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Research Article

High-Molecular-Weight Glutenin 1Bx17 and 1By18 Subunits Encoded by *Glu-B1i* Enhance Rheological Properties and Breadmaking Quality of Wheat Dough

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The elasticity of wheat dough is mainly determined by high-molecular-weight glutenin subunits (HMW-GSs) encoded by *Glu-1* loci. In this study, we performed the first comprehensive study on the effects of *Glu-B1i*-encoded 1Bx17 and 1By18 subunits on dough rheological properties and breadmaking quality by using a pair of *Glu-B1* near-isogenic lines (NILs) ZM-NIL1 and ZM-NIL2. Comparative analysis of basic quality parameters, rapid visco analyzer (RVA) and farinograph parameters, and C-cell and loaf parameters showed that ZM-NIL2 containing *Glu-B1i*-encoded 1Bx17 and 1By18 subunits had better dough rheological properties and breadmaking quality than ZM-NIL1 carrying *Glu-B1c*-encoded 1Bx7 and 1By9 subunits, including significantly increased protein and gluten content, development time and stability, and loaf volume and score. Particularly, 1Bx17 and 1By18 subunits could significantly enhance bread texture, including significant increase in slice brightness, slice area, circumference, cell contrast, cell extension, and cell quantity. These results demonstrate that 1Bx17 and 1By18 subunits have a significant contribution to dough rheological properties and breadmaking quality.

1. Introduction

Wheat (*Triticum aestivum* L.) is one of the three main agricultural crops in the world, and it acts as the main source of proteins and satisfies the energy needs of huge amount of the world's population. Wheat flour can be used to make a variety of food products such as various breads, noodles, and cookies. Wheat quality is mainly determined by storage protein composition and content. The major storage proteins in wheat endosperm, occupying 85% of total grain protein, consist of glutenins and gliadins that are synthesized and accumulated during seed development. Glutenins and gliadins are the major determinant factors of the viscoelasticity and extensibility of dough, respectively [1, 2]. Glutenins are divided into high- and low-molecular-weight glutenin subunits (HMW-GSs and LMW-GSs) based on their molecular weights. Although HMW-GSs only account for about 10% in wheat grain proteins, they play important roles in dough strength and breadmaking quality. HMW-GS and LMW-GS as well as gliadins are linked into polymers by intermolecular disulfide bonds and form the largest protein molecule glutenin macropolymers (GMPs) in the stage of endosperm development, significantly affecting the rheological properties of wheat dough [2].

HMW-GSs are encoded by genes at the orthologous *Glu-1* loci on the long arms of chromosomes 1A (*Glu-A1*), 1B (*Glu-B1*), and 1D (*Glu-D1*) [1]. Each locus possesses two paralogous genes encoding one larger x-type subunit (80–88 kDa) and one smaller y-type subunit (67–73 kDa), respectively [3]. Although common hexaploid wheat can express 6 HMW-GSs (1Ax, 1Ay, 1Bx, 1By, 1Dx, and 1Dy) in theory, only 3–5 genes express in the individual genotypes due to gene silencing. The 1Bx, 1Dx, and 1Dy genes generally have expression activity while the 1Ay and 1By genes remain silent occasionally, especially the 1Ay gene [4]. The allelic variations at *Glu-1* are closely related to dough quality [5, 6].

Particularly, some subunits confer superior breadmaking quality such as 1Dx5 + 1Dy10 (*Glu-D1d*) and 1Ax1 (*Glu-A1a*), whereas some others are highly related to poor end use properties such as 1Dx2 + 1Dy12 (*Glu-D1a*) and 1Bx20 (*Glu-B1e*) [5, 7].

Molecular characterization showed that a HMW-GS comprises three distinct domains: a central large repetitive domain flanked by short N- and C-terminal nonrepetitive domains [8]. The 1Bx17 and 1By18 subunit genes were firstly cloned and characterized by Reddy and Appels [9] and Liang et al. [10], respectively. 1Bx17 and 1Bx7 genes aligned perfectly except for two amino acid substitutions and a 36-codon deletion in the repetitive domain that results in the loss of a block of three hexapeptide and two nonapeptide repeats [9]. Meanwhile, 1By18 gene containing 2163 bp is highly identical to *1By8*, with only three single-nucleotide polymorphism (SNP) variations at 231, 233, and 1976 sites of the coding sequence. The deduced amino acid sequence of 1By18 only exhibited two amino acid substitutions at positions 78 (Leu-Pro) and 684 (Gly-Glu), respectively, compared to 1By8. 1By18 and 1By8 as well as 1Bx7 and 1Bx17 also displayed the closest phylogenetic relationships among *Glu-B1* genes. Thus, *Glu-B1i* allele could have originated from *Glu-B1b*, which might emerge after the formation of modern hexaploid wheat [10].

Quality analysis with tensile apparatus showed that 1Bx17 + 1By18 subunits are better than 1Bx7 + 1By8 subunits in the dough extensibility [11]. The results from the improved lines Kehan 9 and Kefeng 3 containing 1Bx17 + 1By18 subunits showed higher total gluten content and gluten index than those of the original varieties with 1Bx7 + 1By9 or 1Bx7 + 1By8 subunits [12]. Analysis of the formation time and gluten strength index from 251 varieties and high-generation strains of China, CIMMYT, and Australia found that the quality effects of *Glu-B1* locus were ranked as 1Bx14 + 1By15 > 1Bx7 + 1By8 > 1Bx17 + 1By18 > 1Bx7 + 1By9 = 1Bx20 > 1Bx6 + 1By8 [13]. However, these studies only involved a few of quality parameter analyses by using different wheat varieties and lines, and the effects of *Glu-B1i* among *Glu-B1* alleles on multiple quality parameters, particularly on bread interior structures and loaf quality, are still unknown.

In this work, we used a pair of *Glu-B1* near-isogenic lines (NILs) recently developed in our group and performed a comprehensive study on the effects of *Glu-B1i* on dough rheological properties and breadmaking quality. Particularly, we focused on the changes of dough rapid visco analyzer (RVA), farinograph, and C-cell parameters and loaf score in the *Glu-B1* NILs, which reflect dough rheological properties, loaf interior structures, and breadmaking quality. Our results provided new evidence for further understanding the functional properties of 1Bx17 + 1By18 subunits involved in wheat processing quality formation.

2. Materials and Methods

2.1. Plant Materials and Field Trial. The experimental materials used in this study included a pair of *Glu-B1* near-isogenic lines ZM-NIL1 (1Ax1, 1Bx7 + 1By9, and 1Dx2 + 1Dy12) with *Glu-B1c* allele and ZM-NIL2 (1Ax1, 1Bx17 + 1By18, and 1Dx2 + 1Dy12) with *Glu-B1i* allele, which were developed in our group through crossing between Chinese winter bread wheat cultivar Zhongmai 8601 (1Ax1, 1Bx7 + 1By9, and 1Dx2 + 1Dy12) and spring wheat variety CB037A (1Ax1, 1Bx17 + 1By18, and 1Dx2 + 1Dy12) and consecutive backcross combining with section and identification. Both ZM-NIL1 and ZM-NIL2 were planted in the experimental fields of the China Agricultural University, Beijing, during the 2016-2017 wheat growing season. Field experiments were performed in randomized block design with three biological replicates (each plot with 20 m^2). The cultivation and management were same as local field cultivation conditions.

2.2. Agronomic Traits Measurement. The main agronomic traits from three biological replicates were measured, including plant height, ear length, tiller number per plant, number of fertile spikelets per spike, spikelet number per spike, grain number per spike, and 1000-grain weight.

2.3. HMW-GS Extraction and SDS-PAGE. HMW-GSs were extracted according to the previous report [14]. The albumins, globulins, and gliadins were firstly extracted and excluded from 15 mg seeds by using 75 μL distilled water, 75 μL dilute salt solutions, and 120 μL 30% ethanol, respectively. Then, glutenins were extracted by using the commonly used glutenin extraction buffer (50% isopropanol and 80 μL Tris-HCl, pH 8.0) with 64.83 μL dithiothreitol (DTT) and 1.4% 4-vinylpyridine (v/v). Sodium dodecyl sulfate-polyacrylamide gel electrophoresis (SDS-PAGE) was performed with Bio-Rad PRO-TEAN II XL equipment in 12% gel and electrophoresed at 15 mA for 2 h based on the previously described method [15].

2.4. Quality Testing. Grain quality parameters tested from three biological replicates included ash content, protein and gluten content, grain hardness, water absorption, rapid visco analyzer (RVA) parameters, farinograph parameters, C-cell parameters related to bread inner structures, loaf volume, and appearance score. Student's *t* test was used for data evaluation [16]. The quality parameters were tested according to Sun et al. [17] with minor modifications. Grain hardness was measured using Perten Single Kernel Characterization System (SKCS) 4100 (Perten Instrument North American Inc., Spring-field, IL, USA) according to the AACC approved method 55-31. Flour moisture and ash contents (% dry basis) were determined according to the AACC (2000) 44-15A and 08-02, respectively. The flour protein content was determined by the NIR product analyzer (Instalab 610, NIR Product Analyzer, Dickey-john Co. Ltd, USA) according to the method of AACC 39-10A. The RVA profile was obtained using the AACC (2000) 76-21 with a RVA (Newport Scientific Series 3). The AACC (2000) 54-21 and 54-10 were followed to obtain farinograph parameters (10 g Brabender Farinograph-E) and tensile tester (Brabender Co. Ltd, Germany). Breadbaking and evaluation

were performed based on the AACC 10-10B method according to the previous report [18]. Image analysis of crumb bread was performed using C-cell image analysis software and equipment (Calibre Control International Ltd.; Warrington) based on the established method [19].

3. Results

3.1. Characterization of Two Glu-B1 Near-Isogenic Lines. The main agronomic trait analysis showed that two *Glu-B1* near-isogenic lines ZM-NIL1 and ZM-NIL2 had clear phenotypic differences (Figures 1(a)–1(c)). Compared with ZM-NIL1, plant height and 1000-grain weight of ZM-NIL2 significantly increased, whereas its tiller number per plant, number of fertile spikelets per spike, and grain number per spike significantly reduced. Ear length and spikelet number per spike had no significant differences in both NILs (Table 1). SDS-PAGE analysis of glutenin proteins showed that both ZM-NIL1 and ZM-NIL2 had the same *Glu-A1a*-encoded 1Ax1 and *Glu-D1a*-encoded 1Dx2 + 1Dy12 subunits but contained different subunit compositions at *Glu-B1* locus: *Glu-B1c*-encoded 1Bx7 + 1By9 subunits in ZM-NIL1 and *Glu-B1i*-encoded 1Bx17 + 1By18 in ZM-NIL1. Both NILs had similar LMW-GS compositions at *Glu-3* loci (Figure 1(d)). These results indicated that ZM-NIL1 and ZM-NIL2 are a pair of typical *Glu-B1* near-isogenic lines. According to the studies so far, *Glu-1* loci appear to have no significant effects on the agronomic traits, and the agronomic differences between ZM-NIL1 and ZM-NIL2 may result from other gene loci closely related to the genomic regions containing *Glu-B1* locus.

3.2. Effects of 1Bx17 and 1By18 Subunits on Basic Quality Parameters and Dough Rheological Properties. The basic quality parameters contain protein content, moisture content, ash content, total gluten content, gluten index, and grain hardness. The results showed that ZM-NIL2 with *Glu-B1i* had a significant increase in the protein content, ash content, and total gluten content and a prominent decline in hardness compared to ZM-NIL1 with *Glu-B1c*. Both NILs had no significant differences in moisture content (Table 2). The protein content and total gluten content are closely related to the bread quality. In general, the higher the protein content, the stronger the flour's tendency, and the more suitable it is to make bread. Our results indicated that the contribution of HMW-GSs 1Bx17 + 1By18 to bread quality is greater than 1Bx7 + 1By9 subunits.

The RVA parameters include falling number, peak viscosity, final viscosity, and setback, which are closely associated with starch pasting properties and starch dispersions during heating/stirring and cooling/stirring. The results showed that the peak viscosity, final viscosity, and setback in ZM-NIL2 increased significantly while falling number had no clear changes. Analysis of farinograph parameters including thickness, water absorption, development time, stability, and softening degree showed that ZM-NIL2 had a significant increase in water absorption, developmental time, and stability time and a clear decline in softening degree while thickness had no significant difference compared with ZM-NIL1 (Table 2). These parameters revealed that 1Bx17 + 1By18 subunits have superior dough rheological properties than 1Bx7 + 1By9 subunits.

3.3. Effects of 1Bx17 and 1By18 Subunits on Breadmaking Quality. C-cell image and parameter analyses were performed to evaluate the inner structural features of the bread slices in ZM-NIL1 and ZM-NIL2, including slice brightness, slice area, circumference, attenuation ratio, cell contrast, volume of course cell, cell extension, cell diameter, cell quantity, cell density, and wall thickness (Table 3 and Figure 2(a)). The results showed that, except for attenuation ratio, cell diameter and wall thickness without clear changes and volume of course cell with 16.73% decrease and the other C-cell parameters in ZM-NIL2 were significantly higher than those in ZM-NIL1. Particularly, slice area, cell contrast, and cell quantity increased by 8.38%, 5.80%, and 16.72%, respectively. These results indicated that 1Bx17 + 1By18 subunits confer superior bread inner structures mainly by promoting cell quantity and slice area (Table 3).

Loaf parameters according to the evaluation standard of wheat flour bread baking quality in China (GB/T16411-2008) showed that loaf volume of ZM-NIL2 was up to 804 mL^3, increasing 10.13% compared to ZM-NIL1 with 730 mL^3 (Table 3 and Figure 2(b)). Ultimately, the loaf score of ZM-NIL2 was 51, significantly higher than ZM-NIL1 (44). The results demonstrated that 1Bx17 + 1By18 subunit can significantly improve loaf volume and score.

4. Discussion

Dough rheological properties and breadmaking quality are closely associated with grain protein content and composition [1]. HMW-GS and LMW-GS as well as gliadins are crosslinked to form GMPs by disulfide bonds, which determine the viscoelasticity of the dough [2, 20]. To some extent, high grain protein and gluten content enhances GMP formation, resulting in superior dough quality [21, 22]. Ash is the mass ratio of inorganic impurities after burning of wheat grains to precombustion. Studies found that protein and ash content and gluten index in wheat grain and flour are positively related to gluten content and strength [22–24]. A moderate increase in protein content was accompanied by a marked increase in maximum consistency and gluten index [25]. Our recent study showed that high-nitrogen fertilizer application and water-deficit treatment could significantly promote grain protein and gluten content, leading to the significant improvement of dough rheological properties and breadmaking quality [16, 19]. The results from this study indicated that the presence of 1Bx17 and 1By18 subunits could significantly increase ash, grain protein, and gluten content, leading to superior dough strength and breadmaking quality (Tables 2 and 3).

Compared to 1Bx7 + 1By9, 1Bx17 + 1By18 subunits also enhance RVA and farinograph parameters and dough rheological properties, including significantly

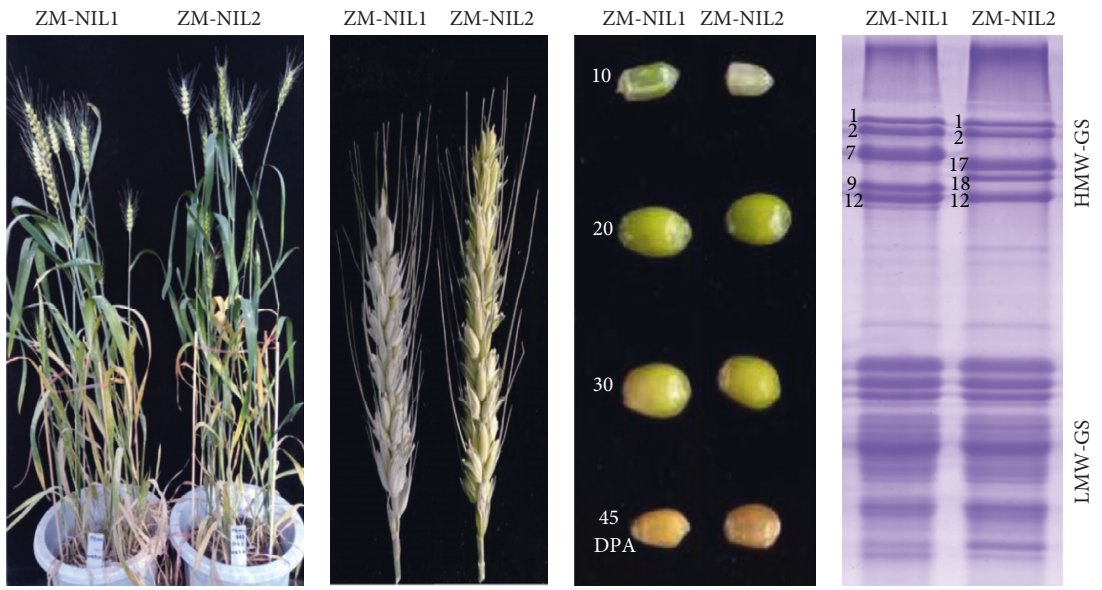

Figure 1: Comparison of growth and development characteristics and glutenin proteins between *Glu-B1* near-isogenic lines ZM-NIL1 and ZM-NIL2. (a) Plant phenotypes. (b) Spike morphology. (c) Grain morphological changes at 10, 20, 30, and 45 days after anthesis (DPA). (d) Seed glutenin subunits identified by SDS-PAGE.

Table 1: Comparison of main agronomic traits and HMW-GS compositions between *Glu-B1* near-isogenic lines ZM-NIL1 and ZM-NIL2.

Glu-B1 NILs	Plant height (cm)	Ear length (cm)	Tiller number per plant	Number of fertile spikelets per spike	Spikelet number per spike	Grain number per spike	1000-grain weight (g)	HMW-GS
ZM-NIL1	72.25 ± 3.03	12.68 ± 0.55	2.38 ± 0.52	12.63 ± 0.74	17.87 ± 0.74	25.22 ± 1.48	42.63 ± 0.30	1, 7 + 9, 2 + 12
ZM-NIL2	80.14 ± 3.63**	12.11 ± 0.45	1.75 ± 0.46**	10.33 ± 0.52**	17.00 ± 0.82	18.80 ± 2.04**	44.13 ± 0.11**	1, 17 + 18, 2 + 12

*Significant at 5%. **Significant at 1%.

increased dough viscosity and setback value, water absorption, development time, and stability as well as significantly decreased softing degree (Table 2). Ultimately, the improved dough rheological properties resulted in significant promotion of bread texture, loaf volume, and score. Particularly, ZM-NIL2 containing 1Bx17 + 1By18 subunits showed significant increase in slice brightness, slice area, circumference, cell extension, cell contrast, and cell quantity and significant decrease in volume of course cell (Table 3). Studies found that some C-cell parameters such as slice brightness, slice area, cell contrast, cell quantity, and elongation are positive to bread texture while the others such as volume of course cell, cell diameter, and wall thickness have negative effects on bread quality [26]. Our results demonstrated that 1Bx17 + 1By18 subunits improve bread texture, loaf volume, and score mainly by promoting slice area, cell contrast, and cell quantity.

Among the world wheat cultivars, especially in Chinese wheat varieties, 1Bx17 + 1By18 subunits occurred in a lower frequency while 1Bx7 + 1By8 and 1Bx7 + 1By9 are frequently present [10]. 1Bx17 and 1Bx7 subunits and 1By18 and 1By8 subunits have similar sequence structures and close phylogenetic relationships, suggesting that *Glu-B1i* allele could originate from *Glu-B1b* through SNP and insertion/deletion variations [9, 10]. Allelic variation and quality analysis showed that 1Bx7 + 1By8 are better than 1Bx17 + 1By18 [13]. The overexpression of 1Bx7 subunit ($1Bx7^{OE}$) also has a positive effect on gluten strength [27, 28]. The results from protein expression, purification, and mixing property analysis confirmed that 1By8 subunit had more contributions to dough strength than 1Bx7 and 1By9 [29, 30]. In addition, the higher β-sheet content has advantage to dough rheological properties. At the *Glu-B1* locus, the β-sheet content in the HMW-GS was ranked as 1Bx17 + 1By18 > 1Bx14 + 1By15 > 1Bx7 + 1By9 > 1Bx7 + 1By8 > 1Bx6 + 1By8 [31]. Thus, 1Bx17 + 1By18 subunits have important contributions to dough rheological properties and breadmaking quality.

5. Conclusion

Analysis of a pair of *Glu-B1* near-isogenic lines revealed that *Glu-B1i*-encoded 1Bx17 + 1By18 subunits significantly enhanced dough rheological properties, including significantly increased grain protein and gluten content and improved

Table 2: Comparison of main quality parameters between *Glu-B1* near-isogenic lines ZM-NIL1 and ZM-NIL2.

Materials	Basic quality parameters							
	Protein content	Moisture content (%)	Ash content (%)	Gluten index (%)	Total gluten content (%)	Hardness	Falling number	
ZM-NIL1	17.10 ± 0.10	15.08 ± 0.14	0.66 ± 0.02	66.79 ± 0.92	4.13 ± 0.05	99.00 ± 14.00	329.00 ± 10.00	
ZM-NIL2	18.88 ± 0.20**	15.08 ± 0.10	0.69 ± 0.01*	72.12 ± 5.27**	4.85 ± 0.05**	77.00 ± 13.00**	331.00 ± 11.00	
Materials	RVA parameters				Farinograph parameters			
	Peak viscosity	Final viscosity	Setback	Thickness	Water absorption (%)	Development time (min)	Stability time (min)	Softening degree
ZM-NIL1	1936.50 ± 67.00	2171.00 ± 90.00	1045.50 ± 99.00	499.00 ± 6.00	60.00 ± 0.20	4.00 ± 0.60	3.70 ± 0.00	317.00 ± 5.00
ZM-NIL2	2192.50 ± 95.00**	2399.00 ± 56.00**	1092.50 ± 39.00*	483.00 ± 13.00	67.45 ± 0.05**	4.50 ± 0.60**	5.35 ± 0.25*	290.00 ± 18.00**

*Significant at 5%. **Significant at 1%.

Table 3: Comparison of main quality parameters between *Glu-B1* near-isogenic lines ZM-NIL1 and ZM-NIL2.

Materials	C-cell parameters						
	Slice brightness	Slice area (px)	Circumference (px)	Attenuation ratio	Cell contrast	Volume of course cell	Cell extension
ZM-NIL1	134.65 ± 1.55	260935.50 ± 4151.50	1928.50 ± 12.50	64.04 ± 2.41	0.69 ± 0.01	14.94 ± 0.47	1.50 ± 0.01
ZM-NIL2	141.05 ± 1.15*	282801.50 ± 2863.50**	1996.5 ± 13.50*	65.72 ± 2.03	0.73 ± 0.01**	12.44 ± 0.45**	1.56 ± 0.01*

Materials	C-cell parameters			Loaf parameters		
	Cell diameter (px)	Cell quantity	Wall thickness (px)	Loaf volume (m^3)	Inner structures	Loaf score
ZM-NIL1	18.56 ± 0.23	2308.50 ± 23.50	3.56 ± 0.03	730.00 ± 20.00	9 ± 0.03	44 ± 0.21
ZM-NIL2	18.09 ± 0.38	2694.50 ± 67.50**	3.49 ± 0.05	804.00 ± 14.00**	9 ± 0.01	51 ± 0.34**

*Significant at 5%. **Significant at 1%.

Figure 2: The C-cell (a) and loaf baking images (b) of *Glu-B1* near-isogenic lines ZM-NIL1 and ZM-NIL2.

RVA and farinograph parameters. These properties improved bread texture and appearance, including significantly increased slice brightness, slice area, circumference, cell contrast, cell extension, cell quantity, loaf volume, and score, resulting in superior breadmaking quality. These results demonstrated that 1Bx17 + 1By18 subunits confer better

breadmaking quality mainly by promoting slice area, cell quantity and contrast, and loaf volume.

Data Availability

The data used to support the findings of this study are available from the corresponding author upon request.

Conflicts of Interest

The authors declare that they have no conflicts of interest.

Authors' Contributions

Haoyu Guo and Jisu Wu contributed equally to this work.

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