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A map of rye chromosome 4R with cytological and isozyme markers

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Abstract. The progeny of two crosses between a structural heterozygote for a reciprocal translocation (4RL/5RL) and a homozygote for the standard chromosome arrangement and of four crosses between standard chromosome homozygotes were analysed in rye (*Secale cereale* L. cv 'Ailés') for the electrophoretic patterns of five different leaf and endosperm isozymes (LAP, PGM, NDH, ADH and EPER). The presence or absence of the quadrivalents at metaphase I (MI) was also tested. Loci *Adh-1*, *Pgm-1* and *Ndh-1* were located on chromosome arm 4RS, and locus *Eper-1* on chromosome arm 4RL. Locus *Lap-2* was located on the 4RS chromosome arm. The estimated distances among the different linked loci support the following gene order: *Eper1*.. (breakpoint-centromere).. *Lap-2*.. ..*Adh-1* .... *Pgm-1*.... *Ndh-1*. These results provide evidence for the chromosomal location of *Lap-2* locus on chromosome arm 4RS in cv 'Ailés'. A high negative interference was detected between the zones delimited by centromere and *Lap-2*, and *Lap-2* and *Pgm-1* in plants with the 4RL/5RL translocation.

Key words: Isozymes – Translocation – Cytogenetic maps – Chromosome 4R – Rye

Abbreviations: LAP, leucine aminopeptidase; PGM, phosphoglucomutase; NDH, NADH dehydrogenase; ADH, alchohol dehydrogenase; EPER, endosperm peroxidase

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Introduction

Loci coding for isozyme markers have been located in different rye chromosome arms (Figueiras et al. 1989, 1991a, b; Wehling 1991; Benito et al. 1991a, b; Melz et al. 1992). The polymorphism for reciprocal translocations that is present in *Secale cereale* cv 'Ailés' provides additional markers for constructing accurate linkage maps (see Figueiras et al. 1985). These cytogenetics markers may include not only the translocation "per se" (that is, the breakpoint) but also the centromere, as in many instances chiasmata are not formed in the interstitial centromere-breakpoint segments of the quadrivalents. Thus, translocations have already proved useful, in improving the genetic maps of chromosomes 1R, 3R and 4R (Figueiras et al. 1985, 1989, 1991a, b). Chromosome 4R, however, presents a comparatively poorer picture: although several loci have been located on this chromosome (Melz et al. 1992), the genetic maps have only two or three points, and linkage data between them are scarce (Figueiras et al. 1991a, b; Wehling 1991; Wricke 1991).

In this report we present linkage data among five isozyme loci and two cytogenetic markers (translocation breakpoint and centromere) located on the 4R chromosome.

Materials and methods

The offspring of two different backcrosses (named LE1 and LE2) between a structural heterozygote (HT, 1IV + 5II) for the reciprocal interchange 4RL/5RL (Figueiras et al. 1990) from *Secale cereale* L. cv 'Ailés' (polymorphic for reciprocal translocations) and a homozygote for the standard chromosome arrangement (HM, 7II) were analysed. In addition, the offspring of another four backcrosses (named PA1, RA1, RA2 and AA1) between homozygotes for the standard chromosome arrangement were

also analysed. Plants of 'Ailés' were crossed with the inbred line 'Riodeva' (backcrosses RA1 and RA2), with the inbred line 'Pool' (backcross PA1) and with another plant of 'Ailes' (cross AA1). Both the chromosome constitution and the isozyme patterns were studied in the progeny of these crosses.

The cytological study was made on the pollen mother cells (PMCs) at metaphase I (MI) following the aceto-orcein stain procedure. Those plants showing 1IV + 5II were classified as structural heterozygotes for the interchange and those showing 7II as structural homozygotes.

The seed set from the six different progenies was allowed to germinate. The biochemical analyses were carried out on 12-day-old leaves and a portion of the dry endosperms. The isozymic systems were studied following the protocols described by Figueiras et al. (1985) for leaf phosphoglucomutase (PGM) and endosperm cathodal peroxidases and by Figueiras et al. (1991b) for leaf NADH dehydrogenase (NDH). The endosperm alcohol dehydrogenase (ADH) was analyzed with the same buffer systems used for PGM and the staining method described by Salinas et al. (1981). The leaf leucine aminopeptidase (LAP) also named aminopeptidase (AMP) was studied with the same buffer systems used for NDH and the staining method described by Benito et al. (1991a).

The following genetic stocks were examined for the chromosomal location of the structural genes for leucine aminopeptidase-2 (LAP-2) (or aminopeptidase-2, AMP-2) isozymes: 'Chinese Spring' hexaploid wheat (*Triticum aestivum* L.), 'Imperial' rye (*Secale cereale* L.), 'Chinese Spring- Imperial' wheat-rye disomic addition line 4R and wheat-rye ditellosomic addition lines 4RS and 4RL (These materials were kindly supplied by Dr. T. E. Miller and Dr. A. J. Lukaszewski). The chromosomal location of structural genes for LAP-2 (AMP-2) isozymes was performed using 10 m*M* DTT (dithiothreitol) crude extracts from the endosperm or embryo of mature seed. The isoelectric focusing separations and the staining procedures with *L*-arginine β-Naphtyl-amide or with *L*-lysine β-Naphtyl-amide were made using the method described by Koebner and Martin (1989) with minor modifications.

Results

A genetic map of the chromosome 4R in rye

The isozymic pattern for both the parental and the progeny plants of the six crosses studied are shown in Fig. 1. These progenies segregated for five different loci located on chromosome 4R. The segregation for the individual isozymic loci was the expected (1:1) in the six crosses analysed (Table 1). The *Pgm-1*, *Ndh-1* and *Lap-2* loci showed two active alleles in all of the crosses analysed, as well as monomeric behaviour (Figs. 1 and 2). The *Adh-1* locus presented two active alleles in all crosses and a dimeric behaviour (Figs. 1 and 2). Finally, the *EPer-1* locus showed one active allele and one null allele and a monomeric behaviour (Fig. 1). In the two crosses with the 4RL/5RL translocation, the segregation observed for the quadrivalent at metaphase I was the expected 1:1 (Table 1).

The linkage relationships (two-point linkage test) between the isozymic loci and between those loci linked to the interchange and the translocation are shown in Table 2. When a same pair of markers was involved in different crosses, the data could be pooled since the χ^2 heterogeneity test was not significant at the 5% level. It can be seen that the *Eper-1* and *Adh-1*, *Eper-1* and *Pgm-1*, *Adh-1* and *Pgm-1*, *Pgm-1* and *Ndh-1*, *Eper-1* and *Lap-2*, *Lap-2* and *Pgm-1* and *Lap-2* and *Ndh-1* loci were linked. All of these loci have been located on chromosome 4R. Moreover, the loci *EPer-1*, *Lap-2*, *Pgm-1* and *Ndh-1* were clearly associated with the translocation (Table 2).

The chromosomal location of the structural genes for rye leucine aminopeptidase-2

The leucine aminopeptidase (LAP-2) patterns obtained using L-arginine β-Naphtyl-amide or L-lysine β-Naphtyl-amide were the same.

Two LAP-2 bands (embryo and endosperm extracts with DTT) were visualized by isoelectric focusing in standard 'Chinese Spring' wheat (Fig. 3). The LAP-2 pattern of 'Imperial' rye had one band. The wheat-rye disomic addition line 4R and the wheat-

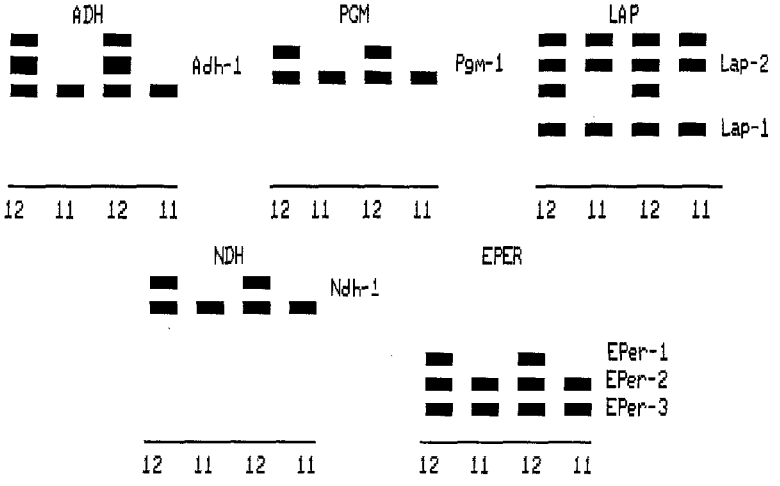

Fig. 1. Diagrammatic representation of the leaf (*PGM*, *LAP* and *NDH*) and endosperm isozymes (*ADH* and *EPER*). The different activity zones studied in each isozyme system are indicated on the *right*. All of the isozymes studied show anodal migration except for the EPER isozymes, which present cathodal migration. The numbers *11* and *12* indicate the different genotypes shown by the plants for loci demonstrating segregation (*Adh-1*, *Pgm-1*, *Lap-2 Ndh-1* and *Eper-1*). The *Adh-1*, *Pgm-1*, *Lap-2* and *Ndh-1* loci show two active alleles, while the *EPer-1* locus show one active and one null allele. The two parents of the backcross and the two types of offspring are indicated from left to right

Table 1. Single-locus segregation of the five isozymic loci located on chromosome 4Rand the translocation 4RL/5RL (T) in the six different crosses studied

Crosses	Loci[a] (Parental genotypes)	Distribution of progeny (phenotype) 11	12	$\chi^2_{1:1}$
PA-1	*Adh-1*(*11*) × (*12*)	49	51	0.04
	Ndh-1(*11*) × (*12*)	20	30	2.00
RA-1	*Pgm-1*(*11*) × (*12*)	22	20	0.10
	Ndh-1(*11*) × (*12*)	19	23	0.38
RA-2	*Pgm-1*(*11*) × (*12*)	22	25	0.19
	Adh-1(*11*) × (*12*)	26	21	0.53
	EPer-1(*11*) × (*12*)	20	27	1.04
	Ndh-1(*11*) × (*12*)	26	21	0.53
AA-1	*Pgm-1*(*11*) × (*12*)	33	33	0.00
	Adh-1(*11*) × (*12*)	35	31	0.24
	EPer-1(*11*) × (*12*)	36	30	0.54
LE-1	*Pgm-1*(*12*) × (*11*)	59	60	0.01
	Ndh-1(*12*) × (*11*)	62	57	0.21
	Lap-2(*12*) × (*11*)	61	58	0.07
	T(1IV + 5II) × (7II)	22	29	0.96
LE-2	*Pgm-1*(*12*) × (*11*)	40	54	2.08
	Ndh-1(*12*) × (*11*)	46	48	0.04
	Lap-2(*12*) × (*11*)	44	50	0.38
	EPer-1(*12*) × (*11*)	21	29	1.28
	T(1IV + 5II) × (7II)	47	43	0.18
Pooled data	*Adh-1*	101	97	0.08
	Pgm-1	176	192	0.69
	Ndh-1	153	149	0.05
	Lap-2	105	108	0.04
	EPer-1	86	83	0.05
	Translocation	69	72	0.06

[a] The *Adh-1*, *Pgm-1*, *Ndh-1* and *Lap-2* loci present two active alleles (*1* and *2*); the (*12*) and (*11*) phenotypes are heterozygous and homozygous plants, respectively. The *EPer-1* locus has one active (*2*) and one null allele (*1*); phenotypes (*11*) are homozygous plants for the null allele. In the case of translocation (T), phenotypes (*12*) and (*11*) are plants with 1IV + 5II and 7II, respectively

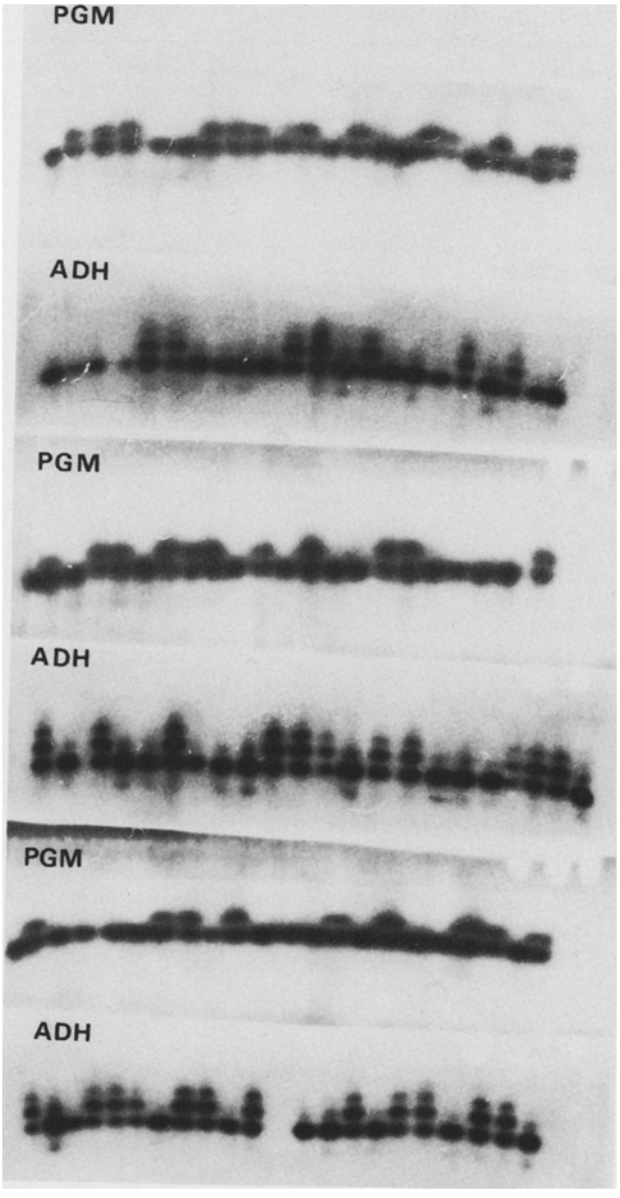

Fig. 2. Phosphoglucomutase (*PGM*) and alcohol dehydrogenase (*ADH*) zymograms shown by the 66 plants of the backcross AA-1. The heterozygous plants (*12*) for the *Pgm-1* and *Adh-1* loci present two and three bands, respectively; the homozygous plants present one band in each locus. The *PGM* and *ADH* isozymes show monomeric and dimeric behaviour, respectively. In this backcross there are only 10 recombinant plants (heterozygous or homozygous plants in both loci). The recombination frequency is 10/66 = 0.1515, and the genetic distance is 15.15 cM

rye ditellosomic addition line 4RS showed the two bands of parental 'Chinese Spring' and another band with the same migration as the band of 'Imperial' rye. The wheat-rye ditellosomic addition line 4RL showed always the same pattern as the standard 'Chinese Spring' (Fig. 3). These results indicate that rye locus *Lap-2* (syn *Amp-2*) is located on the *4RS* chromosome arm of 'Imperial' rye.

The chromosomal location of the *Pgm-1*, *Ndh-1* and *Adh-1* structural genes was also carried out using the same seeds. The results indicated that these rye loci (*Pgm-1*, *Ndh-1* and *Adh-1*) are also located on the 4RS chromosome arm.

Discussion

The number of genes coding for isozymes that have now been located in rye is substantial (Schlegel et al. 1986; Hart 1987; Melz et al. 1992), but linkage data among isozyme loci appear to be scarce. Several isozyme loci have been located on chromosome 4R, but there is little data on linkage among them. The isozyme loci located in the chromosome arm 4RS are *Ndh-1*, *Dia-2* (diaphorase), *Adh-1*, *Pgm-1* and *Ep-2*

Table 2. Linkage data observed among loci located on the 4R chromosome and translocation 4RL/5RL (T)

Crosses	Loci[a]	Distribution of progeny (phenotype)				$\chi^2_{Linkage}$	Distance (cM)
		1111	*1211*	*1112*	*1212*		
RA-1	*Pgm-1, Ndh-1*	3	19	16	4	18.66	16.66 ± 5.27
RA-2	*Pgm-1, Adh-1*	2	20	24	1	35.76	6.38 ± 3.01
	Pgm-1, EPer-1	13	9	7	18	4.76	34.04 ± 5.38
	Adh-1, EPer-1	6	20	14	7	9.38	27.66 ± 5.51
AA-1	*Pgm-1, Adh-1*	6	27	29	4	32.06	15.15 ± 4.41
	Adh-1, EPer-1	24	11	12	19	6.07	34.85 ± 5.86
LE-1	*Pgm-1, Ndh-1*	40	19	22	38	11.49	34.45 ± 4.36
	Pgm-1, Lap-2	8	51	53	7	66.57	12.60 ± 3.04
	Ndh-1, Lap-2	24	38	37	20	8.07	36.97 ± 4.42
	T, *Pgm-1*	18	4	1	28	37.23	9.80 ± 4.16
	T, *Lap-2*	2	20	26	3	34.39	9.80 ± 4.16
LE-2	*Pgm-1, Ndh-1*	13	27	33	21	7.19	36.17 ± 4.95
	Pgm-1, Lap-2	9	31	35	19	14.92	29.78 ± 4.71
	Pgm-1, EPer-1	3	16	17	13	5.91	32.65 ± 6.70
	Lap-2, EPer-1	13	10	7	19	4.59	34.69 ± 6.80
	T, *Pgm-1*	36	11	3	40	42.62	15.55 ± 3.82
	T, *Lap-2*	9	38	35	8	35.26	18.88 ± 4.12
	T, *EPer-1*	4	17	15	9	8.03	28.88 ± 6.75
RA-2 + AA-1	*Pgm-1, Adh-1*	8	47	53	5	67.76	11.50 ± 3.00
LE-1 + LE-2	*Adh-1, EPer-1*	17	44	33	19	17.09	31.86 ± 4.38
	Pgm-1, EPer-1	31	24	19	39	8.03	38.05 ± 4.56
	Pgm-1, Ndh-1	67	32	45	71	18.63	35.21 ± 3.27
	Pgm-1, Lap-2	17	82	88	26	75.71	20.19 ± 2.75
	Ndh-1, Lap-2	43	65	62	43	7.89	40.37 ± 3.36
	T, *Pgm-1*	54	15	4	68	75.24	13.47 ± 2.87
	T, *Lap-2*	11	58	61	11	66.72	15.60 ± 3.05

[a] The *Adh-1*, *Pgm-1*, *Ndh-1* and *Lap-2* loci present two active alleles (*1* and *2*); the (*12*) and (*11*) phenotypes are heterozygous and homozygous plants, respectively. The *EPer-1* locus has one active (*2*) and one null allele (*1*), phenotypes (*11*) are homozygous plants for the null allele. In the case of translocation (T), phenotypes (*12*) and (*11*) are plants with 1IV + 5II and 7II, respectively

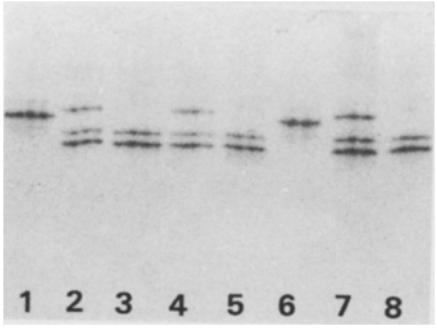

Fig. 3. Leucine aminopeptidase patterns of: *1 Secale cereale* L. cv 'Imperial', *2* 'Chinese Spring-Imperial' disomic addition line 4R, *3* 'Chinese Spring-Imperial' ditelocentric addition line 4RL, *4* 'Chinese Spring-Imperial' ditelocentric addition line 4RS, *5* euploid *Triticum aestivum* L. cv 'Chinese Spring', *6 Secale cereale* L. cv 'Imperial', *7* 'Chinese Spring-Imperial' disomic addition line 4R, *8* 'Chinese Spring-Imperial' ditelocentric addition line 4RL. The seeds used in growing ascensions 1–4 were supplied by Dr. T. E. Miller, and those in ascensions 5–8 by Dr. A. J. Lukaszewski

(endopeptidase). *Aat-4* (Aspartate aminotransferase, syn *Got-1*), *Eper-1*, and *Est-B* and *Est-10* (leaf esterases) loci have been located on the 4RL chromosome arm (see review of Liu and Gale 1991; Melz et al. 1992). Other loci such as *Cat-1* (catalases), *Ldh-1*, *Ldh-2* (lactate dehydrogenase) and *Lap-2* (syn *Amp-2*) have been associated with chromosome 4R but not precisely with one or the other chromosome arm (Melz et al. 1992; Thiele and Melz 1992).

The data obtained from the crosses RA-2 and AA-1 (without translocations) revealed that *EPer-1*, *Adh-1* and *Pgm-1* loci are linked (Table 2). The linkage map obtained using a three-point linkage analysis is consistent with previous data regarding the chromosome arm location of these loci. Our linkage data favour the gene order: *Eper-1*....(centromere)....*Adh-1*....*Pgm-1*. As given in Table 2, locus *Ndh-1* was linked to *Pgm-1* (16.66 ± 5.27 cM), and in a different cross (PA-1) *Ndh-1* and *Adh-1* showed an independent assortment (data not presented), indicating that *Ndh-1* had a more telomeric location (also stated by Figueiras et al. (1991a, b)). So, the data obtained in our crosses without translocations support the loci order: *EPer-1*....(centromere)....*Adh-1*....*Pgm-1*....*Ndh-1* (Fig. 4).

The loci *EPer-1*, *Lap-2*, *Pgm-1* and *Ndh-1* were linked in crosses with the interchange *4RL/5RL*(LE-1 and LE-2). In addition, the presence of chiasmata at interstitial segments in these quadrivalents was never detected in MI configurations. Therefore, the es-

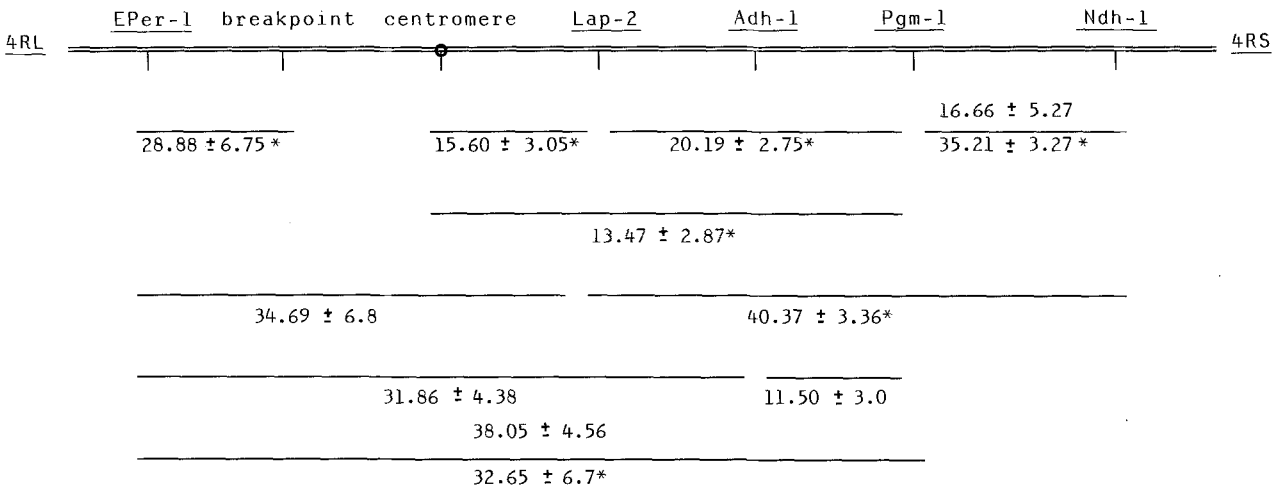

Fig. 4. A map of rye chromosome 4R with isozyme and cytological markers. The *Eper-1* locus is located on the 4RL chromosome arm and the *Adh-1*, *Lap-2*, *Pgm-1* and *Ndh-1* loci are located on the 4RS chromosome arm. The order of the loci has been estimated using three-point linkage analyses, and the distances between the loci were estimated by means of maximum likelihood method and two-point linkage analyses. In the backcrosses, distance = (recombinant/total progeny) × 100. *Genetic distances obtained in backcrosses involving translocation 4RL/5RL

timated distances between loci located on the 4RS chromosome arm (non-translocated arm) and the translocation 4RL/5RL in fact represent the distance between the loci and the centromere. In the same way, the estimated distances between loci located on the 4RL chromosome arm (that is the translocated arm) and the translocation 4RL/5RL really represent the distance between those loci and the breakpoint.

The most probable gene order using three-point linkage analysis in all possible combinations is: *EPer-1*.. (breakpoint-centromere) .. *Lap-2*.. *Pgm-1*.... *Ndh-1* (Fig. 4). However, three-point linkage analysis among breakpoint-centromere, *Lap-2* and *Pgm-1* suggests the gene order: *Lap-2*.. (breakpoint-centromere).. *Pgm-1*. This gene order on chromosome 4R suggests that the *Lap-2* locus could be located on the 4RL chromosome arm. Previous data obtained by Koebner and Martin (1989) indicated that the *Lap-2* locus (syn *Amp-2*) is located on the 4RL chromosome arm. However, in a more recent review about non-homoeologous translocations between groups 4, 5 and 7 chromosomes within wheat and rye, Liu et al. (1992) suggested a 4RS chromosome arm location for the locus *Lap-2* based on a personal communication of R. M. D. Koebner. This misinterpretation was also observed in our results presented here: on the one hand, linkage data suggest a 4RL location and, on the other hand, isoelectric focusing of wheat-rye disomic and ditellocentric addition lines indicates a 4RS location. We calculated the coincidence coefficient (c) and chromosomal interference (I) between the zones delimited by these three points (breakpoint-centromere, *Lap-2* and *Pgm-1*) in the two crosses with the 4RL/5RL interchange (LE-1 and LE-2). The results obtained indicate a high negative interference in the LE-1 cross, ($c = 4.0833$ and $I = -3.0833$) and $c = 1.1354$ and $I = -0.1354$ in the LE-2 cross. Negative interference has been found in interchange heterozygotes of rye reported by Sybenga and Mastenbroeck (1980), who stated that sometimes it is possible to get an order that is actually different from the real gene order. Therefore, the different gene order obtained (*Lap-2*.. (breakpoint-centromere) .. *Pgm-1*) could come from the fact that the chromosomal location was obtained from 'Imperial' rye, while our cytogenetic map came from 'Ailes'. However, we believe that the different order obtained for breakpoint-centromere, *Lap-2* and *Pgm-1* is probably due to the high negative interference detected and that the locus *Lap-2* is in fact located, together with the loci *Pgm-1*, *Adh-1* and *Ndh-1*, on the 4RS chromosome arm, as demonstrated by isoelectric focusing (Fig. 3). The linkage data obtained in all of our crosses favour the gene order: *EPer-1*.. (breakpoint-centromere).. *Lap-2*.... *Adh-1*.... *Pgm-1*.... *Ndh-1* (Fig. 4).

The chromosomal location and the linkage data are consistent with data previously reported (Melz et al. 1992). Wricke (1991) and Wheling (1991) have obtained a map of the 4R chromosome with three isozyme loci: *Got-1*.... *LEst-10*... (centromere).. *Pgm-1*. The genetic distances estimated between *Got-1* and *LEst-10* and between *LEst-10* and *Pgm-1* were 36 ± 3.8 cM and 22 ± 4.1 cM, respectively. The genetic distances obtained by Wheling (1991) and our results suggest that the most probably gene order is: *Got-1*.... *EPer-1*.... *LEst-10*.. (centromere).. *Lap-2*.... *Adh-1*.... *Pgm-1*.... *Ndh-1*.

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References

Benito C, Gallego FJ, Zaragoza C, Frade JM, Figueiras AM (1991a) Biochemical evidence of a translocation between 6RL/7RL chromosome arms in rye (*Secale cereale* L.). A genetic map of 6R chromosome. Theor Appl Genet 82: 27–32

Benito C, Zaragoza C, Gallego FJ, De la Peña A, Figueiras AM (1991b) A map of rye chromosome 2R using isozyme and morphological markers. Theor Appl Genet 82:112–116

Figueiras AM, González-Jaen MT, Salinas J, Benito C (1985) Association of isozymes with a reciprocal translocation in cultivated rye (*Secale cereale* L.). Genetics 109:177–193

Figueiras AM, Elorrieta MA, Benito C (1989) Association of four isozyme loci with a reciprocal translocation between 1R/4R chromosomes in cultivated rye (*Secale cereale* L.). Theor Appl Genet 78:224–228

Figueiras AM, González-Jaén MT, Candela M (1990) Chromosomal identification and meiotic behavior of reciprocal translocations in a rye polymorphic population. Evolutionary implications. Theor Appl Genet 79:686–692

Figueiras AM, Zaragoza C, Gallego FJ, Benito C (1991a) NADH dehydrogenase: a new molecular marker for homoeology group 4 in Triticeae. A map of the 4RS chromosome arm in rye. Theor Appl Genet 83:169–172

Figueiras AM, Elorrieta MA, Benito C (1991b) Genetic and cytogenetic maps of chromosomes 1R, 4R and 7R in cultivated rye (*Secale cereale* L.). Genome 34:681–685

Hart GE (1987) Genetic and biochemical studies of enzymes. In: Heyne EG (ed) Agronomy Series, vol 13: wheat and wheat improvement. Madison, Wis., pp 169–215 Madison, Wisconsin

Koebner RMD, Martin PK (1989) Chromosomal control of the aminopeptidase of wheat and its close relatives. Theor Appl Genet 78:657–665

Liu CJ, Gale MD (1991) The chromosomal location of genes encoding NADH dehydrogenase isozymes in hexaploid wheat and related species. Genome 34:44–51

Liu CJ, Atkinson MD, Chinoy CN, Devos KM, Gale MD (1992) Non-homoeologous translocations between group 4, 5 and 7 chromosomes of wheat and rye. Theor Appl Genet 83:305–313

Melz G, Schlegel R, Thiele V (1992) Genetic linkage map of rye (*Secale cereale* L.) Theor Appl Genet 85:33–45

Salinas J, Pérez de la Vega M, Benito C (1981) The chromosomal location of the embryo plus scutellum alcohol dehydrogenase isozymes in the hexaploid wheat kernel. Euphytica 30:729–734

Schlegel R, Melz G, Mettin D (1986) Rye cytology, cytogenetics and genetics. Current status. Theor Appl Genet 72:721–734

Sybenga J, Mastenbroeck I (1980) Combined genetic and cytological analysis of positive and negative interference in an interchange heterozygote of rye (*Secale cereale* L.). Heredity 44:83–92

Thiele V, Melz G (1991) Chromosomal location of genes controlling lactate dehydrogenase in rye, wheat and barley. Genome 35:32–34

Wehling P (1991) Inheritance, linkage relationships and chromosomal localization of the glutamate oxaloacetate transaminase, acid phosphatase and diaphorase isozyme genes in *Secale cereale* L. Theor Appl Genet 82:569–576

Wricke G (1991) A molecular marker linkage map of rye for plant breeding. Votr Pflanzenzuecht 20:72–78