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Biochemical evidence of a translocation between *6RL/7RL* chromosome arms in rye (*Secale cereale* L.). A genetic map of *6R* chromosome

C. Benito *, F. J. Gallego, C. Zaragoza, J. M. Frade and A. M. Figueiras
Department of Genetics, Faculty of Biology, University Complutense, E-28040 Madrid, Spain

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Summary. The segregation of different isozymic loci was investigated in backcrosses and F_2s in rye. The leucin aminopeptidase-1 (*Lap-1*), Aconitase-1 (*Aco-1*), Esterase-6 (*Est-6*), Esterase-8 (*Est-8*), and Endopeptidase-1 (*Ep-1*) loci were linked. The *Aco-1*, *Est-6*, and *Est-8* loci have been previously located on the *6R*L chromosome arm. The *Lap-1* locus has been located on the *6R*S chromosome arm. The results favor the gene order: *Lap-1* . . . (centromere) . . . *Aco-1* . . . *Est-8* . . . *Est-6* . . . *Ep-1*. The isoelectric focusing separations of aqueous extracts from mature embryo tissue of wheat-rye addition and substitution lines involving the chromosomes of cereal rye *Secale cereale* L. confirmed the gene location of locus *Ep-1* on the *6R*L chromosome arm. Screening of wheat-rye addition lines involving the chromosomes of *Secale montanum* revealed that *Ep-1* locus is not located on chromosome *6R* of *S. montanum*. These results are the first biochemical evidence of the translocation between chromosome arms *6R*L/*7R*L in the evolution of *S. cereale* from *S. montanum*.

Key words: Isozymes – Genetic mapping – Chromosome *6R* – Endopeptidase – *Secale cereale*

Introduction

Genetic and cytogenetic maps that consider both seed protein polymorphism and isozyme loci have been reported in rye by Singh and Shepherd (1984, 1988 a, b), Lawrence and Appels (1986), and Benito et al. (1990). On the other hand, cytogenetic maps including data on translocations and morphological markers have been reported by De Vries and Sybenga (1984), and on translocations and isozyme markers by Figueiras et al. (1985, 1989). Linkage data are available for esterases (Wehling and Schmidt-Stohn 1984; Wehling et al. 1985), endosperm and embryo peroxidases (García et al. 1982), leaf peroxidases (Benito et al. 1990), 6-phosphogluconate dehydrogenase and glucose phosphate isomerase (Lawrence and Appels 1986), 6-phosphogluconate and malate dehydrogenase, glutamate oxaloacetate transaminase and malate dehydrogenase (Figueiras et al. 1985), endosperm alkaline phosphatases (Figueiras et al. 1987), and esterases and malate dehydrogenase and glutamate oxaloacetate transaminase (Figueiras et al. 1991).

Although loci codifying for isozyme markers have been located in rye chromosome arms (Bergman and Maan 1973; Tang and Hart 1975; Hart 1979; Rao and Rao 1980; Chojecki and Gale 1982; Salinas and Benito 1984 a, b, 1985 a, b; Lawrence and Appels 1986; Chenicek and Hart 1987), the corresponding genetic and cytogenetic maps are poorly developed. On the other hand, several isozyme loci have been located on chromosome *6R* (see Tables 1 and 3), but linkage data are not available.

Here we present linkage data among isozyme loci located on the *6R* chromosome (a map of chromosome *6R*), the chromosomal location of the endopeptidase-1 locus in rye, and biochemical evidence of the translocation between chromosome arms *6R*L/*7R*L in the evolution of *Secale cereale* L. from *Secale montanum* L.

Materials and methods

Plant materials

(i) The following genetics stocks were examined during the chromosomal location of the structural genes for endopeptidase isozymes: "Chinese Spring," "Holdfast," and "Kharkov"

* To whom correspondence should be addressed

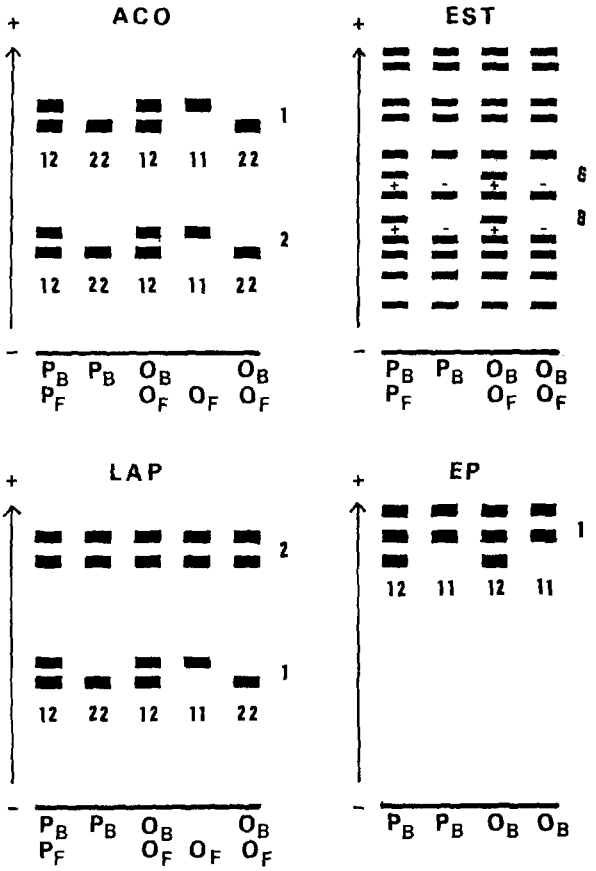

Fig. 1. Diagrammatic representation of the leaf isozymes. The different activity zones observed in each isozyme system are indicated on the *right*, and the different genotypes (11, 12, and 22) or phenotypes (+ and −) shown by the plants are indicated *below* each activity zone. The *Aco-1*, *Aco-2*, *Lap-1*, and *Ep-1* loci show two active alleles; the *Est-6* and *Est-8* loci show one active and one null allele. P_F = parent of F_2-like progenies, P_B = parent of backcrosses, O_F = offspring of the F_2-like progenies, O_B = offspring of the backcrosses

hexaploid wheats (*Triticum aestivum* L.); "Imperial," "King II," and "Dakold" ryes (*Secale cereale* L.); *Secale montanum* L.; wheat-rye addition and substitution lines involving the chromosomes of cereal rye, *S. cereale*, varieties "Imperial," "King II," and "Dakold;" and wheat-rye addition lines involving the chromosomes of *S. montanum*. (These materials were supplied by Prof. E. R. Sears, Dr. T. E. Miller, and Dr. J. P. Gustafson.)
(ii) The following crosses were analyzed in order to map the *6R* chromosome: three F_2-like progenies (called S1, S2, and S3) obtained by self-pollination of plants belonging to the rye cultivar "Ailés" and two backcrosses (named R1 and R2) between plants of cultivar "Ailés" and the inbred line "Riodeva."

Electrophoresis

(i) Chromosomal location of structural genes for endopeptidase isozymes was performed as follows. Crude extracts for electrophoresis were prepared by incubating a small segment of mature seed, including the embryo, in 40 l of distilled water at room temperature for 1–2 h. The isoelectric focusing separations were made using the method described by Koebner et al. (1988), and the staining method was adapted from Hart and

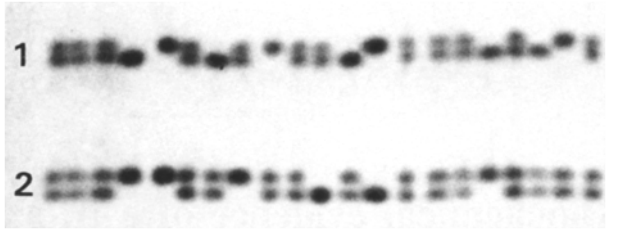

Fig. 2. Aconitase (ACO) zymograms shown by the plants of the F_2-like progeny. The different activity zones are indicated on the *left*. The heterozygous plants for *Aco-1* and *Aco-2* loci present two bands in each activity zone, the homozygous plants present one band in each activity zone. The aconitase isozymes show monomeric behavior

Table 1. Chromosomal location of isozyme structural genes that segregated in the three F_2-like progenies and the two backcrosses analyzed

Loci	Chromosome or chromosome arm
Mdh-1	*1RL*
Per-2 (leaf peroxidases)	*2RS*
Got-3	*3RL*
Aco-2	*5RL*
Lap-1	*6RS*
Aco-1	*6RL*
Est-6	*6RL*
Est-8	*6RL*
Ep-1	*6R* or *7R?*
Acph-1	*7RL*

Langston (1977). The gels were incubated at room temperature for about 1 h in a 0.5% agar solution containing 1 mg/ml Fast Black K (Sigma) and 0.5 mg/ml BANA (Sigma) in 0.1 *M* Trizma-maleate-NaOH, pH 5.8. Fast Black K and BANA were predissolved in 0.5–1.0 ml N-N′-dimethylformamide (Koebner et al. 1988).

These analyses were carried out by Dr. A. Delibes in the School of Agricultural Engineering of Madrid (Department of Biochemistry).
(ii) The following methods were used in order to map the *6R* chromosome. Electrophoresis was performed in horizontal 12% starch gels, using buffers and staining methods described by Brewer and Sing (1970), Figueiras et al. (1985, 1989), and Chenicek and Hart (1987). The following isozymatic systems were carried out simultaneously over 12-day-old leaves extracts: acid phosphatase (ACPH), peroxidase (PER), aconitase (ACO), esterase (EST), endopeptidase (EP), Leucin aminopeptidase (LAP), glutamate oxaloacetate transaminase (GOT), and malate dehydrogenase (MDH).

Results

A genetic map of the 6R chromosome in rye

The isozymic pattern for both the parental and the progeny plants of the three F_2-like progenies (S1, S2, and S3) and the two backcrosses (R1 and R2) is shown in Fig. 1.

Table 2. Linkage data observed among the loci located on the *6 R* chromosome

Loci	Distribution of progeny (phenotype)				χ^2 Linkage	Distance (cM)
	++	+−	−+	−−		
Pooled data of the three F_2-like progenies: S1+S2+S3						
Aco-1, Lap-1	162	38	31	25	14.06***	33.66±3.77
Lap-1, Est-6	115	39	35	9	0.38	–
Pooled data of the two backcrosses: R1+R2						
Ep-1, Est-6	18	61	54	33	24.67***	30.72±3.58
Ep-1, Est-8	61	18	34	56	23.16***	31.33±3.60
Ep-1, Aco-1	25	31	40	26	3.28	–
Aco-1, Est-6	46	19	19	41	19.21***	30.40±4.11
Aco-1, Est-8	19	46	42	18	20.81***	29.60±4.08
Est-6, Est-8	1	83	114	0	194.02***	0.51±0.50

In the F_2-like progenies, the phenotype+ indicates homozygous for allele 1 (11) and heterozygous for alleles 1 and 2 (12). Phenotype − indicates homozygous for allele 2 (22). In the backcrosses, the phenotype+ indicates heterozygous for alleles 1 and 2 (12) and phenotype− indicates homozygous for allele 2 (22). The *Est-6* and *Est-8* loci showed null alleles; therefore the phenotype− always indicates homozygous for the null allele, whereas phenotype+ indicates heterozygous for active and null alleles, and homozygous for active alleles in F_2-like progenies (see Fig. 1)
*** $P<0.001$

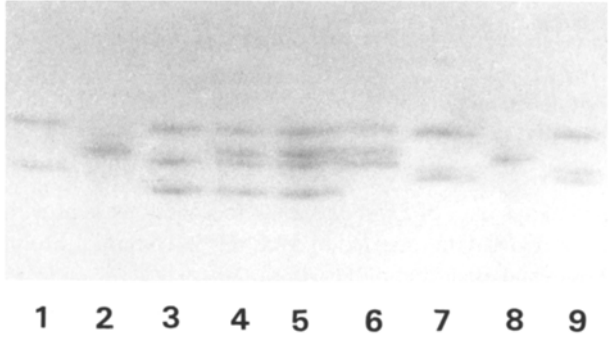

Fig. 3. Endopeptidase patterns of: *1* "Chinese Spring – *Secale montanum*" addition line *6 R, 2 Secale montanum, 3 Triticum aestivum* cv "Holdfast," *4* "Holdfast – King II" telocentric substitution line *6 A/6 R*L, *5* telocentric substitution line *6 B/6 R*L, *6* telocentric substitution line *6 D/6 R*L, *7 Secale cereale* cv King II or cv "Imperial", *8 Triticum aestivum* cv "Chinese Spring," *9* "Chinese Spring – Imperial" disomic addition line *1R*

These progenies segregated for ten different loci located on six of the seven different rye chromosomes (Table 1). The *Got-3*, *Acph-1*, and *Mdh-1* loci showed two active alleles in all crosses analyzed, as well as dimeric behavior. The *Aco-1*, *Aco-2* (Fig. 2), *Lap-1*, and *Ep-1* loci also showed two active alleles in all crosses and monomeric behavior (Fig. 1). The *Per-2*, *Est-6*, and *Est-8* showed one active and one null allele. Therefore, for the last group of loci, it is not possible to distinguish the homozygotes for active alleles from the heterozygotes.

The linkage relationships between the isozymic loci are shown in Table 2. It can be seen that *Lap-1*, *Aco-1*, *Est-8*, *Est-6*, and *Ep-1* loci were linked. The remaining loci analyzed (*Per-2*, *Mdh-1*, *Got-3*, *Acph-1*, and *Aco-2*) showed independent assortment. The data of the three F_2-like progenies (S1+S2+S3) and the two backcrosses (R1+R2) can be pooled, since the X heterogeneity test was not significant at the 5% level.

The chromosomal location of the structural genes for rye endopeptidase-1

The endopeptidase patterns of standard "Chinese Spring" and "Holdfast" wheats as visualized by isoelectric focusing (Figs. 3 and 4) consisted of three bands. The endopeptidase patterns of *S. montanum* and *S. cereale* cultivars "Imperial" and "King II" had one band (Figs. 3 and 4), while the endopeptidase patterns of hexaploid wheat "Kharkov" and rye "Dakold" showed two bands (Fig. 4). The seven wheat-rye addition lines "Chinese Spring – Imperial" showed the same three bands as standard "Chinese Spring," but only the addition line with rye chromosome *6R* showed a pattern with a different relative staining intensity, being one band more intense (Fig. 4). The three wheat-rye telocentric substitution lines "Holdfast–King II" involving the rye chromosome arm *6R*L (*6A/6R*L, *6B/6R*L, and *6D/6R*L) showed the three bands of the parental wheat "Holdfast" (except *6D/6R*L line, which had two wheat bands) and another band with the same migration as the band of rye cultivars ("Imperial" and King II") (Fig. 3). The wheat-rye addition line "Kharkov–Dakold" with chromosome *6R* had the two bands of "Kharkov" and another band with a similar migration to the "Dakold" rye band. The wheat-rye addition line "Chinese Spring–*S. montanum*" with chromosome *6R* showed the same pattern as standard "Chinese Spring" (Fig. 3). The wheat-rye addition line "Chinese Spring–*S. montanum*" involving chromosome

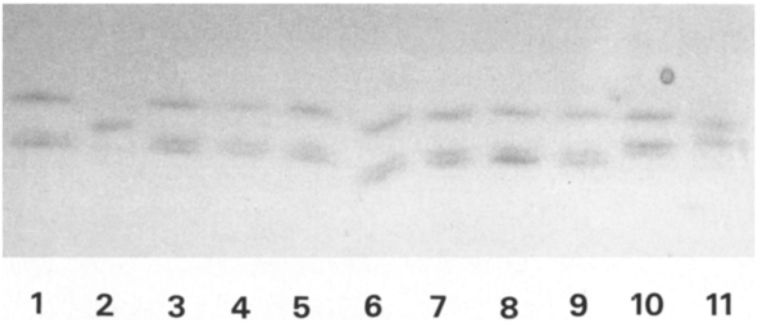

Fig. 4. Endopeptidase patterns of: *1 Triticum aestivum* cv "Chinese Spring," *2 Secale cereale* cv "Imperial" or cv "King II," "Chinese Spring – Imperial" disomic addition lines, *3 1R, 4 2R, 5 3R, 6 4R, 7 5R, 8 6R, 9 7R, 10* "Kharkov – Dakold" disomic addition line *6R, 11 Secale cereale* cv "Dakold"

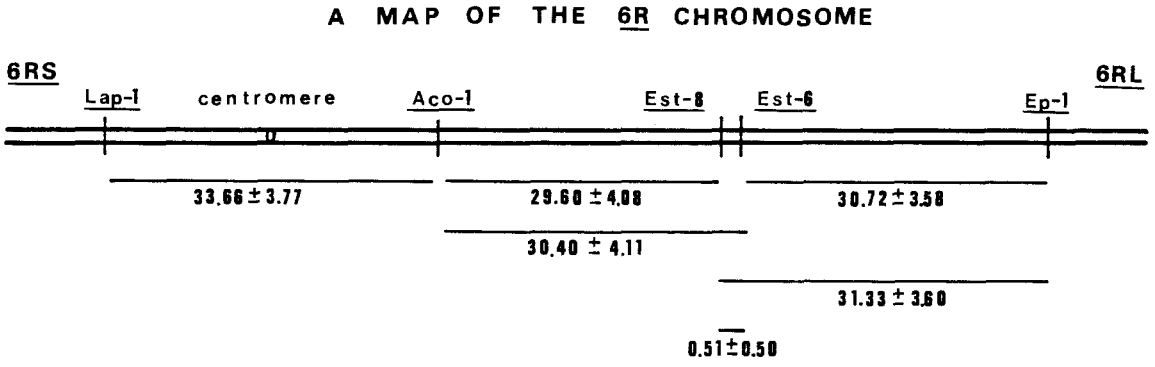

Fig. 5. A map of rye chromosome *6 R* with isozyme markers. The *Lap-1* locus is located on the *6 RS* chromosome arm and the *Aco-1*, *Est-8*, *Est-6*, and *Ep-1* loci are located on the *6 R*L chromosome arm. The distances between the loci were estimated by means of the maximum likelihood method. In the backcrosses, distance = (recombinant/total progeny) × 100

7R was not available. The results indicate that the rye *Ep-1* locus is located on chromosome *6R* of the "Imperial" and "Dakold" cultivars, and on the *6R*L chromosome arm of "King II." The *6R* chromosome of *S. montanum* does not carry information for endopeptidase isozymes.

Discussion

The number of structural genes coding for isozymes that have now been located in rye is substantial (Hart and Tuleen 1983; Figueiras et al. 1985; Schlegel et al. 1986; Hart 1987), but linkage data among isozyme loci appears to be infrequent. Several isozyme loci have been located on chromosome *6R* (see Table 3), but linkage data among these loci are not available.

Our data reveal that *Lap-1*, *Aco-1*, *Est-8*, *Est-6*, and *Ep-1* loci are linked (Table 2). The linkage map obtained for these five loci on chromosome *6R* is consistent with the previous data regarding chromosome arm location of these loci (Table 3). The remaining five loci analyzed showed independent assortment and also with the loci of chromosome *6R*. These results are in agreement with the previous location data (Table 1). The linkage data favor the gene order: *Lap-1* . . . (centromere) . . . *Aco-1* . . . *Est-8* . . . *Est-6* . . . *Ep-1* (Fig. 5). The chromosomal location and the linkage data of *Est-6* and *Est-8* loci are consistent with the previous data reported by Wehling and Schmidt-Stohn (1984) and Benito et al. (1990).

Previous data on the chromosomal location of the *Ep-1* locus in rye are inconsistent. In a review of Hart and Tuleen (1983), the *Ep-1* locus is located on chromosome 6/7. Later, Schlegel et al. (1986), in another review, indicated that the *Ep-1* locus is on chromosome *7R* [they cited the review of Hart and Tuleen (1983)]. Koebner et al. (1988), using isoelectric focusing, indicated that the *Ep-1* locus is located on the *7R*L chromosome arm of "King II" rye and on chromosome *7R* of "Imperial" rye. In a new review of Hart (1987), the *Ep-1* locus is placed on chromosome *6R* of "Imperial" rye (he cited an unpublished paper of G. E. Hart and N. A. Tuleen).

At this moment, the only endopeptidase pattern of wheat-rye addition lines has been published by Koebner et al. (1988). These authors used isoelectric focusing techniques and pointed out that "Chinese Spring" wheat have two or three endopeptidase bands (the seeds of "Chinese Spring" were heterogeneous). The wheat-rye addition lines with the *7R* chromosome have three endopeptidase bands, and these bands probably came from the "Chinese Spring" cultivar. Our chromosomal location data pointed out that locus *Ep-1* is located on the *6R*L chromosome arm of the "King II" cultivar, because the three telocentric substitution lines (Fig. 3) showed the three endopeptidase

Table 3. Rye characters located on chromosome *6R*

Locus	Chromosome/arm	References
Lap-1 = Amp-1	*6RS*	Schlegel et al. 1986 Tang and Hart 1975
Got-2 = Aat-2	*6RL*	Schmidt et al. 1984 Tang and Hart 1975
6-Pdg-1	*6RL*	Rao and Rao 1980 Salinas and Benito 1985a
Aadh-2 = Adh-3	*6RL*	Schmidt et al. 1984 Hart and Tuleen 1983
Aco-1	*6RL*	Chenicek and Hart 1987
Est-2	*6RL*	Schmidt et al. 1984 Artyomova 1982
Est-5	*6RL*	Miller 1984
Est-6, Est-8	*6RL*	Salinas and Benito 1983 Wehling et al. 1985
-Amy-1	*6RL*	Miller 1984
Ep-1	*6RL* *6R*	Our data Hart 1987 (unpublished results)
SPer (embryo)	*6R*	Salinas and Benito 1984b
Co Corroded plant habit	*6RS*	Miller 1984
Alt1 Aluminum tolerance	*6RS*	Aniol and Gustafson 1984
wh White plant	*6RS*	De Vries and Sybenga 1984
Ha3 Hairy peduncle	*6R*	Schlegel et al. 1986
Pro Prolin	*6R*	Evans and Scoles 1980
Sf4 Self-fertility	*6R*	Schlegel et al. 1986
Pm5 Powdery mildew (*Erisiphe graminis*) resistance	*6R*	Lind 1982
Yr3 Stripe rust (*Puccinia striiformis*) resistance	*6RL*	Miller 1984
Reg Red grain	*6RL*	Miller 1984
Rog Round grain	*6RL*	Miller 1984

bands on "Holdfast" wheat (except the *6D/6R*L line) and another endopeptidase band with the same migration as rye band. The endopeptidase pattern on the wheat-rye "Chinese Spring–Imperial" addition line with chromosome *6R* showed a different relative staining intensity of the three bands (Fig. 4). One of the endopeptidase bands observed in the "Dakold" rye was present in the wheat-rye "Kharkov–Dakold" addition line with chromosome *6R*. However, the "Chinese Spring–*Secale montanum*" addition line chromosome *6R* did not show the rye band. Therefore, our linkage data pointed out that the *Ep-1* locus is located on the *6R*L chromosome arm; these are consistent with our chromosomal location data. Moreover, the *Acph-1* locus, located on the *7R*L chromosome arm (Salinas and Benito 1985), and the *Ep-1* locus showed independent assortment.

It has been proposed that in the evolution of *S. cereale* from *S. montanum*, at least two interchanges involving chromosome arms *7RS/4RL* and *6RL/7RL* (Koller and Zeller 1976) have taken place. The *Ep-1* locus has been located on the *6R*L chromosome arm of *S. cereale*, but no information was found on chromosome *6R* of *S. montanum* (addition line with chromosome *7R* is not available). In *Triticum aestivum*, the structural genes for endopeptidase have been located on the *7B*L and *7D*L chromosome arms (Hart and Langston 1977; Koebner et al. 1988). These results are biochemical evidence of the translocation *6RL/7RL* in the evolution of *S. cereale* from *S. montanum*. Also, these data suggest that chromosome *6R* of rye is partially homoeologous with chromosomes *7B*L and *7D*L of wheat.

A series of morphological and resistance genes have been located on chromosome *6R* (Table 3). Moreover, the locus for eyespot disease resistance caused by the fungus *Pseudocercosporella herpotrichoides* (this locus came from *Aegilops ventricosa* and has been introduced by recombination into *T. aestivum*) is closely linked to the *Ep-1* loci located on the long arms of group 7 chromosomes of wheat (Law et al. 1988; Worland et al. 1988). Studies on the resistance to *Ps. herpotrichoides* carried out by Riley and Macer (1966) indicated a poligenic control of this character in *Secale cereale*. Other resistance genes have been located on the *6R*L chromosome arm in rye (stem rust resistance caused by the fungus *Puccinia striiformis*) and on chromosome *6R* (powdery mildew resistance caused by the fungus *Erisiphe graminis*). Several resistances to diseases caused by fungus have been related with rye chromosome *6R*, and it will be interesting to learn the linkage relationships between these resistances and the *Ep-1* locus. Genetic maps simultaneously using isozymes, morphological, and resistance markers have been poorly developed, and the exploitation of linkages between chromosomal markers and genes controlling agronomic traits can be expected to increase with the development of further biochemical and molecular markers in the Triticeae species.

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