Theor Appl Genet (1987) 73:690–698



# Chromosomal location of structural genes controlling isozymes in *Hordeum chilense*

## 3. Esterases, glutamate oxaloacetate transaminase and phosphoglucomutase

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Received June 30, 1986; Accepted August 12, 1986
Communicated by F. Mechelke

**Summary.** Polyacrylamide and starch gel electrophoresis of esterase (EST), glutamate oxaloacetate transaminase (GOT) and phosphoglucomutase (PGM) isozymes in *Hordeum chilense, Triticum turgidum* conv. *durum,* the amphiploid *H. chilense* × *T. turgidum* (Tritordeum), and the *durum* wheat/*H. chilense* monosomic addition lines revealed the chromosomal location of one EST locus, two GOT loci and one PGM locus. Loci *Est-H$^{ch}$1* and *Got-H$^{ch}$2* were found on chromosome 6H$^{ch}$, *Got-H$^{ch}$3* on chromosome 3H$^{ch}$, and *Pgm-H$^{ch}$1* on chromosome 4H$^{ch}$. These results lend evidence for the assumed homoeology relationships between chromosomes of Triticeae species.

**Key words:** *Hordeum chilense* – Tritordeum – Esterases – Glutamate oxaloacetate transaminase – Phosphoglucomutase – Isozymes

### Introduction

Data on the arrangement of alien isozyme loci, namely in *Aegilops, Agropyron, Secale* and *Hordeum* species, that are orthologous to genes with known chromosomal locations in wheat, have contributed substantially to our knowledge of homoeology and the highly conservative synteny of genes within Triticeae species.

In *Hordeum chilense* (2n = 14, genomes H$^{ch}$ H$^{ch}$), one glucose phosphate isomerase (Chojecki and Gale 1982), two leaf peroxidase (Ainsworth et al. 1984 b), a malate dehydrogenase and a 6-phosphogluconate dehydrogenase (Fernández and Jouve 1987) structural genes have been located on chromosome 1H$^{ch}$. Likewise, Miller et al. (1985) described an α-amylase locus on chromosome 7H$^{ch}$ and Fernández and Jouve (submitted) identified two leaf cathodal peroxidase loci on chromosomes 2H$^{ch}$ and 7H$^{ch}$, and one acid phosphate gene on chromosome 7H$^{ch}$. Lastly, an esterase gene has been assigned to chromosome 3H$^{ch}$ (Ainsworth et al. 1986 a).

Esterases (EST, E.C. 3.1–) are enzymes of comparatively low specifity. Although they are specific for the ester link, they hydrolyse a very large number of different esters, though not at the same time. Arylesterases (3.1.1.2), carboxilic ester hydrolases, have often been used in gene location studies in Triticeae species (see revisions of Salinas and Benito 1985 b; Wehling et al. 1985; Salinas et al. 1985). Glutamate oxaloacetate transaminase (GOT), or aspartate amino transferase (AAT, E.C. 2.6.1.1), are pyridoxal-phosphate-proteins which transfer amino group from L-aspartate to 2-oxoglutarate, producing oxaloacetate and L-glutamate. Chromosomal localizations of GOT genes have been extensively carried out in Triticeae (see revisions of Salinas and Benito 1985 a; Benito et al. 1985; Díaz and Jouve 1986). Phosphoglucomutase (PGM, E.C. 2.7.5.1) is an enzyme involved in the biosynthesis of saccharides which has also been used in genetic mapping in cereals (Benito 1982; Brown and Munday 1982; Nielsen et al. 1982; Benito et al. 1984, 1985; Schmidt et al. 1984; Wehling et al. 1985; Salinas and Benito 1985 a).

In this report we describe the chromosomal location and genetic control of EST, GOT and PGM isozymes in *H. chilense,* by means of an analysis of their electrophoretic expression in tetraploid wheat/*H. chilense* monosomic addition lines, obtained beginning from the amphiploid *H. chilense* × *Triticum turgidum* conv. *durum* (Tritordeum).

### Materials and methods

Plant materials analysed in this study were the following:

*Triticum turgidum* conv. *durum* (2n = 28, genomes AA BB), cv. 'Mexican 248 × Andalucía 344' (MA).

*Hordeum chilense* Brong. var. 'muticum' (Presl) Hauman (2n = 14, genomes H$^{ch}$ H$^{ch}$).

Amphiploid *H. chilense* × *T. turgidum* conv. *durum,* Tritordeum, (2n = 42, genomes AA BB H$^{ch}$ H$^{ch}$), line 'CHMA', obtained by Martin and Sánchez-Monge Laguna (1982).

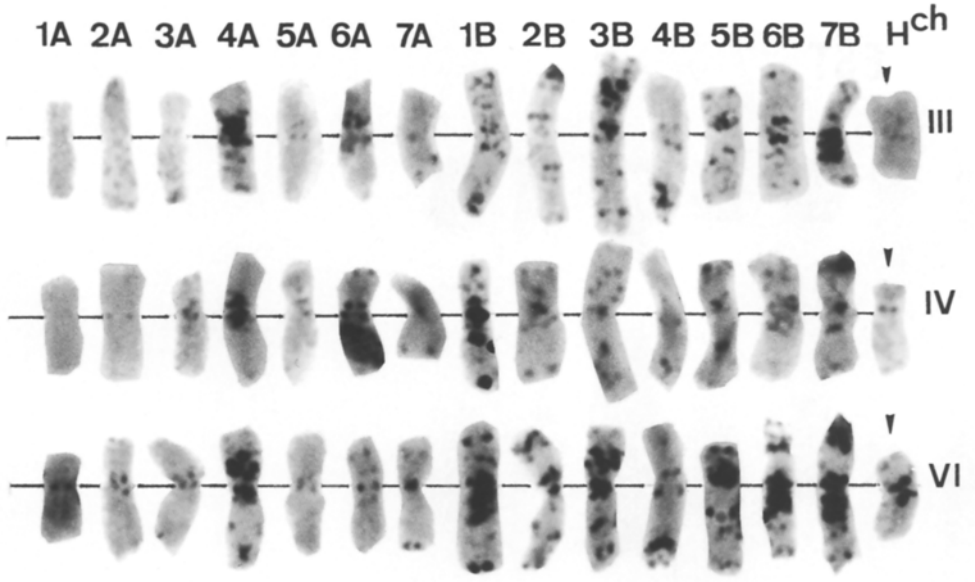


**Fig. 1.** Giemsa C-banded karyotype of *T. turgidum* conv. *durum* addition chromosomes III, IV and VI (*arrows* indicate the *chilense* chromosome)

Tetraploid wheat/*H. chilense* monosomic addition lines, (2n=29), obtained as described by Fernández and Jouve (1987).

*T. aestivum* (2n=42, genomes AA BB DD), cv. 'Chinese Spring' (CS).

*H. vulgare* (2n=14, genomes HH), cv. 'Hassan'.

Chromosomal identification of addition lines was carried out by C-banding as described by Fernández and Jouve (1984) (Fig. 1).

Isozyme analysis was made an extracts of young leaves. Polyacrylamide gels (8%) were used to analyse EST and GOT isozyme expression and starch gels (Connaught 12%) were employed in PGM studies. Electrophoretic techniques and staining methods have been previously described by Salinas and Benito (1985b), Díaz and Jouve (1986) and Benito et al. (1984) for the analysis of EST, GOT and PGM isozymes, respectively. A minimum of ten electrophoretic assays were made for each material in each enzymatic system. No intraspecific variation was detected.

## Results

### *Esterases*

When polyacrylamide gels were stained alternatively using $\alpha$- or $\beta$-naphthyl acetate, no differences in enzymatic activity of isozyme bands were found. Therefore, we have considered only one group of esterases. Because of its clear and repetitive isozymatic patterns, the most anodic region (EST-1) has been studied (Figs. 2 and 5).

*T. turgidum* showed a minimum of four bands, three at zone 1 (Est-w1, EST-w2 and EST-w3), and the fourth (EST-w4) at zone 2.

*H. chilense* esterase zymograms showed a degree of variability (Sanz et al. 1986). However, one of the most frequent phenotypes is indicated in Fig. 2. It consists of six bands, EST-ch1 to EST-ch6, in the most anodic region. Occassionally EST-ch5 and EST-ch6 appeared as a single thicker band, probably as a result of imperfect electrophoretic separation. *H. chilense* esterase isozyme phenotypes lacked a well defined EST-2 region, but a faint isozyme band sometimes appeared in less migrating positions.

Tritordeum and the *durum* wheat/*H. chilense* addition chromosome VI showed seven isozyme bands, from which *band-1* corresponded to EST-w1, *band-2* approximately to EST-w2, *band-3* to EST-w3 and EST-ch3, *band-4* to EST-ch4, *band-5* to EST-ch5, and *band-6* to EST-ch6.

Common wheat and cultivated barley revealed esterase zymograms coincident with previous studies (Salinas and Benito 1985b; Salinas et al. 1985). Some variability in *H. vulgare* isozyme phenotypes was detected.

### *Glutamate oxaloacetate transaminase*

All isozyme phenotypes consisted of three regions GOT-1, GOT-2 and GOT-3 (Figs. 3 and 5).

Common and *durum* wheats, Tritordeum and the addition lines showed a single GOT-1 isozyme, whereas *H. chilense* and *H. vulgare* presented faint isozyme bands.

Tetraploid wheat exhibited a single band at zone 2, called GOT-2-w1. The *H. chilense* zymogram also

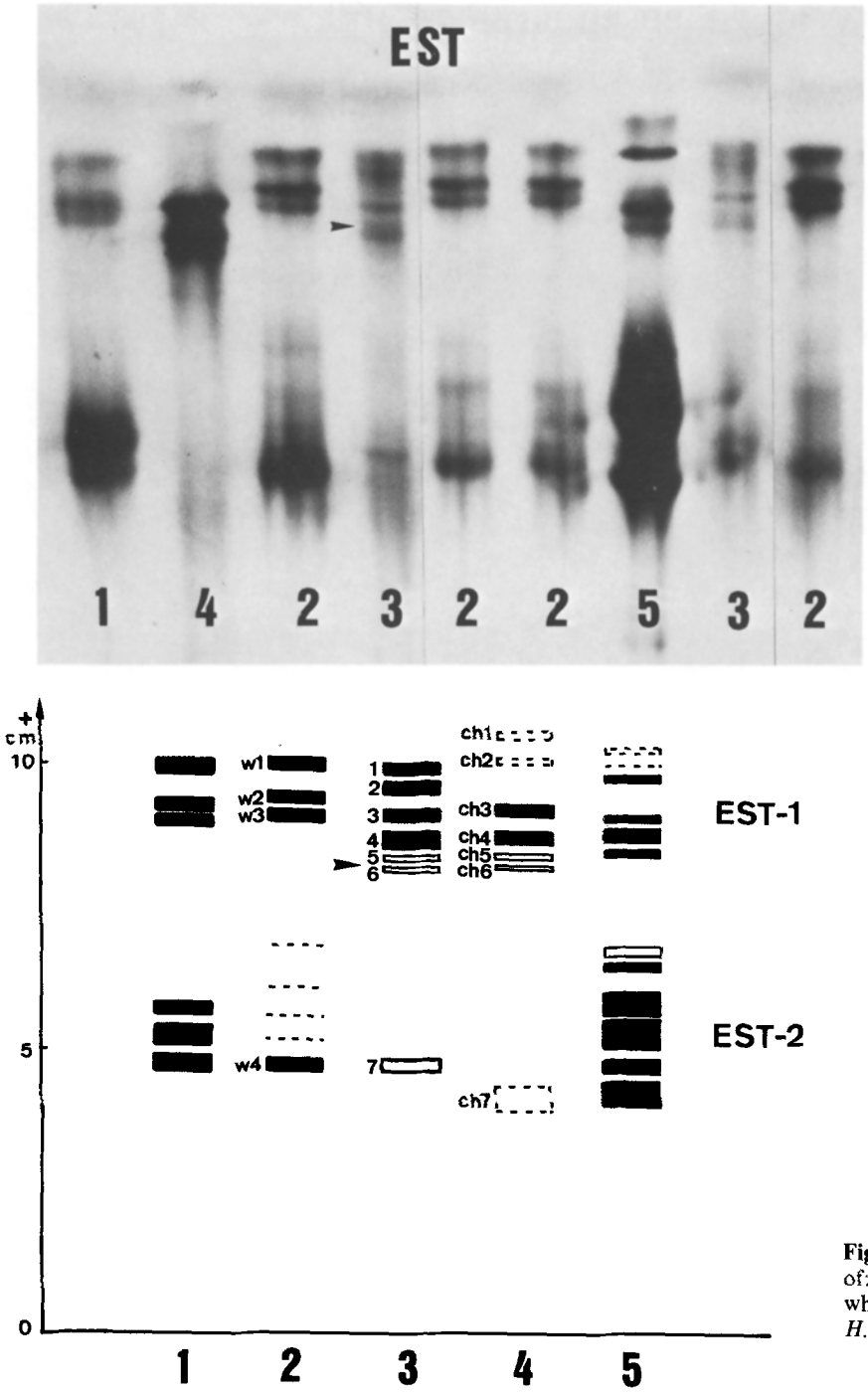


**Fig. 2.** Esterase (EST) isozyme phenotype of: (1) common wheat (CS); (2) *durum* wheat (MA); (3) Tritordeum (CHMA); (4) *H. chilense*; (5) *H. vulgare*

showed a single less migrating band, GOT-2-ch1. The amphiploid and the addition chromosome VI presented three GOT-2 isozymes: *band-1* coincident with GOT-2-w1, *band-3* with GOT-2-ch1, and *band-2* of an intermediate migration rate. Hexaploid wheat and barley showed electrophoretic patterns previously described by Hart (1975) and Hart et al. (1980).

The lowest migrating region, GOT-3, revealed three bands, GOT-3-w1, GOT-3-w2 and GOT-3-w3 in *durum* wheat zymograms with a relative staining intensities of 1 : 2 : 1. *H. chilense* showed two isozyme bands, GOT-3-ch1 and GOT-3-ch2. Tritordeum and the addition chromosome IV also exhibited three bands, *1*, *2* and *3*, with relative intensities of 1 : 4 : 4. Likewise, common

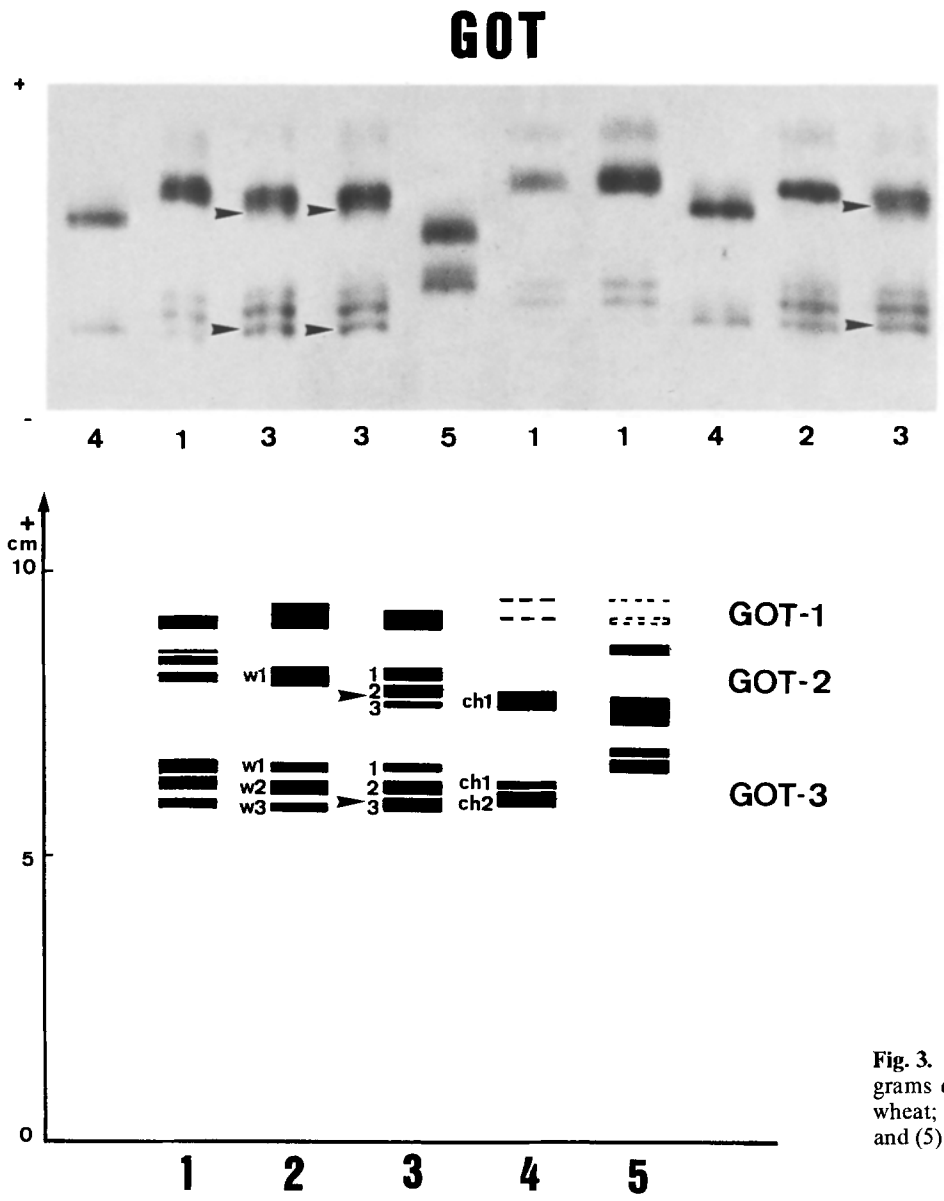


**Fig. 3.** Polyacrylamide gel GOT zymograms of: (1) common wheat; (2) *durum* wheat; (3) Tritordeum; (4) *H. chilense*; and (5) *H. vulgare*

wheat presented three isozyme bands of similar migration speeds but of different staining rates (4 : 4 : 1), which is in accordance with the results reported by Hart (1975). *H. vulgare* showed two addition migrating isozyme bands.

Both GOT-2 and GOT-3 systems constitute good isozyme markers for *H. chilense* chromosomes VI and IV, respectively.

*Phosphoglucomutase*

In starch gels, common and *durum* wheats had a zymogram with four isozyme bands, named PGM-w1 to PGM-w4 from top to bottom. *H. chilense* revealed a double banded phenotype, PGM-ch1 and PGM-ch2. This second isozyme band is not present in all zymograms analyzed (Figs. 4 and 5).

The amphiploid and the *durum* wheat/*H. chilense* addition chromosome III exhibited a PGM isozyme phenotype with six bands, just as an addition of both wheat and *chilense* isozymes. Cultivated barley showed a zymogram similar to the *chilense* one, but with lower migrating isozymes (Sanz et al. 1986).

## Discussion

*Esterase gene location*

Esterase isozymes have been described as monomers in different plants of the genera *Avena* (Marshall and Allard 1969),

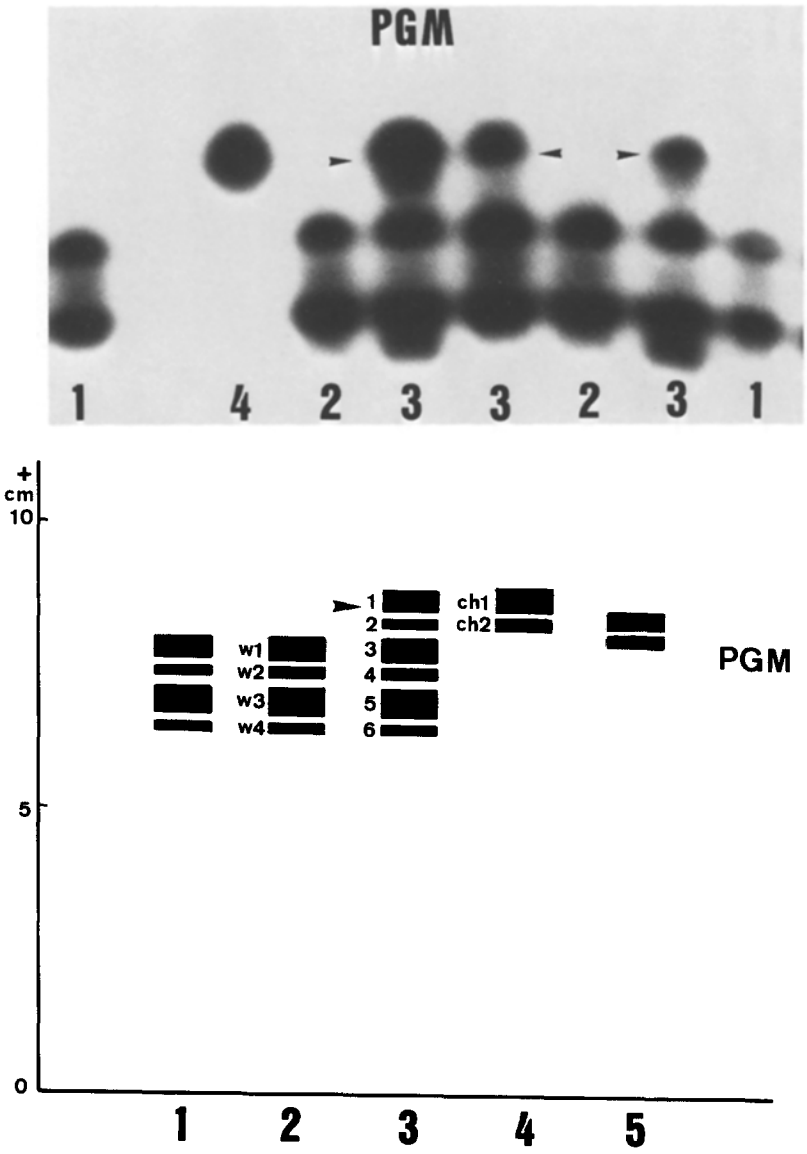


**Fig. 4.** PGM isozyme phenotypes of: (1) *T. aestivum*; (2) *T. turgidum*; (3) Tritordeum; (4) *H. chilense*; (5) *H. vulgare*

*Picea* (Lundkvist and Rudin 1977), *Oriza* (Nakagahra 1977), or as dimers in *Zea mays* (Scandalios 1969), *H. jubatum* (Babbel and Waine 1977) and *Elytrigia elongata* (Hart and Tuleen 1983). Both monomeric and dimeric esterases have been described in *T. aestivum* (Barber et al. 1968; May et al. 1973; Jaaska 1980), *S. cereale* (Barber et al. 1968; Bergman and Maan 1973; Koller and Zeller 1976; Salinas and Benito 1985 b) and *Lycopersicon* spp. (Tanksley and Rick 1980).

In hexaploid wheat, most anodic esterases have been assigned to structural genes on chromosome arms 3A$\alpha$, 3BS and 3DS (Barber et al. 1968, 1969; Bergman 1972; Bozzini et al. 1973; May et al. 1973; Nakai 1976; Jaaska 1980; Ainsworth et al. 1984). Likewise, loci codifying lower migrating esterases have been identified on the long arms of homoeologous group 6 chromosomes (Barber et al. 1968; Bergman 1972; May et al. 1973; Nakai 1976; Jaaska 1980) and on group 7 (May et al. 1973; Jaaska 1980).

In rye, *Secale cereale,* orthologous genes of the above mentioned of wheat have been located on chromosomes 3R (Barber et al. 1968; Bergman and Maan 1973; Salinas and Benito 1985 b) and 6R, specifically on its long arm (Bergman and Maan 1973; Wehling et al. 1985; Salinas and Benito 1985 b). Genetic control of most anodic esterases and alkaline IP esterases has been assigned to chromosome arms 4RL and 5RL, respectively (Wehling et al. 1985).

Hart and Tuleen (1983) have described an esterase gene on the long arm of chromosome 3E in *E. elongata.*

In *H. vulgare,* esterase control has been assigned to the following chromosomes: 3H (Kahler and Allard 1970; Nielsen and Frydenberg 1971; Hvid and Nielsen 1977; Hart et al. 1980; Brown and Munday 1982; Brown 1983; Salinas et al. 1985), 1H (Hart et al. 1980), 2H (Brown and Munday 1982), and 6H (Salinas et al. 1985). Finally, Ainsworth et al. (1986 a) have identified the *Est-H$^{ch}$5* locus on chromosome 3H$^{ch}$ of *H. chilense.*

Dimeric wheat and rye esterases are more anodic than the monomeric ones and their structural genes are

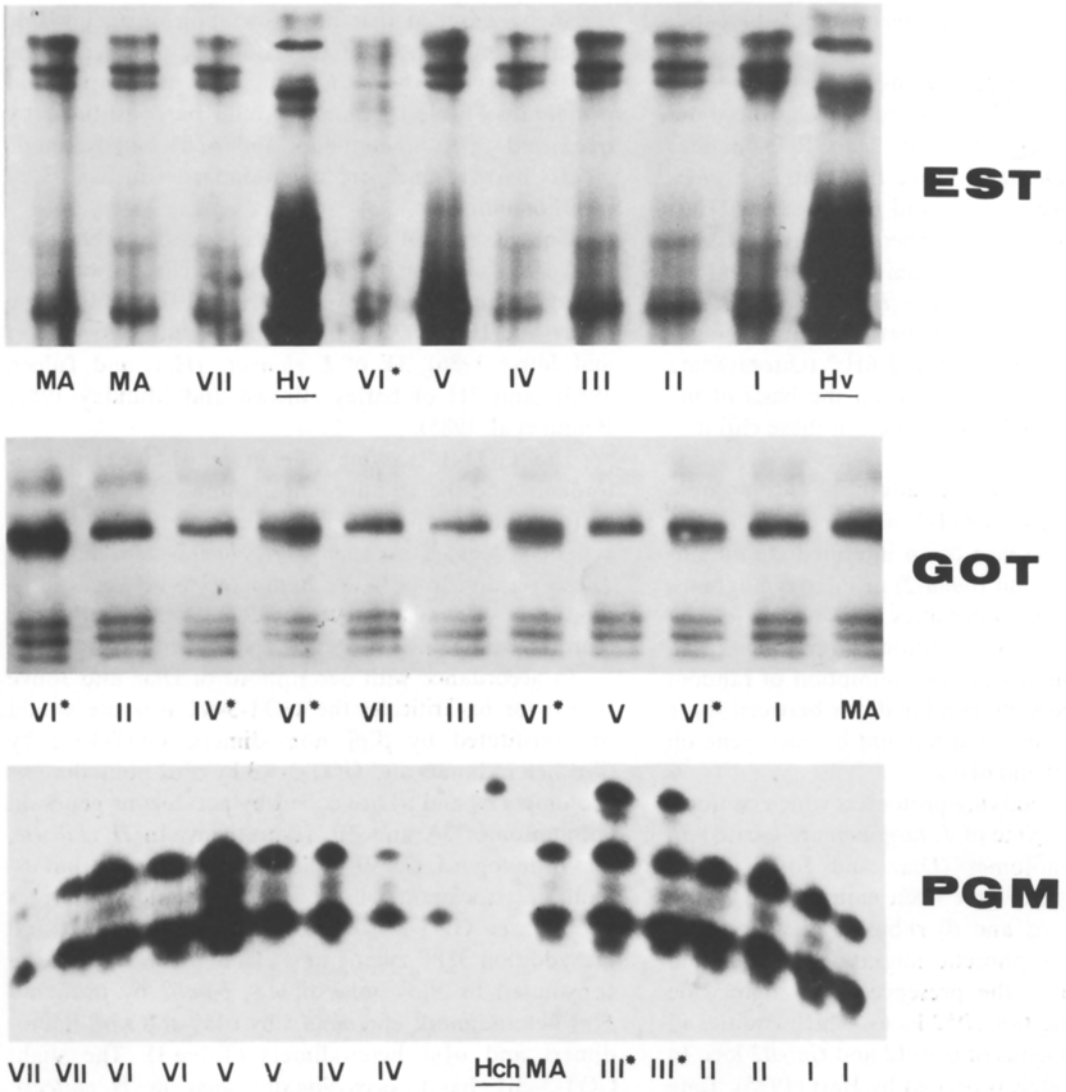


**Fig. 5.** EST, GOT and PGM zymograms of the tetraploid wheat/*H. chilense* monosomic addition lines. (*) EST-1 and GOT-2 isozyme markers are revealed by the addition chromosome VI ($6H^{ch}$). The addition chromosome IV ($3H^{ch}$) presents the GOT-3 isozyme marker, and the addition chromosome III ($4H^{ch}$) shows the PGM marker

located on the short arm of group 3 chromosomes, whereas most cathodic esterase genes have been identified on the long arm of group 6 chromosomes. On the contrary, barley anodic esterases are controlled by genes on the 6H chromosome, and less migrating isozymes on 3H (Salinas et al. 1985). Dimeric esterases have never been described in *H. vulgare* (Kahler and Allard 1970, 1981).

The EST isozymatic patterns showed by Tritordeum and the addition chromosome VI reveal the existence of at least an anodic esterase gene on chromosome VI. We have called this gene *Est-Hch1* in accordance with the rules for wheat genes symbolization (McIntosh 1983). These results support the homoeology between *H. chilense* chromosome VI (that can be named $6H^{ch}$, 6H of *H. vulgare* 6R of rye and the wheat group 6 chromosomes.

*Glutamate oxaloacetate transaminase gene location*

The dimeric structure of active GOT molecules has been proved in different *Poaceae* species such as *Z. mays* (MacDonald and Brewbaker 1972), *T. aestivum* (Hart 1975), *Agropyron* and *Hordeum* spp. (Hart et al. 1976; Babbel and Wain 1977), and 6x-Triticale (Díaz and Jouve 1986).

Genetic control of common wheat GOT-1 isozymes has been assigned to chromosomes of group 6 and 7 (Hart 1975). Likewise, Salinas and Benito (1985a) described a GOT-1 isozyme locus on rye chromosome arm 7RL. The localization of genes controlling GOT-1

isozymes in *Hordeum* spp. has been impossible until the present time.

Genes codifying GOT-2 isozymes have been identified on the long arms of wheat group 6 chromosomes (Hart 1975), 6R of rye (Tang and Hart 1975; Salinas and Benito 1985a; Díaz and Jouve 1986), 6E of *E. elongata* (Hart and Tuleen 1983), and 6H of barley (Hart et al. 1980). GOT-2 isozyme phenotypes showed by Tritordeum and the addition chromosome VI reveal the existence of a structural gene, *Got-H$^{ch}$2,* on this *H. chilense* chromosome. Homoeology between chromosomes of wheat group 6, 6E, 6R, 6H and 6H$^{ch}$ (chromosome VI) is deduced from this analysis, on the basis of the location of orthologous GOT-2 genes on these chromosomes.

The amphiploid and the addition chromosome 6Hch express dimeric GOT-2 isozymes, which is deduced from the presence of an intermediate migrating GOT-2 isozyme band (*band-2*) in their zymograms. Band staining relative intensities showed by *durum* wheat, Tritordeum and the addition chromosome 6H$^{ch}$, are in good agreement with an assumption of random association of all possible combinations between three protomers produced in equal amount by each gene on chromosomes 6A, 6B and 6Hch.

Structural genes codifying protomers which conform to the GOT-2-w1 isozyme of *T. turgidum* are located on 6A and 6B chromosomes (Diaz and Jouve 1986). These paralogous genes have been named *Got-A2* and *Got-B2,* and codify $\alpha_6^2$ and $\beta_6^2$ subunits in wheat. The coincidence in electrophoretic migration rate of both peptides brings about the presence of a single wide isozymatic band. The *Got-H$^{ch}$2* locus, which codifies $\eta_6^2$ protomers, is orthologous of *Got-A2* and *Got-B2* loci. In accordance with models proposed by Hart (1975), Tang and Hart (1975), Hart et al. (1980), Salinas and Benito (1985a) and Díaz and Jouve (1986) in different cereals, it can be assumed that the association of all possible dimeric combinations of $\eta_6^2$, $\alpha_6^2$ and $\beta_6^2$ produces three GOT-2 isozymes (*bands 1, 2* and *3*) in the amphiploid zymogram (Table 1). *Band-1* would be constituted by $\alpha_6^2\alpha_6^2$ and $\beta_6^2\beta_6^2$ homodimers and $\alpha_6^2\beta_6^2$ heterodimers, *band-2* by $\alpha_6^2\eta_6^2$ and $\beta_6^2\eta_6^2$ heterodimers, and *band 3* by $\eta_6^2\eta_6^2$ homodimers.

Genetic control of GOT-3 isozymes has been assigned to genes on the long arm of chromosomes of wheat homoeologous group 3 (Hart 1975), 3R of rye (Tang and Hart 1975; Salinas and Benito 1985a; Díaz and Jouve 1986), 3E of *E. elongata* (Hart and Tuleen 1983), and 3H of barley (Brown and Munday 1982; Benito et al. 1985).

The GOT-3 isozyme phenotype showed by Tritordeum and the addition chromosome IV reveals that a structural gene, *Got-H$^{ch}$3,* coding for this enzymatic system is located on such a *H. chilense* chromosome. These results support the homoeology between chromosomes of wheat group 3, 3R, 3E, 3H and 3H$^{ch}$ (chromosome IV).

In accordance with descriptions of Díaz and Jouve (1986) for 6x-Triticale, the GOT-3-w1 isozyme would be constituted by $\beta_3^3\beta_3^3$ homodimers, GOT-3-w2 by $\beta_3^3\alpha_3^3$ heterodimers and GOT-3-w3 by $\alpha_3^3\alpha_3^3$ homodimers. Protomers $\alpha_3^3$ and $\beta_3^3$ are coded by paralogous genes on chromosomes 3A and 3B, respectively. In *H. chilense,* the orthologous *Got-H$^{ch}$3* locus codifies $\eta_3^3$ subunits. Dimeric associations of $\alpha_3^3$, $\beta_3^3$ and $\eta_3^3$ protomers brings about three GOT-3 isozymes in the amphiploid, and the addition 3H$^{ch}$ zymograms. Thus, *Band 1* would be constituted by $\beta_3^3\beta_3^3$ homodimers, *band 2* by $\beta_3^3\alpha_3^3$ and $\beta_3^3\eta_3^3$ heterodimers, and *band 3* by $\alpha_3^3\alpha_3^3$ and $\eta_3^3\eta_3^3$ homodimers and $\alpha_3^3\eta_3^3$ heterodimers (Table 1). The slight GOT-3-ch1 band, occassionally seen in *H. chilense* phenotypes, seems to be a conformational molecule and does not participate in GOT-3 subunit organization.

**Table 1.** Schematic model showing the conformation of active dimeric molecules of the GOT isoenzyme system in *durum* wheat (MA), Tritordeum (CHMA) and *H. chilense*

| 'MA' | | 'CHMA' & addition chr. 6 H$^{ch}$ | | *H. chilense* | |
|---|---|---|---|---|---|
| Isoenzymes | Composition of subunits | Isoenzymes | Composition of subunits | Isoenzymes | Composition of subunits |
| GOT-2∼w1 | $\alpha_6^2\alpha_6^2$ $\alpha_6^2\beta_6^2$ $\beta_6^2\beta_6^2$ | GOT-2∼1 | 4/9 $\alpha_6^2\alpha_6^2$ $\alpha_6^2\beta_6^2$ $\beta_6^2\beta_6^2$ | | |
| | | GOT-2∼2 | 4/9 $\alpha_6^2\eta_6^2$ $\beta_6^2\eta_6^2$ | | |
| | | GOT-2∼3 | 1/9 $\eta_6^2\eta_6^2$ | GOT-2-ch1 | $\eta_6^2\eta_6^2$ |
| | | | & 3 H$^{ch}$ | | |
| GOT-3∼w1 | 1/4 $\beta_3^3\beta_3^3$ | GOT-3∼1 | 1/9 $\beta_3^3\beta_3^3$ | | |
| GOT-3∼w2 | 2/4 $\beta_3^3\alpha_3^3$ | GOT-3∼2 | 4/9 $\beta_3^3\alpha_3^3$ $\beta_3^3\eta_3^3$ | | |
| GOT-3∼w3 | 1/4 $\alpha_3^3\alpha_3^3$ | GOT-3∼3 | 4/9 $\alpha_3^3\alpha_3^3$ $\alpha_3^3\eta_3^3$ $\eta_3^3\eta_3^3$ | GOT-3-ch2 | $\eta_3^3\eta_3^3$ |

*Phosphoglucomutase gene location*

Genes codifying PGM isozymes have been located on chromosome arms 4A$\alpha$, 4BL and 4DS of common wheat (Benito 1982; Benito et al. 1984), 4RS of rye (Schmidt et al. 1984; Wehling et al. 1985; Salinas and Benito 1985a), and on *H. vulgare* chromosome 4H (Brown and Munday 1982; Nielsen et al. 1982; Benito et al. 1985).

PGM isozyme phenotypes presented by the amphiploid and the addition chromosome III reveal the existence of at least a structural gene, *Pgm-H$^{ch}$1*, on such a *H. chilense* chromosome. This locus codifies PGM-ch1 isozyme (*band 1* in the Tritordeum zymogram). The PGM-ch2 isozyme band could be an electrophoresis artefact or a conformational molecule, as was reported by Benito et al. (1984) for the PGM-w2 band.

Clear evidence of homoeology between wheat group 4 chromosomes, 4R, 4H and *H. chilense* chromosome III (that can be called 4H$^{ch}$) is revealed in our study.

Our results are in agreement with monomeric behaviour for PGM isozymes, previously described by Brown et al. (1978) in *Hordeum*, Mitton et al. (1979) in *Pinus*, Wendel and Parks (1982) in *Camelia japonica*, and Pérez de la Vega and Allard (1984) in *S. cereale*.

*Chromosomal homoeology*

The location of *Est-H$^{ch}$1* and *Got-H$^{ch}$2* linked loci on chromosome 6H$^{ch}$ reveals the homoeology between this *H. chilense* chromosome and those of group 6 of wheat and related species. Fernández (1986) observed the expression of some morphological traits in *durum* wheat/*H. chilense* monosomic and multisomic addition forms and pointed out the influence of the 6H$^{ch}$ chromosome on plant shape, number of nodes, width of flag leaf, clorosis in young leaves, number of spikes/plant, thickness of wall stem, shape and laxity of spikes, length and pigmentation of awns, shape and size of grains and fertility. Some of these characters are also controlled by complex genetic systems on wheat group 6 chromosomes (see review of McIntosh 1983).

Genes coding for aminopeptidase (AMP, E.C. 3.4.11.1) and dipeptidase (DIP, E.C. 3.4.13.11) have been located on wheat group 6 chromosomes (Hart 1973; Hart and Langston 1977) and 6H of barley (Hart et al. 1980; Brown and Munday 1982). These gene locations have been impossible in *H. chilense* until the present time, because of monomorphism for such enzymatic systems showed by the wild barley, *durum* wheat, Tritordeum and the addition lines (Fernández 1986; Sanz et al. 1986).

Chromosome 3H$^{ch}$ carries *Est-H$^{ch}$5* (Ainsworth et al. 1986a) and *Got-H$^{ch}$3* loci, that demonstrate its homoeology with group 3 chromosome of wheat and related species.

The *Pgm-H$^{ch}$1* locus on chromosome 4H$^{ch}$, orthologous of those of group 4 chromosomes of wheat, rye and barley, is proof of the homoeology between these chromosomes. A locus coding low molecular weigth proteins of grain has been identified on chromosome 4H$^{ch}$ (Fernández 1986), which is in agreement with A-hordeins gene location previously reported by Salcedo et al. (1984) in *H. vulgare*.

Our results permit us to establish clear homoeology relationships between *H. chilense* chromosomes and those of related species, which agrees with the maintenance of linkage groups throughout the evolution of Triticeae (Hart 1979).

*Acknowledgements.* The authors are grateful to Dr. C. Benito for technical assistance, and Dr. A. Martín for providing the plant material. This article is part of a study supported by a grant of the "Plan de Formación del Personal Investigador, M.E.C., Spain".

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