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Biochemical evidence of homoeology between *Triticum aestivum* and *Agropyron intermedium* chromosomes

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Summary. The alcohol dehydrogenase (ADH), phosphoglucose mutase (PGM), glucosephosphate isomerase (GPI), glutamic oxaloacetic transaminase (GOT), malate dehydrogenase (MDH), leaf esterases (ESTL), leaf acid (ACPH) and endosperm alkaline (PHE) phosphatases, leaf peroxidases (PERL) zymogram phenotypes of *Triticum aestivum, Agropyron intermedium, Triticum aestivum – Agropyron intermedium* octoploids and six *Agropyron intermedium* chromosome additions to *Triticum aestivum* and two ditelocentric addition lines were determined. It was found that the six disomic chromosome addition lines and one ditelocentric chromosome addition line could be distinguished from one another and from the other possible lines on the basis of the zymogram phenotypes of these isozymes. The structural gene *Acph-X1* was located on *Agropyron* chromosome L1, the genes *Got-X3* and *Mdh-X2* on chromosome L2, the gene *Gpi-X1* on chromosome L3, the genes *Adh-X1, Pgm-X1* and *Phe-3* on chromosome L4, gene *Perl-1* on chromosome L5 and the gene *Estl-2* on chromosome L7 and chromosome arm L7d2. These gene locations provide evidence of homoeology between *Agropyron* chromosomes L1, L2, L3, L4, L5 and L7 and the *Triticum aestivum* chromosomes of homoeologous groups 7, 3, 1, 4, 2 and 6, respectively.

Key words: Chromosomal location – Isozyme markers – *Agropyron intermedium*

Introduction

In genetic studies, enzyme markers for chromosomes facilitate the detection of the presence of specific chromosomes or chromosome segments. Such markers are also useful in the mapping of chromosomes and in the identification of chromosomal translocation.

A considerable number of wheat lines which contain alien genetic material (added or substituted) have ben produced by cytogeneticists taking advantage of the ability of hexaploid wheat to admit aneuploidy. The chromosomal location of structural genes for isozymes can provide information on chromosome homology and homoeology as well as on genetic relationships among related species (Tang and Hart 1975; Hart and Langston 1977; Hart et al. 1980; Powling et al. 1981; Hart and Tuleen 1983 a). The genetics of wheat isozymes and the characterization of alien genetic material using isozyme markers have been recently reviewed by Hart (1983, 1984) and Hart and Tuleen (1983 b).

This paper reports the locations of various structural genes controlling different isozymes of the hexaploid *Agropyron intermedium* (genome X). Also, biochemical evidence of homoeology among hexaploid wheat, rye, barley, *Agropyron elongatum (Elytria elongata)* and *Agropyron intermedium* is discussed.

Material and methods

This study was carried out with material produced by Dr. Y. Cauderon (C.N.R.A., 78000-Versailles). The material consisted of *Triticum aestivum* cv. 'Vilmorin 27' (V-27), *Agropyron intermedium* (AI) (the particular line of *A. intermedium* used in the original cross was not available) and the V-AI disomic addition lines, except for the L6 line, the ditelocentric addition lines L7d1 and L7d2 and the amphiploid TAF-46 (octoploid).

The analyses were carried out with both parts of individual kernels, specifically the endosperm (E), and 12-day-old seedling leaves (L). The zymogram phenotypes of the leaf isozymes for phosphoglucose mutase (PGM), glucosephosphate isomerasa (GPI), glutamic oxaloacetic transaminase (GOT), malate dehydrogenase (MDH), esterases (ESTL), acid phosphatases (ACPH) and peroxidases (PERL) was determined. Also, the endosperm alkaline phosphatases (PHE) and the endosperm alcohol dehydrogenase (ADH) zymogram were analyzed.

Information on PHE was obtained using polyacrilamide gel slabs (10%) following the protocol described by Salinas and Benito (1984). The nomenclature used for these isozymes has been described by Salinas and Benito (1985). ADH was analyzed in starch gels following the protocol described by Salinas et al. (1981).

The remaining isozymes analyzed (PGM, GPI, GOT, MDH, ESTL, ACPH and PERL) were electrophoresed following the protocols described by Benito et al. (1985); Salinas et al. (1985); Figueiras et al. (1985) and Salinas and Benito (1984a), and the staining methods used have been previously described by Brewer and Singh (1970). The nomenclature used for these isozymes is also described in the works mentioned above.

In the addition lines studied all enzyme systems showed the presence of the wheat isozymes and, sometimes, the additional presence of specific *Agropyron* isozymes.

Results

1 Alcohol dehydrogenase (ADH) (Fig. 1)

The ADH zymogram phenotype of 'Vilmorin-27' wheat showed three isozymes: ADH-1, ADH-2 and ADH-3, in order of decreasing electrophoretic mobility; with relative staining intensities of 1:4:4, respectively. The octoploid TAF-46 and the addition line with L4 chromosome express five ADH isozymes. The zymogram phenotype of *Agropyron intermedium* showed one isozyme, named ADH-1, with a slower migration than V-27 ADH-3 isozyme. The mobility of the three more anodal isozymes corresponds to the V-27 isozymes and the most cathodal isozyme to *Agropyron* ADH-1. The fifth form, not expressed by either V-27 or *Agropyron,* is intermediate in mobility between V-27 ADH-3 and *Agropyron* ADH-1. The relative staining intensities observed in order of decreasing electrophoretic mobility for these five isozymes were 1:4:6:4:1, respectively.

The triplicate structural genes which produce the wheat ADH isozymes are located on chromosomes 4A, 4B and 4D (Hart 1970; Hart and Langston 1977). These structural genes code subunits which have been designated α, β and δ, respectively. It has been proposed that random association of these protomers results in the production of six types of dimers which are expressed as ADH-1 ($\alpha\alpha$ dimers), ADH-2 ($\alpha\beta$ and $\alpha\delta$ dimers), and ADH-3 ($\beta\beta$, $\delta\delta$ and $\beta\delta$). The *Agropyron* structural gene codes for a subunit designated γ. A hypothesis consistent with the results of this study is that the five isozymes observed in octoploids and addition line L4 are composed of all possible dimeric combinations of four subunits, namely α, β and δ produced by wheat and an additional protomer designated γ, which is encoded by an *Agropyron* gene. An schematic model for the subunit composition of the three ADH isozymes of V-27, of *Agropyron* ADH-1 and of the five isozymes observed in octoploids and disomic addition line L4 is shown in Table 1. Three dimeric forms which were not found in either parents are assumed to be produced by octoploids and the addition line L4. ADH-4 is composed of $\delta\gamma$ and $\beta\gamma$ dimers while the $\alpha\gamma$ dimers have the same mobility as V-27 ADH-3.

If the four subunits are produced in the same quantities and associate randomly to form active dimeric molecules, the expected distribution of the 10 dimeric types contained in the octoploids and in the addition line L4 will be based on $(p+q+r+s)^2$, where p, q, r and s would be the frequencies of α, β, δ and γ, respectively. In the octoploids and the disomic addition line L4, $p=q=r=s=1/4$.

The expected distribution of the isozymes are shown in Table 1. The observed relative staining intensities of the five bands are in good agreement with this distribution.

2 Phosphoglucose mutase (PGM) (Figs. 1 and 2)

The V-27 had two major isozymes, designated PGM-1 and PGM-3, with relative staining intensities of 1:2, respectively. AI showed an isozyme, PGM-1, with a faster anodal migration than those of V-27. The octoploids and the addition line L4 exhibited a three band zymogram: the most cathodal isozymes have the same migration as V-27 bands and the most anodal isozyme

Table 1. Schematic models for the subunit composition of the ADH isozymes produced by *T. aestivum* cv. 'Vilmorin', *Agropyron intermedium* (AI), amphiploid (octoploid) TAF-46 and the V-AI addition line L4

Isozymes	V	AI	V-AI-L4	TAF-46
ADH-1	1/9[a] $\alpha\alpha$		1/16 $\alpha\alpha$	1/16 $\alpha\alpha$
ADH-2	4/9 $\alpha\beta$, $\alpha\delta$		4/16 $\alpha\beta$, $\alpha\delta$	4/16 $\alpha\beta$, $\alpha\delta$
ADH-3	4/9 $\beta\beta$, $\beta\delta$, $\delta\delta$		6/16 $\beta\beta$, $\beta\delta$, $\delta\delta$, $\alpha\gamma$	6/16 $\beta\beta$, $\beta\delta$, $\delta\delta$, $\alpha\gamma$
ADH-4			4/16 $\beta\gamma$, $\delta\gamma$	4/16 $\beta\gamma$, $\delta\gamma$
ADH-5		$\gamma\gamma$	1/16 $\gamma\gamma$	1/16 $\gamma\gamma$

[a] The expected quantitative distribution of the isozymes is indicated by the ratios preceding the dimers

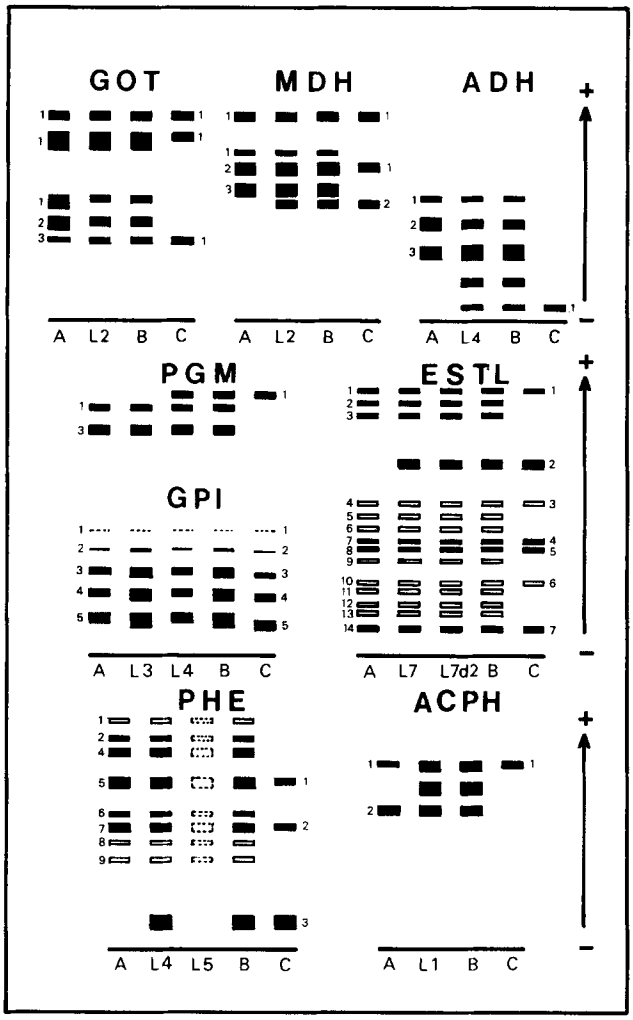

Fig. 1. Diagramatic representation of the zymograms of the hexaploid wheat 'Vilmorin' (A), *Agropyron intermedium* (C), amphiploid (octoploid) TAF-46 (B) and the wheat-*Agropyron intermedium* addition lines for the isozymes: glutamate oxaloacetate transaminase (GOT), malate dehydrogenase (MDH), alcohol dehydrogenase (ADH), phopshoglucose mutase (PGM), glucose phosphate isomerase (GPI), leaf esterases (ESTL), alkaline phosphatases of the endosperm (PHE) and leaf acid phosphatases (ACPH). All these isozymes migrated from the cathode to the anode

corresponds, in mobility, to the AI PGM-1 band. New bands with an intermediate migration were not observed.

3 Glucosephosphate isomerase (GPI) (Fig. 1)

The GPI patterns observed in V-27 had five bands (from GPI-1 to GPI-5). AI showed also five bands, all with a slower migration than GPI-1, GPI-2, GPI-3, GPI-4 and GPI-5 wheat bands, respectively. The octoploid TAF-46 and the addition line L3 exhibited a zymogram of five bands with a greater staining than the wheat and AI bands. These patterns would be the sum of the wheat and AI patterns.

4 Glutamic oxaloacetic transaminase (GOT) (Figs. 1 and 2)

V-27, TAF-46 AI and all the addition lines showed three activity zones: GOT-1, GOT-2 and GOT-3 (in order of decreasing electrophoretic mobility). V-27, AI and all the addition lines exhibited the same patterns for GOT-1 and GOT-2 zones. GOT-1 showed one band and GOT-2 another band.

V-27 showed three isozymes, designated GOT-3 a, GOT-3 b and GOT-3 c, in order of decreasing anodal electrophoretic migration, in the GOT-3 zone. The relative staining intensities of these isozymes were 4:4:1, respectively. The AI pattern had a GOT-3 isozyme with the same migration as the V-27 GOT-3 c isozyme. The addition line L2 and TAF-46 had three isozymes displaying the same mobility as the V-27 bands but with relative staining intensities of 1:2:1, respectively.

The triplicate structural genes which produce wheat GOT-3 isozymes are located on chromosome arms 3AL, 3BL and 3DL (Hart 1970). The subunits encoded by these genes have been designated α, β and δ, respectively. It has been proposed (Hart 1970) that random association of these protomers results in the production of six types of dimers, which are expressed as GOT-3 a ($\beta\beta$, $\delta\delta$, $\beta\delta$ dimers), GOT-3 b ($\alpha\beta$, $\alpha\delta$) and GOT-3 c ($\alpha\alpha$). *Agropyron* structural gene *Got-3* codes for a subunit named γ. The pattern observed in L2 and TAF-46 could be explained if we suppose that all subunits (α, β, δ and γ) occur in all possible dimeric combinations. A schematic model for the subunit composition for AI, TAF-46, V-27 and L2 is shown in

Fig. 2A–H. Zymograms of the hexaploid wheat 'Vilmorin' (9), amphiploid (octoploid) TAF-46 (10) and the wheat-*Agropyron intermedium* addition lines L1, L2, L3, L4, L5, L7, L7d1 and L7d2 (1, 2, 3, 4, 5, 6, 7 and 8, respectively). **A** glutamate oxaloacetate transaminase (GOT). **B** phosphoglucose mutase (PGM). **C** glucose phosphate isomerase (GPI). **D** malate dehydrogenase (MDH). **E** endosperm alkaline phosphatases (PHE). **F** leaf acid phosphatases (ACPH). **G** leaf esterases (ESTL). **H** leaf peroxidases (PER). All these isozymes, except for PER, migrated from the cathode to the anode

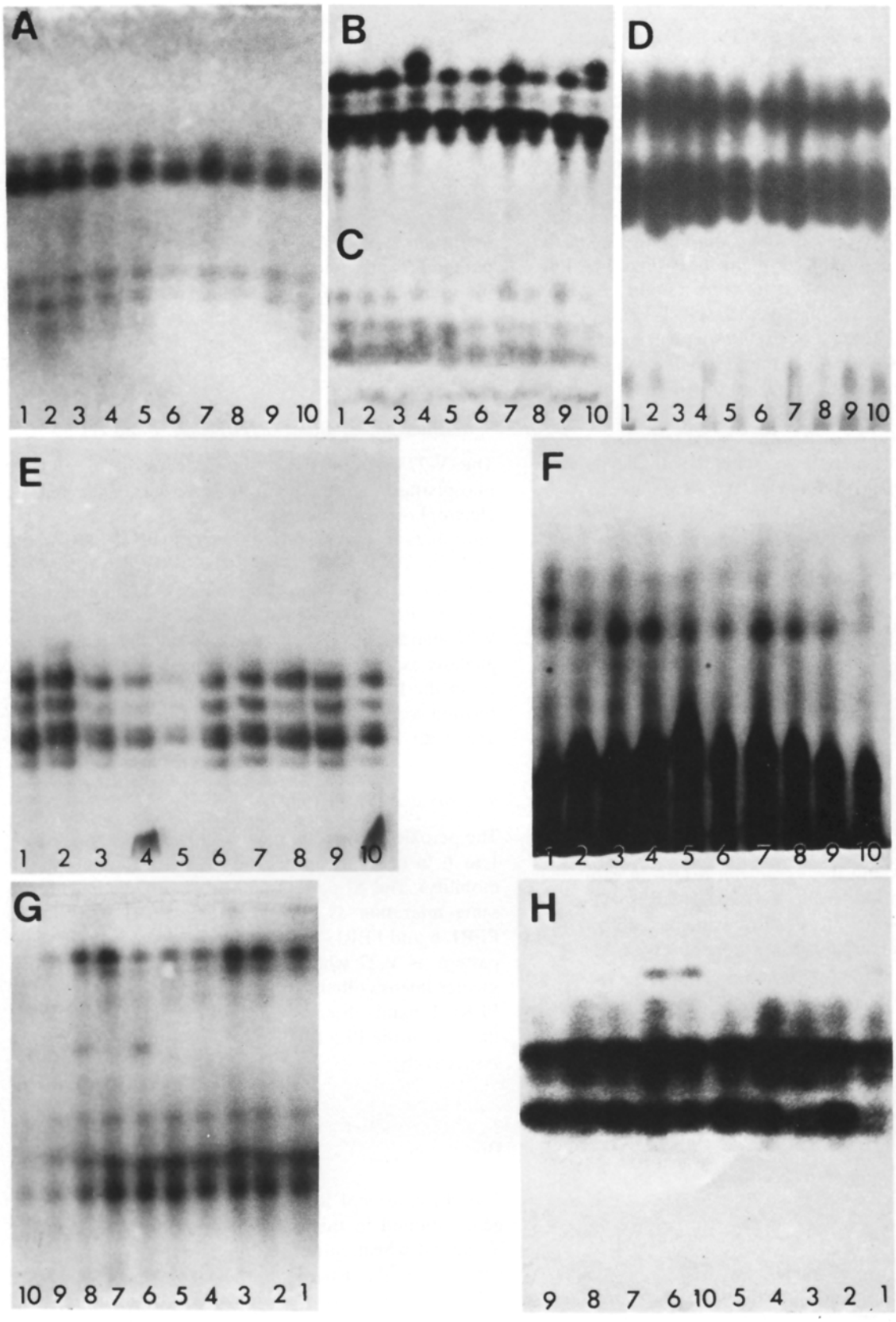
A
1 2 3 4 5 6 7 8 9 10
B
C
1 2 3 4 5 6 7 8 9 10
D
1 2 3 4 5 6 7 8 9 10
E
1 2 3 4 5 6 7 8 9 10
F
1 2 3 4 5 6 7 8 9 10
G
10 9 8 7 6 5 4 3 2 1
H
9 8 7 6 10 5 4 3 2 1

Table 2. Schematic models for the subunit composition of the GOT-3 isozymes produced by *T. aestivum* cv. 'Vilmorin', *Agropyron intermedium* (AI), amphiploid (octoploid) TAF-46 and the V-AI addition line L2

Isozymes	V	AI	V-AI-L2	TAF-46
GOT-3a	4/9[a] $\beta\beta, \delta\delta, \beta\delta$		1/4 $\beta\beta, \beta\delta, \delta\delta$	1/4 $\beta\beta, \beta\delta, \delta\delta$
GOT-3b	4/9 $\alpha\beta, \alpha\delta$		2/4 $\alpha\beta, \alpha\delta, \beta\gamma, \delta\gamma$	2/4 $\alpha\beta, \alpha\delta, \beta\gamma, \delta\gamma$
GOT-3c	1/4 $\alpha\alpha$	$\gamma\gamma$	1/4 $\alpha\alpha, \alpha\gamma, \gamma\gamma$	1/4 $\alpha\alpha, \alpha\gamma, \gamma\gamma$

[a] The expected quantitative distribution of the isozymes is indicated by the ratios preceding the dimers

Table 2. The three dimers which were not found in the parents would be produced by the TAF-46 and L2 line. The $\gamma\beta$ and $\gamma\delta$ dimers have the same mobility as GOT-3b and the $\alpha\gamma$ dimer migrates like GOT-3c. If $p=q=r=s=1/4$, p, q, r and s being the frequencies of α, β, δ and γ, respectively, and if they associate randomly to form active dimers, the expected distribution of the 10 dimeric types contained in TAF-46 and L2 will be based on $(p+q+r+s)^2$. The proposed distribution (shown in Table 2) is in agreement with the relative staining intensities observed in TAF-46 and L2.

5 Malate dehydrogenase (MDH) (Figs. 1 and 2)

V-27, AI TAF-46 and all the addition lines showed two activity zones: MDH-1 and MDH-2 (in order or decreasing anodal electrophoretic mobility). V-27, TAF-46, AI and all addition lines exhibited only one band with the same migration in the MDH-1 zone.

V-27 showed three isozymes, designated MDH-2a, MDH-2b and MDH-2c, in order of decreasing anodal electrophoretic mobility, for the MDH-2 zone. The relative staining intensities of these three bands were 1:4:4, respectively. The AI pattern had two MDH isozymes designated MDH-2a and MDH-2b. The *Agropyron* MDH-2b isozyme migrated slower than the wheat isozymes, but the *Agropyron* MDH-2a exhibited the same migration as the V-27 MDH-2b isozyme. In TAF-46 and L2 all the V-27 isozymes as well as the MDH-2b isozyme of *Agropyron* were observed.

6 Esterases (ESTL) (Figs. 1 and 2)

The V-27 pattern had 14 isozymes and the *Agropyron* zymogram showed 7 esterase bands. Only the ESTL-2 isozyme of *Agropyron* exhibited a different migration as did the V-27 esterases. In the TAF-46, L7 disomic line and in the L7d2 ditelocentric lines all the esterase bands of V-27 as well as *Agropyron* ESTL-2 were observed.

7 Acid phosphatases (ACPH) (Figs. 1 and 2)

V-27 displayed two isozymes: ACPH-1 and ACPH-3. AI had only one band (ACPH-1) having the same migration as V-27 ACPH-1. TAF-46 and L1 showed the parental bands and as well as a new band with an intermediate migration between the AI ACPH-1 band and the V-27 ACPH-3 band. This new band is probably an heterodimer with the subunit of wheat and *Agropyron.*

8 Alkaline phosphatases (PHE) (Figs. 1 and 2)

The V-27 pattern showed nine endosperm alkaline phosphatases (from 1 to 9, in order of decreasing electrophoretic mobility). The AI pattern had three phosphatase isozymes, designated PHE-5, PHE-7 and PHE-10. The AI PHE-5 and PHE-7 bands showed the same migration as the corresponding V-27 phosphatases. The AI PHE-10 isozymes migrated slower than the V-27 bands. In TAF-46 and L4 all the V-27 phosphatases as well as the AI PHE-10 band were observed.

In the L5 line a decreased intensity of V-27 PHE in relation to the rest of the addition lines and wheat was detected.

9 Peroxidases (PERL) (Fig. 2)

The peroxidase pattern of V-27 showed six bands (from 1 to 7, in order of decreasing cathodal electrophoretic mobility). The AI pattern had five peroxidases with the same migration as V-27: PERL-1, PERL-3, PERL-4, PERL-6 and PERL-7. TAF-46 and L5 showed the same pattern as V-27 wheat, but PERL-1 was present in a greater intensity than V-27 and other addition lines. The PERL-1 band observed in addition line L5 would be the sum of the PERL-1 bands of wheat and *Agropyron,* respectively.

Discussion

The chromosomal locations of the isozyme structural genes studied in this paper have been carried out in hexaploid wheat cultivar 'Chinese Spring', in rye cultivars 'Imperial', 'King II' and 'Dakold', and in barley cultivar 'Betzes'. The results obtained, including the

Table 3. Chromosomal locations of isozyme structural genes in hexaploid wheat cultivar 'Chinese Spring' (CS), rye cultivar 'Imperial' (I), 'King II' (KII) and 'Dakold' (D), and in barley cultivar 'Betzes' (B)

Gene	*T. aestivum* CS Genomes A, B, D	*S. cereale* I, KII, D Genome R	*H. vulgare* B Genome H
Adh-1	4 Ap, 4 Bp, 4 Dp	4 Rp	4
Mdh-2	1 Aq, 1 Bq, 1 Dq	1 Rq, 3 Rq	1, 3
Got-1	6 Ap, 6 Bp, 6 Dp	7 R	–
Got-2	6 Aq, 6 Bq, 6 Dq	6 Rq	6
Got-3	3 Aq, 3 Bq, 3 Dq	3 Rq	3
Acph(L)	4 Aq, 4 Bq, 4 Dq	7 Rq	4
Phe(E)	4 Aq, 4 Bq, 4 Dq	7 Rq	7, 3
Cpxe(E)	7 Ap, 4 Bp, 7 Dp	4 Rq, 7 Rp	7
Per1(L) (1)	2 Ap, 2 Bp, 2 Dp	2 Rp	2
Est1(L)-1	3 Ap, 3 Bp, 3 Dp	3 R	6
Est1(L)-4	6 Aq, 6 Bq, 6 Dq	6 R	3
Pgm-1 (2)	4 Ap, 4 Bp, 4 Dp	4 Rp	4
Gpi-1	1 Ap, 1 Bp, 1 Dp	1 Rp	1
Glyadins (3)	1 Ap, 1 Bp, 1 Dp	1 R	–
β-Amy (4)	4 Aq, 4 Dq	–	4

See Hart (1983); Hart und Tuleen (1983) and Benito et al. (1985 b) excepting (1) (Benito et al. 1985 a; Boch et al. 1986); (2) (Benito et al. 1984); (3) (Shepherd 1968) and (4) (Joudrier and Cauderon 1976)

Table 4. Chromosomal location of the isozyme structural genes in *Agropyron intermedium* and *Elytrigia elongata* (=*Agropyron elongatum*)

Gene	*Agropyron intermedium* (genome X) Addition line (chromosome)	Gene	*Elytrigia elongata* (genome E) Chromosome arm
Gliadins	L3 (1X) (1)	*Gpi-E1*	1 S
Gpi-X1	L3 (1X)	*Est-E1*	3 S
Per1	L5 (2X)	*Got-E3*	3 L
PHE (– effect)	L5 (2X)	*Adh-E1*	4 S
Got-X3	L2 (3X)	*Lpx-E1*	4 S
Mdh-X2	L2 (3X)	*Adh-E2*	5 L
β-Amy	L4 (4X) (1)	*Lpx-E2*	5 L
Pgm-X1	L4 (4X)	*Amp-E1*	6^{α}
Adh-X1	L4 (4X)	*Adh-E3*	6^{β}
Phe	L4 (4X)	*Got-E2*	6^{β}
Est-X2	L7, L7 d2 (6X)	*Ep-E1*	7 L
Cpxe	L1 (7X)		
Acph-X1	L1 (7X)		

See Hart and Tuleen (1983 b) for chromosomal locations on *E. elongata*.
The chromosomal locations for *A. intermedium* reported are carried out in this work except for (1) (Cauderon et al. 1978)

subunit structure postulated for these isozymes, are indicated in Table 3.

The six CS-AI addition lines examined in this work can be identified by different isozyme markers and the isozyme structural genes that have been located on *Agropyron intermedium* chromosomes are indicated in Table 4.

The isozyme stuctural genes that have been located on *A. intermedium* and *Elytrigia elongata* (=*Agropyron elongatum*) chromosomes are also indicated in Table 4.

Therefore, the results obtained in this study indicate that *A. intermedium* chromosomes L1, L2, L3, L4, L5 and L7 are homoeologous of the wheat and rye chromosomes 7, 3, 1, 4, 2 and 6, respectively. Consequently, on the basis of these results, we propose the following homoeologous nomenclature for the *A. intermedium* (genome X) chromosomes: L1 (7X), L2 (3X), L3 (1X), L4 (4X), L5 (2X), L6 (not available) (5X?) and L7 (6X).

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