Journal of Genetics, Vol. 97, No. 4, September 2018, pp. 905–910
https://doi.org/10.1007/s12041-018-0985-x

RESEARCH ARTICLE

Allelic variation of high molecular weight glutenin subunits of bread wheat in Hebei province of China

ZHENXIAN GAO*, GUOYING TIAN, YANXIA WANG, YAQING LI, QIAO CAO, MEIKUN HAN and ZHANLIANG SHI

Shijiazhuang Academy of Agricultural and Forestry Sciences, Shijiazhuang 050041, Hebei, People's Republic of China
*For correspondence. E-mail: zhenxiangao@163.com.

Received 24 October 2017; revised 31 December 2017; accepted 30 January 2018; published online 4 September 2018

Abstract. In common wheat (*Triticum aestivum* L.), allelic variations of Glu-1 loci have important influences on grain end-use quality. The allelic variations in high molecular weight glutenin subunits (HMW-GSs) were identified in 151 hexaploid wheat varieties representing a historical trend in the cultivars introduced or released in Hebei province of China from the years 1970s to 2010s. Thirteen distinct alleles were detected for Glu-1. At Glu-A1, Glu-B1 and Glu-D1, we found that the most frequent alleles were the 1 (43.0%), 7+8 (64.9%), 2+12 (74.8%) alleles, respectively, in wheat varieties. Twenty two different HMW-GS compositions were observed in wheat. Twenty-five (16.6%) genotypes possessed the combination of subunits 1, 7+8, 2+12, 25 (16.6%) genotypes had subunit composition of 2*, 7+8, 2+12; 20 (13.2%) genotypes had subunit composition of null, 7+8, 2+12. The frequency of other subunit composition was less than 10%. The Glu-1 quality score greater than or equal to 9 accounted for 20.6% of the wheat varieties. The percentage of superior subunits (1 or 2* subunit at Glu-A1 locus; 7+8, 14+15 or 17+18 at Glu-B1 locus; 5+10 or 5+12 at Glu-D1 locus) was an upward trend over the last 40 years. The more different superior alleles correlated with good bread-making quality should be introduced for their usage in wheat improvement efforts.

Keywords. allelic variation; high molecular weight glutenin subunits; wheat.

Introduction

Wheat is one of the most important food crops and can be processed into multiple types of food products (e.g. bread, noodles and cakes). Bread-making quality of wheat is determined to a large extent by the properties of the major storage proteins (Figueroa *et al.* 2011). Based on extraction and solubility in aqueous alcohol, the wheat storage proteins are classified as gliadins or glutenins (Shewry *et al.* 1986). These two protein types are important contributors for the rheological properties of dough. In general, gliadins are responsible for extensibility and viscosity of dough, while the glutenins contribute to elasticity (Anjum *et al.* 2007; Figueroa *et al.* 2011). According to categories based on electrophoretic behaviour and genetic control, the glutenins can be further divided into two subfamilies, high molecular weight glutenin subunits (HMW-GSs) and low molecular weight glutenin subunits (LMW-GSs) (Shewry 2009). The HMW-GSs are particularly important in determining dough elasticity (Anjum *et al.* 2007). In wheat, the allelic variation in the HMW-GS composition has been reported to account for ~70% of the genetic variations of dough properties (Payne *et al.* 1988).

In hexaploid wheat, the HMW-GS genes are encoded at the *Glu-1* loci (*Glu-A1*, *Glu-B1* and *Glu-D1*) on the long arm of group-1 chromosomes (Payne *et al.* 1980; Shewry and Halford 2002). In each locus, there are two duplicated HMW-GS genes, designated as x-type and y-type subunits (Dong *et al.* 2017). Because of the allelic variation and gene inactivation, these loci are highly polymorphic in nature without environmental influence (Gale 2005). These variations frequently result in the expression of allelic x-type and y-type subunits differing in sodium dodecyl sulphate polyacrylamide gel electrophoresis (SDS-PAGE), or the

Electronic supplementary material: The online version of this article (https://doi.org/10.1007/s12041-018-0985-x) contains supplementary material, which is available to authorized users.

silencing of one or more HMW-GS genes in certain genotypes (Dong *et al.* 2017). In the 1980s, according to the SDS-PAGE allelic variation in HMW-GS, three (*Glu-A1a*, *Glu-A1b* and *Glu-A1c*), 11 (*Glu-B1a* and *Glu-b-k*) and seven (*Glu-D1a* and *Glu-b-g*) common alleles have been found in each locus (Payne *et al.* 1984; Anjum *et al.* 2007). To date, more alleles and HMW-GSs have been identified from wheat and its related species and have been studied (Gu *et al.* 2004; Jiang *et al.* 2012; Dong *et al.* 2013). In common wheat, x-type subunits at *Glu-B1* and *Glu-D1* loci, y-type subunits at *Glu-D1* locus are always expressed, whereas x-type subunits at *Glu-A1* and y-type at *Glu-B1* are not always expressed (Izadi-Darbandi *et al.* 2010). Therefore, three to five HMW-GSs are usually expressed in wheat, with the HMW-GS composition often differing among different cultivars (Wang *et al.* 2017). It is known that the action of HMW-GSs in controlling wheat end-use quality is *Glu-D1*>*Glu-B1*>*Glu-A1* (Lawrence *et al.* 1988; Uthayakumaran *et al.* 2002; Jiang *et al.* 2012; Yang *et al.* 2014). Further genetic studies have found that the subunit compositions of these proteins are also correlated with wheat end-use quality. For example, at the *Glu-A1* locus, subunits Ax1 and Ax2* were better than those of the null allele having positive effects on bread-making quality (Payne 1987; Branlard *et al.* 2001). The subunits Bx7 (at the *Glu-B1* locus) and Dx5 (at the *Glu-D1* locus) have been proposed to be particularly important for loaf volume and dough quality (Wieser and Zimmermann 2000). Since the genetic diversity of HMW-GSs may be an important source of genes for quality improvement, uncovering the composition of HMW-GSs in different wheat varieties is essential for molecular design breeding in controlling wheat end-use quality.

In Hebei province, the study of genetic improvement of wheat quality has begun since 1980s, and some strong gluten wheat varieties have been cultivated, such as Shiluan 02-1, Gaoyou 2018 etc. However, the overall level is still not as good as those of the United States, Canada, Australia and so on. In this study, by means of the SDS-PAGE method, HMW-GSs were detected from 151 hexaploid wheat released by the Hebei Crops Varieties Approval Committee (1970s–2010s). The objectives of the studies are: (i) to elucidate the genetic basis and the law of evolution in wheat quality of Hebei province, further explore the main problems of wheat quality and corresponding countermeasures, and (ii) to screen some wheat varieties with excellent genetic basis for quality, providing support for breeders for good-quality wheat.

Materials and methods

Plant materials

In total, 151 winter wheat varieties (see table 1 in electronic supplementary material at http://www.ias.ac.in/jgenet/) suitable for sowing in the south of Hebei province were used. The wheat varieties were released from 1970s until now. We also included Shiluan 02-1 and Chinese spring cultivars as standard cultivars for identification of banding patterns of wheat HMW glutenin proteins.

SDS-PAGE analysis

Two seeds were selected randomly from each wheat variety. The whole seed was crushed and extracted into 200 μL SDS-PAGE sample buffer, 2% SDS, 10% glycerol, 5% 2-mercaptoethanol, 0.002% bromophenol blue, 62.5 mM Tris-HCl pH 6.8 and placed in a refrigerator at 4°C for 12 h. After centrifugation, the supernatant was analysed using 10% SDS-PAGE and a mini-cell apparatus (Liuyi, Beijing, China) at 20 mA for 3.5 h. Then, gels were stained overnight with 12% (w/v) trichloroacetic acid solution containing 0.05% Coomassie Brilliant Blue R250 in the absolute ethanol (5% w/v) and destained with 25% methanol and 10% acetic acid. A gel documentation system (Bio-Rad, California, USA) was used to scan the gel.

Results and discussion

Allelic variation at Glu-1 loci for HMW glutenin subunits

The results obtained from this study demonstrated as HMW glutenin subunit compositions and allele frequencies in 151 winter wheat varieties are described in table 1 and table 1 in electronic supplementary material. The allelic variability in part wheat varieties at 10% gel is presented in figure 1. A total of 13 different allele variants were detected for HMW-GSs: three at *Glu-A1*, seven at *Glu-B1* and three at *Glu-D1* (table 1).

For the *Glu-A1* locus, 1 or 2* subunits have positive effects on bread-making quality whereas the null allele appears inferior (Luo *et al.* 2001). The frequencies of the two active types 1 (*Glu-A1a*) and 2* (*Glu-A1b*) were 43.0

Table 1. Allelic variation and frequency at the *Glu-1* loci.

Glu-1 loci	Allele	Subunit	Frequency	Number of cultivars
Glu-A1	a	1	43.0	65
	b	2*	31.8	48
	c	Null	25.2	38
Glu-B1	a	7	2.0	3
	b	7+8	64.9	98
	c	7+9	23.2	35
	d	6+8	2.6	4
	f	13+16	0.7	1
	h	14+15	6.0	9
	i	17+18	0.7	1
Glu-D1	a	2+12	74.8	113
	d	5+10	9.9	15
	h	5+12	15.2	23

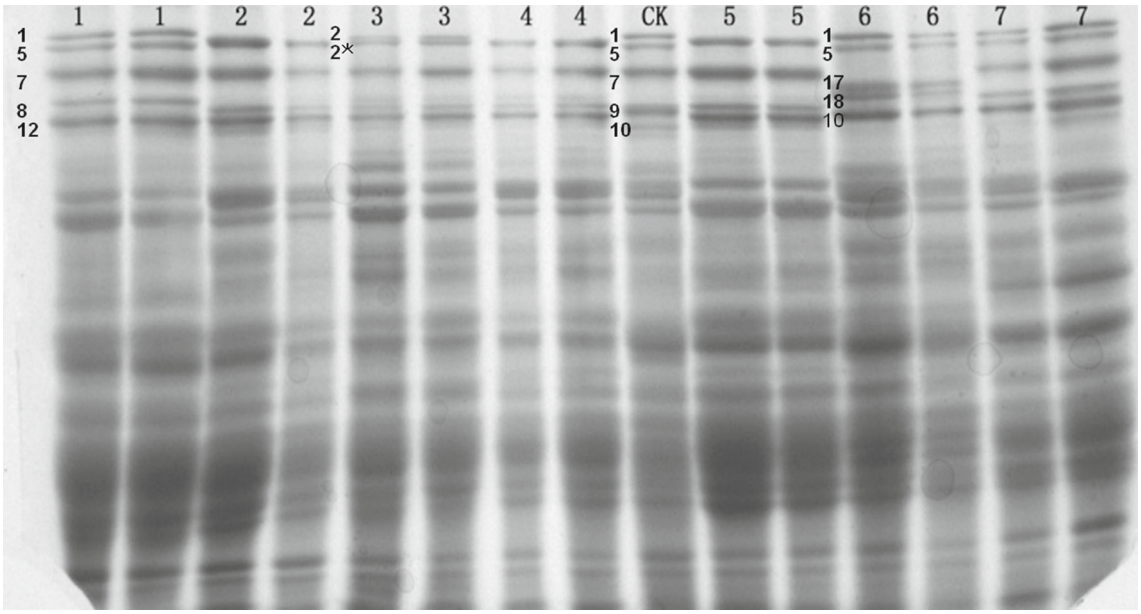

Figure 1. Electrophoretic patterns of HMW-GS in part of wheat varieties tested. 1, 71-3; 2, Shi 5093; 3, Zhongmai 9; 4, Han 4564 9; 5, Henong 85-9; 6, 5099; 7, 8901-11; CK, Shiluan 02-1.

and 31.8%, respectively, the rest (25.2%) were null-type gene *Glu-A1c* (table 1). The sum of the frequencies (74.8%) of subunits 1 and 2* was far higher than those obtained in the wheat varieties released from other wheat regions of China. For example, a low proportion, 37.5, 37.2 and 30.7%, contains the *Glu-A1*, 1 or 2* alleles, respectively, in Hubei, Gansu and Xinjiang province of China (Hao *et al.* 2004; Liu *et al.* 2004; Cao *et al.* 2009). However, a high proportion had been found in Argentinean (97.5%), Spanish (98.4%) and Moroccan (85.0%) wheat varieties (Caballero *et al.* 2004; Lerner *et al.* 2009; Henkrar *et al.* 2017). This implies that targeting for continuing to improve frequency of 1 or 2* alleles at the *Glu-A1* locus would be a strategy for promoting quality for the national wheat.

At the *Glu-B1* locus, seven alleles were detected, 2.0, 64.9, 23.2, 2.6, 0.7, 6.0 and 0.7%, accounting for 7 (*Glu-B1a*), 7+8 (*Glu-B1b*), 7+9 (*Glu-B1c*), 6+8 (*Glu-B1d*), 13+16 (*Glu-B1f*), 14+15 (*Glu-B1h*) and 17+18 (*Glu-B1i*), respectively. In Hebei province, the most frequent alleles were 7+8 and 7+9, which were also the most predominant in the bread wheat varieties of China, France and Argentina (Branlard *et al.* 2003; Song *et al.* 2006; Lerner *et al.* 2009). Subunit 6+8 is very common in synthetic hexaploids and durum wheat but its frequency is very low in bread wheat (Rasheed *et al.* 2012) and 14+15 is the unique subunit type of wheat in China (Liu *et al.* 2007). In fact, the *Glu-B1* locus possesses a significantly greater diversity of alleles than the*Glu-A1* and *Glu-D1* loci in hexaploid wheats (Li *et al.* 2004). Four types of subunits at the *Glu-B1* locus, 20 (*Glu-B1e*), 13+19 (*Glu-B1f*), 21 (*Glu-B1j*) and 22 (*Glu-B1k*) were observed in the previous study (Payne 1987) that are no longer found in the current study, but were present in other province wheat varieties of China at low frequency (Liang *et al.* 2008; Zhang *et al.* 2008; Hua *et al.* 2009).

At the *Glu-D1* locus, three subunits 2+12, 5+10 and 5+12 encoded by alleles *Glu-D1a*, *Glu-D1d* and *Glu-D1h*, respectively, were found. Subunit 2+12 was found most frequently in 113 (74.8%) genotypes followed by subunit 5+12 in 23 (15.2%) genotypes while subunit 5+10 was observed in 15 (9.9%) genotypes. Subunit 5+10 frequently confers superior end-use qualities to commercial wheat varieties (Dong *et al.* 2013). Yet synthetic hexaploids (*Triticum turgidum* × *Aegilops tauschii*; $2n = 6x = 42$) with subunit 5+12 showed better overall quality characteristics and bread loaf volume compared with any other *Glu-D1* encoded glutenin subunits (Peña *et al.* 1995). Subunits 5+12 are common in synthetic hexaploids (Peña *et al.* 1995; Rasheed *et al.* 2012). These results showed that subunits 5+12 have been successfully introduced into bread wheat through the excellent crossability of synthetic wheats with conventional bread wheats in China. On the other hand, 32.9% of the entries contain subunits 5+10 or 5+12, compared with 80.6% from the previous study of cultivars released from America, indicating that subunits 5+10 or 5+12 is not in great use in the Hebei province of China.

HMW-GS composition in hexaploid wheat

Twenty-two allelic combinations were observed in the survey of 151 Hebei province wheat varieties (table 2) of which 5.3% genotypes possessed the combination of subunits 1, 7+8 and 5+10; 2.0% genotypes had subunit composition of 1, 7+9 and 5+10; 8.6% genotypes had subunit

Table 2. HMW-GS combination frequencies and quality scores of tested wheat.

No.	1A	1B	1D	Frequency (%)	Quality score
1	1	7+8	5+10	5.3	3+3+4=10
2	1	7+9	5+10	2.0	3+2+4=9
3	1	7+8	2+12	16.6	3+3+2=8
4	1	7+9	2+12	3.3	3+2+2=7
5	1	7	2+12	0.7	3+2+2=7
6	1	7+8	5+12	8.6	3 + 3+?≥10
7	1	7+9	5+12	2.6	3 + 2+?≥9
8	1	13+16	5+12	0.7	3 + 2+?≥9
9	1	14+15	5+10	0.7	3+3+4=10
10	1	14+15	2+12	2.0	3+3+2=8
11	1	17+18	5+10	0.7	3+3+4=10
12	2*	6+8	2+12	2.6	3+1+2=6
13	2*	7+8	2+12	16.6	3+3+2=8
14	2*	7+9	2+12	9.3	3+2+2=7
15	2*	7	2+12	0.7	3+2+2=7
16	2*	14+15	2+12	2.6	3+3+2=8
17	Null	7+8	5+10	1.3	1+3+4=8
18	Null	7+8	2+12	13.2	1+3+2=6
19	Null	7+9	2+12	6.0	1+2+2=5
20	Null	14+15	2+12	0.7	1+3+2=6
21	Null	7	2+12	0.7	1+2+2=5
22	Null	7+8	5+12	3.3	1 + 3+?≥8

'?' indicates wheat varieties with 5+12 showed better overall quality characteristics than any other *Glu-D1* encoded glutenin subunits (Peña *et al.* 1995).

composition of 1, 7+8 and 5+12; 2.6% genotypes had subunit composition of 1, 7+9 and 5+12; 0.7% genotypes had subunit composition of 1, 13+16 and 5+12; 0.7% genotypes had subunit composition of 1, 14+15 and 5+10 and 0.7% genotypes had subunit composition of 1, 17+18 and 5+10. All the above combinations' quality score with 9 corresponded to good bread-making quality according to the *Glu-1* score of Payne (1987). The high potency of *Glu-D1* over *Glu-A1* and *Glu-B1* in promoting the incorporation of HMW-GSs and LMW-GSs into glutenin macropolymers (GMPs) had also been suggested by prior studies using a new series of deletion mutants lacking one or two of the three *Glu-1* loci (*Glu-A1*, *Glu-B1* and *Glu-D1*) specifying HMW-GSs (Wang *et al.* 2017). Whereas, subunits 2+12 encoded by alleles *Glu-D1a* are considered deleterious for bread-making quality but favourable for biscuit making (Payne *et al.* 1987). In this study, the wheat varieties with a high-quality score do not contain 2+12 subunits (table 2). The x–x and x–y dimers of HMW-GSs were found, but those consisting of solely y-type HMW-GSs to form the backbone of the GMPs by the interchain disulphide bonds were not found (Wieser 2007). It is likely that the number and distribution of cysteine residues differ within the subunits which influence the structure of glutenin polymers (Lindsay *et al.* 2000). Distinguishing from other x-type subunits, 1Dx5 subunit containing an additional cysteine in the central repetitive domain might be the major factor which explains why this gluten subunit is associated

Table 3. Frequency and composition of HMW-GS of wheat varieties in different decades from 1970 to 2010.

		1970s		1980s		1990s		2000s		2010s	
Locus	Subunit	Number	Frequency (%)	Number	Frequency (%)	Number	Frequency (%)	Number	Frequency (%)	Number	Frequency (%)
Glu-A1	1	0	0	5	20.8	8	32.0	35	56.5	17	54.8
	2*	6	66.7	8	33.3	12	48.0	15	24.2	7	22.6
	Null	3	33.3	11	45.8	5	20.0	12	19.4	7	22.6
Glu-B1	6+8	3	33.3	0	0	1	4.0	0	0	0	0
	7	2	22.2	1	4.2	0	0	0	0	0	0
	7+8	3	33.3	16	66.7	11	44.0	46	74.2	22	71.0
	7+9	1	11.1	7	29.2	10	40.0	11	17.7	6	19.4
	14+15	0	0	0	0	2	8.0	4	6.5	3	9.7
	17+18	0	0	0	0	1	4.0	0	0	0	0
	13+16	0	0	0	0	0	0	1	1.6	0	0
Glu-D1	2+12	9	100	20	83.3	19	76.0	46	74.2	19	61.3
	5+10	0	0	1	4.2	3	12.0	6	9.7	5	16.1
	5+12	0	0	3	12.5	3	12.0	10	16.1	7	22.6

with good quality (Ribeiro *et al.* 2013). Further, the high abundance of 1Dx+1Dy in insoluble glutenin preparation (relative to that of 1Bx+1By or 1Ax) is also an important factor for the functional dominance of *Glu-D1* (Wang *et al.* 2017). The results suggest that the majority of the wheat cultivars in Hebei province possess 5+10 or 5+12 subunits in their *Glu-D1* locus and 1 or 2* subunits in the *Glu-A1* locus and consequently relatively higher quality assessment score was found to be one of the key strategies to hold for improved wheat quality in our breeding programmes.

Historical evolution of Glu-1 locus

Our results showed that the frequencies of 1 subunit, 7+8 subunits, 5+10 subunits and 5+12 subunits have increased from 0 to 54.8, 33.3 to 71.0, 0 to 16.1 and 0 to 22.6%, respectively, in Hebei province winter wheat varieties over the last 40 years (table 3). While subunit 2* declined from 66.7 of 1970s entries to 22.6% of 2010 entries, and 2+12 subunits declined from 100 to 61.3% of entries in the same period (table 3). Although subunit 2* declined about 40%, the combined percentages of subunits 2* and 1 increased by 11.8% over the past 40 years. Subunits 2* and 1 have equivalent effects on bread-making quality according to Payne's observation (Payne *et al.* 1987), while subunit 1 appears to have increased in frequency at the expense of subunit 2* which is similar to the situation in American wheat, where subunit 2* declined from 84.2 of 1970–1990 entries to 76.1% of 1991–2005 entries, and subunit 1 increased from 13.4 to 21.2% of entries in the same period (Shan *et al.* 2007). The tendency of variation differences between the subunits 2* and 1 may also contribute to the choice of breeding parents or other functional dominance. Further work is needed to validate this possibility. At the end of the last century, 17+18 subunits, 14+15 subunits and 13+16 at the *Glu-B1* locus began to appear at a low frequency (table 3). The functional dominance was ranked in the order 17+18>15+14>7+8>7+9 subunits based on data on the secondary structure of gluten using a series of near-isogenic lines. This allelic richness for the *Glu-B1* locus is compatible with hybridized among different wheat varieties and can be transferred through standard breeding procedures. The increased frequency of both subunits 5+10 and 5+12 and the reduced frequency of subunits 2+12 are consistent with the important contribution of the *Glu-D1d* and *Glu-D1h* alleles to dough strength and greater attention was paid to end-use quality in the region's wheat breeding programmes.

Acknowledgements

Fund was provided by the National Key Research and Development Programme of China (nos 2016YFD0300407 and 2016YFD0101802). The authors are indebted to Dr Dongcheng Liu (IGDB-CAS, Beijing, China) for advice on methods and interpretation of results.

References

Anjum F. M., Khan M. R., Din A., Saeed M., Pasha I. and Arshad M. U. 2007 Wheat gluten: high molecular weight glutenin subunits - structure, genetics, and relation to dough elasticity. *J. Food Sci.* **72**, 56–63.

Branlard G., Dardevet M., Saccomano R., Lagoutte F. and Gourdon J. 2001 Genetic diversity of wheat storage proteins and bread wheat quality, wheat in a Global Environment: Proceedings of the 6th International Wheat Conference. Springer, The Netherlands.

Branlard G., Dardevet M., Amiour N. and Igrejas G. 2003 Allelic diversity of HMW and LMW glutenin subunits and omega-gliadins in French bread wheat (*Triticum aestivum* L.). *Genet. Resour. Crop Evol.* **50**, 669–679.

Caballero L., Martin L. M. and Alvarez J. B. 2004 Intra- and interpopulation diversity for HMW glutenin subunits in Spanish spelt wheat. *Genet. Resour. Crop. Evol.* **51**, 175–181.

Cao J. M., Zhou A. D., Li D., Huang T. R., Gao Y. H., Zhang X. Z. *et al.* 2009 Analysis of genetic diversity of HMW-GS in wheat varieties and strains of Xinjiang. *Xinjiang Agric. Sci.* **46**, 1192–1197.

Dong Z. Y., Yang Y. S., Li Y. W., Zhang K. P., Lou H. J., An X. L. *et al.* 2013 Haplotype variation of *Glu-D1* locus and the origin of *Glu-D1d* allele conferring superior end-use qualities in common wheat. *PLoS ONE* **8**, e74859.

Dong Z. Y., Yang Y. S., Zhang K. P., Li Y. W., Wang J. J., Wang Z. J. *et al.* 2017 Development of a new set of molecular markers for examining *Glu-A1* variants in common wheat and ancestral species. *PLoS ONE* **12**, e0180766.

Figueroa J. D. D., Peña R. J., Maucher T. and Khan K. 2011 Kernel elastic properties and sedimentation: influence of high and low molecular weight glutenin allelic composition. *Cereal Chem.* **88**, 41–44.

Gale K. R. 2005 Diagnostic DNA markers for quality traits in wheat. *J. Cereal Sci.* **41**, 181–192.

Gu Y. Q., Coleman-Derr D., Kong X. Y. and Anderson O. D. 2004 Rapid genome evolution revealed by comparative sequence analysis of orthologous regions from four triticeae genomes. *Plant Physiol.* **135**, 459–470.

Hao C. Y., Shang X. W. and Zhang H. Q. 2004 Composition of high molecular weight glutenin subunits of spring wheat varieties in Gansu Province. *J. Plant Genet. Res.* **5**, 38–42.

Henkrar F., El-Haddoury J., Iraqi D., Bendaou N. and Udupa S. M. 2017 Allelic variation at high-molecular weight and low-molecular weight glutenin subunit genes in Moroccan bread wheat and durum wheat cultivars. *3 Biotech.* **7**, 287–296.

Hua C., Ikeda T., Wang H. F., Takata K., Zhang Y. F., Yanaka M. *et al.* 2009 Genetic diversity of high molecular weight glutenin subunit (HMW-GS) composition in common wheat landraces from Xinjiang, China. *J. Agric. Biotechnol.* **17**, 1070–1074.

Izadi-Darbandi A., Yazdi-Samadi B., Shanejat-Boushehri A.-A. and Mohammadi M. 2010 Allelic variations in *Glu-1* and *Glu-3* loci of historical and modern Iranian bread wheat (*Triticum aestivum* L.) cultivars. *J. Genet.* **89**, 193–199.

Jiang Q. T., Ma J., Wei Y. M., Liu Y. X., Lan X. J., Dai S. F. *et al.* 2012 Novel variants of HMW glutenin subunits from *Aegilops* section *Sitopsis* species in relation to evolution and wheat breeding. *BMC Plant Biol.* **12**, 73–85.

Lawrence G. J., MacRitchie F. and Wrigley C. W. 1988 Dough and baking quality of wheat lines deficient in glutenin subunits

controlled by the *Glu-A1*, *Glu-B1* and *Glu-D1* loci. *J. Cereal Sci.* **7**, 109–112.
Lerner S. E., Kolman M. A. and Rogers W. J. 2009 Quality and endosperm storage protein variation in Argentinean grown bread wheat. I. Allelic diversity and discrimination between cultivars. *J. Cereal Sci.* **49**, 337–345.
Li W., Wan Y., Liu Z., Liu K., Liu X., Li B. *et al.* 2004 Molecular characterization of HMW glutenin subunit allele *1Bx14*: further insights into the evolution of *Glu-B1-1* alleles in wheat and related species. *Theor. Appl. Genet.* **109**, 1093–1104.
Liang W., Yuan M. P., Jun X. H., Li L., Hu H. Z., Chun X. X. *et al.* 2008 Compositions of HMW-GS in wheat varieties and advanced lines from Xinjiang. *J. Triticeae Crops* **28**, 430–435.
Lindsay M. P., Tamas L., Appels R. and Skerritt J. H. 2000 Direct evidence that the number and location of cysteine residues affect glutenin polymer structure. *J. Cereal Sci.* **31**, 321–333.
Liu F. Y., Huang S. Q., Zhang D. L., Li Y. G. and Li S. P. 2007 Composition analysis of high molecular weight glutenin subunit from some good quality wheat varieties in China. *J. Yangzhou Univ.* **28**, 47–51.
Liu Y., He G. Y., Li T. E., Chen M. J., He Y. G. and Shewry P. R. 2004 Analysis of high-molecular-weight glutenin subunit compositions from Hubei commercial hexaploid wheat (*Triticum aestivum* L.) cultivars. *J. Wuhan Bot. Res.* **22**, 105–110.
Luo C., Griffin W. B., Branlard G. and McNeil D. L. 2001 Comparison of low- and high molecular-weight wheat glutenin allele effects on flour quality. *Theor. Appl. Genet.* **102**, 1088–1098.
Payne P. I. 1987 Genetics of wheat storage proteins and the effect of allelic variation on breadmaking quality. *Plant Physiol.* **38**, 141–153.
Payne P. I., Law C. N. and Mudd E. E. 1980 Control by homoeologous group 1 chromosomes of the high-molecular-weight subunits of glutenin, a major protein of wheat endosperm. *Theor. Appl. Genet.* **58**, 113–120.
Payne P. I., Holt L. M., Hutchinson J. and Bennett M. D. 1984 Development and characterisation of a line of bread wheat, *Triticum aestivum*, which lacks the short-arm satellite of chromosome 1B and the Gli-B1 locus. *Theor. Appl. Genet.* **68**, 327–334.
Payne P. I., Nightingale M. A., Krattiger A. F. and Holt L. M. 1987 The relationship between HMW glutenin subunit composition and the bread-making quality of British-grown wheat varieties. *J. Sci. Food Agric.* **40**, 51–65.
Payne P. I., Holt L. M., Krattiger A. F. and Carrillo J. M. 1988 Relationships between seed quality characteristics and HMW glutenin subunit composition determined using wheats grown in Spain. *J. Cereal Sci.* **7**, 229–235.
Peña R. J., Zarco-Hernandez J. and Mujeeb-Kazi A. 1995 Glutenin subunit compositions and breadmaking quality characteristics of synthetic hexaploid wheats derived from *Triticum turgidum* × *Triticum tauschii* (coss.) Schmal crosses. *J. Cereal Sci.* **21**, 15–23.
Rasheed A., Safdar T., Gul-Kazi A., Mahmood T., Akram Z. and Mujeeb-Kazi A. 2012 Characterization of HMW-GS and evaluation of their diversity in morphologically elite synthetic hexaploid wheats. *Breed Sci.* **62**, 365–370.
Ribeiro M., Bancel E., Faye A., Dardevet M., Ravel C., Branlard G. *et al.* 2013 Proteogenomic characterization of novel x-type high molecular weight glutenin subunit 1Ax1.1. *Int. J. Mol. Sci.* **14**, 5650–5667.
Shan X., Clayshulte S. R., Haley S. and Byrne P. 2007 Variation for glutenin and waxy alleles in the US hard winter wheat germplasm. *J. Cereal Sci.* **45**, 199–208.
Shewry P. R. 2009 Wheat. *J. Exp. Bot.* **60**, 1537–1553.
Shewry P. R. and Halford N. G. 2002 Cereal seed storage proteins: structures, properties and role in grain utilization. *J. Exp. Bot.* **53**, 947–958.
Shewry P. R., Tatham A. S., Forde J., Kreis M. and Miflin B. J. 1986 The classification and nomenclature of wheat gluten proteins: a reassessment. *J. Cereal Sci.* **4**, 97–106.
Song J. M., Liu A. F., Jiang G. H., Li H. S., Liu J. J. and Zhao Z. D. 2006 Comparison of allelic variations at high-molecular-weight glutenin subunit loci in wheat cultivars released in different periods in China. *J. Agric. Sci.* **14**, 728–735.
Uthayakumaran S., Beasley H. L., Stoddard F. L., Keentok M., Phan-Thien N., Tanner R. I. *et al.* 2002 Synergistic and additive effects of three high molecular weight glutenin subunit loci. I. Effects on wheat dough rheology. *Cereal Chem. J.* **79**, 294–300.
Wang Z. J., Li Y. W., Yang Y. S., Liu X., Qin H. J., Dong Z. Y. *et al.* 2017 New insight into the function of wheat glutenin proteins as investigated with two series of genetic mutants. *Sci. Rep.* **7**, 3428–3441.
Wieser H. 2007 Chemistry of gluten proteins. *Food Microbiol.* **24**, 115–119.
Wieser H. and Zimmermann G. 2000 Importance of amounts and proportions of high molecular weight subunits of glutenin for wheat quality. *Eur. Food Res. Technol.* **210**, 324–330.
Yang Y. S., Li S. M., Zhang K. P., Dong Z. Y., Li Y. W., An X. L. *et al.* 2014 Efficient isolation of ion beam-induced mutants for homoeologous loci in common wheat and comparison of the contributions of *Glu-1* loci to gluten functionality. *Theor. Appl. Genet.* **127**, 359–372.
Zhang S., Li P., Geng G., Zhang Q. and Yang J. 2008 Composition analysis of high molecular weight subunits of glutenin of the progenies of wheat wide hybridization. *Acta Agric. Boreali-Occident. Sin.* **17**, 62–65.

Corresponding editor: Manoj Prasad