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Functions and Composition Variations of Wheat Glutenin Proteins in Steamed Bread and Noodles

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Abstract

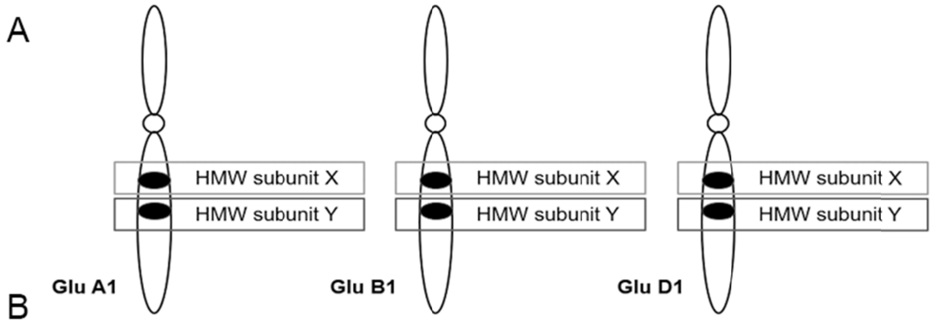
As a major food crop, wheat offers indispensable energy and nutrients to humans worldwide. With the living standards rising, the demand of high-quality wheat increases sharply. Wheat gluten proteins (glutenins and gliadins) are important components of seed storage proteins that affect the elasticity, strength or viscosity of dough. In this review, we summarize the composition of glutenin subunits in wheat grain and analyze the impact of glutenin on the traditional Chinese foods: steamed bread and noodles. Furthermore, we summarize the molecular markers used for wheat quality breeding. The advent of the recent wheat genomic will speed up the identification and quality breeding of novel glutenins.

Keywords: wheat, glutenins, food quality, traditional Chinese foods

1. The Composition of the Glutenin Subunits in Wheat Grain

Hexaploid wheat (*Triticum aestivum* L.), one of the most widely cultivated crops, provides about 20% calories and proteins to human daily diets (Wang et al., 2020). With the increasing world population, food production need to increase by at least 50% by 2050 to meet the huge consumption (FAO, 2017). Meanwhile, because of rising living standards, more and more healthy foods with good qualities are demanded. Thus, substantial efforts were needed for improving the yield of good-quality wheats. Wheat quality mainly refers to the end-use value of flour, which depends on the properties of seed storage proteins (SSPs), such as the content and composition of gluten proteins (Gao et al., 2021; Rasheed et al., 2014; Wang et al., 2020).

Wheat glutenin is a complex mixture, which can be divided into HMW-GSs (70000-90000 Da) and LMW-GSs (20000-45000 Da), accounting for ~13% and ~20% of SSPs, respectively (Ma et al., 2019). There are three general domains in glutenin protein, including a β-reverse turn and two terminal α-helix domains. More β-reverse turn structures are considered to be beneficial for wheat flour quality (Ma et al., 2019; Patil et al., 2015; Tilley et al., 2001). HMW-GSs could explain up to 70% of the genetic variations in dough processing quality, but only makes up about 10% of gluten proteins (Liu et al., 2005). Six HMW-GS genes are located on the long arms of homoeologous chromosomes 1A, 1B and 1D, and each locus has two tightly linked genes that encodes X-and Y-type subunits, namely, *TaGlu-1Ax*, *TaGlu-1Ay*, *TaGlu-1Bx*, *TaGlu-1By*, *TaGlu-1Dx*, and *TaGlu-1Dy* (Galili & Feldman, 1985) (Figure 1). Due to gene silencing, there are always three to five HMW-GSs in hexaploid wheat (Payne et al., 1981), but in some wild wheat lines diploid (AA) and tetraploid (AABB) 1Ay subunit could express (Hu et al. 2008; Xu et al. 2009).



B

Glu-1	Subunit	Gross protein content	Sedimentation	Water absorption	Wet gluten content	Stability time	Variety number
Glu-D1	5+10	12. 07a	40. 02a	60. 6a	31. 7a	5. 36B	9
	2+12	12. 78a	32. 4a	62. 19a	34. 28a	2. 85A	20
	5+12	12. 3	25. 8	58. 6	32. 1	2. 4	1
Glu-B1	17+18	12. 43a	34. 13a	60. 97a	33. 87a	3. 87a	3
	14+15	13. 85a	28. 15a	63. 4a	35. 35a	1. 75a	2
	7+8	12. 49a	33. 37a	62. 36a	34. 07a	3. 19a	17
	7+9	12. 23a	35. 73a	58. 81a	30. 88a	4. 22a	6
	7+8 7+9	12. 55a	46. 7a	62. 75a	33. 25a	5. 85a	2
Glu-A1	N	12. 39a	30. 48a	61. 09a	34. 87a	2. 99a	17
	1	12. 39a	42. 93b	63. 99a	35. 07a	4. 83b	12
	2*	14. 3	31. 9	62. 2	39. 9	3. 9	1

Figure 1. The composition of HMW-GSs. (A) The subunits are split up into three groups: 1A, 1B and 1D; (B) Effect of loci Glu-1 on quality characters (Yang et al., 2003)

LMW-GSs account for about 60% of the wheat glutenin and are encoded by *TaGlu-3* loci on the short arm of homoeologous chromosomes 3A, 3B and 3D (Lee et al., 2016; Lindsay & Skerritt, 1999). LMW-GS is divided into three-type subunits including LMW-i, LMW-m and LMW-s based on the first amino acid residues of the mature proteins (Clarke et al., 2003; Cloutier et al., 2001). LMW-GS could form intermolecular and intramolecular disulphide bonds because of the eight conserved cysteine residues (Shewry & Halford, 2002). Previous studies have found that cysteine residues for intermolecular disulphide bonds display an important role in the quality of gluten proteins and are significantly correlated with the properties of dough (Dong et al., 2013; Herpen et al., 2008; Ram et al., 2006).

2. Wheat Glutenin Variations and Their Roles in Dough Quality

Variations in amount and composition of wheat gluten account for some variation in properties of dough. In hexaploid wheat, the *Glu-A1* locus has been found to have three different subunits, including 1, 2* and Null, which reported that Ax1 and Ax2* were associated to good bread making quality, while AxNull was responsible for poor quality (Kocourkova et al., 2008; Payne, 1987). Rogers et al. (1997) found that 1Ay subunit from diploid *T. boeoticum* Boiss. ssp. *thaoudar* could increase the gluten strength of hexaploidy wheat. *Glu-B1* exhibits the richest variation in 1Bx + 1By subunit pairs of hexaploid wheat, such as 1Bx7, 1Bx7 + 1By8, 1Bx7 + 1By9, 1Bx6 + 1By8, 1Bx13 + 1By16, 1Bx13 + 1By19, 1Bx14 + 1By15, 1Bx17 + 1By18, 1Bx20 and 1By20 (Anjum et al., 2007). 1Bx7 + 1By8, 1Bx7 + 1By9, 1Bx13 + 1By16, 1Bx17 + 1By18 and 1By20 are more common variation types of HMW-GSs at *Glu-B1* locus (Hu, 2003). Compared to hexaploid wheat, there were more variations in tetraploid at *Glu-B1* locus, and 1Bx6 + 1By8 was the most frequent allele in *Triticum spelta* (Xu et al. 2009). Jondiko et al. (2012) reported that 1Bx7 + 1By9 could increase dough strength, and another study found that the recombinant inbred lines (RILs) containing 1Bx7 + 1By9 displayed a higher SDS-sedimentation volume than that with 1Bx20 at *Glu-B1* locus (Jondiko et al., 2012; Nishio et al., 2007). Chen et al. (2019) reported that the absence of 1Bx7 + 1By9 could lead to weaker dough strength and inferior sponge cake performance (Chen et al., 2019). The 1Bx14 + 1By15 subunits are beneficial to the accumulation of endosperm in the near-isogenic lines (NILs) with Glu-1Bh (Zhao et al., 2020). The 1Bx17 + 1By18 subunits are tightly associated with strong dough quality, while 1Bx20 + 1By20 are associated with weak dough (Cornish et al., 2001; Ma et al., 2019). Tang et al. (2008) reported that the subunits 1Bx6 + 1By8 from synthetic hexaploid wheat exhibited better overall quality characteristics than 1Bx7 + 1By8. Compared to *Glu-B1*, *Glu-D1* locus exhibit less variation, including 1Dx2 + 1Dy12, 1Dx3 + 1Dy12, 1Dx4 + 1Dy12, 1Dx5 + 1Dy10, 1Dx2 + 1Dy10, 1Dx2.2 + 1Dy12 and 1Dx2 + 1Dy11 (Deng et al., 2006). Among these subunits, 1Dx5 + 1Dy10 subunits are usually beneficial to wheat processing quality (Gupta et al., 1994; Lafiandra et al., 1993; Ma et al., 2005; Xu et al., 2008). Yanaka et al. (2007) found that the novel allelic locus *Glu-D1d* at *Glu-D1* was positively associated to dough strength. The subunits 1Dx5 + 1Dy10 exhibits more effects on SDS sedimentation value, dough mixing time and dough strength than 1Dx2 + 1Dy12 (Liang et al., 2010). 1Dx5', the same electrophoretic mobility as the traditional one 1Dx5 in sodium dodecyl sulfate polyacrylamide gel electrophoresis (SDS-PAGE), was identified associated with good baking quality (Feng et al., 2011; Yan et al., 2008). The allele *Glu-D1d* (1Dx5 + 1Dy10) was found associated with good quality in 1 *T. aestivum* ssp. *spelta* accession, 5 *T. aestivum* ssp. *macha* accessions and 7 *T. aestivum* ssp. *compactum* accessions (Xu et al. 2009). On the basis of relationship between wheat quality and HMW-GS alleles, several scoring systems have been established for the processing quality's prediction (Wang et al., 2018). Comparing the contribution rates of *Glu-1*, the decreasing order was: *Glu-D1* > *Glu-A1* > *Glu-B1* (Payne et al., 1981). But another study reported that because of the rich variation of *Glu-B1* and *Glu-D1* locus, the decreasing order was: *Glu-D1* > *Glu-B1* > *Glu-A1* (Lawrence et al., 1988). According to quality contributions, the different subunits were ranked as: 1Ax1 > 1Ax2* > 1AxNull at *Glu-A1* locus, 1Bx14 + 1By15 > 1Bx7 + 1By8 > 1Bx17 + 1By18 > 1Bx7 + 1By9 at *Glu-B1* locus, and 1Dx5 + 1Dy10 > 1Dx2 + 1Dy12 > 1Dx4 + 1Dy12 at *Glu-D1* locus (Gao et al., 2002). Ma et al. (2019) found that the wheat genotypes that had subunits 13 + 16 or 7* + 8 at *Glu-B1* locus and 5 + 10 at *Glu-D1* locus without 1BL/1RS translocation were expected to contain strong-gluten proteins in wheat grain.

As one of the major components of wheat storage proteins, the LMW-GS plays an important role in dough quality in terms of allele variations and expression levels. Dong et al. (2010) found that high expression of LMW-GS in Xiaoyan 54 exhibited better dough quality than Jing 411. There are many kinds of variations in *Glu-3*, i.e., seven alleles at *Glu-A3* locus (*Glu-A3a*, *Glu-A3b*, *Glu-A3c*, *Glu-A3d*, *Glu-A3e*, *Glu-A3f*, *Glu-A3g*), nine alleles at *Glu-B3* locus (*Glu-B3a*, *Glu-B3b*, *Glu-B3c*, *Glu-D3d*, *Glu-D3e*, *Glu-D3f*, *Glu-D3g*, *Glu-D3h*, *Glu-D3i*), eleven alleles at *Glu-D3* locus (*Glu-D3a*, *Glu-D3b*, *Glu-D3c*, *Glu-D3d*, *Glu-D3e*, *Glu-D3f*, *Glu-D3g*, *Glu-D3h*, *Glu-D3i*, *Glu-D3j*, *Glu-D3k*) (Appelbee et al., 2009; Cherdouh et al., 2010). It has been reported that the variation of *Glu-3* significantly affected wholemeal flour protein content (WFP) and mid-line peak value (MPV) (Luo et al., 2001). *Glu-A3g*, *Glu-A3b* and *Glu-A3i* were found associated with elite dough quality by analyzing the near-isogenic lines (NILs) of the variety Aroona (Zhang et al., 2012). Lee et al. (2016) found that the wheat varieties containing *Glu-B3b*, *Glu-A3d*, *Glu-B3g* and *Glu-B3i* displayed better bread baking quality than *Glu-A3e* and *Glu-B3c*. The *Glu-A3m* and *Glu-A1b* were more significantly correlated with dough resistance and extensibility than *GluA1c* and *Glu-A3k* respectively (Gupta et al., 1989). *LMW-N13*, a novel LMW-GS identified from *Aegilops uniaristata*, was found to display superior dough properties (Du et al., 2020). Together, the variations between gluten subunits and dough properties provides useful data for quality breeding in wheat.

3. Impacts of Glutenin on the Traditional Wheat Food

Chinese steamed bread and noodles are the most popular products of wheat in the north China. There is about 72% Chinese wheat used for human consumption (Lin et al., 2020). Previous study indicated that protein content of flour was significantly associated with steamed bread quality (Deng et al., 2007). He et al. (2003) found that extension of extensograph and gluten strength were positively correlated with steamed bread volume and springiness. Liang et al. (2015) showed that the appropriate proportion of strong and weak gluten chose for the high-quality traits of steamed bread and noodles.

Noodles, one of the most popular consumptive styles of wheat, quality is mainly evaluated by color, surface appearance, texture, firmness, cohesiveness and tensile strength (Zhou et al., 2013). Hou et al. (2013) showed that gluten quality was positively correlated with noodles texture. HMW-GS, one of the most important storage protein, plays a key role in the elasticity and strength of gluten (Liu et al., 2009). HMW-GS content and combinations are positively associated with cooking time, hardness, elasticity, cohesiveness and chew ability of noodles (Zhang et al., 2013). Influences of different subunits on noodle quality were 1AxNull > 1Ax1, 1Bx7 + 1By8 > 1Bx7 + 1By9 > 1Bx14 + 1By15, 1Dx4 + 1Dy12 > 1Dx5 + 1Dy10≥1Dx2 + 1Dy12, and the 1Bx7 + 1By8 at *Glu-B1* locus is the most important subunit for high-quality noodles, while Null/7 + 8/2 + 12, 1/7 + 8/4 + 12 and 1/7 + 8/5 + 10 are the recommended combination (Zhang et al., 2013). Nieto et al. (1994) found that the increasing Y-type HMW-GS speed up the improvement of gluten macropolymers and gluten strength. He et al. (2005) selected 158 winter and facultative cultivars for detecting the effects of HMW-GS and LMW-GS on Chinese noodles quality, and the results indicated that *Glu-A3d* and *Glu-B3d* were slightly better for noodles quality. Park et al. (2011) found that *Glu3* together with *Glu-1* was able to improve the quality of cooked noodles. Meanwhile, Tang et al. (2010) found that *Glu-B1d* (6 + 8) had a positive influence on Chinese noodles, especially combined with the subunits *Glu-A1* and *Glu-D1*. In order to find the relationship between wheat gluten and the processing quality of Xinjiang hand-stretched noodles (XHSN), 195 wheat varieties were used to analysis, and the results identified that the variation of subunits displayed different effects on the quality of

XHSN, such as 1, 2*, 7 + 9, 17 + 18, 5 + 10, *gluA3a*, *gluB3a*, *gluB3b*, *gluB3d* and *gluB3g* significantly increased the quality of proteins, but *Glu-A3c* was positively associated with protein amount (Xiang et al., 2015).

Steamed bread is an important staple food in China, and about 40% of wheat is used for making Chinese steamed bread (He et al., 2003). Steamed bread is generally divided into two types, southern and northern types. There are more studies focusing on northern type steamed bread, because of its popular production. In modern time, steamed bread is usually made by mechanized or semi-mechanized method, which require different flour quality. Zhao et al. (1995) found that the most optimum wheat varieties for cooking steamed bread were middle gluten wheat, through studying the relationship between wheat quality and steamed bread in Heilongjiang province. 33 wheat varieties were used to analyze the effect of HMW-GS on the quality of steamed bread, and the results showed that HMW-GS mainly influenced the volume and whiteness of steamed bread (Zhang et al., 2015). Investigations on steamed bread quality and the HMW-GS have shown that *Glu-1Ax1* and *Glu-1Dx2* were positively associated with the volume of steamed bread, *Glu-1Bx7* and Glu-1By8 were only positively associated with the score, and Glu-1Dx5 + 1Dy10, Glu-1By9 and Glu-1Dy12 were positively associated with both the score and volume of steamed bread (Deng et al., 2007). The subunits of 1Bx13 + 1By16 were beneficial to steamed bread processing because of its positive association with subsidence volume and farinograph stability (Li et al., 2009).

Many previous reports have shown that most leading wheat cultivars in China are not suitable for mechanically processed food because of their weak gluten content (He, 1999; He et al., 2004; Wan et al., 1989; Wang et al., 1989; Zhang et al., 2007). In wheat cultivars, the richest variations are AxNull (66%), 1Bx7 + 1By8 (54%) and 1Dx2 + 1Dy12 (80%), however, the high-quality subunits 1Dx5 + 1Dy10 or 1Ax2* rarely appear (Vaiciulyte-Funk et al., 2015). Thus, increasing gluten strength to meet the quality need of wheat products, such as steamed bread and noodles, should be the direction of wheat quality improvement in future.

4. The Molecular Markers Used for Wheat Quality Breeding

With the improvement of our living standard, the demand for high-quality wheat is increasing. Wheat cultivars lack high-quality subunits or combination in China, such as 1Dx5 + 1Dy10, 1Ax2* and 1Bx17 + 1By18, which limit the progress of wheat quality breeding (He et al., 2003). Molecular marker assisted selection combined with conventionality breeding are regarded as a useful tool for the improvement of wheat quality.

SDS-PAGE is usually considered an efficient method for profiling gluten, but some different subunits with similar molecular weight were not differentiated readily (Lafiandra et al., 1994). For example, 1Bx7 and 1Bx7*, only a little difference in electrophoretic mobility, cannot be easily resolved by their elution time (Marchylo et al., 1992; Ragupathy, 2008). The molecular marker could distinguish the identical molecular-weight clearly. According to the sequence of *Glu-1Dy10* and *Glu-1Dy12*, Smith et al. (1994) designed the specific primer and generated DNA marker. Butow et al. (2003) designed the PCR marker to discriminate the two types of *Glu-1Bx7*, and it created the opportunity for quality characteristics. Meanwhile, $1Bx7^{OE}$ was designed as the marker due to its contribution to dough strength (Butow et al. 2003). Subsequently, the specific molecular markers for the subunits of 1Ax2*, 1Axl, 1AxNull, 1Dx5, 1Dy10, 1Dx2, 1Dyl2, 1Bx7, 1Bx7*, 1Bx17, 1By8, 1By9 and 1By16 were designed (Ahmad, 2000; Debustos et al., 2001; Lei, 2006). Xu et al. (2006) analyzed the composition and distribution of HMW-GS in China by 250 wheat varieties and 175 RILs, and identified the specific marker for high-quality 1Bx14 + 1By15 and codominant marker for 1Bx17 + 1By18. Some major and stable QTLs of gluten strength were found on chromosomes 1A and 1B, and several candidate markers assisted with durum wheat quality improvement through molecular breeding were identified (Johnson et al., 2013). Zhen et al. (2014) developed a specific PCR marker for *Glu-A3a* allele and validate it using NILs and RILs, which could be used as a molecular marker for the improvement of gluten quality by marker assisted selection. A molecular marker that tightly linked with *Glu-D1* double dull was developed, and this codominant molecular marker enhanced the speed of improvement for better biscuit making quality (Ram et al., 2019). In order to study the relationship between the subunits composition of HMW-GSs and wheat germplasm resources in China, molecular marker identification was used to analyze the quality composition of HMW-GSs among 105 winter wheat variety resources, and the results displayed that the frequency distribution of different type subunits varied greatly, such as the frequency of the high-quality subunit "1Ax1" was 42.6%, but "1Ax2*" was 14.5% (Wang et al., 2016).

5. Conclusions

According to our summarization, extensive studies have demonstrated that the proportion and composition of gluten have important impact on dough quality. However, the HMW glutenins play one of the most important roles in the quality of steamed bread and noodles. The availability of wheat reference genome sequence accelerated the identification of novel glutenins, and may enable to develop efficient molecular markers for the breeding of high-quality wheat.

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