

Genetic Diversity of High and Low Molecular Weight Glutenin Subunits in Saharan Bread and Durum Wheats from Algerian Oases

INES BELLIL¹, MOHAMMED CHEKARA BOUZIANI² and DOUADI KHELIFI¹

¹Laboratory of Genetics Biochemistry and Plant Biotechnologies, Faculty of the Sciences of Nature and Life, Mentouri University, Constantine, Algeria; ²Department of the Sciences of Nature and Life, Faculty of precise Sciences and the Sciences of Nature and Life, Mohamed Khider University, Biskra, Algeria

Abstract: Saharan wheats have been studied particularly from a botanical viewpoint. Genotypic identification, classification and genetic diversity studies to date were essentially based on the morphology of the spike and grain. For this, the allelic variation at the glutenin loci was studied in a set of Saharan bread and durum wheats from Algerian oases where this crop has been traditionally cultivated. The high molecular weight and low molecular weight glutenin subunit composition of 40 Saharan bread and 30 durum wheats was determined by SDS-PAGE. In Saharan bread wheats 32 alleles at the six glutenin loci were detected, which in combination resulted in 36 different patterns including 17 for HMW and 23 for LMW glutenin subunits. For the Saharan durum wheats, 29 different alleles were identified for the five glutenin loci studied. Altogether, 29 glutenin patterns were detected, including 13 for HMW-GS and 20 for LMW-GS. Three new alleles were found in Saharan wheats, two in durum wheat at the *Glu-B1* and *Glu-B3* loci, and one in bread wheat at the *Glu-B1* locus. The mean indices of genetic variation at the six loci in bread wheat and at the five loci in durum wheat were 0.59 and 0.63, respectively, showing that Saharan wheats were more diverse. This information could be useful to select Saharan varieties with improved quality and also as a source of genes to develop new lines when breeding for quality.

Keywords: allelic variation; genetic diversity; glutenin subunits; polymorphism; Saharan wheats

Improving grain quality is a major challenge for many wheat breeding programmes. Wheat storage proteins, namely gliadins and glutenins, are the main components of gluten, which is the main contributor to the rheological and bread-making properties of wheat (BRANLARD *et al.* 2001). Genetic studies have revealed that these proteins are encoded at several, complex and highly polymorphic loci. Glutenin subunits are classified as high molecular weight (HMW) and low molecular weight (LMW) subunits on the basis of their mobility in SDS-PAGE. The LMW-GS are subdivided into B, C and D (JACKSON *et al.* 1983), with B subunits playing a major role in

gluten quality (RUIZ & CARRILLO 1995; TURCHETTA *et al.* 1995). HMW subunits are encoded at the *Glu-1* loci on the long arm of the group 1 chromosomes (PAYNE *et al.* 1980). B-LMW-GS are inherited as groups controlled at *Glu-3* and *Glu-B2* loci (SINGH & SHEPHERD 1988). The natural variation found for all these protein loci is very important for improving wheat quality. Saharan wheats have remained poorly studied for a long time; several reasons may explain this fact: the isolation of the Saharan areas, the consumption of produced wheat, and the difficulty to study Saharan wheats out of their original environment, particularly because of their

extreme sensitivity to yellow rust. Considerable work of collecting and describing Saharan wheat populations was presented in studies by MIEGE (1924) and ERROUX (1958). These studies were devoted to the morphological variability of ears and grains with the aim of classifying the different types encountered. This approach has limitations, and faced many difficulties due to the heterogeneity of the populations, the abundance of intermediate forms and the vagueness of the nomenclature. In this context, the diversity of Saharan wheat varieties and forms represents an important source of genetic variability and consequently, of valuable traits for wheat improvement. On the other hand, proteins are valuable biochemical markers for genetic analysis, and for the quantification of genetic diversity present in wheat collections (KUDRYAVTSEV *et al.* 1996). The objective of this study was to determine the allelic composition at glutenin loci encoding for high and low molecular weight glutenin subunits within Saharan bread and durum wheat cultivars. The allelic frequencies were used to analyse the genetic diversity of these proteins for both durum and bread Saharan wheats from Algerian oases.

MATERIAL AND METHODS

Plant material

A total of 70 cultivars of Saharan wheats originating from Algerian oases were analysed for high and low molecular weight glutenin subunits. This collection included 40 Saharan bread wheats and 30 Saharan durum wheats (Tables 1 and 2). These wheats were mostly collected and maintained at the National Institute of Agronomical Research (INRAA-Adrar, Algeria), the Technical Institute of Saharan Agricultural Development (ITDAS-Adrar, Djamaa-EL oued and Biskra, Algeria) and the Centre of Scientific and Technical Research in Dry Areas (CRSTRA-Biskra, Algeria). Ten of these cultivars were provided by farmers (Agini, Beliouni, Guemgoum Erkham1, Jenah Khotaiifa, Hassi Ben Abdallah, Saba, Ghouff, Ramla, Hedba, and Touatia3).

Protein analysis

Glutenins were extracted following a sequential procedure (SINGH *et al.* 1991). Electrophoresis of glutenin subunits was performed using SDS-PAGE

according to SINGH *et al.* (1991). High molecular weight (HMW) glutenin alleles at *Glu-A1*, *Glu-B1* and *Glu-D1* loci were identified using the nomenclature of PAYNE and LAWRENCE (1983) completed by BRANLARD *et al.* (2003). B-low molecular weight (B-LMW) glutenin alleles at *Glu-A3*, *Glu-B3*, *Glu-D3* and *Glu-B2* loci were designated according to NIETO-TALADRIZ *et al.* (1997) for durum wheats, and according to BRANLARD *et al.* (2003) for bread wheats.

Statistical analysis

Allelic frequencies were calculated at each glutenin locus. The genetic diversity at each locus was calculated as follows: $H = 1 - \sum Pi^2$, with H and Pi denoting the genetic variation index and the frequency of the number of alleles at the locus, respectively (NEI 1973).

RESULTS

Polymorphism for HMW-GS and LMW-GS patterns in Saharan wheats

In Saharan bread wheats, 32 alleles were identified in total at the six loci *Glu-A1*, *Glu-B1*, *Glu-D1*, *Glu-A3*, *Glu-B3* and *Glu-D3*. On the basis of genetic diversity found at the six loci, 36 patterns were established among the 40 Saharan bread wheat cultivars analysed (Table 1). Thirty three patterns were specific to one cultivar each. Extensive variability was observed for the HMW glutenins. A total of 16 HMW subunits were revealed from the analysis of different Saharan bread wheats. The majority of the forty cultivars analysed possessed three to five bands and 17 types of patterns were determined (Table 1). Each combination was encountered in one to ten cultivars. Concerning the B-LMW subunits, large variability in patterns was detected and 23 combinations were listed (Table 1). The number of cultivars for each combination of B-LMW subunits varied from one to six. The results showed that the greatest polymorphism of storage proteins in Saharan bread wheats was on chromosome 1B with nine allelic forms at the *Glu-B1* and *Glu-B3* loci.

In Saharan durum wheats, 29 different alleles at the *Glu-1*, *Glu-3* and *Glu-B2* loci were identified resulting

Table 1. Allelic composition at the six HMW and LMW loci found in 40 bread wheats from Algerian oases

No.	Cultivars	Origin	HMW			LMW		
			<i>Glu-A1</i>	<i>Glu-B1</i>	<i>Glu-D1</i>	<i>Glu-A3</i>	<i>Glu-B3</i>	<i>Glu-D3</i>
1	Cheguira	Djanet	<i>a</i>	<i>a</i>	<i>e</i>	<i>a</i>	<i>g</i>	<i>a</i>
2	Bouchouka	Ouargla	<i>a</i>	<i>d</i>	<i>a</i>	<i>a</i>	<i>g</i>	<i>a</i>
3	Bousbiba	Timimoun	<i>a</i>	<i>d</i>	<i>b</i>	<i>f</i>	<i>j</i>	<i>c</i>
4	Sebaga1	Tidmane, Touat, Adrar	<i>b</i>	<i>a</i>	<i>a</i>	<i>a</i>	<i>d</i>	<i>a</i>
5	Bent Mbarek	Liada, Tsabit, Touat, Adrar	<i>b</i>	<i>a</i>	<i>a</i>	<i>a</i>	<i>d</i>	<i>c</i>
6	Saharaoui	Biskra	<i>b</i>	<i>a</i>	<i>d</i>	<i>a</i>	<i>c</i>	<i>c</i>
7	Belbaida	Timimoun	<i>b</i>	<i>c</i>	<i>d</i>	<i>b</i>	<i>b</i>	<i>b</i>
8	Belmabrouk1	Touat, Gourrara	<i>b</i>	<i>e</i>	<i>a</i>	<i>a</i>	<i>d</i>	<i>b</i>
9	Belmabrouk2	Ouled El Hadj Mamoun, Touat	<i>b</i>	<i>e</i>	<i>a</i>	<i>d</i>	<i>g</i>	<i>c</i>
10	Chater1	Tidmane, Touat, Adrar	<i>b</i>	<i>e</i>	<i>a</i>	<i>d</i>	<i>j</i>	<i>c</i>
11	Ben Salem	Hiba, Tsabit, Adrar	<i>b</i>	<i>e</i>	<i>a</i>	<i>b</i>	<i>g</i>	<i>b</i>
	Mansouri	Touat, Adrar	<i>b</i>	<i>e</i>	<i>a</i>	<i>b</i>	<i>g</i>	<i>b</i>
12	Eskandaria 1	Aougrou, Gourrara, Adrar	<i>b</i>	<i>e</i>	<i>a</i>	<i>a</i>	<i>d</i>	<i>c</i>
13	Touatia3	Mekkid, Touat, Adrar	<i>b</i>	<i>g</i>	<i>a</i>	<i>a</i>	<i>h</i>	<i>c</i>
14	Chetla	Taghit	<i>b</i>	<i>i</i>	<i>d</i>	<i>a</i>	<i>b</i>	<i>a</i>
15	Fritas	M'rara, El oued	<i>b</i>	<i>new3</i>	<i>a</i>	<i>a</i>	<i>d</i>	<i>b</i>
16	El Menea	El Habla, Tsabit, Adrar	<i>b</i>	<i>o</i>	<i>a</i>	<i>a</i>	<i>i</i>	<i>c</i>
17	Bakli	Aougrou, Gourrara, Adrar	<i>b</i>	<i>o</i>	<i>a</i>	<i>a</i>	<i>d</i>	<i>b</i>
	Manga	Touat, Adrar	<i>b</i>	<i>o</i>	<i>a</i>	<i>a</i>	<i>d</i>	<i>b</i>
	Oum Rokba1	Ouled El Hadj, Zaouiat Kounta, Adrar	<i>b</i>	<i>o</i>	<i>a</i>	<i>a</i>	<i>d</i>	<i>b</i>
18	Sebaga2	Tiouliline, Touat, Adrar	<i>c</i>	<i>a</i>	<i>a</i>	<i>a</i>	<i>d</i>	<i>a</i>
19	Moumena	Ouled Rached, Gourrara, Adrar	<i>c</i>	<i>a</i>	<i>a</i>	<i>d</i>	<i>g</i>	<i>b</i>
20	Hamra	Aguril, Touat, Adrar	<i>c</i>	<i>a</i>	<i>a</i>	<i>b</i>	<i>j</i>	<i>b</i>
21	Touatia2	Touat, Gourrara, Adrar	<i>c</i>	<i>a</i>	<i>a</i>	<i>a</i>	<i>f</i>	<i>b</i>
22	Tafertat	Touat, Gourrara	<i>c</i>	<i>a</i>	<i>a</i>	<i>a</i>	<i>c</i>	<i>b</i>
23	Hassi Ben Abdallah	Hassi Ben Abdallah, Ouargla	<i>c</i>	<i>b</i>	<i>a</i>	<i>d</i>	<i>f</i>	<i>b</i>
24	Oum Rokba2	Tittaouine E'chorfa, Aoulef, Adrar	<i>c</i>	<i>c</i>	<i>a</i>	<i>a</i>	<i>h</i>	<i>b</i>
25	Tabelballa	Benni-Abbès	<i>c</i>	<i>c</i>	<i>d</i>	<i>a</i>	<i>g</i>	<i>c</i>
26	Boukarnafa	Benni-Abbès	<i>c</i>	<i>d</i>	<i>a</i>	<i>d</i>	<i>g</i>	<i>c</i>
	Yahia	Gourrara, Adrar	<i>c</i>	<i>d</i>	<i>a</i>	<i>d</i>	<i>g</i>	<i>c</i>
27	Bahamoud	Gourrara, Adrar	<i>c</i>	<i>e</i>	<i>a</i>	<i>a</i>	<i>i</i>	<i>b</i>
28	Oum Zhira	El Ksar Ain Zeghlouf-Reggane, Adrar	<i>c</i>	<i>e</i>	<i>a</i>	<i>d</i>	<i>g</i>	<i>c</i>
29	Kedoura	Tiouliline, Touat, Adrar	<i>c</i>	<i>e</i>	<i>a</i>	<i>d</i>	<i>j</i>	<i>b</i>
30	Chater2	Tamantit, Touat, Adrar	<i>c</i>	<i>e</i>	<i>a</i>	<i>a</i>	<i>d</i>	<i>c</i>
31	El Farh	Tittaouine E'chorfa, Aoulef, Adrar	<i>c</i>	<i>e</i>	<i>a</i>	<i>d</i>	<i>b'</i>	<i>b</i>
32	Zaghloul	Tsabit, Touat, Adrar	<i>c</i>	<i>e</i>	<i>a</i>	<i>a</i>	<i>h</i>	<i>b</i>
33	Masraf	Tsabi, Touat, Adrar	<i>c</i>	<i>e</i>	<i>a</i>	<i>a</i>	<i>d</i>	<i>b</i>
34	Chouitar	Tamantit, Touat, Adrar	<i>c</i>	<i>e</i>	<i>a</i>	<i>d</i>	<i>f</i>	<i>b</i>
35	Touatia1	Ouled Rached, Gourrara, Adrar	<i>c</i>	<i>e</i>	<i>a</i>	<i>a</i>	<i>h</i>	<i>b</i>
36	Mekaouia	Gourrara, Adrar	<i>c</i>	<i>e</i>	<i>a</i>	<i>d</i>	<i>g</i>	<i>b</i>

Table 2. Allelic composition at the five HMW and LMW loci found in 30 Saharan durum wheats from Algerian oases

No.	Cultivars	Origin	HMW		LMW		
			<i>Glu-A1</i>	<i>Glu-B1</i>	<i>Glu-A3</i>	<i>Glu-B3</i>	<i>Glu-B2</i>
1	Kahla	Touat	<i>b</i>	<i>b</i>	<i>h</i>	<i>b</i>	<i>a</i>
2	Merouani	El Oued	<i>b</i>	<i>e</i>	<i>j</i>	<i>a</i>	<i>a</i>
3	M'zirâa	M'zirâa, Biskra	<i>c</i>	<i>b</i>	<i>b</i>	<i>new2</i>	<i>a</i>
4	Beds	Beds, Biskra	<i>c</i>	<i>b</i>	<i>c</i>	<i>c</i>	<i>b</i>
5	Chegga	Chegga, Biskra	<i>c</i>	<i>b</i>	<i>d</i>	<i>c</i>	<i>b</i>
6	Tazzi	Aougrou, Gourrara, Adrar	<i>c</i>	<i>b</i>	<i>d</i>	<i>h</i>	<i>b</i>
7	Ouled Khoudir	Bechar	<i>c</i>	<i>b</i>	<i>h</i>	<i>new2</i>	<i>a</i>
	El Ksor	El Ksor, Lioua, Biskra	<i>c</i>	<i>b</i>	<i>h</i>	<i>new2</i>	<i>a</i>
8	Agini	Adrar	<i>c</i>	<i>d</i>	<i>b</i>	<i>b</i>	<i>b</i>
9	Beliouni	Adrar	<i>c</i>	<i>d</i>	<i>c</i>	<i>a</i>	<i>a</i>
10	Saba	Mekkid, Touat, Adrar	<i>c</i>	<i>e</i>	<i>a</i>	<i>a</i>	<i>a</i>
11	Jenah Khotaifa	Adrar	<i>c</i>	<i>e</i>	<i>a</i>	<i>a</i>	<i>b</i>
12	Ghouff	Ahaggar	<i>c</i>	<i>e</i>	<i>b</i>	<i>b</i>	<i>a</i>
13	Bidi2	Ain Ennaga, Biskra	<i>c</i>	<i>e</i>	<i>c</i>	<i>h</i>	<i>b</i>
14	Guemgoum Erksam2	Adrar	<i>c</i>	<i>e</i>	<i>c</i>	<i>c</i>	<i>b</i>
15	Romani	El Fid, Biskra	<i>c</i>	<i>e</i>	<i>d</i>	<i>d</i>	<i>b</i>
16	Megarine	Megarine, Djamaa	<i>c</i>	<i>f</i>	<i>a</i>	<i>b</i>	<i>b</i>
17	Biskri	Biskra	<i>c</i>	<i>f</i>	<i>b</i>	<i>b</i>	<i>b</i>
18	Kahlaya	Doucen, Biskra	<i>c</i>	<i>f</i>	<i>c</i>	<i>c</i>	<i>b</i>
19	Amakawia	Ahaggar	<i>c</i>	<i>f</i>	<i>e</i>	<i>f</i>	<i>b</i>
20	Hedba	Megarine, Djamaa	<i>c</i>	<i>h</i>	<i>a</i>	<i>a</i>	<i>a</i>
21	Djebli	Sidi Okba, Biskra	<i>c</i>	<i>new1</i>	<i>c</i>	<i>h</i>	<i>b</i>
22	Guemgoum Erksam1	Marmoutha, Lioua, Biskra	<i>c</i>	<i>new1</i>	<i>c</i>	<i>c</i>	<i>b</i>
23	Khangat Sidi Naji	Khangat Sidi Naji, Biskra	<i>c</i>	<i>o</i>	<i>d</i>	<i>h</i>	<i>b</i>
24	Zribet El Oued	Zribet El Oued, Biskra	<i>c</i>	<i>o</i>	<i>e</i>	<i>h</i>	<i>b</i>
25	Souda	Timimoun	<i>c</i>	<i>u</i>	<i>b</i>	<i>i</i>	<i>a</i>
26	Ahaggar	Ahaggar	<i>c</i>	<i>VI</i>	<i>a</i>	<i>a</i>	<i>b</i>
27	Ain Zaatout	Ain Zaatout, Biskra	<i>c</i>	<i>VI</i>	<i>c</i>	<i>h</i>	<i>a</i>
28	El Waha	Adrar	<i>VI</i>	<i>b</i>	<i>b</i>	<i>b</i>	<i>b</i>
29	Ramla	Adrar	<i>VI</i>	<i>d</i>	<i>b</i>	<i>h</i>	<i>b</i>

in twenty-nine patterns in this collection. Twenty eight patterns were specific of one cultivar each as shown in Table 2. Three and nine HMW glutenin subunits alleles were identified at the *Glu-A1* and *Glu-B1* loci, respectively. 17 alleles encoding LMW glutenin subunits were observed in the collection. Seven, eight and two alleles corresponded to the *Glu-A3*, *Glu-B3* and *Glu-B2* loci. Combinations of these alleles gave thirteen HMW-GS patterns and twenty LMW-GS patterns (Table 2). The highest allelic variability for

HMW and LMW glutenin subunits was found for chromosome 1B with nine and eight allelic forms at the *Glu-B1* and *Glu-B3* loci, respectively.

Allelic diversity of glutenins in Saharan wheats

The HMW-GS composition and allele frequencies in the 40 Saharan bread cultivars are shown in Table 3.

Table 3. Allele frequencies of HMW and LMW glutenin and genetic index diversity at the *Glu-1* and *Glu-3* loci of Saharan bread wheats

Locus	Allele	Subunit	Frequency (%)
<i>Glu-A1</i>	<i>a</i>	1	7.50
	<i>b</i>	2*	42.50
	<i>c</i>	null	50.00
	H index		0.56
<i>Glu-B1</i>	<i>a</i>	7	22.50
	<i>b</i>	7+8	2.50
	<i>c</i>	7+9	7.50
	<i>d</i>	6+8	10.00
	<i>e</i>	20	40.00
	<i>g</i>	13+19	2.50
	<i>i</i>	17+18	2.50
	<i>o</i>	6+22	10.00
	<i>new3</i>		2.50
H index		0.76	
<i>Glu-D1</i>	<i>a</i>	2+12	85.00
	<i>b</i>	3+12	2.50
	<i>d</i>	5+10	10.00
	<i>e</i>	2+11	2.50
H index		0.27	
<i>Glu-A3</i>	<i>a</i>		60.00
	<i>b</i>		7.50
	<i>d</i>		30.00
	<i>f</i>		2.50
	H index		0.54
<i>Glu-B3</i>	<i>b</i>		5.00
	<i>b'</i>		2.50
	<i>c</i>		5.00
	<i>d</i>		27.50
	<i>f</i>		7.50
	<i>g</i>		27.50
	<i>h</i>		10.00
	<i>i</i>		5.00
	<i>j</i>		10.00
	H index		0.81
<i>Glu-D3</i>	<i>a</i>		12.50
	<i>b</i>		52.50
	<i>c</i>		35.00
	H index		0.59

Table 4. Allele frequencies of HMW and LMW glutenin and genetic index diversity at the *Glu-1*, *Glu-3* and *Glu-B2* loci of Saharan durum wheats

Locus	Allele	Subunit	Frequency (%)
<i>Glu-A1</i>	<i>b</i>	2*	6.67
	<i>VI</i>	2***	6.67
	<i>c</i>	null	86.67
	H index		0.24
<i>Glu-B1</i>	<i>b</i>	7+8	26.67
	<i>d</i>	6+8	10.00
	<i>e</i>	20	23.33
	<i>f</i>	13+16	13.33
	<i>h</i>	14+15	3.33
	<i>u</i>	7*+8	3.33
	<i>o</i>	6+22	6.67
	<i>VI</i>	19	6.67
	<i>new1</i>		6.67
	H index		0.83
<i>Glu-A3</i>	<i>a</i>	6	16.67
	<i>b</i>	5	23.33
	<i>c</i>	6+10	26.67
	<i>d</i>	6+11	13.33
	<i>e</i>	11	6.67
	<i>h</i>	null	10.00
	<i>j</i>	8+	3.33
H index		0.81	
<i>Glu-B3</i>	<i>a</i>	2+4+15+19	20.00
	<i>b</i>	8+9+13+16	20.00
	<i>c</i>	2+4+14+15+19	16.67
	<i>d</i>	2+4+14+17+19	3.33
	<i>f</i>	2+4+15+19	3.33
	<i>h</i>	1+3+14+18	23.33
	<i>i</i>	7+8+14+18	3.33
	<i>new2</i>		10.00
H index		0.82	
<i>Glu-B2</i>	<i>a</i>	12	36.67
	<i>b</i>	null	63.33
H index		0.46	

Sixteen different *Glu-1* alleles were found, three at *Glu-A1*, nine at *Glu-B1* and four at the *Glu-D1* locus, included one allele at the *Glu-B1* locus which had not previously been described in bread

wheat. This novel allele encoded a subunit with slightly faster mobility than subunit 7 encoded by the *Glu-B1a* allele. This new subunit, designated *new3*, was present in the cultivar Fritas. TAHIR *et al.* (1996) reported subunit 7f in bread wheat landraces from Pakistan and FANG *et al.* (2009) identified subunit 7** in Chinese endemic wheats with faster mobility than subunit 7. However, without making a direct comparison, it is not possible to decide whether subunit 7 detected in the study is identical or not to subunit 7f or 7**. At the *Glu-A1* locus, allelic distribution among the 40 cultivars was 50% and 42.5% for the two alleles *c* and *b*, respectively, and lower for allele *a* with 7.5%. At the *Glu-B1* locus, alleles *b* encoding for subunits 7+8, *g* encoding for subunits 13+19, *i* for subunits 17+18, and the new one were rare at 2.5%. Otherwise, the most frequent alleles were *Glu-B1e* and *Glu-B1a* encoding for subunits 20 and 7 with 40% and 22.5%, respectively. At the *Glu-D1* locus, subunits 2+12 encoded by *Glu-D1a* were predominant (85%). The less frequent alleles were *Glu-D1d* (5+10), observed only in four cultivars, *Glu-D1b* (3+12) and *Glu-D1e* (2+11) were found only in one cultivar each. Using the bread

wheat nomenclature proposed by BRANLARD *et al.* (2003) for LMW glutenin subunits, we were able to identify 16 LMW subunits among the 40 cultivars. The *Glu-B3d* and *Glu-B3g* alleles were frequent in the collection (27.5%). Otherwise, the less frequent alleles were the allele *b'* (2.5%), allele *b*, *c* and *i* (5%) and alleles *f*, *h* and *j* (7.5% and 10%), respectively. Concerning the *Glu-A3* locus, 90% of the collection analysed can be characterized by two alleles only: *Glu-A3a* and *Glu-A3d* found in 60% and 30% of the cultivars, respectively. The two other alleles *b* and *f* were less common. For the *Glu-D3* locus, we observed one allele at a low frequency: *Glu-D3a* encoded only in five cultivars (12.5%). The most frequently observed allele was *Glu-D3b* (52.5%). Moreover *Glu-D3c* was found in fourteen cultivars (35%).

In Saharan durum wheats up to 12 allelic forms were detected at the *Glu-1* loci encoded for HMW-GS (Table 4). Three different alleles were detected at *Glu-A1* and nine at *Glu-B1*. Although three alleles were observed at the *Glu-A1* locus, the null allele (*Glu-B1c*) was found in most cultivars studied (86.67%). The *Glu-A1b* and *Glu-A1VI* alleles (encoding the 2* and 2*** subunits, respectively)

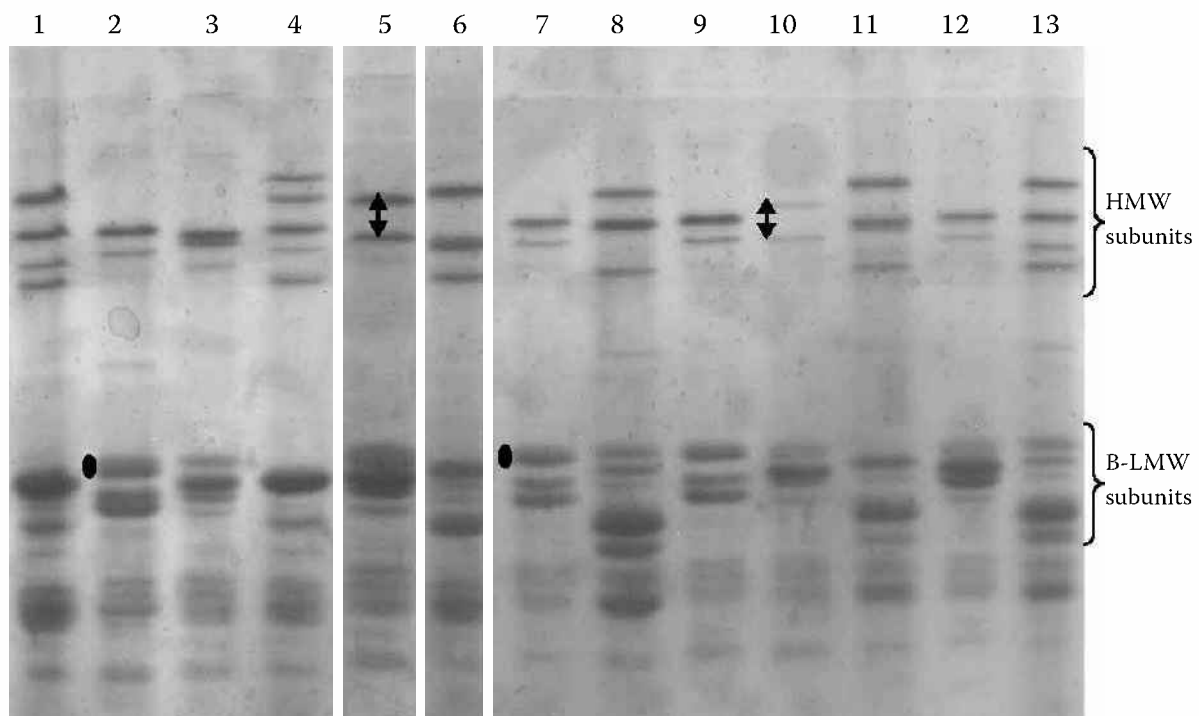


Figure 1. SDS-PAGE patterns of high molecular weight and low molecular weight glutenin subunits of Saharan durum wheat from Algerian oases; 1 – Democrat; 2 – M'zirâa; 3 – Kahlaya; 4 – Rempart; 5 – Djebli; 6 – Gabo; 7 – Ouled Khoudir; 8 – Vilmorin 53; 9 – El Ksor; 10 – Guemgoum Erkhani; 11 – Atlass 66; 12 – Chegga; 13 – Recital (lanes 1, 4, 6, 8, 11 and 13 wheat checks); ↑ – *Glu-B1new1*, ● – *Glu-B3new2*

appeared at a lower frequency (6.67%), as each was present only in two cultivars among the 30 cultivars analysed. At the *Glu-B1* locus, a total of 9 alleles were detected, of which one allele and two subunits were not described previously. The *Glu-B1b* allele (encoding the subunit pair 7+8) and *Glu-B1e* (subunit 20) were the most frequent at a frequency of 26.67% and 23.33%, respectively. Other alleles occurring at a relatively high frequency (13.33% and 10%) were *Glu-B1f* (encoding subunit pairs 13+16) and *Glu-B1d* (encoding subunit pairs 6+8). The alleles *Glu-B1h*, encoding for subunit 14+15, and *Glu-B1u* encoding for 7*+8, were rare (3.33%). The new allele was found in two cultivars only: Djebli and Guemgoum Erksam1. This allele encodes two subunits, of which one had a slightly lower mobility than that of band 6 of pair 6+8 encoded by the *Glu-B1d* allele, the other new subunit moved slightly slower than subunit 18 (Figure 1). This set of Saharan durum wheat germplasm displays abundant allelic variation for LMW-GS. A total of 17 alleles were identified (Table 4). The identified low molecular weight glutenin subunits were those previously described by NIETO-TALADRIZ *et al.* (1997), except subunit 8+ encoded by the allele *Glu-A3j*, which was identified by CHERDOUH *et al.* (2005). The most common allele at *Glu-A3* was *Glu-A3c* encoding subunits 6+10 with a frequency of 26.67%, followed by *Glu-A3b* encoding subunit 5 at 23.33%. The allele classified as rare was *Glu-B3j* (subunit 8+) detected at a lower frequency of 3.33%. At the *Glu-B3* locus, the frequency of *Glu-B3h* allele was 23.33%, and it was the most frequent followed by *Glu-B3a* and *Glu-B3b* with 20% each. Two other alleles, *Glu-B3c* and the new allele were considered relatively abundant at 16.67% and 10% respectively. At the *Glu-B2* locus, 36.66% of the collection was characterized as carrying the *Glu-B2a* allele. The null allele (*Glu-B2b*) was present in 63.33% of the collection.

DISCUSSION

Saharan bread wheats

The genetic diversity index of 0.59 was higher than the value 0.40 obtained in winter wheat cultivars from the Czech Republic (BRADOVÁ & ŠTOČKOVÁ 2010). All the loci, except *Glu-D1*, displayed a genetic variability higher than 0.50, *Glu-B3* being the most polymorphic (Table 3). The

number of alleles detected at the *Glu-1* and *Glu-3* loci was higher than that in other collections. The HMW-GS composition had been widely used to assess the genetic diversity and grain quality of wheat. The frequency of a number of subunits in the Saharan bread wheats differed considerably from that noted in the previous study. Subunit 1 at *Glu-A1*, subunits 7+8, 7+9, 6+8, 13+19, 17+18, 6+22 and the new allele at *Glu-B1* and subunits 3+12 and 2+11 at *Glu-D1* appeared less frequently in this study while subunits 20 and 7 at *Glu-B1* were observed more frequently. A total of 16 alleles encoding for HMW-GS were present in only 40 cultivars of Saharan bread wheat and this high level of diversity agrees with the results of FANG *et al.* (2009) and with the results of WEI *et al.* (2001). Major differences between Saharan wheats and other collections were observed in the frequency of subunit 7 although Saharan wheats had subunit pair 6+22 (4 varieties) controlled by *Glu-B1o*. The effect of these subunits on wheat quality still remains unclear. No Saharan varieties possessed subunit pair 14+15 controlled by *Glu-B1h*, which was in the other collections. The forty Saharan bread wheats had a somewhat rare subunit pair; 17+18 (Chetla), subunit 20 (16 varieties), and subunit 13+19 (Touatia3). It is thus clear that allelic variation among the Saharan bread wheats is considerable at the *Glu-B1* locus. Subunit pair 5+10 at the *Glu-D1* allele is seen more frequently in European (PAYNE *et al.* 1984) than in Saharan wheat cultivars, possibly owing to their correlation with good bread-making quality. The mean genetic variation index at *Glu1* was 0.53. It was higher than that reported for other collections, showing that Saharan hexaploid wheats have relatively high genetic diversity. High diversity was found in the Saharan wheats for LMW-GS. The *Glu-A3a* allele was the most frequent as it was in French cultivars (BRANLARD *et al.* 2003) and winter wheats from the Czech Republic (BRADOVÁ & ŠTOČKOVÁ 2010). The number of alleles detected at *Glu-B3* (9 alleles) was the same as that found by DARBANDI *et al.* (2010) in Iranian cultivars and seven of them were present in both collections. The most frequent alleles were *Glu-B3d* and *Glu-B3g*. The same results were observed in French cultivars and winter wheat cultivars from the Czech Republic for *Glu-B3g* allele, but *Glu-B3d* was less frequent in both collections. The allele *b* was the most frequent at the *Glu-D3* locus in Saharan cultivars as it was in Iranian cultivars.

Conversely, BRANLARD *et al.* (2003) and BRADOVÁ and ŠTOČKOVÁ (2010) found that *Glu-D3c* was the predominant allele.

Saharan durum wheats

The results obtained showed rather a high polymorphism in HMW-GS and LMW-GS variation, especially for the *Glu-B1* and *Glu-B3* loci. A total of 29 different alleles were identified for the five glutenin loci studied. Two new alleles were found, one at *Glu-B1* and the other at *Glu-B3*. For the *Glu-B1* locus, some alleles are very frequent: more particularly the alleles *Glu-B1b* and *Glu-B1e* encoding subunits 7+8 and 20, respectively. These results are in agreement with those of MORAGUES *et al.* (2006), three alleles at *Glu-A1* and 14 alleles at the *Glu-B1* locus, where *Glu-B1e* and *Glu-B1b* were the most frequent. They agreed also with the results reported by CARRILLO (1995). However, most cultivars of Saharan durum wheat analysed do not have subunit 6+8 encoded by *Glu-B1d*. Conversely, HAMDÍ *et al.* (2010) found that *Glu-B1e* and *Glu-B1d* were predominant in 856 accessions of durum wheat collected in Algeria. Similar results were obtained by CHERDOUH *et al.* (2005), who studied genetic diversity in a set of 45 Algerian durum wheat landraces and old cultivars and observed that *Glu-B1e* and *Glu-B1d* alleles were predominant. For the B-LMW glutenins, seven, eight and two were observed at *Glu-A3*, *Glu-B3* and *Glu-B2*, respectively, in Saharan wheats. Six of the seven alleles detected at the *Glu-A3* locus were the same as those found by HAMDÍ *et al.* (2010). The *Glu-A3c* allele was the most frequent in our study. Most of the glutenin alleles found among modern cultivars (NIETO-TALADRIZ *et al.* 1997, 2000; IGREJAS *et al.* 1999) are present in the analysed Saharan durum wheat collection. On the other hand, rare LMW glutenin alleles have only been found in old Spanish and Portuguese cultivars (NIETO-TALADRIZ *et al.* 1997; BRITES & CARRILLO 2000). Among those rare alleles (*Glu-A3e, f, g, i, Glu-B3d, e, f, g, h, i, j, k, Glu-A3e, Glu-B3d, Glu-B3f, Glu-B3h, Glu-B3i*) were present in Saharan durum wheats. The genetic variability at 0.63 was higher than 0.36, which was obtained in cultivars from Portugal (IGREJAS *et al.* 1999), contrary, it was lower than 0.72 found in durum wheat landraces from Spain (AGUIRIANO *et al.* 2008), and 0.67 obtained in Mediterranean landraces (MOR-

AGUES *et al.* 2006). From the quality point of view, Saharan durum wheats from Algeria have a high percentage of HMW and B-LMW glutenin alleles related to grain quality such as *Glu-A1a* (KAAN *et al.* 1993; AGHAI *et al.* 1996), *GluB1a* and *Glu-B1d*, but the HMW glutenin subunits appear to play a much less important role in the end-use quality of durum wheat (DU CROS 1987), and only *Glu-B1e* has been related with poor quality (CARRILLO *et al.* 1990; NIETO-TALADRIZ *et al.* 2000). B-LMW glutenin alleles related to high gluten strength were observed such as *Glu-A3a, Glu-A3c, Glu-A3d, Glu-A3h* and *Glu-B3a, Glu-B3c* (CARRILLO *et al.* 2000). It would be interesting to make a quality evaluation of these lines, mainly to determine the effect on quality of the alleles and allele combinations for which no data are available. This information could be useful to select local varieties with improved quality, and also to use them as a source of genes to develop new lines when breeding for quality.

In conclusion, this work shows that Saharan wheats from Algerian oases have extensive allelic variation in HMW-GS and LMW-GS, including new alleles. This indicates that Saharan wheats have a potential value in wheat breeding, and that further studies of their diversity are warranted.

References

- AGHAI J., ABD-MISHANI S., KHODABANDEH N. (1996): Genetic variation and geographical diversity for seed storage proteins of Iranian durum wheat collection. *Iranian Journal of Agricultural Sciences*, **27**: 105–113.
- AGUIRIANO E., RUIZ M., FITÉ R., CARRILLO J.M. (2008): Genetic variation for glutenin and gliadins associated with quality in durum wheat (*Triticum turgidum* L. ssp. *turgidum*) landraces from Spain. *Spanish Journal of Agricultural Research*, **6**: 599–609.
- BRADOVÁ J., ŠTOČKOVÁ L. (2010): Evaluation of winter wheat collection in terms of HMW- and LMW-glutenin subunits. *Czech Journal of Genetic and Plant Breeding*, **46** (Special Issue): S96–S99.
- BRANLARD G., DARDEVET M., SACCOMANO R., LA-GOUTTE F., GOURDON J. (2001): Genetic diversity of wheat storage proteins and bread wheat quality. *Euphytica*, **119**: 59–67.
- BRANLARD G., DARDEVET M., AMIOUR N., IGREJAS G. (2003): Allelic diversity of HMW and LMW glutenin subunits and omega gliadins in French bread wheat (*Triticum aestivum* L.). *Genetic Resources and Crop Evolution*, **50**: 669–679.

- BRITES C., CARRILLO J.M. (2000): Inheritance of gliadin and glutenin proteins in four durum wheat crosses. *Cereal Research Communication*, **28**: 239–246.
- CARRILLO J.M. (1995): Variability for glutenin proteins in Spanish durum wheat landraces. *CIHEAM – Options Méditerranéennes Serie A, Seminars Méditerranéennes*, 143–147.
- CARRILLO J.M., VAZQUEZ J.F., ORELLANA J. (1990): Relationship between gluten strength and glutenin proteins in durum wheat cultivars. *Plant Breeding*, **104**: 325–333.
- CARRILLO J.M., MARTÍNEZ M.C., MOITA BRITES C., NIETO-TALADRIZ M.T., VÁSQUEZ J.F. (2000): Relationship between endosperm proteins and quality in durum wheat (*Triticum turgidum* var. *durum*). *CIHEAM – Options Méditerranéennes Serie A/40*, 463–467.
- CHERDOUH A., KHELIFI D., CARRILLO J.M., NIETO-TALADRIZ M.T. (2005): The high and low molecular weight glutenin polymorphism of Algerian durum wheat landraces and old cultivars. *Plant Breeding*, **124**: 338–342.
- DARBANDI A.I., SAMADI B.Y., BOUSHEHRI A.A.S., MOHAMMADI M. (2010): Allelic variations in *Glu-1* and *Glu3* loci of historical and modern Iranian bread wheat (*Triticum aestivum* L.) cultivars. *Journal of Genetics*, **89**: 193–199.
- DU CROS D.L. (1987): Glutenin protein and gluten strength in durum wheat. *Journal of Cereal Sciences*, **5**: 3–12.
- ERROUX J. (1958): Note sur les blés des oasis du Sahara algérien. *Bulletin de la Société des Histoires de la Nature de l'Afrique du Nord*, **49**: 56.
- FANG J., LIU Y., LUO J., WANG Y., SHEWRY P.R., HE G. (2009): Allelic variation and genetic diversity of high molecular weight glutenin subunit in Chinese endemic wheats (*Triticum aestivum* L.). *Euphytica*, **166**: 177–182.
- HAMDI W., BELLIL I., BRANLARD G., KHELIFI D. (2010): Genetic variation and geographical diversity for seed storage proteins of seventeen durum wheat populations collected in Algeria. *Notulae Botanicae Horti Agrobotanici Cluj-Napoca*, **38**: 22–32.
- IGREJAS G., GUEDES-PINTO H., CARNIDE V., BRANLARD G. (1999): The high and low molecular weight glutenin subunits and ω -gliadin composition of bread and durum wheats commonly grown in Portugal. *Plant Breeding*, **118**: 297–302.
- JACKSON E.A., HOLT L.M., PAYNE P.I. (1983): Characterisation of high molecular weight gliadin and low-molecular-weight glutenin subunits of wheat endosperm by two-dimensional electrophoresis and the chromosomal location of their controlling genes. *Theoretical and Applied Genetics*, **66**: 29–37.
- KAAN F., BRANLARD G., CHIHAAB B., BORRIS C., MONNEVEUX P. (1993): Relations between genes coding for grain storage protein and two pasta cooking quality criteria among durum wheat (*T. durum* Desf.) genetic resources. *Journal of Genetics and Breeding*, **47**: 151–156.
- KUDRYAVTSEV A.M., BOGGINI G., BENEDETTELLI S., ILLICHEVSKII N.N. (1996): Gliadins polymorphism and genetic diversity of modern Italian durum wheat. *Journal of Genetics and Breeding*, **50**: 239–248.
- MIEGE E. (1924): Sur les divers *Triticum* cultivés au Maroc. *Bulletin de la Société des Sciences Naturelles du Maroc*, **4**: 5–6.
- MORAGUES M., ZARCO-HERNANDEZ J.F., MORALEJO M.A., ROYO C. (2006): Genetic diversity of glutenin protein subunits composition in durum wheat landraces (*Triticum turgidum* ssp. *Tugidum* convar. *durum* (Desf.) Mackey) from the Mediterranean basin. *Genetic Resources and Crop Evolution*, **53**: 993–1002.
- NEI M. (1973): Analysis of gene diversity in subdivided populations. *Proceedings of the National Academy of Sciences of the United States of America*, **70**: 3321–3323.
- NIETO-TALADRIZ M.T., RUIZ M., MARTÍNEZ M.C., VÁSQUEZ J.F., CARRILLO J.M. (1997): Variation and classification of B low-molecular-weight glutenin subunit alleles in durum wheat. *Theoretical and Applied Genetics*, **95**: 1155–1160.
- NIETO-TALADRIZ M.T., RODRIGUEZ-QUIJANO M., CARRILLO J.M. (2000): Glutenin proteins as markers for durum wheat quality selection. In: *Actes du 1^{er} Symposium International sur la Filière Blé, Office Algérien Interprofessionnel des céréales*, 267–270.
- PAYNE P.I., LAWRENCE G.J. (1983): Catalogues of alleles for the complex gene loci, *Glu-A1*, *Glu-B1* and *Glu-D1* which code for high-molecular-weight subunits of glutenin in hexaploid wheat. *Cereal Research Communication*, **11**: 29–35.
- PAYNE P.I., LAW C.N., MUDD E.E. (1980): Control of homoeologous group 1 chromosomes of the high-molecular-weight subunits of glutenin, a major protein of wheat endosperm. *Theoretical and Applied Genetics*, **58**: 113–120.
- PAYNE P.I., HOLT L.M., JACKSON E.A., LAW C.N., DAMANIA A.B. (1984): Wheat storage proteins: their genetics and their potential for manipulation by plant breeding. *Philosophical Transactions of the Royal Society B*, **304**: 359–371.
- RUIZ M., CARRILLO J.M. (1995): Relationships between different prolamins and some quality properties in durum wheat. *Plant Breeding*, **114**: 40–44.
- SINGH N.K., SHEPHERD K.W. (1988): Linkage mapping of the genes controlling endosperm storage proteins in

- wheat. 1. Genes on the short arms of group-1 chromosome. *Theoretical and Applied Genetics*, **75**: 642–650.
- SINGH N.K., SHEPHERD K.W., CORNISH G.B. (1991): A simplified SDS-PAGE procedure for separating LMW subunits of glutenin. *Journal of Cereal Science*, **14**: 203–208.
- TAHIR M., TURCHETTA T., ANWAR R., LAFIANDRA D. (1996): Assessment of genetic variability in hexaploid wheat landraces of Pakistan based on polymorphism for HMW glutenin subunits. *Genetic Resources and Crop Evolution*, **43**: 211–220.
- TURCHETTA T., CIAFFI M., PORCEDDU E., LAFIANDRA D. (1995): Relationship between electrophoretic pattern of storage proteins and gluten strength in durum wheat landraces from Turkey. *Plant Breeding*, **114**: 406–412.
- WEI Y.M., ZHENG Y.L., ZHOU Y.H., LIU D.C., LAN X.J., YAN Z.H. et al (2001): Genetic diversity of *Gli-1*, *Gli-2* and *Glu-1* alleles among Chinese endemic wheats. *Acta Botanica Sinica*, **43**: 834–839.

Received for publication August 22, 2011
Accepted after corrections January 10, 2012

Corresponding author:

Prof. DOUADI KHELIFI, Université Mentouri, Faculté des Sciences de la Nature et de la Vie,
Laboratoire de Génétique Biochimie et Biotechnologies Végétales, 25 000 Constantine, Algérie
e-mail: dkhelifi@yahoo.fr
