig. 2 Some examples of chromosomes 1R, 3R, 4R, 6R, 4R/6R and 6R/4R appearing in the progenies analyzed. The different segregating C-bands are indicated

Table 1 Joint segregation, contingency χ^2 values for independence, recombination percentages and map distances for the most relvant pairs of markers of chromosomes 1R, 3R, 4R and 6R analyzed in this work

Markers (*Aa*, *Bb*)	Genotype of the heterozygous parental (*AB*/*ab*)	Recovered gametes				Contingency χ^2	Recombination frequency (%)	Map distance in cM
		AB	*Ab*	*aB*	*ab*			
Chromosome 1R								
Gpi-R1, 1S2	$Gpi^{1}\ 1S2^{+}/Gpi^{3}\ 1S2^{-}$	52	21	26	60	26.550**	29.6 ± 3.6	33.9 ± 5.6
Gpi-R1, Mdh-R1	$Gpi^{1}\ Mdh1^{1}/Gpi^{3}\ Mdh1^{3}$	52	21	27	59	25.055**	30.2 ± 3.6	34.9 ± 5.7
1S2, Mdh-R1	$1S2^{+}\ Mdh1^{1}/1S2^{-}\ Mdh1^{3}$	73	5	6	75	118.071***	6.9 ± 2.0	7.0 ± 2.0
1S2, 1L1	$1S2^{+}\ 1L1^{-}/1S2^{-}\ 1L1^{+}$	72	6	6	75	114.617***	7.6 ± 2.1	7.6 ± 2.1
Mdh-R1, 1L1	$Mdh1^{1}\ 1L1^{-}/Mdh1^{3}\ 1L1^{+}$	77	2	1	79	147.265***	1.9 ± 1.1	1.9 ± 1.1
Mdh-R1, Pgd2	$Mdh1^{1}\ Pgd2^{1}/Mdh1^{3}\ Pgd2^{2}$	62	17	18	62	49.850***	22.0 ± 3.3	23.6 ± 4.1
1L1, Pgd2	$1L1^{-}\ Pgd2^{1}/1L1^{+}\ Pgd2^{2}$	62	16	18	63	52.132***	21.4 ± 3.2	22.8 ± 3.9
1L1, 1Lt	$1L1^{-}\ 1Lt^{-}/1L1^{+}\ 1Lt^{+}$	47	31	42	39	1.136 ns	45.9 ± 3.9	Independent
Pgd2, 1Lt	$Pgd2^{1}\ 1Lt^{-}/Pgd2^{2}\ 1Lt^{+}$	44	36	45	34	0.061 ns	50.9 ± 4.0	Independent
Chromosome 3R								
Mdh-R2, Cen3	$Mdh2^{1}\ Cen3^{DT}/Mdh2^{2}\ Cen3^{N}$	70	0	3	86	147.373***	1.9 ± 1.1	1.9 ± 1.1
Mdh-R2, 3St	$Mdh2^{1}\ 3St^{+}/Mdh2^{2}\ 3St^{-}$	34	36	0	3	2.727 ns	49.3 ± 5.8[a]	Independent
Mdh-R2, 3Lt	$Mdh2^{1}\ 3Lt^{+}/Mdh2^{2}\ 3Lt^{-}$	35	35	1	2	0.315 ns	49.3 ± 5.8[a]	Independent
Chromosomes 4R and 6R								
4Lt, 4L2	$4Lt^{+}\ 4L2^{-}/4Lt^{-}\ 4L2^{+}$	28	13	15	25	7.712**	34.6 ± 5.3[b]	42.5 ± 10.1
4L2, Pgm-R1	$4L2^{-}\ Pgm^{1}/4L2^{+}\ Pgm^{2}$	41	2	37	1	0.228 ns	48.2 ± 5.6[b]	Independent
TR01, Pgm-R1	$TR01^{N}\ Pgm^{2}/TR01^{T}\ Pgm^{1}$	73	5	3	78	128.670***	5.0 ± 1.7	5.1 ± 1.8
Pgm-R1, Aco-R1	$Pgm^{1}\ Aco1^{2}/Pgm^{2}\ Aco1^{1}$	47	36	22	54	12.384***	36.5 ± 3.8	46.4 ± 8.2
TR01, Aco-R1	$TR01^{N}\ Aco1^{1}/TR01^{T}\ Aco1^{2}$	56	22	34	47	14.376***	35.2 ± 3.8	43.8 ± 7.5
TR01, 6L4	$TR01^{N}\ 6L4^{+}/TR01^{T} 6L4^{-}$	55	23	33	48	14.265***	35.2 ± 3.8	43.8 ± 7.5
Aco-R1, 6L4	$Aco1^{1}\ 6L4^{+}/Aco1^{2}\ 6L4^{-}$	88	2	0	69	151.078***	1.3 ± 0.9	1.3 ± 0.9
Aco-R1, 6Lt	$Aco1^{1}\ 6Lt^{-}/Aco1^{2}\ 6Lt^{+}$	57	33	32	37	4.561*	40.9 ± 3.9	57.5 ± 11.8
6L4, 6Lt	$6L4^{+}\ 6Lt^{-}/6L4^{-}\ 6Lt^{+}$	56	32	33	38	4.699*	40.9 ± 3.9	57.5 ± 11.8

[a] The segregation of C-bands 3St and 3Lt was determined only in the telocentric chromosomes

[b] The segregation of C-bands 4Lt and 4L2 was determined only in translocated chromosomes

*** $P<0.001$; ** $0.01>P>0.001$; * $0.05>P>0.01$; ns, not significant

of the recovered gametes from plant 6-2 could be determined in all progeny plants. The segregating telomere C-banding pattern (markers *3St* and *3Lt*) coming from plant 6-2 could only be unequivocally established in the telocentric chromosomes (Fig. 2).

The joint segregations and the recombination percentages for the most relevant pairs of markers of chromosome 3R are shown in Table 1. The inheritance of each individual marker fitted the expected 1:1 segregation.

Isozyme locus *Mdh-R2* was assigned to chromosome 3R by Salinas and Benito (1985). Figueiras et al. (1985) found no recombinants between *Mdh-R2* and a translocation involving chromosomes 1R and 3R that did not have interstitial chiasmata and concluded that *Mdh-R2* is located between the centromere and the translocation breakpoint, very close to the centromere. The distance of 1.9 ± 1.1 cM between loci *Mdh-R2* and *Cen3* obtained in this work (Table 1) and the absence of linkage with the two telomere C-bands of chromosome 3R are consistent with these earlier observations. However, if we consider that in rye chromosomes recombination around the centromere is low (Fig. 4) and that the telocentrics used in this work had reduced it even more, the physical location of *Mdh-R2* being very close to the centromere is highly doubtful. Its location not far apart from the middle of the arm is more realistic.

Chromosomes 4R and 6R

Plants 3-2 and 3-3 were heterozygous for translocation *TR01* involving chromosomes 4R and 6R. The alternative structural arrangements have been designated $TR01^{N}$ (chromosomes 4R and 6R) and $TR01^{T}$ (chromosomes 4R/6R and 6R/4R). The C-banding analysis of the translocated chromosomes (Fig. 2) indicated that the translocation breakpoint is located in the long arm of chromosome 6R (between bands 6L1 and 6L2) and in the short arm of chromosome 4R. In order to determine more accurately the physical location of the translocation breakpoint, the synaptonemal complexes of seven pachytene cells of a plant heterozygous for translocation *TR01*, ditelocentric for chromosome 1R and ditelocentric for chromosome 3R were analyzed. Figure 3 shows the spread synaptonemal complexes from one of these cells. The four quadrivalent segments in which the translocation breakpoint (TB) divides the chromosomes involved in this translocation (I, between TB and telomere of 4RS; II, between TB and the telomere of 4RL; III, between TB and the telomere of 6RS; and IV, between TB and the telomere of 6RL) could be unequivocally distinguished since: (1) the four chromosomes involved in the quadrivalent have fixed relative positions (Fig. 3c) and (2) from the analysis of the C-banding pattern at mitosis, it can be concluded that quadrivalent segments I and II are the shortest and the longest ones, respectively.

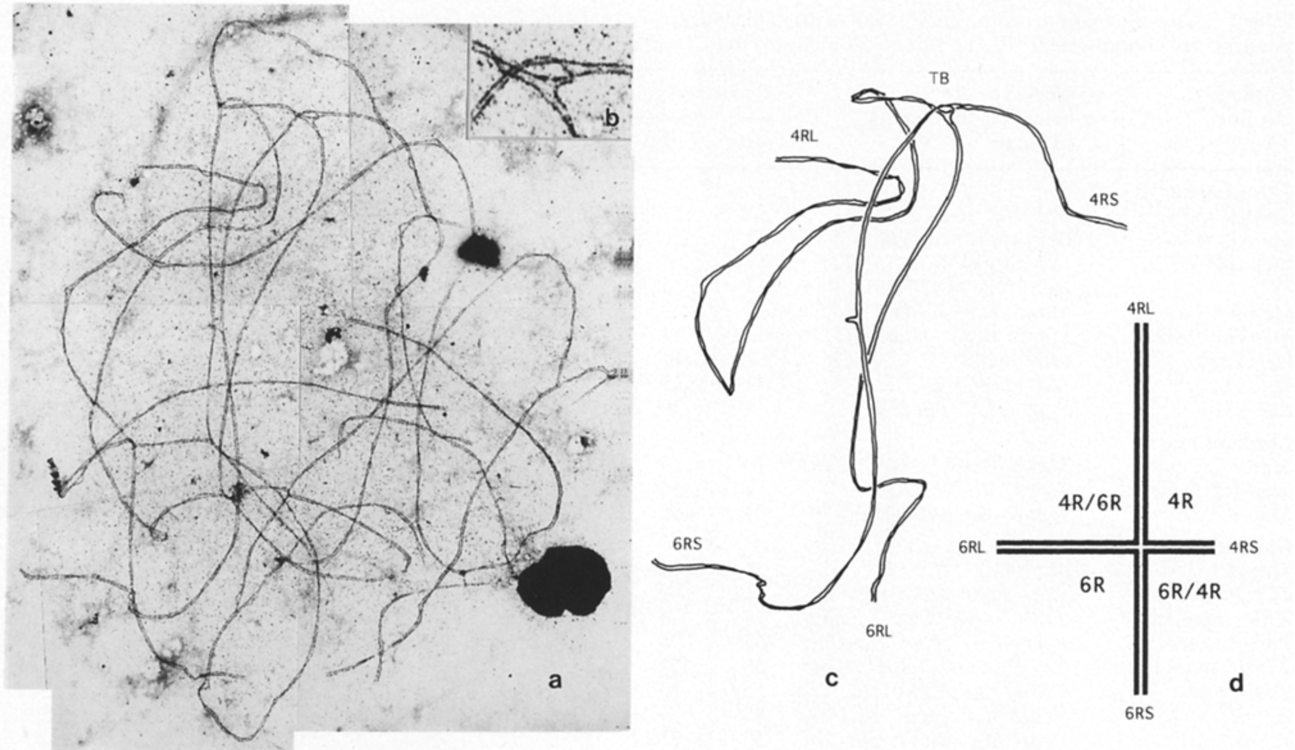


Fig. 3a–d Electron micrograph of the spread synaptonemal complexes from a pachytene nucleus of a heterozygote for translocation *TR01* (**a**), with the corresponding drawing of the quadrivalent (**c**) and the pairing diagram of the multivalent formed (**d**). The region of partner exchange corresponding to the translocation breakpoint is enlarged in **b**

Table 2 shows the mean length of the different synaptonemal complex segments of the *TR01* quadrivalent. The relative lengths of the short arms of chromosomes 4R and 6R at mitosis have been estimated to be 38% and 34% of the total chromosome lengths, respectively (Giraldez et al. 1979). From the results obtained in this work the translocation breakpoint was located (Fig. 4) near the middle of chromosome 6R (corresponding to a rather proximal location in the long arm) and near the middle of the short arm of chromosome 4R.

Plant 3-2 and 3-3 were also heterozygous for isozyme loci *Pgm-R1* (alleles Pgm^1 and Pgm^2) and *Aco-R1* (alleles Aco^1 and Aco^2) and for the amount of C-heterochromatin in two C-bands of chromosome arm 4RL (*4L2*, alternatives $4L2^+$ and $4L2^-$; and *4Lt*, alternatives $4Lt^+$ and $4Lt^-$) and two C-bands of chromosome arm 6RL (*6L4*, alternatives $6L4^+$ and $6L4^-$; and *6Lt*, alternatives $6Lt^+$ and $6Lt^-$); they were homozygous for a small telomere C-band on chromosome arm 6RS ($6St^-$).

Concerning chromosomes 4R and 6R, plant 6-2 had the standard, non-translocated karyotype. It was homozygous for isozyme loci *Pgm-R1* (allele Pgm^1) and *Aco-R1* (allele Aco^1), heterozygous for the C-band 4L2 and homozygous for the C-banding pattern of chromosome 6R, showing a large C-band in the telomere of the short arm ($6St^+$) of this chromosome.

Table 2 Length (μ) of the different synaptonemal complex (SC) segments of the multivalent formed in pachytene cells of a plant heterozygous for translocation *TR01* (*4St* Telomere of 4RS, *TB* translocation breakpoint, *4Lt* telomere of 4RL, *6St* telomere of 6RS, *6Lt* telomere of 6RL)

	Quadrivalent segments						Mean total SC length	Number of cells
	Chromosome 4R		Chromosome 6R		Chromosome 3R			
	4St-TB	TB-*4Lt*	6St-TB	*6Lt*-TB	3RS[a]	3RL[a]		
SC mean length	19.3 ± 2.2	62.1 ± 5.0	40.3 ± 2.6	39.6 ± 3.1	36.9 ± 3.2	43.5 ± 2.5	526.3 ± 39.3	7
Mean % of the corresponding chromosome	23.7 ± 2.0	76.3 ± 2.0	50.7 ± 1.5	49.3 ± 1.5	45.7 ± 1.4	54.3 ± 1.4		

[a] In all pachytene nuclei analyzed, the shortest telocentric lateral element of the trivalent formed by the 3R chromosomes was taken as chromosome arm 3RS. Then, the difference between 3RS and 3RL length could be smaller

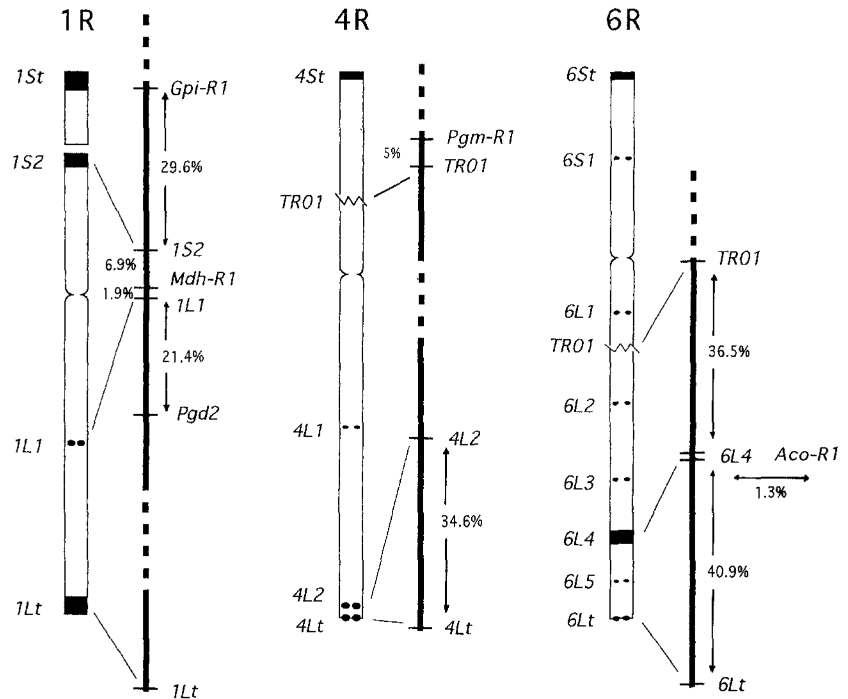


Fig. 4 Comparison of the physical maps of chromosomes 1R, 4R and 6R, based on mitotic C-banding and (or) synaptonemal complex analyses, and the corresponding genetic maps, based on recombination (%) between adjacent markers, in the progenies studied

The *Pgm-R1*, *Aco-R1* and *TR01* constitution of the recovered gametes from plants 3-2 and 3-3 could be determined in all progeny plants. Also, the difference in C-banding pattern between the parental plants concerning the telomere C-band of 6RS allowed the unequivocal identification of the C-banding pattern of the segregating 6R chromosomes coming from plants 3-2 and 3-3. However, the segregating C-bands *4L2* and *4Lt* coming from plants 3-2 and 3-3 could only be unequivocally established in the translocated chromosomes (Fig. 2).

The inheritance of each individual marker of chromosomes 4R and 6R fitted the expected 1:1 segregation. The joint segregations and the recombination percentages for the most relevant pairs of markers of these chromosomes are shown in Table 1. A comparison between the physical and the genetic maps of chromosomes 4R and 6R is also shown in Fig. 4.

Isozyme locus *Pgm-R1* has been assigned to chromosome arm 4RS by Benito et al. (1984). Figueiras et al. (1989, 1991) found that the genetic distances between *Pgm-R1* and three different translocations involving chromosome arm 4RL are very similar to one another (14.98%, 16.82% and 14.63% respectively). Since all three translocations did not have interstitial chiasmata, Figueiras et al. (1991) concluded that the distance estimated in all cases was that between *Pgm-R1* and the centromere. The results obtained in the present work agree with these previous observations and increase the precision concerning the physical location of *Pgm-R1*. Translocation *TR01* has no interstitial chiasmata (Goicoechea et al. 1991) and its breakpoint is located near the middle of chromosome arm 4RS (Table 2, Fig. 4). The 5% recombination found between locus *Pgm-R1* and translocation *TR01* (Table 1) indicates that this isozyme locus is located in the distal half of chromosome arm 4RS.

The comparison between the genetic and the physical maps of chromosome 6R shown in Fig. 4 indicates that C-band *6L4* is located in a chromosome region in which chiasma frequency in relatively high. From the low recombination value obtained in this work between isozyme locus *Aco-R1* and C-band *6L4* ($1.3 \pm 0.9\%$, Table 1), it can be concluded that these two markers must be located at a short physical distance from one another. It was not possible to determine the relative order of *Aco-R1* and *6L4* within the chromosome because they showed identical recombination values with the two adjacent markers, *TR01* and *6Lt* (Table 1), with the two recovered gametes recombinant for *Aco-R1* and *6L4* having the genotypes $TR01^{T}$, $Aco1^{1}$, $6L4^{-}$, $6Lt^{-}$ and $TR01^{N}$, $Aco1^{1}$, $6L4^{-}$, $6Lt^{+}$, respectively.

Devos et al. (1993), after their analysis of a restriction fragment length polymorphism-based genetic map of the rye genome, confirmed the pairing results of Naranjo and Fernández-Rueda (1991) and concluded that 6RL comprises a proximal region with homoeology to the wheat group 6 chromosomes, an interstitial region with homoeology to the long arms of the wheat group 3 chromosomes, and a distal region with homoeology to the long arms of the wheat group 7 chromosomes. Since *Aco-1* loci are located on the long arms of the homoeologous group 6 chromosomes of Triticeae (Chenizek and Hart 1987), the close linkage between *Aco-R1* and C-band *6L4* obtained in the present work indicates that the physical extent of the translocated segments

coming from homoeology groups 3 and 7 considered together represents only the distal 25–30% of the 6RL arm length.

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