Cereal Research Communications 39(3), pp. 405–414 (2011)
DOI: 10.1556/CRC.39.2011.3.10

Genetic Diversity of Gluten Proteins in *T. turgidum* L.

C. RIEFOLO, D.B.M. FICCO, L. CATTIVELLI and P. DE VITA*

C.R.A. Cereal Research Centre, S.S. 16, km 675, 71122 Foggia, Italy

(Received 17 May 2010; accepted 5 October 2010;
Communicated by F. Békés)

The genetic variations of high and low molecular weight glutenin subunits (HMW-GS and LMW-GS) as well as of ω- and γ-gliadins in 562 accessions of 7 tetraploid *Triticum turgidum* L. subspecies were investigated using sodium dodecyl sulfate polyacrylamide-gel electrophoresis (SDS-PAGE). A total of 26 HMW-GS alleles (7 at *Glu-A1* and 19 at *Glu-B1* loci) with 63 allelic combinations, as well as 11 LMW-GS alleles (5 at *Glu-A3,* 4 at *Glu-B3* and 2 at *Glu-B2* loci) with 26 allelic combinations, were detected. Two novel HMW-GS, called *B1cf* and *B1cg,* were discovered in *T. dicoccum, B1cg* was also found in *T. turanicum*. The *Glu-B1* locus showed the highest values of genetic diversity index (H), with a mean of 0.72. As regards gliadins, 8 alleles at *Gli-B1* locus have been found. The dendrogram based on allelic frequencies, revealed that *T. durum, T. carthlicum* and *T. polonicum* grouped a part from the other subspecies. This behaviour suggested probably different evolutive pathways among the tetraploid wheats.

Keywords: HMW, LMW, gluten, *Triticum turgidum* subspecies, tetraploid wheats

Introduction

Gluten proteins are constituted by two classes called gliadins and glutenins both characterized by high glutamine and proline contents. Gliadins are monomeric proteins responsible for gluten viscoelasticity, encoded by genes located on the distal part of the short arm of homoeologous chromosomes 1 *(Gli-1)* and 6 *(Gli-2)* both in durum (Lafiandra et al. 1983) and bread wheat (Lafiandra et al. 1984). Glutenins are polymeric proteins and their disulphide bonds link high-molecular-weight (HMW-GS) with low-molecular-weight (LMW-GS) glutenin subunits (Shewry et al. 1992). In tetraploid wheats HMW-GS are encoded by the *Glu-1* (*Glu-A1* and *Glu-B1*) locus, while LMW-GS are encoded by *Glu-3 (Glu-A3, Glu-B3)* and *Glu-B2* loci. Their chemical characteristics explain the gluten strength. A number of studies have already reported on the allelic composition of gliadins and glutenins in *T. turgidum* L. subsp. *durum* (Branlard et al. 1989; Nieto-Taladriz et al. 1997; Xu et al. 2009) and *T. turgidum* subsp. *dicoccum* (Vallega and Waines 1987; Li et al. 2006). Few reports are available for *T. turgidum* subsp. *dicoccoides* (Levy et al. 1988), while almost any report has been published on other tetraploid wheats (Sissons and Batey 2003), particularly on LMW-GS composition. In this study, alleles of HMW-GS,

* Corresponding author; E-mail: pasquale.devita@entecra.it; Phone: 0039 0881 742972;
Fax: 0039 0881 713150

LMW-GS, ω- and γ-gliadins were evaluated in 562 accessions of 7 tetraploid *Triticum turgidum* L. subspecies to provide an overview of the genetic variability of gluten proteins in ancestral tetraploid wheats in comparison with cultivated subspecies.

Materials and Methods

Plant materials

A total of 562 accessions of tetraploid wheat were evaluated. The collection consists of 325 *T. turgidum* L. subsp. *durum* (Desf.), 12 *T. turgidum* L. subsp. *carthlicum* (Nevski) Á. Löve & D. Löve, 21 *T. turgidum* L. subsp. *polonicum* (L.) Thell, 19 *T. turgidum* L. subsp. *turgidum* (L.) Thell, 142 *T. turgidum* subsp. *dicoccum* (Shrank ex Schübler) Thell., 20 *T. turgidum* subsp. *dicoccoides* (Korn. ex Asch. & Graebn.) Thell., and 23 *T. turgidum* L. subsp. *turanicum* (Jakubz.) Á. Löve & D. Löve accessions.

Durum wheat genotypes and some Italian emmer populations were collected by the C.R.A. Cereal Research Centre, while the remaining wild and domesticated wheat accessions were kindly provided by Dr. Harold Bockelaman (USDA-ARS, National Small Grain Collection Aberdeen, USA), Dr Mike Ambrose (John Innes Centre Park Colney Lane Norwich, UK) and Dr. Iva Faberova Research (Institute of Crop Production, Genebank Department, Czech Republic).

Electrophoresis

Glutenins were extracted from flour samples (50 mg) according to Laemmli (1970). Electrophoresis was performed in SE 600 Ruby Hoefer vertical unit with stacking and running gel concentration 3% and 10%, respectively. The identification of HMW-GS was based on the classification of Branlard et al. (1989). The new subunits and alleles were designed according to Li et al. (2006) and McIntosh et al. (2006). LMW-GS were classified according to Nieto-Taladriz et al. (1997). Gliadins were extracted from single seeds and fractionated in acid (pH 3.1) polyacrylamide gel electrophoresis (A-PAGE) according to Lafiandra and Kasarda (1985) and their classification was performed according to Boggini et al. (1995) and Aguirano et al. (2008).

Data analysis

The genetic diversity at each locus was calculated on the basis of Nei (1973): $H = 1 - pi^2$ (H is Nei's genetic variation index and *pi* is the frequency of a particular allele at that locus). Genetic distances among groups of cultivars were computed by NTSYS-pc 2.0 software according to the modified Roger's distance (Wright 1978).

Results

Allelic composition of HMW glutenin subunits

The frequencies and the compositions of HMW-GS are shown in Table 1. At the *Glu-A1* locus, 7 HMW-GS alleles were detected. *T. dicoccum* was the only subspecie where all alleles were represented. The allele *Glu-A1c* (null) was the dominant allele detected in all tetraploid subspecies with a frequency ranging from 5.26% *(T. turgidum)* to 91.30% *(T. turanicum),* 97.23% *(T. durum)* and 100.00% *(T. carthlicum)*. The allele *Glu-A1a* was detected in six tetraploid wheats with the highest frequency in *T. turgidum* (52.63%), followed by *T. dicoccum* (45.77%) and *T. polonicum* (42.86%). It was absent in *T. carthlicum*. *Glu-A1b* was also detected in six tetraploid wheats, but with a lower mean frequency (7.12%). Others alleles at *Glu-A1* locus were overall detected at low frequency (≤3%). They were present at a relevant level only in *T. dicoccum* and *T. turgidum;* only exception was the allele *Glu-A1h* highly represented in *T. dicoccoides* (30.00%).

At the *Glu-B1* locus 19 allelic variants were detected. The subunits 7 + 8 (*Glu-B1b)* and 6 + 8 *(Glu-B1d)* were the most common allelic variants (30.96% and 20.64%, respectively). Their frequencies ranged from 58.33% *(T. carthlicum)* to 4.35% *(T. turanicum)* for *Glu-B1b* and from 43.48% *(T. turanicum)* to 10.00% *(T. dicoccoides)* for *Glu-B1d.* The subunit 20 *(Glu-B1e)* (21.89%), was detected in 5 out of 7 tetraploid wheats with a frequency ranging from 32.61% *(T. durum)* to 3.52% *(T. dicoccum)*. The highest number of *Glu-B1* alleles was detected in *T. dicoccum* where the most frequent allele (22.53%) was *Glu-B1b* followed by *Glu-B1d* and *Glu-B1cf* (14.08%). In particular, a new allelic variant *Glu-B1cf* was characterized by a x-type subunit with an intermediate migration rate between the subunits 13 and 14 (13.1), while the y-type subunit moved at a rate greater than the subunit 18 (18.1) (Fig. 1). *Glu-B1cf* was also found in *T. dicoccum* (14.08%), *T. dicoccoides* (10.00%) and *T. turanicum* (8.70%). In addition, in *T. dicoccum* at *Glu-B1* locus, *Glu-B1k* (subunit 22) and *Glu-B1q* (subunit V) showed relatively high frequencies, 9.15% and 3.52%, respectively. The other rare allelic variants detected in the present study confirmed a previous report of Vallega and Waines (1987).

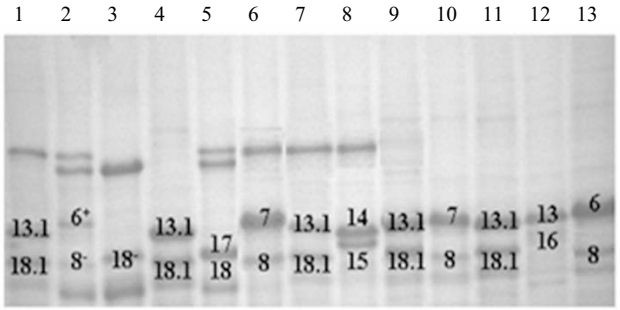

Figure 1. SDS-PAGE patterns of HMW and LMW glutenin subunits in some cultivars of *T. aestivum* (a), *T. durum* (b), *T. dicoccum* (c) and *T. turanicum* (d). (1) PI 272600 (c), (2) Sieve (a), (3) Resistente (a), (4) PI 191599 (d), (5) Loreto (a), (6) Padre Pio (c), (7) PI 286061 (c), (8) Sappo (c), (9) PI 192641 (d), (10) Duilio (b), (11) PI 57536 (c), (12) Solitario (b), (13) Creso (b)

Table 1. Allelic composition of HMW-GS at different loci in 562 cultivars and accessions of *T. turgidum* L. subsp. with H Nei's genetic variation indexes

Locus	Allele	Subunit	Total	%	*T. turgidum* L. subsp. *durum*		*T. turgidum* L. subsp. *dicoccum*		*T. turgidum* L. subsp. *turanicum*		*T. turgidum* L. subsp. *dicoccoides*		*T. turgidum* L. subsp. *polonicum*		*T. turgidum* L. subsp. *turgidum*		*T. turgidum* L. subsp. *carthlicum*	
					No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Glu-A1	*a*	1	93	16.55	2	0.62	65	45.77	1	4.35	6	30.00	9	42.86	10	52.63		–
	b	2*	40	7.12	4	1.23	24	16.90	1	4.35	4	20.00	2	9.52	4	21.05		–
	c	null.	383	68.15	316	97.23	20	14.08	21	91.30	4	20.00	9	42.86	1	5.26	12	100.00
	h	I	16	2.85		–	9	6.34		–	6	30.00		–	1	5.26		–
	j	1' o III	17	3.02	3	0.92	13	9.15		–		–		–	2	10.53		–
	o	2**o V	11	1.96		–	9	6.34		–		–	1	4.76	1	5.26		–
	q	2***o VI	2	0.36		–	2	1.41		–		–		–		–		–
	H					0.05		0.72		0.16		0.74		0.62		0.66		0.00
Glu-B1	*a*	7	3	0.53		–	3	2.11		–		–		–		–		–
	b	7+8	174	30.96	114	35.08	32	22.53	1	4.35	7	35.00	12	57.14	4	21.05	7	58.33
	d	6+8	116	20.64	74	22.76	20	14.08	10	43.48	2	10.00	5	23.81	4	21.05	2	16.67
	e	20	123	21.89	106	32.61	5	3.52		–		–	4	19.05	1	5.26	3	25.00
	f	13+16	15	2.67	12	3.69	1	0.70	1	4.35		–		–	1	5.26		–
	k	22	13	2.31		–	13	9.15		–		–		–		–		–
	n	II	5	0.89	2	0.61	1	0.70		–	2	10.00		–		–		–
	o	III	4	0.71	2	0.61	2	1.41		–		–		–		–		–
	p	23+18	16	2.85	3	0.92	7	4.93		–	6	30.00		–		–		–
	q	V	5	0.89		–	5	3.52		–		–		–		–		–
	r	19	19	3.38	2	0.61	11	7.75		–	1	5.00		–	5	26.32		–
	ag	28+29	13	2.31		–	12	8.45	1	4.35		–		–		–		–
	aw	6.8+20y	1	0.18		–		–		–		–		–	1	5.26		–
	be	6.1+22.1	2	0.36		–	2	1.41		–		–		–		–		–
	bm	6'+22.1	6	1.07		–	6	4.22		–		–		–		–		–
	cb	6+17	10	1.78	10	3.08		–		–		–		–		–		–
	cd	6.1+8.1	5	0.89		–	2	1.41		–		–		–	3	15.78		–
	cf	13.1+18.1	26	4.63		–	20	14.08	2	8.70	2	10.00		–		–		–
	cg	7+17	6	1.07		–		–	8	34.80		–		–		–		–
	H					0.72		0.88		0.68		0.76		0.58		0.81		0.60

In *T. dicoccoides* the alleles *Glu-B1b* and *Glu-B1p* had the highest frequencies (35.00 and 30.00%, respectively) followed by *Glu-B1d, Glu-B1cf* and *Glu-B1n* (10.00%). In *T. turanicum, Glu-B1d* was the most observed allelic variant (43.48%) followed by the novel allelic variant *Glu-B1cg* (34.80%). *Glu-B1cg* was characterized by a x-type and y-type subunits with the same mobility of the subunits 7 and 17, respectively (Fig. 2).

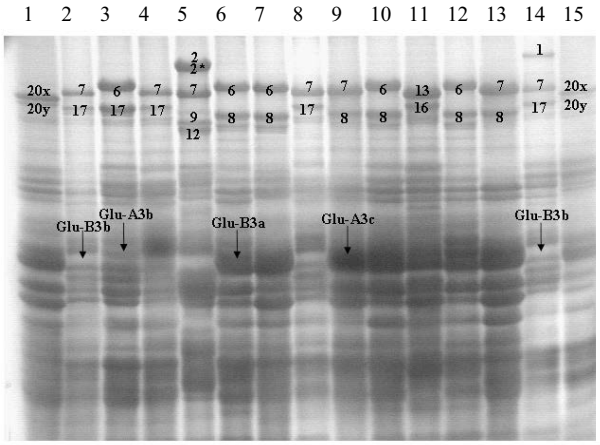

Figure 2. SDS-PAGE patterns of HMW and LMW glutenin subunits in 7 *T. turanicum* accessions (a) along with durum wheat cultivars (b) and Bolero (bread wheat) (lane 5). (1) Appulo (b), (2) PI 67343 (a), (3) Quadruro (b), (4) PI 68104 (a), (5) Bolero, (6) Cltr 11390 (a), (7) Creso (b), (8) 127106 (a), (9) Simeto (b), (10) 166308 (a), (11) Solitario (b), (12) 166450 (a), (13) Simeto (b), (14) 166554 (a), (15) Appulo (b)

In *T. turgidum* the allele *Glu-B1r* was the most detected (26.32%) followed by *Glu-B1b* and *Glu-B1d* (21.05%) and *Glu-B1cd* (15.78%).

In durum wheat the allelic variants *Glu-B1b* (subunit 7 + 8) and *Glu-B1e* (subunit 20) were observed with a similar frequency (35.08% and 32.61%, respectively); other rare alleles as *Glu-B1o* and *Glu-B1r* (0.61%), *Glu-B1cb* (3.08%) were also present.

The allelic variants *Glu-B1d* and *Glu-B1h* associated to high gluten quality in durum wheat genotypes (Carrillo et al. 2000), were the less represented in all other tetraploid wheats.

The most frequent allele combinations examined among 562 tetraploid wheat accessions were N + 7 + 8 (22.95%), N + 20 (19.57%) and N + 6 + 8 (15.98%) present in *T. durum, T. carthlicum* and *T. turanicum* (data not shown).

Allelic composition of LMW glutenin subunits and gliadins

Ten alleles were detected at *Glu-3* loci, five each for *Glu-A3* and *Glu-B3* (Table 2). *Glu-A3a* (subunit 6) was the most abundant allele (49.29%), present in all subspecies with frequencies ranging between 72.00% *(T. durum)* and 4.35% *(T. turanicum),* followed by *Glu-A3c* (subunit 6 + 10) (26.33%) and *Glu-A3b* (subunit 5) (17.62%) with the latter present in all species evaluated with the exception on *T. carthlicum*. The subunit 11 *(Glu-A3e)*

Table 2. Allelic composition of LMW-GS, ω- and γ-gliadins at different loci in 562 cultivars and accessions of *T. turgidum* L. subsp. with H Nei's genetic variation indexes

Locus	Allele	Subunit and gliadin	Total	%	*T. turgidum* L. subsp. *durum*		*T. turgidum* L. subsp. *dicoccum*		*T. turgidum* L. subsp. *turanicum*		*T. turgidum* L. subsp. *dicoccoides*		*T. turgidum* L. subsp. *polonicum*		*T. turgidum* L. subsp. *turgidum*		*T. turgidum* L. subsp. *carthlicum*	
					No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Glu-A3	*a*	6	269	49.29	234	72.00	24	17.61	1	4.35	3	15.00	2	9.52	2	10.53	3	25.00
	b	5	100	17.62	31	9.54	46	31.69	10	43.48	7	35.00	3	14.29	3	15.79		–
	c	6 + 10	154	26.33	59	18.15	49	34.51	12	52.17	10	50.00	11	52.38	4	21.05	9	75.00
	e	11	2	0.36		–	2	1.41		–		–		–		–		–
	h	null.	37	6.41	1	0.31	21	14.79		–		–	5	23.81	10	52.63		–
	H					0.44		0.73		0.54		0.60		0.64		0.64		0.38
Glu-B3	*a*	2 + 4 + 15 + 19	380	67.62	285	87.69	38	26.76	12	52.17	7	35.00	18	85.71	8	42.10	12	100.00
	b	8 + 9 + 13 + 16	116	20.64	38	11.69	51	35.91	11	47.83	7	35.00	3	14.29	6	31.58		–
	d	2 + 4 + 15 + 17 + 19	7	1.24	1	0.31	6	4.22		–		–		–		–		–
	h	1 + 3 + 14 + 18	28	4.98	1	0.31	21	14.79		–	6	30.00		–		–		–
	i	7 + 8 + 14 + 18	31	5.52		–	26	18.31		–		–		–	5	26.32		–
	H					0.22		0.74		0.50		0.67		0.24		0.65		0.00
Gli-B1	a^a	ω-33–35–38, γ-42	121	21.53	39	12.00	56	39.44	12	52.17	7	35.00	2	10.00	5	26.31	–	
	c^a	ω-35, γ-45	351	62.46	283	87.08	25	17.61	11	47.83	7	35.00	18	85.00	3	15.79	4	33.33
	e^a	ω-35, γ-47	1	0.18	1	0.31		–		–		–		–		–		–
	f^a	ω-35, γ-42	1	0.18	1	0.31		–		–		–		–		–		–
	g^a		1	0.18	1	0.31		–		–		–		–		–		–
	i^a		1	0.18		–	1	0.70		–		–		–		–		–
	l^a		27	4.80		–	12	9.68		–		–	1	5.00	6	31.58	8	66.67
	new-1[b]	γ-44	28	4.98		–	22	15.49		–	6	30.00		–		–		–
	null.		31	5.52		–	26	18.31		–		–		–	5	26.32		–
	H					0.23		0.75		0.50		0.66		0.26		0.74		0.44
Glu-B2	*a*	12	411	52.85	278	85.54	68	47.89	11	47.83	10	50.00	19	90.50	13	56.48	12	100.00
	b	null.	151	47.15	47	14.46	74	52.11	12	52.17	10	50.00	2	9.50	6	43.52		–
	H					0.25		0.50		0.50		0.50		0.17		0.49		0.00

[a] Allele classification at *Gli-B1* according to Boggini et al. (1995)
[b] Allele classification at *Gli-B1* according to Aguirano et al. (2008)

was the allelic variant less represented at locus *Glu-A3,* and detected only in *T. dicoccum* with a frequency of 1.41%. Comparing the subspecies, the allele *Glu-A3a* was the most abundant (72.00%) only in *T. durum,* whereas in all other tetraploid wheats the allele most abundant was *Glu-A3c*.

Among all the possible alleles at *Glu-B3* locus, the most frequent were *Glu-B3a* (subunit 2 + 4 + 15 + 19) (67.62%) and *Glu-B3b* (subunit 8 + 9 + 13 + 16) (20.64%) detected in all tetraploid wheats with the exception of *Glu-B3b,* absent in *T. carthlicum*. The first is correlated with a good durum wheat quality, the second with a poor one (Ruiz and Carrillo 1995a, b; Vazquez et al. 1996). *Glu-B3a* was the prevalent allele in *T. carthlicum* (100.00%), *T. durum* (87.69%) and *T. polonicum* (85.71%), whereas in *T. dicoccum* the *Glu-B3b* allele was the most represented (35.91%).

At *Gli-B1* locus 9 allelic variants were detected and the allele *Gli-B1*c (ω-35 and γ-45 gliadins) (62.46%) and *Gli-B1*a (ω-33-35-38 and γ-42 gliadins) (21.53%) were the most represented among the tetraploid. An exception is *T. carthlicum* where the allele *Gli-B1a* was absent and the most abundant allelic variant was *Gli-B1l* (66.67%). At this locus the frequency of the new alleles was small (<5.0 %) except for *Gli-B1null*.

At *Glu-B2* locus, two allelic variants *Glu-B2a* and *Glu-B2b* were detected. The first was the most abundant, particularly in *T. carthlicum* (100.00%), *T. durum* (85.54%), *T. polonicum* (90.50%) and *T. turgidum* (56.48%), while in the other subspecies they were equally distributed. The most frequent LMW-GS combination among 562 tetraploid wheat genotypes was 2 + 4 + 6 + 12 + 15 + 19 (44.84%) (data not shown).

Genetic diversity

In Tables 1 and 2 the Nei's genetic variation index (H) for HMW-GS and LMW-GS loci are reported. The highest H value was detected for *Glu-B1* locus with a mean of 0.72, confirming this locus as the one with the highest polymorphic level, whereas the lowest polymorphic content was detected for *Glu-B2* (0.25). *T. dicoccum* showed the highest H values (0.88) at *Glu-B1* locus together *T. turgidum* (0.81), whereas the lowest belonged to *T. polonicum* (0.58). At *Glu-A1* locus, lower H values were calculated for *T. carthlicum, T. durum* and *T. turanicum* (0.00, 0.05 and 0.16, respectively), whereas higher H values were detected in *T. dicoccoides* (0.74) and *T. dicoccum* (0.72).

Discussion

The analysis of storage protein variation can provide important information for the assessment of genetic variability in germplasm. Twenty-six allelic variants were found at the two *Glu-1* loci, among them two alleles, *Glu-B1cf* (subunit 13.1 + 18.1) and *Glu-B1cg* (subunit 7 + 17) (Figs 1 and 2), were never reported before in tetraploid wheat accessions. In *T. dicoccum*, 45.77% of the accessions possessed *Glu-A1a* (subunit 1), 16.90% *Glu-A1b* (subunit 2*) and 14.08% *Glu-A1c* (subunit null) with a similar trend reported by Li et al. (2006). In *T. polonicum* the most common alleles were *Glu-A1a* and *Glu-A1c* detected in the 42.86% of the accessions, differently by Pan et al. (2007) and Xu et al. (2009). In *T. carthlicum Glu-A1c* was the only allele detected, whereas Zhuang et al. (2006) found

both *Glu-A1a* and *Glu-A1b*. In *T. turanicum Glu-A1c* presented a similar frequency (91.30%) to those already reported by Xu et al. (2009) (84.70%).

At the *Glu-B1* locus the allelic variants detected in our study have confirmed the high polymorphic level emphasized by Vallega (1988) and Xu et al. (2009). Some allelic variants detected in *T. dicoccum* were also found by other authors as *Glu-B1be* (6.1 + 22.1) (An et al. 2005), *Glu-B1bm* (6' + 22.1) and *Glu-B1cd* (6.1 + 8.1) (Li et al. 2006), although in the present work *Glu-B1cd* was detected both in *T. dicoccum* and in *T. turgidum,* with a frequency greater than that found by Li et al. (2006). The allele *Glu-B1b* was also the most detected in *T. carthlicum* accessions (58.33%) as reported by Xu et al. (2009) followed by *Glu-B1e* (25.00%) and *Glu-B1d* (16.67%). A similar electrophoretic pattern at *Glu-B1* locus was also found in *T. polonicum*, a finding different from Xu et al. (2009). In addition, in the tetraploid accessions investigated in this work two typical allelic variants of hexaploid wheats were also found: *Glu-B1aw* (6.8 + 20y) in *T. turgidum*, previously reported only in triticale by Amiour et al. (2002), and *Glu-B1ag* (28 + 29) in *T. dicoccum* and *T. turanicum* (Pogna et al. 1989). The allelic variants *Glu-B1d* and *Glu-B1h* associated to high gluten quality in durum wheat genotypes (Carrillo et al. 2000), were the less represented in all other tetraploid wheats.

LMW-GS and γ-gliadins are considered very important for gluten quality in durum wheat (Payne et al. 1984; Pogna et al. 1990; Ruiz and Carrillo 1995a). Ten alleles were detected at *Glu-3* loci, five each for *Glu-A3* and *Glu-B3* (Table 2) and since *Glu-B3* locus is tightly linked to *Gli-B1* one (Singh and Shepherd 1988; Nieto-Taladriz et al. 1997; Carrillo et al. 2000), the frequencies of allelic composition of ω- and γ-gliadins were also considered.

In the present work a large variability had been found in tetraploid wheats subspecies. *T. dicoccum, T. turgidum* and *T. dicoccoides* represented the tetraploid wheats with the highest level of polymorphism (0.72 and 0.66, respectively), a possible source of new alleles for durum wheat breeding. On the contrary *T. carthlicum* was characterized by a low mean H (0.24) as well as *T. durum* (0.32). In particular, *T. carthlicum, T. durum* and *T. polonicum* showed lower means H for *Glu-B3* (0.00, 0.22, 0.24, respectively) and *Gli-B1* loci (0.44, 0.23, 0.26, respectively). These results were confirmed by a cluster analysis among 562 accessions of seven *T. turgidum* L. subspecies (Fig. 3). *T. durum, T. carthlicum* and *T. polonicum* clustered in the first part of the dendrogram while in the second clustered *T. dicoccoides* together *T. dicoccum,* underlining the different polymorphism between these two groups of tetraploid wheats. Also, the accessions of *T. turgidum* and *T. turanicum* were represented in the second group. The separation between *T. durum* and *T. dicoccum* and *T. dicoccoides* could be the consequence of the selection for some allelic variants correlated with a better gluten quality in *T. durum,* as also reported by other authors (Ruiz and Carrillo 1995a, b; Vazquez et al. 1996).

Numerous studies have been conducted with the main objective to explore the composition of seed storage proteins of various *Triticum* wheats subspecies such as *T. durum* and *T. dicoccum* and exploit as potential sources of useful alleles for qualitative improvement of modern durum wheat cultivars. The present data provide an overview of the allelic composition of almost all *T. turgidum* subspecies and confirm that *T. dicoccum* is the

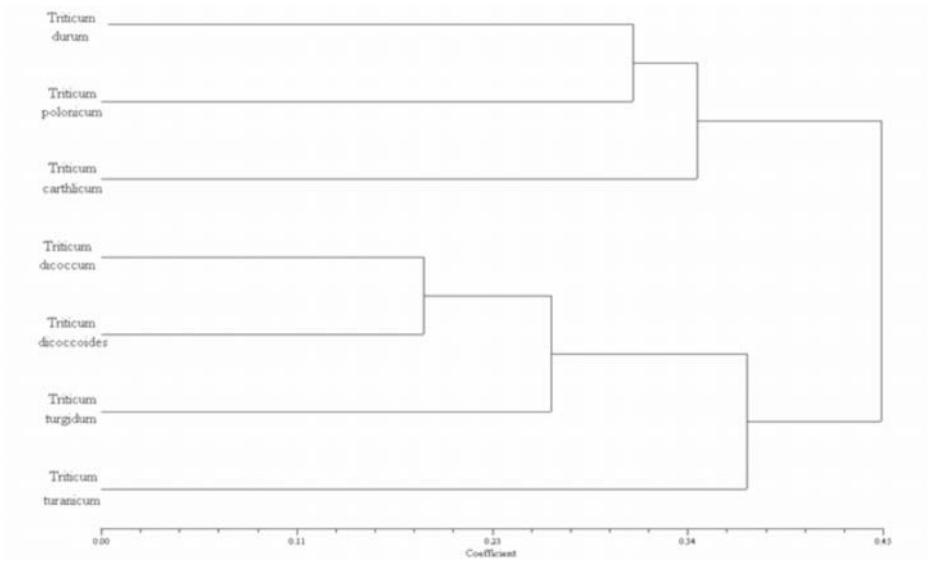

Figure 3. Dendrogram based on modified Roger's (Wright 1978) genetic distances among *T. turgidum* L. subspecies considering loci *Glu-A1, Glu-B1, Glu-A3, Glu-B3, Glu-B2* and *Gli-B1*

subspecies with the highest level of polymorphisms. Nevertheless, the exploitation of the other related subspecies has allowed the identification of few new allelic variants suggesting that further unexplored genetic variability for gluten composition is still available.

Acknowledgements

This work was supported by Italian Ministry of University and Research (MIUR) project AGROGEN and by Italian Ministry of Agriculture Project RGV-FAO.

References

Aguirano, E., Ruiz, M., Fitè, 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. Span. J. Agric. Res. **4**:599–609.

Amiour, N., Bougennac, A., Marcoz, C., Sourdille, P., Bourgoin, M., Khelifi, D., Branlard, G. 2002. Diversity of seven glutenin and secalin loci within triticale cultivars grown in Europe. Euphytica **123**:295–305.

An, X., Li, Q., Yan, Y., Xiao, Y., Hsam, S.L.K., Zeller, F.J. 2005. Genetic diversity of European spelt wheat (*Triticum aestivum* ssp. *spelta* L. em. Thell) revealed by glutenin subunit variations at the *Glu-1* and *Glu-3* loci. Euphytica **146**:193–201.

Boggini, G., Tusa, P., Pogna, N.E. 1995. Breadmaking quality of durum wheat genotypes with some novel glutenin subunit composition. J. Cereal Sci. **22**:105–113.

Branlard, G., Autran J.C., Monneveux, P. 1989. High molecular weight subunit in durum wheat *(T. durum)*. Theor. Appl. Genet. **78**:353–358.

Carrillo, J.M., Martinez, M.C., Brites, C., Nieto-Taladriz, M.T., Vazquez, J.F. 2000. Relationships between endosperm proteins and quality in durum wheat (*Triticum turgidum* L. var. *durum*). Options Méditerranéennes **40**:463–467.

Laemmli, U.K. 1970. Cleavage of structural proteins during the assembly of the head of bacteriofage T4. Nature **227**:680–685.

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

Lafiandra, D., Kasarda, S.S., Morris, R. 1984. Chromosomal assignment of genes coding for the wheat gliadin protein components of the cultivars Cheyenne and Chinese Spring by two-dimensional (two-pH) electrophoresis. Theor. Appl. Genet. **68**:531–539.

Lafiandra, D., Benedettelli, S., Spagnoletti-Zeuli, P.L., Porceddu, E. 1983. Genetic aspects of durum wheat gliadins. In: Porceddu, E. (ed.), Breeding Methodologies in Durum Wheat and Triticale. Viterbo, Italy, pp. 29–37.

Levy, A.A., Galili, G., Feldman, M. 1988. Polymorphism and genetic control of high molecular weight glutenin subunits in wild tetraploid wheat *Triticum turgidum* var. *dicoccoides*. Heredity **61**:63–72.

Li, Q.Y., Yan, Y.M., Wang, A.L., An, X.L., Zhang, Y.Z., Hsam, S.L.K., Zeller, F.J. 2006. Detection of HMW glutenin subunit variations among 205 cultivated emmer accessions (*Triticum turgidum* ssp. *dicoccum*). Plant Breed. **125**:120–124.

McIntosh, R.A., Devos, K.M., Dubcovsky, J., Rogers, W.J., Morris, C.F., Appels, R., Anderson, O.A. 2006. Catalogue of gene symbols for wheat: 2006 Supplement. http://www.shigen.nig.ac.jp/wheat/komugi/genes/macgene//supplement2006.pdf

Nei, M. 1973. Analysis of gene diversity in subdivided populations. Proc. Nat. Acad. Sci. USA **70**:3321–3323.

Nieto-Taladriz, M.T., Ruiz, M., Martinez, M.C., Vazquez, J.F., Carrello, J.M. 1997. Variation and classification of B low-molecular-weight glutenin subunit alleles in durum wheat. Theor. Appl. Genet. **95**:1155–1160.

Pan, D., Hong, L., Wei, L., Peng-Fei, Q., Yu-Ming, W., Zheng, Y.L. 2007. Genetic diversity of storage proteins in *Triticum polonicum* L. J. Plant Sci. **2**:416–424.

Payne, P.I., Jackson, E.A., Holt, L.M. 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, N.E., Autran, J.C., Mellini, F., Lafiandra, D. 1990. Chromosome 1B-encoded gliadins and glutenin subunits in durum wheat: genetics and relationship to gluten strenght. J. Cereal Sci. **11**:15–34.

Pogna, N.E., Mellini, F., Beretta, A., Dalbelin Deruffo, A. 1989. The high molecular weight subunits of common wheat cultivars grown in Italy. J. Genet. Breed. **43**:17–24.

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

Shewry, P.R., Halford, N.G., Tatham, A.S. 1992. High-molecular weight subunits of wheat glutenin. J. Cereal Sci. **15**:105–120.

Singh, N.K., Shepherd, K.W. 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.

Sissons, M.J., Batey, I. 2003. Protein and starch properties of some tetraploid wheats. Cereal Chem. **80**:468–475.

Vallega, V. 1988. Comparative analysis of high-molecular weight glutenin subunit composition in various *Triticum* species. Plant Breed. **100**:241–246.

Vallega, V., Waines, J.G. 1987. High molecular weight glutenin subunit variation in *Triticum turgidum* var. *dicoccum*. Theor. Appl. Genet. **74**:706–710.

Vazquez, J.F., Ruiz, M., Nieto-Taladriz, M.T., Albuquerque, M.M. 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.

Wright, S. 1978. Evolution and the Genetics Populations, Vol. 4. Variability within and among Natural Populations. University of Chicago Press, Chicago, USA.

Xu, L., Li, W., Wei, Y., Yan, Z., Zheng, Y. 2009. Genetic diversity of HMW glutenin subunits in diploid, tetraploid and hexaploid *Triticum* species. Gen. Res. Crop Evol. **56**:377–391.

Zhuang, P., Guo, Z., Yan, Z., Wei, Y., Zheng, Y. 2006. Analysis of HMW glutenin subunits in *Triticum carthlicum nevski*. Southwest China J. Agric. Sci. **9**:5–9.