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Variation and classification of B low-molecular-weight glutenin subunit alleles in durum wheat

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Abstract The B low-molecular-weight (LMW) glutenin subunit composition of a collection of 88 durum wheat cultivars was analyzed. Extensive variation has been found and 18 different patterns were detected. Each cultivar exhibited 4–8 subunits, and altogether 20 subunits of different mobility were identified. The genetic control of all these subunits was determined through the analysis of nine F_2 populations and one backcross. Five subunits were controlled at the *Glu-A3* locus, 14 at *Glu-B3* and 1 at *Glu-B2*. At the *Glu-A3* locus each cultivar possessed from zero to three bands and eight alleles were identified. At the *Glu-B3* locus each cultivar showed four or five bands and nine alleles were detected. Only one band was encoded by the *Glu-B2* locus. A nomenclature for these alleles is proposed and the relationship between them and the commonly used LMW-model nomenclature is discussed.

Key words Durum wheat · LMW glutenin subunits · Allelic variants

Introduction

The gluten composition of durum wheat cultivars is the main factor that determines the quality of the end-use products. Studies have been focused on the analysis of glutenins and gliadins, the main components of gluten. Early studies (Damidaux et al. 1978; Kosmolak et al. 1980; du Cros et al. 1982) demonstrated the usefulness of gliadins γ-45 and γ-42, encoded at the *Gli-B1* locus (Joppa et al. 1983), as markers of good and poor pasta quality, respectively. Further studies (Payne et al. 1984; Pogna et al. 1988, 1990; Ruiz and Carrillo 1995 a) found that low-molecular-weight (LMW) glutenin subunits, encoded at the *Glu-3* loci and tightly linked to the *Gli-1* loci (Singh and Shepherd 1988), were responsible for the differences in quality.

Durum wheats had been classified according to their LMW glutenin patterns and these patterns have been related to quality (Payne et al. 1984; Pogna et al. 1988, 1990; Carrillo et al. 1990, 1991; Kovacs et al. 1995). The LMW-models include chromosome 1A- and 1B-encoded LMW glutenin subunits (Gupta and Shepherd 1988; Ruiz and Carrillo 1993). Recently, the effect of a few allelic variants at the *Glu-A3*, *Glu-B3* and *Glu-B2* loci on pasta quality has been reported (Ruiz and Carrillo 1995 a, b, 1996; Vázquez et al. 1996). The aim of the present work was to study the variability and the genetic control of the B-LMW glutenin subunits in durum wheat in order to determine the allelic variation at each of the loci implicated. A nomenclature for these alleles is proposed.

Material and methods

Plant material

Eighty eight durum wheat cultivars were analyzed (see Table 1). Except for Langdon, which was from our Laboratory, seed samples were from the Instituto Nacional de Semillas y Plantas de Vivero (Spain). Seed samples of the 11 cultivars proposed as standards (see Table 1) are available on request. F_2 seeds from nine crosses and seeds from one backcross (see Table 2) were analyzed to determine the inheritance of particular B-LMW glutenin subunits.

Electrophoresis

Proteins were extracted from crushed endosperm halves following the sequential procedure of Singh et al. (1991). The first propanol-1

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extract was evaporated and gliadins were dissolved in 1.5 M dimethyl formamide and fractionated by acid polyacrylamide-gel electrophoresis (A-PAGE; Lafiandra and Kasarda 1985). Electrophoresis of reduced and alkylated proteins [high-molecular-weight (HMW) and LMW glutenin subunits] were performed on sodium dodecyl sulphate polyacrylamide gels (SDS-PAGE) according to Nieto-Taladriz et al. (1994).

Results

Intervarietal variation in B-LMW glutenin subunits

The B-LMW glutenin subunit pattern was determined in at least ten seeds per cultivar, and all of them were homogeneous. 'Mexicali' and 'Langdon' were used as references to determine the relative mobilities of these subunits. Bands were numbered according to their increasing mobility.

In the analysis of 88 durum wheat cultivars a total of 18 different B-LMW glutenin subunit patterns were detected (Fig. 1). Each cultivar possessed 4–8 subunit bands and altogether 20 subunits of different mobility were identified. Seventy six per cent of the collection analyzed can be characterized by only four patterns: 40% showed the same pattern as 'Mexicali' (Fig. 1, slots a, m), 18% were as 'Cocorit' (slot b), and 9% were as 'Antón' (slot o) and 'Langdon' (slot p). Four cultivars were as 'Jiloca' (slot d), four as 'Esquilache' (slot e), and two as 'Mundial' (slot i). Eleven patterns were rare and were found in only one cultivar each: 'Granja Badajoz' (slot j), 'Ardente' (slot k), 'Endural' (slot l), 'Claro de Balazote' (slot h), 'Alaga' (slot n), 'Andalucía 344' (slot q), 'Blatfort' (slot r), 'Peñafiel' (slot c), 'Cibeles' (slot f), 'Clarofino' (slot g) and 'Agudo' (slot s).

Fig. 1 SDS-PAGE patterns of glutenin subunits of durum wheat cultivars 'Mexicali' (slots *a*, *m*), 'Cocorit' (*b*), 'Peñafiel' (*c*), 'Jiloca' (*d*), 'Esquilache' (*e*), 'Cibeles' (*f*), 'Clarofino' (*g*), 'Claro de Balazote' (*h*), 'Mundial' (*i*), 'Granja Badajoz' (*j*), 'Ardente' (*k*), 'Endural' (*l*), 'Alaga' (*n*), 'Antón' (*o*), 'Langdon' (*p*), 'Andalucía 344' (*q*), 'Blatfort' (*r*) and 'Agudo' (*s*). Arrowheads, arrows and dots refer to bands controlled by alleles at the *Glu-A3*, *Glu-B3* and *Glu-B2* loci, respectively, in the cultivars proposed as standards

Genetic control of B-LMW glutenin subunits

The chromosomal location of the genes controlling the B-LMW glutenin subunits was determined on the basis of the segregation patterns observed in the progenies analyzed (90–150 seeds per population). It was assumed that bands with the same relative mobility were the same subunit. The analysis of gliadins showed that parents had either bands γ-45 ('Ardente', 'Senatore Capelli', 'Peñafiel', 'Ferox', 'Claro de Balazote' and 'Mexicali'), γ-42 ('Antón', 'Lakota', 'Safari'), γ-44 ('Alaga'), or γ-null ('Blatfort'). Table 1 includes the γ-gliadins found in the cultivars analyzed. These bands are controlled by genes at the *Gli-B1* locus, on the short arm of chromosome 1B (Joppa et al. 1983), tightly linked to the *Glu-B3* locus (Singh and Shepherd 1988). Therefore, those LMW glutenin subunits which co-segregated with these γ-gliadins were assigned to the *Glu-B3* locus and those which were independent were assigned to the *Glu-A3* locus. Only in one cross, 'Senatore Capelli'/'Claro de Balazote', did both parents have γ-45 and the genetic control of specific subunits was based on the LMW glutenin subunits already determined in other crosses. The parents of the ten progenies analyzed were chosen in order to establish the genetic control of all the 20 subunits detected among the durum wheat collection considered. Table 2

Table 1 Durum wheat cultivars analyzed and their allelic classification at the loci considered[a]

Cultivar	*Gli-B1*	*Glu-A3*	*Glu-B3*	*Glu-B2*	Cultivar	*Gli-B1*	*Glu-A3*	*Glu-B3*	*Glu-B2*
Abadía	42	b	b	b	Férox	45	c	a	a
Acalón	45	c	a	a	Gallareta	45	a	a	a
Agridur	45	a	a	a	Gamex	45	a	a	a
Agudo	42	h	b	b	**Granja Badajoz**	45	e	e*	a
Alacón	45	a	a	a	ID 1039	45	a	a	a
Alaga	44	d*	h*	b	Jabato	42	b	b	a
Aldeano	42	b	b	a	Jaguar	45	c	a	a
Aldura	42	b	b	b	Jerez 36	45	a	a	a
Almanzor	45	c	a	a	**Jiloca**	45	h*	c*	b
Andalucía 344	Null	b	i	b	Kidur	42	b	b	b
Anento	45	a	a	a	Kronos	45	c	a	a
Angre	45	a	a	a	Lakota	42	b	b	a
Antón	42	b	b	a	**Langdon**	42	b*	b*	b*
Arcobaleno	45	a	a	a	Lebrija	45	a	a	a
Ardente	45	e	f*	a	Ledesma	45	a	a	a
Artena	45	c	a	a	**Mexicali**	45	a*	a*	a*
Ascani	45	a	a	a	Minos	45	c	a	a
Benor	42	b	b	b	**Mundial**	45	e	d*	a
Bidi 17	45	a	a	a	Nita	42	b	b	b
Blatfort	Null	e*	i*	b	Nuño	45	a	a	a
Boira	45	a	a	a	P 3114-88	45	c	a	a
Bonzo	45	c	a	a	Páramo	45	d	a	b
Boreal	45	a	a	a	Pastanero	45	a	a	a
Bravadur	45	a	a	a	Pedrisco	45	a	a	a
Brindur	45	c	a	a	Pedroso	45	a	a	a
Camacho	45	h	c	b	Peñafiel	45	h	a	a
Castronuevo	45	h	c	b	Pingüino	42	b	b	a
Cibeles	45	c	c	b	Randur	42	b	b	b
Claro de Balazote	45	g*	g*	a	Recio Raspinegro	45	d	a	b
Clarofino	45	f*	a	a	Regallo	45	d	a	b
Cocorit	45	c*	a	a	Rocky	45	a	a	a
Colorón	45	e	d	a	Rocio	45	a	a	a
Cosmodur	45	c	a	a	Roqueño	45	c	a	a
D 104	45	a	a	a	Safari	42	b	b	a
D 2971	45	c	a	a	Senadur	45	a	a	a
Dédalo	45	c	a	a	Senatore Capelli	45	a	a	a
Don Pedro	45	a	a	a	Simeto	45	c	a	a
Duradero	45	a	a	a	Sula	45	a	a	a
Durati	45	a	a	a	Tejón	42	b	b	a
Durbel	45	a	a	a	Valgera	45	a	a	a
Endural	45	c	f	a	Valira	45	a	a	a
Epidur	45	h	c	b	Valnova	45	a	a	a
Esquilache	45	d	a	b	Vento	42	b	b	b
Fabio	45	a	a	a	Vitrón	42	b	b	a

[a] Varieties in bold characters are proposed as standards for each allele indicated by *

Table 2 B-LMW glutenin subunits studied at each of the progenies analyzed and their genetic control. Subunits are numbered according to their relative mobility in SDS-PAGE

Cross	*Glu-A3*					*Glu-B3*													*Glu-B2*
	5	6	10	11	20	1	2	3	4	7	8	9	13	14	15	16	17	18	19	12
Antón/Ardente	x			x			x		x		x	x	x		x	x	x			
Ferox/Lakota			x				x		x		x	x	x		x	x			x	
Alaga/Safari				x		x		x			x	x	x	x		x		x		x
Alaga/Blatfort		x				x		x		x	x									
Alaga/Ferox						x	x	x	x				x		x			x	x	x
Blatfort/Ferox		x	x	x			x		x	x	x			x	x			x	x	x
Peñafiel/Blatfort				x			x		x	x	x			x	x			x	x	x
S.Capelli/C.Balazote			x		x											x			x	
Mexicali/Blatfort		x		x			x		x	x	x			x	x			x	x	x
Antón/2*Mexicali											x	x	x			x				

summarizes the subunits studied in each of the progeny populations and their genetic control.

Segregation data showed that five LMW glutenin subunits were controlled at the *Glu-A3* locus and 14 at the *Glu-B3* locus. One subunit (subunit 12) was found to be at a distance of 17 cM from the *Gli-B1/Glu-B3* complex locus and was thus controlled by the *Glu-B2* locus (Ruiz and Carrillo 1993; Liu 1995).

Table 1 summarizes the allelic composition at the *Glu-A3, Glu-B3* and *Glu-B2* loci of the durum wheat cultivars analyzed. At the *Glu-A3* locus each cultivar possessed from zero to three bands (Fig. 1). Eight alleles were identified and the glutenin subunits encoded by them are shown in Fig. 2. The *Glu-A3a* allele encodes one subunit, numbered 6, and was present in the cultivars that exhibited the same pattern as 'Mexicali' ('Mexicali'-type cultivars; 40% of the collection analyzed). The *Glu-A3b* allele also encodes one subunit, numbered 5, slightly slower than subunit 6 and present in the 'Langdon'-type and 'Antón'-type cultivars and in 'Andalucía 344' (19% of the collection). This subunit should correspond to that detected by Liu and Shepherd (1995) at the same locus in 'Langdon' and denoted by them as •. The *Glu-A3c* allele encodes two bands (6 + 10) and was detected in the 'Cocorit'-type cultivars and in 'Endural' and 'Cibeles' (20% of the collection). The *Glu-A3d* allele also encodes two bands (6 + 11) and was present in 'Alaga' and in the 'Esquilache'-type cultivars (6% of the collection). The *Glu-A3e* allele encodes band 11 and was present in 'Blatfort', 'Granja Badajoz', 'Ardente' and in the 'Mundial'-type cultivars (6% of the collection). The *Glu-A3f* allele encodes three bands (6 + 11 + 20) and was found in 'Clarofino'. The *Glu-A3g* allele encodes three bands (6 + 10 + 20) and was found in 'Claro de Balazote'. The *Glu-A3h* allele corresponds to the null allele and was detected in the 'Jiloca'-type cultivars and in 'Peñafiel' and 'Agudo' (7% of the collection).

At the *Glu-B3* locus each cultivar possessed four or five bands of different mobility (Fig. 1). Nine different alleles were identified and the glutenin subunits encoded by them are shown in Fig. 2. The *Glu-B3a* allele encodes four bands numbered 2 + 4 + 15 + 19 and was present in the 'Mexicali'-type, 'Cocorit'-type and 'Esquilache'-type cultivars and in 'Peñafiel' and 'Clarofino' (65% of the collection). The *Glu-B3b* allele encodes four bands (8 + 9 + 13 + 16) and was found in the 'Langdon'-type and 'Antón'-type cultivars and in 'Agudo' (19% of the collection). The *Glu-B3c* allele encodes five bands (2 + 4 + 14 + 15 + 19) and was detected in the 'Jiloca'-type cultivars and in 'Cibeles' (6% of the collection). The *Glu-B3d* allele encodes bands 2 + 4 + 15 + 17 + 19 and was present in the 'Mundial'-type cultivars (two cultivars). The *Glu-B3e* allele encodes bands 2 + 4 + 15 + 16 + 18 and was only found in 'Granja Badajoz'. The *Glu-B3f* allele encodes bands 2 + 4 + 15 + 17 and was present in 'Ardente' and 'Endural'. The *Glu-B3 g* allele encodes bands 2 + 4 + 15 + 16 and was only detected in 'Claro de Balazote'. The *Glu-B3h* allele encodes bands 1 + 3 + 14 + 18 and was present in 'Alaga'. Finally, the *Glu-B3i* allele encodes bands 7 + 8 + 14 + 18 and was found in 'Blatfort' and 'Andalucía 344'.

At the *Glu-B2* locus only two allelic variants were detected and the glutenin subunits encoded by them are shown in Fig. 2. The *Glu-B2a* allele encodes subunit 12 (Fig. 1) and was found in the 'Mexicali'-type, 'Cocorit'-type, 'Mundial'-type and 'Antón'-type cultivars and in 'Peñafiel', 'Clarofino', 'Granja Badajoz', 'Ardente', 'Endural' and 'Claro de Balazote' (76% of the collection). The null allele *Glu-B2b* was present in the 'Langdon'-type, 'Jiloca'-type and 'Esquilache'-type cultivars and in 'Cibeles', 'Alaga', 'Andalucía 344', 'Blatfort' and 'Agudo' (24% of the collection).

Discussion

Extensive variation has been found among the 88 durum wheat cultivars analyzed. A total of 18 different electrophoretic patterns was detected. The number of bands per cultivar (4–8) is similar to that reported by Gupta et al. (1988), but slightly higher than that found by Liu and Shepherd (1996). A high proportion of the cultivars were 'Mexicali'-type and 'Cocorit'-type, and this fact could probably be due to the effect of modern breeding, which reduces genetic variability. Moreover, rare LMW patterns have been found only in old cultivars.

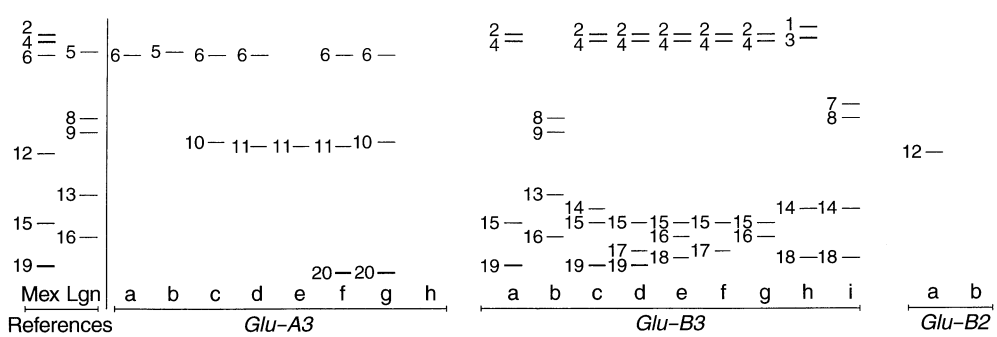

Fig. 2 Diagram showing the *Glu-A3-*, *Glu-B3-* and *Glu-B2*-encoded B-LMW glutenin subunits identified as allelic variants in the analysis of the progenies studied. Cultivars 'Mexicali' (*Mex*) and 'Lang-don' (*Lgn*) are included as references. Letters indicate the alleles at each locus

Three loci control the synthesis of B-LMW glutenin subunits, *Glu-A3, Glu-B3* (Singh and Shepherd 1988) and *Glu-B2* (Ruiz and Carrillo 1993; Liu 1995). Eight, nine and two different alleles located at the *Glu-A3, Glu-B3* and *Glu-B2* loci, respectively, were identified. Table 1 includes the cultivars proposed for use as standards for each allele. The extent of the allelic variation at the *Glu-B3* locus described in this study is similar to that reported by Gupta and Shepherd (1990) at the same locus in bread wheat. The *Glu-A3* locus exhibits a similar allelic polymorphism to *Glu-B3*, higher than that found by Gupta and Shepherd (1990) in bread wheat. On the other hand, the results show that the *Glu-A3* locus encodes a minimum number of bands and includes the null allele, as in bread wheat (Gupta and Shepherd 1990).

The γ-gliadins 42 and 45, encoded at the *Gli-B1* locus, have generally proved to be good markers of poor and good pasta quality, respectively (Damidaux et al. 1978, 1980; du Cros et al. 1982). This locus is tightly linked to *Glu-B3* (Singh and Shepherd 1988) and our results show that wheats carrying γ-45 can exhibit six different alleles at the *Glu-B3* locus (*a*, *c*, *d*, *e*, *f* and *g*). This variability could explain why cultivars with γ-45 have pasta quality ranking from medium to high (Damidaux et al. 1980; Leisle et al. 1981, 1985; du Cros et al. 1982; Carrillo et al. 1990, 1991), depending on the allele present at the *Glu-B3* locus.

Among the alleles found at the *Glu-A3* locus, only two were rare (*f* and *g*) and present in only one cultivar each. At the *Glu-B3* locus one allele (*a*) was present in 65% of the cultivars analyzed, and six alleles (*d*, *e*, *f*, *g*, *h*, and *i*) were rare, exhibited by only one or two cultivars each. The high frequency of the *Glu-B3a* allele can be explained because of the selection pressure towards good pasta-making quality in a narrow genetic background.

Several studies have demonstrated that LMW glutenin subunits and not gliadins, are responsible for durum wheat quality (Payne et al. 1984; Pogna et al. 1990; Ruiz and Carrillo 1995 a). Earlier studies classified durum wheats into several models, LMW-1 and LMW-2 (Payne et al. 1984), LMW-1$^-$, LMW-2$^-$ and LMW-2* (Carrillo et al. 1990), based only on the B-LMW glutenin subunits of slower mobility. Thus LMW-1 and LMW-1$^-$ have been related to poor quality and LMW-2 and LMW-2$^-$ to good quality (Carrillo at al. 1990, 1991; Pogna et al. 1990). This nomenclature has been widely used, and in some cases wrongly extended, to all the B-LMW subunit patterns, or else considered as allelic variants at the *Glu-B3* locus. Recently, the inadequacy of the association between gluten quality and LMW-models has been shown, because durum-wheat quality depends on specific LMW glutenin subunits encoded at the *Glu-A3*, Glu-B3 and *Glu-B2* loci (Ruiz and Carrillo 1995a, b; Vázquez et al. 1996). The results obtained in the present work show that what was considered as LMW-models are a mixture of subunits controlled by different alleles at the *Glu-3* and *Glu-2* loci. So, the LMW-1 model comprises different allelic situations: one allele at the *Glu-A3* locus and two different alleles at both the *Glu-B3* and *Glu-B2* loci. The LMW-1$^-$ model comprises two different alleles at both *Glu-A3* and *Glu-B3* loci and one at *Glu-B2*. The LMW-2 model contains five alleles at the *Glu-A3* locus, four at *Glu-B3* and two at *Glu-B2*. The LMW-2$^-$ model consists of two alleles at *Glu-A3*, five at *Glu-B3* and two at *Glu-B2*. Only the LMW-2* model corresponds to one allele at each of the three loci. Table 3 establishes the equivalence between the LMW-models and the allelic composition found for them.

Table 3 Equivalence between LMW-models (Payne et al. 1984; Carrillo et al. 1990) and the allelic composition found for them

Model	*Glu-A3*	*Glu-B3*	*Glu-B2*
LMW-1	*b*	*b*	*a*
	b	*b*	*b*
	b	*i*	*b*
LMW-1$^-$	*e*	*i*	*b*
	h	*b*	*b*
LMW-2	*a*	*a*	*a*
	c	*a*	*a*
	d	*a*	*b*
	c	*c*	*b*
	f	*a*	*b*
	c	*f*	*a*
	g	*g*	*a*
LMW-2$^-$	*h*	*a*	*a*
	h	*c*	*b*
	e	*d*	*a*
	e	*e*	*a*
	e	*f*	*a*
LMW-2*	*d*	*h*	*b*

The relationship between some *Glu-B3* variants, as determined by the two-step one-dimensional SDS-PAGE procedure (Gupta and Shepherd 1990), and gluten strength has been studied (Ruiz and Carrillo 1995 a, b; Vázquez et al. 1996). Even though the resolution of subunits by that method and the one used in this work is quite different, the translation of those alleles to the allelic classification proposed here was possible because the same cultivars were used. So, from those studies we can establish a rank of alleles based on their effect on gluten strength: *Glu-B3a* = *Glu-B3f* > *Glu-B3g* > *Glu-B3b* = *Glu-B3i*. The study of the effect of allelic variation at the *Glu-A3*, *Glu-B3* and *Glu-B2* loci on pasta quality is in progress. A knowledge of the effect of these alleles on pasta quality will provide plant breeders with a useful tool for selecting in early generations lines which combine the best allelic combinations when breeding for quality.

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References

Carrillo JM, Vázquez JF, Orellana J (1990) Relationship between gluten strength and gluten proteins in durum wheat cultivars. Plant Breed 104 : 325–333

Carrillo JM, Vázquez JF, Ruiz M, Albuquerque MM (1991) Relationships between gluten strength and gluten components in Spanish durum wheat landraces. In : Bushuk W and Tkachuk R (eds). Gluten proteins 1990. AACC, St Paul, Minnesota, pp 268–277

Cros DL du, Wrigley CW, Hare RA (1982) Prediction of durum wheat quality from gliadin-protein composition. Aust J Agric Res 33 : 429–442

Damidaux R, Grignac P, Feillet P (1978) Relation applicable en sélection entre l'électrophoregramme des gliadines et les propriétés viscoélastiques du gluten de *Triticum durum* Desf. C R Acad Sci Paris 287 : 701–704

Damidaux R, Autran JC, Feillet P (1980) Gliadin electrophoregrams and measurements of gluten viscoelasticity in durum wheats. Cereal Foods World 25 : 754–756

Gupta RB, Shepherd KW (1988) Low-molecular-weight glutenin subunits in wheat: their variation, inheritance and association with bread-making quality. In: Miller TE, Koebner RMD (eds) Proc 7th Int Wheat Genet Symp. Bath Press, Bath, England, pp 943–949

Gupta RB, Shepherd KW (1990) Two-step one-dimensional SDS-PAGE analysis of LMW subunits of glutenin. 1. Variation and genetic control of the subunits in hexaploid wheats. Theor Appl Genet 80 : 65–74

Joppa LR, Khan K, Williams ND (1983) Chromosomal location of genes for gliadin polypeptides in durum wheat *Triticum turgidum*. Theor Appl Genet 64 : 289–293

Kosmolak FG, Dexter JE, Matsuo RR, Leisle D, Marchylo BA (1980) A relationship between durum wheat quality and gliadin electrophoregrams. Can J Plant Sci 60 : 427–432

Kovacs MIP, Howes NK, Leisle D, Zawistowski J (1995) Effect of two different low-molecular-weight subunits on durum wheat pasta-quality parameters. Cereal Chem 72 : 85–87

Lafiandra D, Kasarda DD (1985) One- and two-dimensional (two pH) polyacrylamide gel electrophoresis in a single gel: separation of wheat proteins. Cereal Chem 62 : 314–319

Leisle D, Kosmolak FG, Kovacs MI (1981) Association of glume color with gluten strength and gliadin proteins in durum wheat. Can J Plant Sci 61 : 149–151

Leisle D, Kovacs MI, Hows N (1985) Inheritance and linkage relationships of gliadin proteins and glume color in durum wheat. Can J Genet Cytol 27 : 716–721

Liu CY (1995) Identification of a new low Mr gluten subunit locus on chromosome 1B of durum wheat. J Cereal Sci 21 : 209–213

Liu CY, Shepherd KW (1995) Inheritance of B subunits of glutenin and ω- and γ-gliadins in tetraploid wheats. Theor Appl Genet 90 : 1149–1157

Liu CY, Shepherd KW (1996) Variation of B subunits of glutenin in durum, wild and less-cultivated tetraploid wheats. Plant Breed 115 : 172–178

Nieto-Taladriz MT, Perretant MR, Rousset M (1994) Effect of gliadins and HMW and LMW subunits of glutenin on dough properties in the F_6 recombinant inbred lines from a bread wheat cross. Theor Appl Genet 88 : 81–88

Payne PI, Jackson EA, Holt LM (1984) The association between γ-gliadin 45 and gluten strength in durum wheat varieties : a direct causal effect or the result of genetic linkage?. J Cereal Sci 2 : 73–81

Pogna NE, Lafiandra D, Feillet P, Autran JC (1988) Evidence for a direct causal effect of low-molecular-weight glutenin subunits on gluten viscoelasticity in durum wheats. J Cereal Sci 7 : 211–214

Pogna NE, Autran JC, Mellini F, Lafiandra D (1990) Chromosome 1B-encoded gliadins and glutenin subunits in durum wheat: genetics and relationship to gluten strength. J Cereal Sci 11 : 15–34

Ruiz M, Carrillo JM (1993) Linkage relationships between prolamin genes on chromosomes 1A and 1B in durum wheat. Theor Appl Genet 87 : 353–360

Ruiz M, Carrillo JM (1995 a) Separate effects on gluten strength of *Gli-1* and *Glu-3* prolamin genes on chromosomes 1A and 1B in durum wheat. J Cereal Sci 21 : 137–144

Ruiz M, Carrillo JM (1995 b) Relationships between different prolamin proteins and some quality parameters in durum wheat. Plant Breed 114 : 40–44

Ruiz M, Carrillo JM (1996) *Gli-B3*/*Glu-B2*-encoded prolamins do not affect selected quality properties in the durum wheat cross 'Abadía' × Mexicali 75'. Plant Breed 115 : 410–412

Singh NK, Shepherd KW (1988) Linkage mapping of the genes controlling endosperm proteins in wheat. 1. Genes on the short arms of group-1 chromosome. Theor Appl Genet 75 : 628–641

Singh NK, Shepherd KW, Cornish GB (1991) A simplified SDS-PAGE procedure for separating LMW subunits of glutenin. J Cereal Sci 14 : 203–208

Vázquez JF, Ruiz M, Nieto-Taladriz MT, Albuquerque MM (1996) Effects on gluten strength of low Mr glutenin subunits coded by alleles at the *Glu-A3* and *Glu-B3* loci in durum wheat. J Cereal Sci 24 : 125–130