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Encoding genes for endosperm proteins in *Hordeum chilense*

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Summary. The endosperm proteins encoded by the genome *Hch* in *Hordeum chilense,* Tritordeum (amphiploid *Hordeum chilense* × *Triticum turgidum*), common wheat-*H. chilense* addition lines, and the segregating plants resulting from the cross Tritordeum × *T. turgidum,* were fractionated by three electrophoretical techniques: SDS-PAGE, A-PAGE, and bidimensional PAGE. Prolamin subunits with a high molecular weight (HMW) were well visualized by SDS-PAGE, the A-PAGE technique permitted good resolution for many hordeins and gliadins, and two-dimensional electrophoresis allowed new sets of bands coded by gene complexes from *H. chilense* chromosomes to be distinguished. The loci *Hor-Hch1* (up to 11 subunits belonging to the ω-, β- and α-hordeins), *Glu-Hch1* (one HMW prolamin subunit), *Hor-Hch2* (one α-hordein), and *Hor-Hch3* (up to four α-hordeins) were located on the *H. chilense* chromosomes *1Hch, 5Hch,* and *7Hch.*

Key words: *Hordeum* – A-PAGE – SDS-PAGE – Two-dimensional electrophoresis – Hordeins

Introduction

The South American wild barley *Hordeum chilense* has been used in breeding programs since the first hybrid between this species and *Triticum aestivum* was reported by Martin and Chapman (1977). The resulting amphiploid was first obtained by Chapman and Miller (1978), and then by Martin and Sánchez-Monge Laguna (1985), who also obtained the amphiploid *Hordeum chilense* × *Triticum turgidum* conv. *durum* (Martin and Sánchez-Monge Laguna 1982). This amphiploid, called "Tritordeum" by the authors, exhibits high cytological stability, good fertility, high crossability with other related amphiploids such as common wheat and triticale, high protein content (20–24%), and many other promising agronomic characters (Martin and Cubero 1981).

Crosses between Tritordeum and durum wheat have led to the production of pentaploid hybrids (2n = 5× = 35, with genome constitution AABBHch), which were fertile and segregated for the *H. chilense* chromosomes (Fernández and Jouve 1988). Moreover, Miller et al. (1982, 1985) have obtained addition and substitution lines for the common wheat "Chinese Spring"/*Hordeum chilense,* beginning with the amphiploid *H. chilense* × *T. aestivum*. This plant material can be applied in different studies, one of which is genetic mapping. Thus, some of the structural genes controlling isozymes and proteins have been located in *H. chilense* chromosomes (Chojecki and Gale 1982; Ainsworth et al. 1984, 1986; Miller et al. 1985; Fernández and Jouve 1987a, b; Payne et al. 1987; Fernández and Jouve 1990).

This paper reports the chromosomal location of genes controlling seed proteins in the wild barley *Hordeum chilense* using SDS-PAGE, A-PAGE, and two dimensional (2-D) procedures.

Materials and methods

Plant materials used in this study were as follows:

1. *Triticum turgidum* conv. *durum* (AABB, 2n = 28), cv "Mexican 248 × Andalucia 344" (MA), and cv 'Cocorit' (COC).
2. *Hordeum chilense* Brong. var. *muticum* (Prel) Hauman (Hch-Hch, 2n = 14) (CH).
3. The amphiploid *H. chilense* × *T. turgidum* conv. *durum* (AABBHchHch, 2n = 42) line "CHMA." This amphiploid was obtained by Martin and Sánchez-Monge Laguna (1982) after chromosome doubling of the hybrid between durum wheat "MA" and the above-mentioned line of the wild barley.

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4. Monosomic or polysomic addition forms of *H. chilense* chromosomes in tetraploid wheat. These plants were obtained by selfing the pentaploid hybrid (AABBHch, 2n=35) obtained by crossing *durum* wheat (female) and Tritordeum (polinator).
5. The *T. aestivum* cv "Chinese Spring"/*H. chilense* disomic addition lines *1Hch, 5Hch,* and *7Hch*. These aneuploid lines were obtained by Miller et al. (1982), who kindly supplied them from the Plant Breeding Institute (Cambridge, UK).

Polyacrylamid gel (10%) electrophoresis in the presence of sodium dodecyl sulphate (SDS-PAGE)

The extraction conditions and electrophoretic method of Payne et al. (1981) were used to analyze the proteins from a part of the kernels of all the plant material, thereby separating the protein subunits by molecular weight. The following (Sigma) molecular weight markers were employed: phosphorilase b (94 kDa), bovine serum albumin (67 kDa), and carbonic anhydrase (29 kDa).

Polyacrylamide gel (7%) electrophoresis with pH=3.1 aluminum lactate buffer (A-PAGE)

Extraction of proteins and the electrophoretic method were followed as described by Lafiandra and Kasarda (1985). These conditions separated proteins by their charge/mass ratio.

Two-dimensional (2-pH) electrophoresis

The extraction technique and electropheretic method developed by Lafiandra and Kasarda (1985) were used. Minor modifications were applied in gels that were 0.9 instead of 1.5 mm thick. A reduction in time for the buffer balance in the second dimension (10 min) was also made. Gels were prerun for 1.5 h at constant voltage (400 V). In the first dimension (aluminium lactate buffer), voltage was 500 V for 3 h at 4 °C. In the second phase (TRIS-glycine buffer), voltage was 300 V for 16 h (overnight) at 6 °C.

Results

SDS- and A-PAGE electrophoresis

Figures 1 a and 2 a show the SDS- and A-PAGE electrophoretic patterns for "CHMA" (AABBHchHch), 'COC' and "MA" (AABB), *Hordeum chilense* (HchHch), and a series of segregant plants obtained by selfing the pentaploid hybrid "COC" × "CHMA" (AABBHch). The durum wheats, the *Hordeum chilense,* and the synthetic amphiploid gave homogeneous phenotypes with both electrophoretic methods.

SDS-PAGE of the total prolamins from durum wheats (Fig. 1 a, track 1) exhibits four polypeptide migration positions. Although some component overlapping occurs, these groups correspond very broadly to the HMW glutenins (95–136 kDa), the ω-gliadins (44–74 kDa), the LMW subunits of glutenin (36–44 kDa), and the predominantly monomeric α-, β-, and γ-gliadins (44–74 kDa), according to the previous description of Shewry et al. (1988) in durum wheats. Some differences in the HMW glutenins were observed that differentiated the two durum wheats. The pattern for HMW proteins in the *Hordeum chilense* line differs from those of the durum

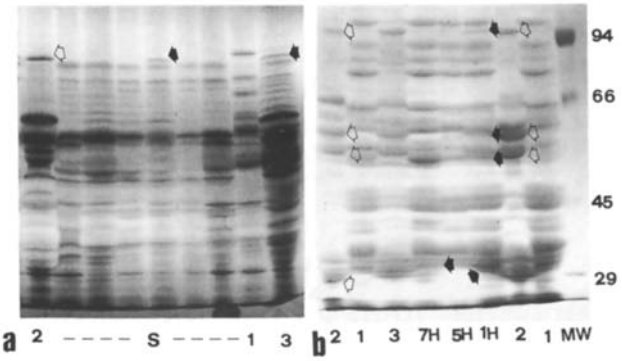

Fig. 1 a and b. Examples of the electrophorenograms obtained by SDS-PAGE of endosperm storage proteins in segregant plants from the pentaploid hybrid AABBHch and the *T. aestivum*/*H. chilense* addition lines. **a** *1*=*T. turgidum* cv "Cocorit"; *2*=*H. chilense* (HchHch); *3*=Tritordeum "CHMA" (AABBHchHch); *S*=segregant plants. **b** *1*=*T. aestivum* cv "Chinese Spring"; *2*=*H. chilense; 3*=addition of extracts of "Chinese Spring"+*H. chilense; 1H, 5H, 7H,* samples of the "Chinese Spring"/*H. chilense* addition lines for chromosomes *1Hch, 5Hch* and *7Hch,* respectively. *Arrows* indicate the *H. chilense* protein markers observed in *H. chilense* (*white*) and segregant plants or addition lines (*black*)

wheats by an intensely stained HMW prolamin (arrowed in Fig. 1 a, track 2), whose migration rate is between the ones observed for the two durum wheats. All HMW prolamins present in durum wheat "MA" and *Hordeum chilense* were present in the SDS-pattern of the amphiploid Tritordeum 'CHMA' (Fig. 1 a, track 3).

According to these results, genes that encode seed proteins in *Hordeum chilense* are expressed in the wheat genetic background and some of their products can be readily distinguished from those of the cultivated species. To determine the chromosomal location of genes controlling seed proteins in the wild barley, 62 segregant plants from progeny of the hybrid AABBHch were tested. These plants showed certain variations, which affected the four major groups of prolamins as follows: 12 out of the 62 plants analyzed (Fig. 1 a, tracks S) showed the HMW *H. chilense* prolamin. Since this band was also present in the SDS-PAGE patterns of the *Hordeum chilense* and Tritordeum "CHMA," this protein must be considered a marker for one of the *H. chilense* chromosomes. It can be reasonably inferred that all the segregates that exhibit it must have added the *H. chilense* chromosome or chromosome region to the durum wheat karyotype.

Figure 1 b illustrates the SDS-PAGE separation of prolamins for the *H. chilense, T. aestivum* "Chinese Spring," and its disomic addition lines *1Hch, 5Hch,* and *7Hch* (tracks 1, *1H, 5H,* and *7H,* respectively). The banding pattern of the "Chinese Spring"-*1Hch* addition line showed four bands that were not present in the pattern of "chinese Spring," but that did coincide with four bands observed in *H. chilense* (Fig. 1 b, tracks 2). The

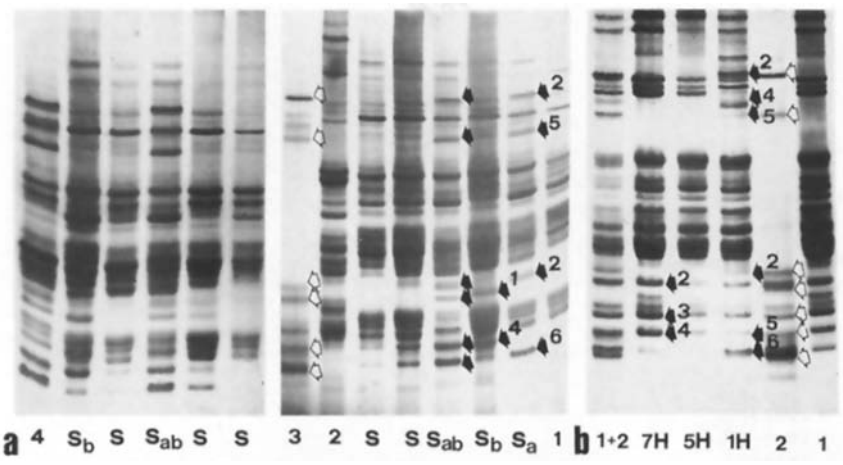

Fig. 2 a and b. Examples of the electrophorenograms obtained by A-PAGE of endosperm storage proteins in segregant plants from the pentaploid hybrid AABBHch, and the *T. aestivum*/*H. chilense* addition lines. **a** *1* = *T. turgidum* cv "MA"; *2* = *T. turgidum* cv "Cocorit"; *3* = *H. chilense* (HchHch), *4* = Tritordeum "CHMA" (AABBHchHch); *S* = segregant plants without *H. chilense* proteins; Sa, Sb, and Sab = segregant plants with different phenotypes; **b** *1* = *T. aestivum* cv "Chinese Spring"; *2* = *H. chilense; 1* + *2* = addition of extracts of "Chinese Spring" + *H. chilense; 1H, 5H, 7H,* samples of the "Chinese Spring"/*H. chilense* addition lines for chromosomes *1Hch, 5Hch,* and *7Hch,* respectively. *Arrows* indicate the *H. chilense* protein markers observed in *H. chilense* (*white*) and segregant plants or addition lines (*black*)

"Chinese Spring"-*7Hch* addition line contained one LMW component, which was also present in the phenotype of *H. chilense*. Finally, the banding pattern for the "Chinese Spring"-*5Hch* addition line presented all the endosperm prolamins from "Chinese Spring" but lacked the barley components.

A-PAGE was applied to study the seed proteins that were extracted with 1.5 *M* 2-methylformamide to exclude the HMW prolamins. The two lines of *durum* wheat, "COC" and "MA" (Fig. 2a, tracks 1 and 2), had patterns of a clearly different type, with major differences in the ω-gliadin region. *Hordeum chilense* (Fig. 2a, track 3) showed a total of 15 polypeptides distributed as follows: 5 ω-prolamins, 2 β-prolamins, and 8 α-prolamins. The pattern for Tritordeum 'CHMA' (Fig. 2a, track 4) showed all the prolamins present in both wheat "MA" and *H. chilense*.

Figure 2 shows A-PAGE separations of seed proteins from segregating plants. Out of the 62 plants analyzed, 39 did not have *H. chilense* hordeins (Fig. 2a, tracks S). The remaining 23 plants had patterns that included some of the distinctive *H. chilense* bands added to the *durum* wheat gliadins. Therefore, and for the purposes of this paper, the plants can be classified into three types: (i) nine plants had the *Sa* phenotype, with *H. chilense* bands ω-ch2, ωch5, β-ch2, and α-ch6 (Fig. 2a, track Sa); (ii) nine plants had the *Sb* phenotype, with hordeins α-ch1 and α-ch4 (Fig. 2a, track Sb); and (iii) five plants presented the *Sab* phenotype (Fig. 2a, tracks Sab) with a pattern that combined all the *H. chilense* hordeins present in both phenotypes *Sa* and *Sb* (Fig. 2a, tracks Sab).

Analysis of the *T. aestivum* "Chinese Spring"/*H. chilense* addition lines (Fig. 2b) by A-PAGE revealed the presence of "Chinese Spring" gliadins plus the following additional *H. chilense* components in each line: (*1Hch*) ω-ch2, ω-ch4, ω-ch5, β-ch2, α-ch5, and α-ch6; (*5Hch*) α-ch4; (*7Hch*) α-ch1, α-ch2, α-ch3, and α-ch4.

When scoring the results obtained by both the SDS-PAGE and A-PAGE methods, it was found that not all the segregant plants with the HMW prolamin (SDS-PAGE) had hordeins from the *Sa* phenotype (A-PAGE). Both kinds of protein components were present in the phenotype of the *T. aestivum* "Chinese Spring" addition line *1Hch*. However, only 7 of the 12 plants exhibiting the HMW barley prolamin showed the *Sa* phenotype. Reciprocally, 7 plants of the 14 with the *Sa* phenotype in A-PAGE lacked the HMW prolamin.

Two-dimensional electrophoresis

When a kernel had bands controlled by *Hordeum chilense* genes, one-third of the kernel was examined by two-dimensional (2-D) electrophoresis. Figure 3 shows photographs of the 2-D separation of gliadins and/or hordeins from *durum* wheat "MA," *H. chilense,* the Tritordeum line "CHMA," and plants that had the *Sa, Sb,* and *Sab* phenotypes on A-PAGE gels.

The *H. chilense* components previously separated by A-PAGE were investigated by the two-pH 2-D system. The first dimension was run under the same conditions as the A-PAGE method (pH = 3.1) and promoted the separation of the four major groups of prolamins resolved by this technique. Many proteins were resolved in conspicuous components (marked by arrows in Fig. 3d–f) after running the second dimension. The set of bands observed by the 2-D system in the *T. aestivum*/*H. chilense* addition lines is illustrated in Fig. 4.

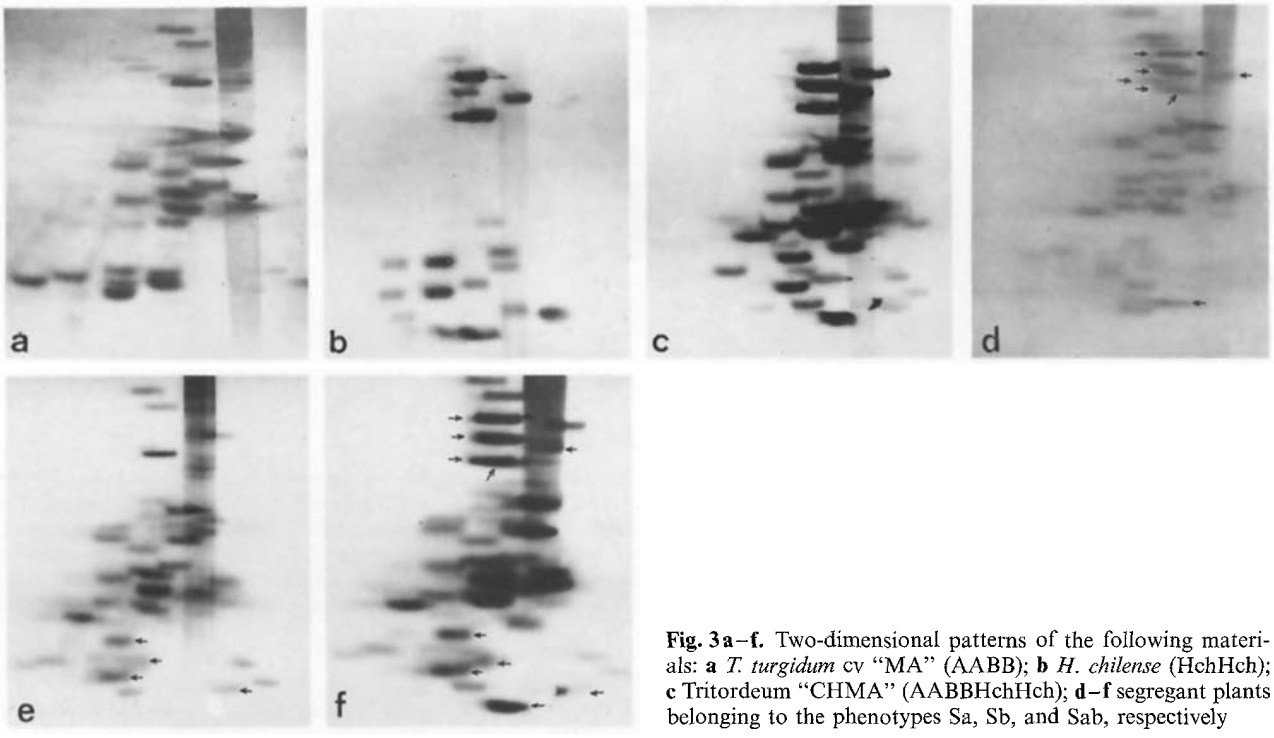

Fig. 3a–f. Two-dimensional patterns of the following materials: **a** *T. turgidum* cv "MA" (AABB); **b** *H. chilense* (HchHch); **c** Tritordeum "CHMA" (AABBHchHch); **d–f** segregant plants belonging to the phenotypes Sa, Sb, and Sab, respectively

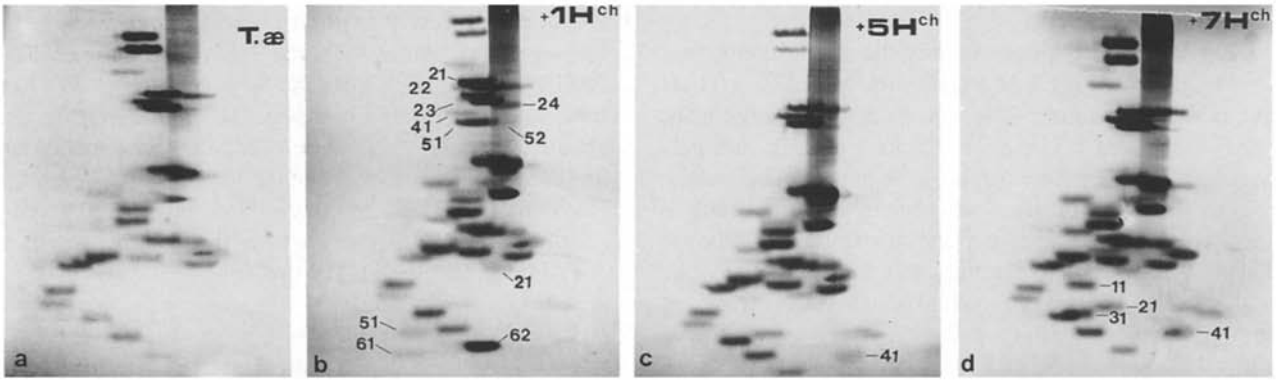

Fig. 4a–d. Two-dimensional patterns of the following materials: **a** *T. aestivum* cv "Chinese Spring"; **b** to **d** the "Chinese Spring"/*H. chilense* addition lines for chromosomes *1Hch, 5Hch,* and *7Hch*, respectively

The correspondence between the *H. chilense* prolamins separated by A-PAGE and the 2-D system in the segregant plants (*Sa, Sb,* and *Sab*) and the "Chinese Spring"/*H. chilense* addition lines (*1Hch, 5Hch,* and *7Hch*) is given in Table 1.

The *1Hch* chromosome addition line (Fig. 4b) showed many bands of *H. chilense* that were also found in the segregant plants with either the *Sa* or *Sab* phenotype. On the other hand, the "Chinese Spring"/*7Hch* addition line showed some of the *H. chilense* components found in plants with the *Sb* phenotype. The *5Hch* addition line had a single *H. chilense* component.

Discussion

The plant material used in this study is formed by segregant plants, in which one or more *H. chilense* chromosomes are lacking in or added to the karyotype of *durum* wheat. Analysis of the chromosome constitution in the progeny obtained by selfing the pentaploid hybrid of the genome formula *AABBHch* was previously reported by Fernández and Jouve (1988). They found that nearly 90% were addition forms of *T. turgidum* with one or more *H. chilense* chromosome. Plants with 29 chromosomes (33%) were more abundant than those with 28 (10%) in

Table 1. Protein composition and chromosomal location of the encoding genes in *Hordeum chilense*, as shown in A-PAGE and 2-D electrophoresis. Sa, Sb and Sab indicate segregant plants belonging to three different phenotypes and three different chromosome constitutions

H. chilense		AABBHch segregant progeny						*T. aestivum*/*H. chilense* add. lines					
		Sa		Sb		Sab		*1Hch*		*5Hch*		*7Hch*	
A-PAGE	2-D	A-PAGE	2-D	A-PAGE	2-D	A-PAGE	2-D	A-PAGE	2-D	A-PAGE	2-D	A-PAGE	2-D
ωch2	ωch21	ωch2	ωch21			ωch2	ωch21	ωch2	ωch21				
	ωch22		ωch22				ωch22		ωch22				
	ωch23		ωch23				ωch23		ωch23				
	ωch24		ωch24				ωch24		ωch24				
ωch4	ωch41	ωch4	ωch41			ωch4	ωch41	ωch4	ωch41				
ωch5	ωch51	ωch5	ωch51			ωch5	ωch51	ωch5	ωch51				
	ωch52		ωch52				ωch52		ωch52				
βch2	βch21	βch2	βch21			βch2	βch21	βch2	βch21				
αch1	αch11			αch1	αch11	αch1	αch11					αch1	αch11
αch2	αch21											αch2	αch21
αch3	αch31											αch3	αch31
αch4	αch41			αch4	αch41	αch4	αch41			αch4	αch41	αch4	αch41
αch5	αch51							αch5	αch51				
αch6	αch61	αch6	αch61			αch6	αch61	αch6	αch61				
	αch62		αch62				αch62		αch62				

the progeny of that hybrid. These addition forms are unstable for *H. chilense* chromosomes, which are frequently eliminated after two generations. However, they have special value for cytogenetic analyses and present certain advantages over the *T. aestivum* addition lines due to their less complex genome constitution.

When both sorts of materials are combined, segregant plants with a variable *H. chilense* chromosome composition and *T. aestivum*/*H. chilense* addition lines, using different electrophoretical methods, can mutually reinforce the results as well as locate new *H. chilense* marker genes. The present paper provides new data on *H. chilense* chromosomes that carry genes which control prolamins and high-molecular-weight seed proteins.

Some 45% of the segregant plants analyzed showed one or more *H. chilense* protein components, distributed as 22.5% for each particular set of proteins (*Sa* and *Sb*). Assuming that *Sa* and *Sb* phenotypes are determined by the presence of different *H. chilense* chromosomes, our new data agree with the transmission rates we reported earlier (Fernández and Jouve 1988) in the offspring of the pentaploid hybrid *AABBHch:* *1Hch*=24%; *2Hch*=22%; *3Hch*=17%; *5Hch*=16%; *6Hch*=34%; and *7Hch*=27%.

Payne et al. (1987) demonstrated that the great majority of the prolamin genes, including those coding for a high-molecular-weight subunit, are present on the *1Hch* chromosome. These authors used the *T. aestivum* cv "Chinese Spring"/*H. chilense* disomic addition lines as testers, and also located a few prolamin genes on the *5Hch* and *7Hch* chromosomes.

The comparison between the set of prolamins revealed by A-PAGE in segregant plants and the wheat – *H. chilense* addition lines permits the assumption to be made that the *Sa* and *Sb* phenotypes, respectively, express genes located on the *1Hch* and *7Hch* chromosomes. Moreover, chromosome *1Hch* carries the gene controlling the HMW prolamin, which was easily distinguished from the wheat bands in the "Chinese Spring"/*Hordeum chilense* *1Hch* addition line on SDS gels. This location was previously suggested by Payne et al. (1987), who demonstrated that the *Glu-Hch1* gene that controls the HMW prolamin in *H. chilense* is located on the long arm of the *1Hch* chromosome. The presence or absence of both the HMW *H. chilense* prolamin and the *Sa* phenotype in certain segregant plants can be explained by centromere misdivision. This process is likely to occur as a consequence of the meiotic behavior as univalents of *H. chilense* chromosomes in the pentaploid hybrid *AABB-Hch*. Some segregant plants may incorporate telocentrics for either the short or long arm, instead of the complete chromosomes. Accordingly, one could suggest that at least one compound locus, namely, *Hor-Hch1*, encodes fror the set of *Sa* phenotype *H. chilense* proteins (bands ω-ch21, ω-ch22, ω-ch23, ω-ch24, ω-ch41, ω-ch51, ω-ch52, β-ch21 α-ch51, α-ch61, and α-ch62), and is located on the short arm of the *1Hch* chromosome.

Gene complexes for α-hordein components were located in *H. chilense* chromosomes *5Hch* and *7Hch*. At least two compound loci, designated *Hor-Hch2* and *Hor-Hch3*, respectively, control the α-ch41 protein and the set of α-ch11, α-ch21, α-ch31, and α-ch41 hordeins associated with the presence of chromosomes *5Hch* and *7Hch*.

If the chromosomal locations of protein genes are compared between *H. chilense* and common wheat or rye and cultivated barley, evidence for both homoeologous relationships and chromosome rearrangements is suggested. Thus, homoeology between the chromosomes of group 1 in wheat, *1R* in rye, *1H* in cultivated barley, and *1Hch* in *H. chilense* seems to be well established on the basis of the loci for the HMW (long arms) and other prolamins (short arms) (Shewry et al. 1984; Galili and Feldman 1984; Payne et al. 1984; Sybenga et al. 1990: Benito et al. 1990), and other genes controlling GPI, MDH, and PER isozymes (see Fernández 1989, for a review). On the other hand, in addition to the prolamin loci located on chromosome *1Hch,* two genes have been assigned to chromosomes *5Hch* and *7Hch*. Assuming that protein components coded by the gene on chromosome *7Hch* were actual prolamins, at least one translocation could have occurred between chromosomes *1Hch* and *7Hch* in the ancestor of wheat and *H. chilense*.

Final elucidation of the nature and homoeological relationships of the genes encoding for seed protein components will come when protein isolation, purification, and chemical characterization are methodologically solved.

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