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Linkage relationships between prolamin genes on chromosomes 1A and 1B of durum wheat

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Abstract. Gliadin and glutenin electrophoresis of F_2 progeny from four crosses of durum wheat was used to analyse the linkage relationships between prolamin genes on chromosomes 1A and 1B. The results showed that these genes are located at the homoeoallelic loci *Glu-1*, *Gli-3*, *Glu-3* and *Gli-1*. The genetic distances between these loci were calculated more precisely than had been done previously for chromosome 1B, and the genetic distances between *Gli-A3*, *Glu-A3* and *Gli-A1* on chromosome 1A were also determined. Genes at *Gli-B3* were found to control some ω-gliadins and one B-LMW glutenin, indicating that it could be a complex locus.

Key words: Gliadins – Glutenins – *Triticum* – Gene mapping – Electrophoresis

Introduction

The two major prolamin protein groups in wheat endosperm are the gliadins and glutenins. Gliadins are monomeric proteins, whereas glutenins are multimeric aggregates of high-molecular-weight (HMW = A subunits) and low-molecular-weight (LMW = B and C subunits) subunits held together by disulphide linkage.

Gliadins are coded by genes located on the short arms of homoeologous chromosomes of groups 1 and 6 at the *Gli-1* and *Gli-2* loci, respectively (Wrigley and Shepherd 1973; Payne et al. 1982a). Each locus contains a cluster of tightly linked codominant genes (Doekes 1973) that code for a "block" of proteins inherited as a Mendelian character (Mecham et al. 1978; Sozinov and Poperelya 1980). Additional dispersed gliadin genes have been shown to occur on the short arm of chromosomes 1A (Sobko 1984; Metakovsky et al. 1986) and 1B (Galili and Feldman 1984; Jackson et al. 1985) at a locus denoted *Gli-3* (Payne et al. 1988) placed midway between the centromere and *Gli-1*.

HMW glutenins subunits are coded at *Glu-1* loci on the long arm of chromosomes of group 1 (Bietz et al. 1975; Payne et al. 1980; Lawrence and Shepherd 1981). The genes controlling some of the B-subunits of glutenin, the major group of LMW glutenins, have been mapped on the short arm of chromosomes 1A and 1B (Payne et al. 1984a). Singh and Shepherd (1988a) located these genes at the *Glu-3* loci, very closely linked to *Gli-1*.

In durum wheat it has been shown that γ-gliadins denoted 42, 44 and 45 are codominant alleles at *Gli-B1* (Joppa et al. 1983; Monneveux et al. 1984). Gliadin γ-45 is genetically linked to ω-gliadin 35 and the B-LMW glutenin subunits model referred to as LMW-2, and γ-42 to ω-gliadin triplet 33-35-38 and to the B-LMW glutenins pattern LMW-1 (Payne et al. 1984b). Carrillo et al. (1990) showed that γ-44 is associated with the B-LMW pattern called LMW-2* and, in some cultivars, γ-45 and γ-42 with the B-LMW models referred to as LMW-2$^-$ and LMW-1$^-$, respectively. The control of two B-LMW patterns from cvs 'Langdon' (with γ-42) and 'Edmore' (with γ-45) by the short arm of chromosomes 1A and 1B has been shown by Gupta and Shepherd (1988).

The aim of the investigation presented here was to determine the linkage relationships and genetic distances between the different prolamin genes on chromosomes 1A and 1B by analysing gliadin and glutenin segregation in four crosses of durum wheat.

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Materials and methods

Four crosses using five durum wheat varieties, 'Abadía', 'Mexicali', 'Ardente', 'Oscar' and 'Alaga', and one Spanish landrace, 'Claro of Bazalote', with contrasting prolamin variants were conducted using standard procedures: cross 1 'Abadía' × 'Mexicali'; cross 2 'Oscar' × 'Ardente'; cross 3 'Oscar' × 'Mexicali'; cross 4 'Alaga' × 'Claro of Bazalote'. A total of 246 F_2 grains from cross 1, 163 from cross 2 and 176 from crosses 3 and 4 were analysed for prolamin composition.

Extraction of endosperm proteins

Gliadins and glutenins were extracted from one-half of a F_2 seed according to Gupta and Shepherd (1990). Two residues (dried pellet) were re-dissolved for the analysis of gliadins and glutenins.

Gliadin electrophoresis

Gliadins were fractionated in acid (pH 3.1) polyacrylamide gel electrophoresis (A-PAGE) (Lafiandra and Kasarda 1985). Band numbers were designated according to Sapirstein and Bushuk (1985).

Glutenin electrophoresis

Glutenins were analysed by two-step one-dimensional polyacrylamide gel electrophoresis (SDS-PAGE) as described by Gupta and Shepherd (1990) with minor modifications. B-LMW patterns were termed LMW-1 and LMW-2 (Payne et al. 1984b) and LMW-1$^-$, LMW-2* and LMW-2$^-$ (Carrillo et al. 1990). Band numbers in zone B were designated by us relative to their electrophoretical mobility; number 1 for the slowest band from cv 'Mexicali' to number 15 for the fastest one from cv 'Claro of Bazalote'. HMW glutenins were designated according to Payne and Lawrence (1983).

Recombination fractions were estimated by the method of maximum likelihood, and map distances and their standard errors (in cM) by the Kosambi function (Kosambi 1944).

Results

The chromosomal location of genes controlling the prolamins studied were made on the basis of the segregation observed in the F_2 seeds analysed. The durum wheat cultivars selected had either bands γ-42 ('Abadía' and 'Oscar'), or γ-44 ('Alaga') or γ-45 ('Mexicali', 'Ar-

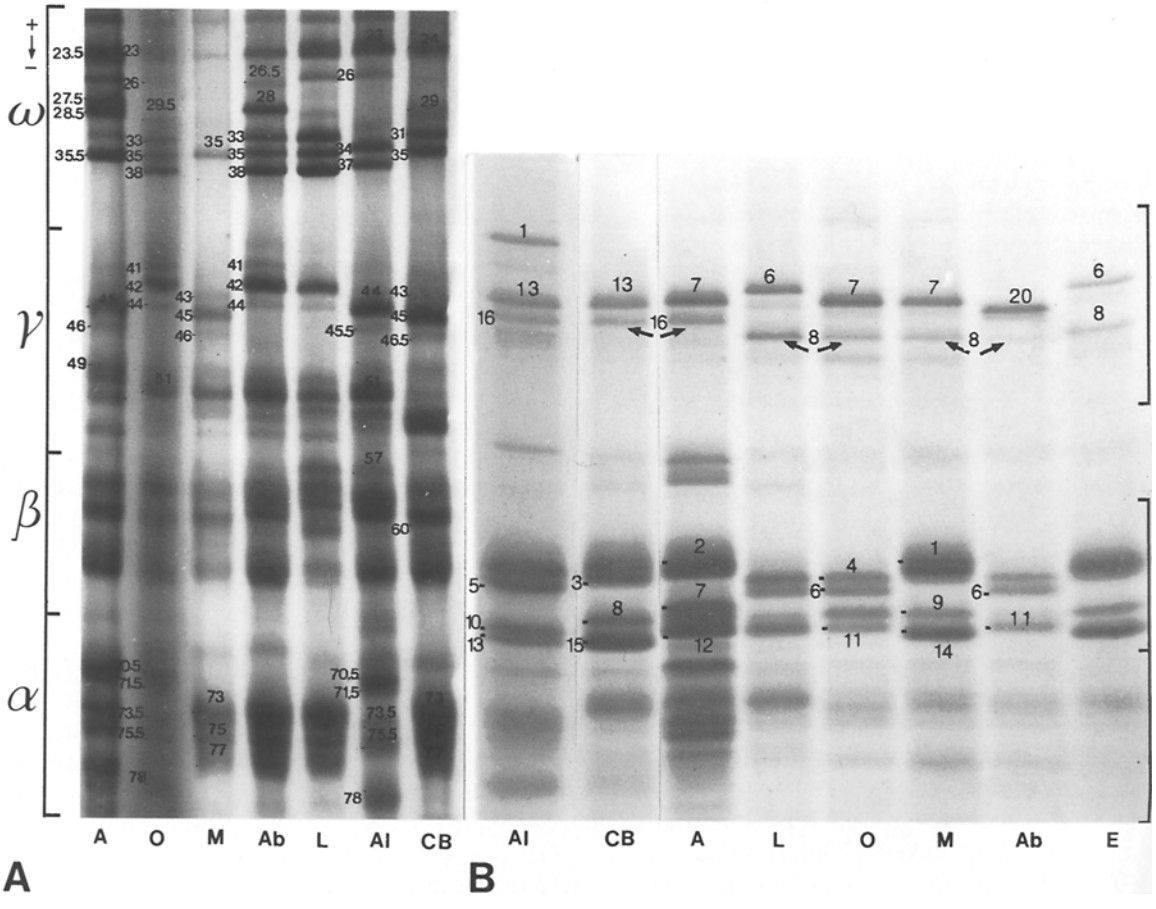


Fig. 1A, B. Gliadin (**A**) and glutenin patterns (**B**) from parental cvs 'Abadía' (*Ab*), 'Oscar' (*O*), 'Ardente' (*A*), 'Alaga' (*Al*), 'C. Bazalote' (*CB*), 'Mexicali' (*M*). Durum wheat cvs 'Langdon' (*L*) and 'Edmore' (*E*) were included for comparison. The contrasting prolamin subunits studied are *numbered*

dente' and 'C. Bazalote') coded by genes at the *Gli-B1* locus. Consequently, those genes coding for the B-LMW glutenin subunits, inherited closely linked to these γ-gliadins, were assigned to the *Glu-B3* locus. Conversely, B-subunits genes inherited independently of *Gli-B1* genes were assigned to *Glu-A3*, and gliadin genes tightly linked to those at *Glu-A3* were assigned to *Gli-A1*. α- and β-gliadins inherited independently of those gliadins located on chromosomes of group 1 were assigned to *Gli-A2* and *Gli-B2* loci, respectively.

Figure 1A shows the gliadin patterns of the parents of the crosses together with the contrasting gliadin bands studied in the F_2 progeny. The latter are ω-26.5, 28, 33, 35, 38 γ-41, 42, 44 from cv 'Abadía' (slot Ab), ω-23, 26, 29.5, 33, 35, 38 γ-41, 42, 44, 51 α-70.5, 71.5, 73.5, 75.5, 78 from cv 'Oscar' (slot O), ω-23.5, 27.5, 28.5, 35.5 γ-45, 46, 49 from cv 'Ardente' (slot A), ω-23, 26, 34, 37 γ-44, 45.5, 51 β-57 α-70.5, 71.5, 73.5, 75.5, 78 from cv 'Alaga' (slot Al). ω-24, 29, 31, 35 γ-43, 45, 46.5 β-60 α-73, 75, 77 from cv 'C. Bazalote' (slot CB) and ω-35 γ-43, 45, 46 α-73, 75, 77 from cv 'Mexicali' (slot M). The α-blocks studied from cvs 'C. Bazalote' and 'Mexicali' and from cvs 'Oscar' and 'Alaga' have also been analysed by Pogna et al. (1990) and designated α-1 and α-2, respectively.

The B-LMW glutenin models selected are shown in Fig. 1B: LMW-2* from 'Alaga' (slot Al), LMW-2$^-$ from 'Ardente' (slot A), LMW-1 from 'Oscar' (slot O), LMW-2 from 'Mexicali' (slot M) and two different models, one from var 'Abadía' (slot Ab) that is similar to model 1 without a band, designated in this work LMW-1(Ab), and another from the landrace 'C. Bazalote' (slot CB) that is composed of four bands and termed here LMW-2(CB). B-LMW subunits studied in the F_2 progeny, those not overlapping, are indicated. They are bands 5, 10, 13 from 'Alaga', 3, 8, 15 from 'C. Bazalote', 2, 7, 12 from 'Ardente', 4, 6, 11 from 'Oscar', 1, 9, 14 from 'Mexicali' and 6, 11 from 'Abadía. The HMW glutenin subunits analysed were: 7 + 16 from 'Ardente', 7 + 8 from 'Oscar' and 'Mexicali' and 20 + 8 from 'Abadía, all coded at *Glu-B1*, and subunits 1 from 'Alaga' and Null from 'C. Bazalote', both coded at *Glu-A1*.

Inheritance of gliadin genes

Gliadin patterns of F_2 grains from crosses 1, 2, 3 and 4 are shown in Fig. 2. The gliadin components that segregated with γ-42, or γ-45 or γ-44 as a block coded at the *Gli-B1* locus were: ω-33-35-38 γ-41-42-44 from 'Abadía', the same block with ω-23 in cross 2 and with ω-23-26 in cross 3 from cv 'Oscar', ω-35.5 γ-45-46 from 'Ardente', ω-35 γ-43-45-46 from 'Mexicali', ω-35 γ-43-45-46.5 from 'C. Bazalote' and ω-23-26-34-37 γ-44-45.5 from 'Alaga'. In cross 1 ω-26.5-28 from 'Abadía' were inherited together in accordance with the expected ratio 3:1 and not included in the *Gli-B1*-encoded block.

Gliadin components coded at *Gli-A1* as allelic variants were the block ω-23.5-27.5-28.5 γ-49 from 'Ardente' and γ-51 from 'Oscar' in cross 2 and γ-51 from 'Alaga' and ω-24-29-31 from 'C. Bazalote' in cross 4.

Band ω-29.5 from 'Oscar' was studied in 102 F_2 grains from cross 2 and in cross 3. It was inherited separately from the *Gli-B1*-encoded block, but some recombinant patterns were found between this component and γ-51 coded at *Gli-A1* (Fig. 2B, slot 7). Its segregation agreed well with a 3:1 ratio.

Blocks α-1 and α-2, in crosses 3 and 4, and β-57 and β-60, in cross 4, were inherited as allelic variants.

The segregation of all of the alternatives was statistically in agreement with a 1:2:1 ratio, which is consistent with the expected ratio for allelic forms.

Inheritance of glutenin genes

Figure 3 shows the fractionation of glutenin subunits of F_2 grains from the four crosses analysed.

B-LMW subunits coded at the *Glu-B3* locus were determined in each cross: bands 6 + 11 from 'Abadía' in cross 1, 1 + 14 from 'Mexicali' in crosses 1 and 3, bands 6 in cross 2 and 6 + 11 in cross 3 from 'Oscar', band 2 from 'Ardente' in cross 2 and 10 + 13 from 'Alaga' and 8 from 'C. Bazalote' in cross 4.

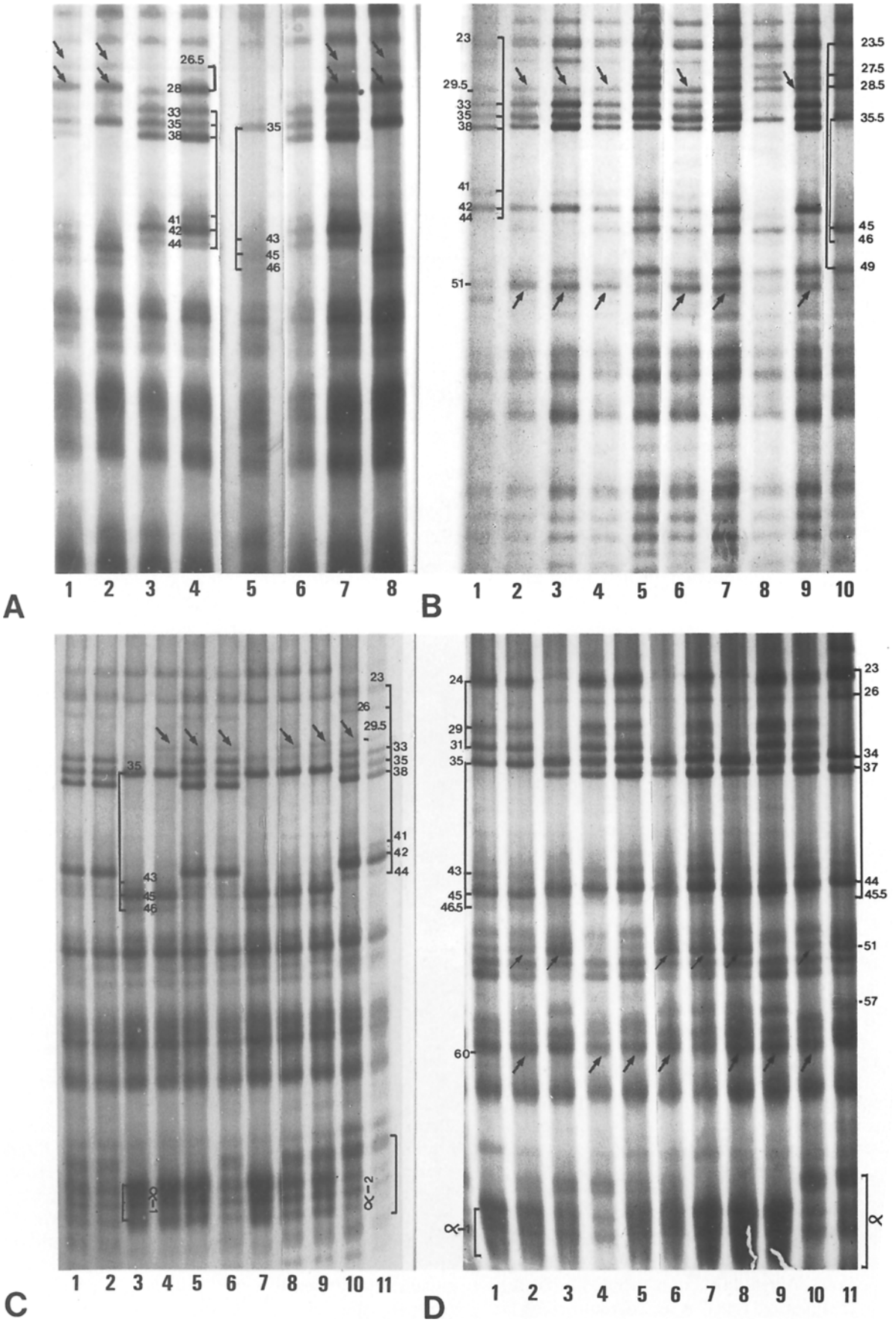
In cross 1 an allelic band of LMW9 from 'Mexicali' was not found in the other parent, 'Abadía'. This subunit was inherited according to a 3:1 segregation and separately from bands 1 + 14, which are coded at the *Glu-B3* locus. The segregation data of this cross revealed that the distribution of F_2 grains for LMW9 and ω-26.5-28 from 'Abadía' was in three phenotype classes, which agreed well with a ratio of 1:2:1, thereby showing that the corresponding genes were allelic.

B-LMW subunits assigned to the *Glu-A3* locus as allelic variants were bands 4 from 'Oscar' and 7 + 12 from 'Ardente' in cross 2 and bands 5 from 'Alaga' and 3 + 15 from 'C. Bazalote' in cross 4.

The alleles at *Glu-B3*, *Glu-A3* and *Glu-B1* all segregated in a 1:2:1 ratio. In cross 4, HMW subunit 1, at *Glu-A1*, was inherited in accordance to a ratio of 3:1.

Prolamin gene mapping

Table 1 shows the linkage relationships of the prolamins controlled by chromosomes 1B and 1A. (Only the first component of each block appears in the table). The genes coding for ω-26.5-28 and LMW9 were located between *Gli-B1* and *Glu-B1*. *Glu-B3-Gli-B1* linkage was 0.8 ± 0.4 cM in cross 1, 1.2 ± 0.6 cM in cross 2 and 4.9 ± 1.1 cM in cross 4. *Glu-B1* was not significantly linked to *Gli-B1*, showing a recombination percentage of 41.2 ± 3.0 with *Glu-B3* and *Gli-B1* in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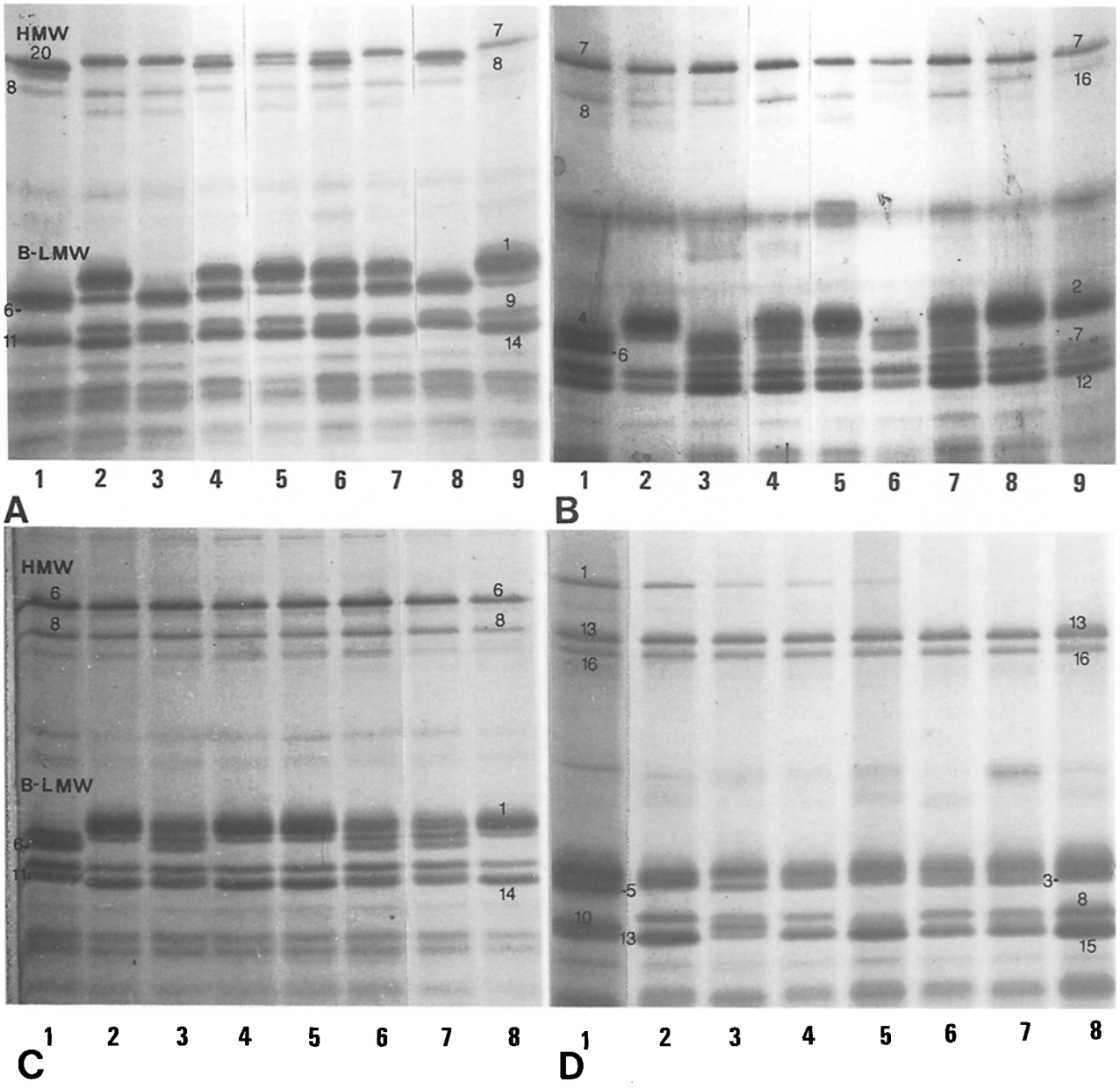

Fig. 3A–D. Glutenin patterns of F_2 grains from **A** cross 1 – 'Abadía' (*1*) × 'Mexicali' (*9*); **B** cross 2 – 'Oscar' (*1*) × 'Ardente' (*9*); **C** cross 3 – 'Oscar' (*1*) × 'Mexicali' (*8*); **D** cross 4 – 'Alaga' (*1*) × 'C. Bazalote' (*8*). Contrasting HMW and B-LMW subunits are *numbered*

cross 1 and 44.8 ± 3.8 and 45.3 ± 3.8, respectively, with these loci, in cross 2.

The data for chromosome 1A indicated that the gene coding for ω-29.5 was located at a distance of 14.0 ± 4.6 cM from *Gli-A1*. It was not possible to calculate the frequency of recombination with *Glu-A1* because both parentals had the Null allele at that locus. In cross 3, ω-29.5 showed no linkage with the rest of prolamins coded by chromosomes 1B, 6A and 6B, which is consistent with the gene for the former being

Fig. 2A–D. Gliadin patterns of F_2 grains from **A** cross 1 – 'Abadía' (*4*) × 'Mexicali' (*5*); **B** cross 2 – 'Oscar' (*1*) × 'Ardente' (*10*); **C** cross 3 – 'Oscar' (*11*) × 'Mexicali' (*3*); **D** cross 4 – 'Alaga' (*11*) × 'C. Bazalote' (*1*). Contrasting studied gliadin bands and blocks are indicated. Bands 26.5, 28, 29.5, 51 and 60 are *arrowed*

Table 1. Linkage relationships between prolamins in chromosomes 1B and 1A in crosses 1, 2 and 4

Chromosome		Prolamin subunits		χ^{2a}	R (%)	Distance (cM)
		Locus 1	Locus 2			
1B	Cross 1	ω-26.5, LMW9	γ-42, γ-45	139.46**	18.6	19.5 ± 2.0
		LMW6, LMW1	γ-42, γ-45	490.08**	0.8	0.8 ± 0.4
		ω-26.5, LMW9	HMW20, HMW7	32.52**	33.1	39.8 ± 4.8
	Cross 2	LMW6, LMW2	γ-42, γ-45	309.15**	1.2	1.2 ± 0.6
	Cross 4	LMW10, LMW8	γ-44, γ-45	254.77**	4.9	4.9 ± 1.1
1A	Cross 2	LMW4, LMW7	γ-51, γ-49	331.56**	1.2	1.2 ± 0.6
		LMW4, LMW7	ω-29.5	41.29**	17.3	18.0 ± 5.3
		ω-29.5	γ-51, γ-49	49.25**	13.7	14.0 ± 4.6
	Cross 4	LMW5, LMW3	γ-51, ω-24	319.99**	1.7	1.7 ± 0.7

** Significant at the 1% level
[a] For joint segregation

controlled by chromosome 1A, as shown in cross 2. *Gli-A1-Glu-A3* linkage was 1.2 ± 0.6 cM in cross 2 and 1.7 ± 0.7 cM in cross 4. *Glu-A1* was not significantly linked to *Gli-A1* and *Glu-A3*, with a recombination of 46.3 ± 4.5% and 45.9 ± 4.5%, respectively. The most likely order with respect to the centromere was studied from the *Glu-A1* allele composition of the recombinants between *Gli-A1* and *Glu-A3*. Several F_3 seeds from each recombinant were analysed to determine the homozygous genotypes for HMW subunit 1. These data indicated that if *Gli-A1* is distal, this order would involve one double recombinant less than if *Gli-A1* was between *Glu-A1* and *Glu-A3*.

Genes coding for α-1 and α-2 blocks in crosses 3 and 4 were inherited independently of the rest of the prolamin loci studied as well those of β-gliadins 57 and 60 in cross 4. Therefore, they were assigned to *Gli-A2* and *Gli-B2*, respectively.

Discussion

The data from this investigation allowed us to locate the genes controlling the synthesis of six and three allelic variants at *Gli-B1* and *Gli-A1*, respectively, and two allelic variants at *Gli-B2* and *Gli-A2*. No recombinant types were detected between the genes of the same block as was found by Sozinov and Poperelya (1980) and Metakovsky et al. (1986).

The chromosomal control of six different B-LMW glutenin models was determined (Fig. 4). The majority of the B bands were inherited as two groups controlled at the *Glu-A3* and the *Glu-B3*, which agrees with the conclusion of Gupta and Shepherd (1988), except for a subunit, designated as 9 in this work, of the LMW-2 pattern (* in Fig. 4). The loci of this B subunit and two ω-gliadins, occurred on the short arm of chromosome 1B at a distance of 19.5 cM from *Gli-B1* and 39.8 cM from *Glu-B1*. Galili and Feldman (1984) located, in common wheat, one ω-gliadin at 28.1 cM from *Gli-B1*. Jackson et al. (1985) mapped a D-subunit prolamin at 22.4 cM from *Gli-B1* and 16.7 cM from *Glu-B1*. Payne et al. (1988) showed that both prolamins were allelic, being more closely related to ω-gliadins in terms of their electrophoretic mobilities and isoelectric points, and called the locus *Gli-B3*. Because of the close genetic relationship between common and durum wheats it is extremely likely that we have mapped this locus. However, our results indicate that genes at *Gli-B3* are controlling a B-LMW glutenin in addition to the ω-gliadins, since if subunit 9 was a gliadin-type prolamin it would have run in the first step of electrophoresis with the rest of the gliadins. Also, it is not a D-subunit because its electrophoretic mobility was faster than that of zone D and it would have been produced in relatively small amounts (Payne et al. 1988). However, this glutenin had the electrophoretic mobility and staining intensity of the B-subunits (Figs. 1B and 3A). These results suggest that *Gli-B3*, similarly to other loci of endosperm proteins, could be a complex locus with genes tightly linked that codes for ω-gliadins and B-LMW glutenins.

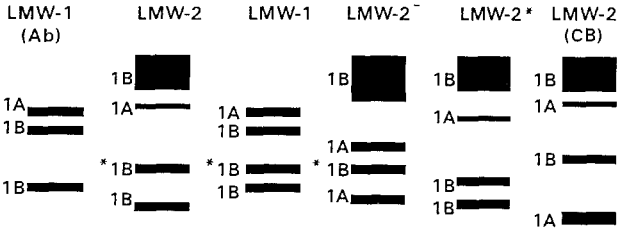

Fig. 4. Diagram of the allelic types of LMW glutenin B-subunits from different patterns of durum wheat cultivars. * coded by *Gli-B3*

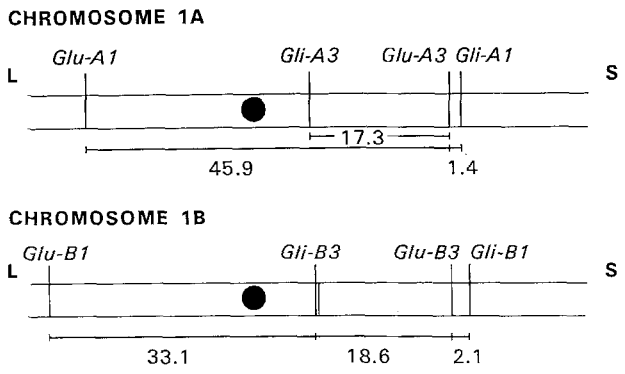

Fig. 5. Genetic map of chromosomes 1A and 1B showing different prolamin loci and their distances (in cM). *L* long arm, *S* short arm

The locus on chromosome 1A coding for the ω-gliadin 29.5 showed a recombination of 13.7% with *Gli-A1*. Because of the *Gli-A1* position at the distal end of the short arm (Singh and Shepherd 1988a), the most probable location of this locus would be proximal to the centromere. This chromosome map position was similar to that of *Gli-B3*, mapped in cross 1, indicating that it could be *Gli-A3*, the homoeologous locus on chromosome 1A. In common wheat Sobko (1984) and Metakovsky et al. (1986) found a percentage of recombination of 31% and 13%, respectively, between *Gli-A1* and a few ω-gliadins.

Pooled linkage data were homogeneous for each chromosome. Analysis of the joint segregation of crosses 1, 2 and 4 indicated that the percentage of recombination and its standard error between *Glu-B1* and *Glu-B3* was 42.8 ± 2.4, which agrees with the data of Lawrence and Shepherd (1981), Payne et al. (1982b), Snape et al. (1985), Singh and Shepherd (1988b) and Pogna et al. (1990). *Glu-B3-Gli-B1* linkage was 2.0 ± 0.4 cM, which is consistent with the 1.7 ± 0.8 cM obtained by Singh and Shepherd (1988a) in common wheat and the 2.0 ± 0.8 cM obtained by Pogna et al. (1990) in durum wheat. *Gli-A1-Glu-A3* linkage was 1.3 ± 0.4 cM. This genetic distance had not been determined so far in wheat because of the failure to find recombinants between the genes of both loci. In cross 2 a higher recombination frequency was obtained between *Gli-A3* and *Glu-A3* (17.3%) than between *Gli-A3* and *Gli-A1* (13.7%), indicating a distal position of *Glu-A3* on the chromosome short arm. However, this locus order was based on a low precise estimate of the recombination frequency (standard error was 4.7 and 4.3, respectively) since *Gli-A3* was defined only by a single allele. On the other hand, although statistically not proven, the recombinant progeny obtained in cross 4 indicated that the most probably location of *Glu-A3* is between *Glu-A1* and *Gli-A1*. This order would be the same as that on chromosome 1B, thereby reflecting the homoeologous relationship of the group 1 chromosomes in wheat.

On the basis of the results of this work the genetic map for chromosomes 1A and 1B is as shown in Fig. 5.

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