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Influence of Low-molecular Weight Glutenin Subunits on Wheat Kernel Elasticity and Sedimentation Volume

J.D.C. FIGUEROA[1]*, R.J. PEÑA[2], P. RAYAS-DUARTE[3] and K. KHAN[4]

[1]Centro de Investigación y de Estudios Avanzados-Unidad Querétaro, Libramiento Norponiente 2000, Fracc. Real de Juriquilla, Querétaro, C.P. 76230 Qro., Mexico
[2]CIMMYT, km 45, Carretera México-Veracruz, El Batán, Texcoco, Mexico C.P. 56130
[3]Robert M. Kerr Food & Agricultural Products Center, Oklahoma State University, 123 FAPC, Stillwater, OK 74078-6055, USA
[4]Department of Cereal and Food Sciences, North Dakota State University, 111 Harris Hall, Dept. 7640, P.O. Box 6050, Fargo, ND 58108-6050, USA

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The effect of low molecular weight (LMW) glutenin subunits (GS) in presence of high molecular weight (HMW)-GS has over SDS sedimentation volume (SDSS) and kernel elasticity is presented. Twenty-six wheat lines having different origins and classified by SDS-PAGE into 14 different LMW-GS genotypic allelic groups were analyzed. When good HMW-GS background, i.e. Glu-1 1, 2*, 7 + 9 or 17 + 18 and 5 + 10 was associated with a number of allelic variants of *Glu-3* loci (LMW-GS), i.e. *Glu-A3 c* and *b; Glu-B3 g, h, d,* higher kernel modulus of elasticity and SDSS were generally present. However, when poor HMW-GS background was present, i.e. *Glu-1* null, 7 + 8, 2 + 12, a poor to medium modulus of elasticity and SDSS were generally found. *Glu-B3* j allelic group, which possesses the wheat–rye translocation showed a tendency to have low elastic modulus, high plastic work (WP) and low SDSS. The effects of good LMW-GS are enhanced by a good HMW-GS background, yielding higher kernel elasticity and SDSS.

Keywords: LMW-GS, HMW-GS, sedimentation volume, modulus of elasticity, kernel elasticity

Introduction

Glutenins are of great importance in explaining the variation that occurs in rheological and "bread-making" properties of wheat. High molecular weight-glutenin subunits (HMW-GS) and low molecular weight-glutenin subunits (LMW-GS) form the so-called glutenin polymers, which are among the largest molecules in nature, with molecular weights in the order of 1 to 5 million with a wide distribution (Southan and MacRitchie, 1999). The genes encoding LMW-GS are mostly located at the *Glu*-3 loci (*Glu-A3, Glu-B3* and *Glu-D3*) on the short arms of group 1 homologous chromosomes (Singh and Shepherd 1988; Luo et al. 2001). The HMW-GS encoding genes occur at the Glu-1 loci

* Corresponding author; E-mail: jfigueroa@qro.cinvestav.mx

(*Glu-A1, Glu-B1* and *Glu-D1*), located on the long arms of group 1 homologous chromosomes (Payne et al. 1987). The LMW-GS represent about 30% of the total protein and about 60% of the total glutenins, and they seem to have a great effect on dough visco-elastic properties in both bread wheat and durum wheat (Jood et al. 2000; Luo et al. 2001). Not only is the total amount of protein important but also the amount and type of the individual glutenin subunits. HMW-GS make a larger contribution to Rmax than the LMW-GS on a constant weight basis (Cornish et al. 2006). Despite their abundance and important effect on dough and bread, LMW-GS have been researched much less than HMW-GS due in part to the difficulty in identifying them in one-dimensional SDS-PAGE. Several alleles at the *Glu-3* loci have been ranked with respect to their effect on dough resistance and extensibility (Gupta et al. 1989; Luo et al. 2001; Maucher et al. 2009). Most of the characterization work has been done in dough and bread related to visco-elastic properties (Beasley et al. 2002; Uthayakumaran et al. 2002; Wang et al. 2006). Little attention has been given to the influence of glutenin proteins on mechanical and visco-elastic properties of kernels, in spite of its high importance not only in the quality of the bread-making process but also during harvesting, storage, drying, tempering, milling, and final use (Figueroa et al. 2009).

Recently, several studies on the elastic properties of wheat kernels were reported for genotypes with different HMW-GS (Figueroa et al. 2009) and LMW-GS (Maucher et al. 2009) composition. Additionally, the association of LMW-GS alleles with the modulus of elasticity and kernel size may help to select an ample range of quality within the same allelic group. A better understanding of the effect of individual alleles on quality parameters is required in order to perform a more specific selection of quality-related components for breeding programs and end use. Thus, tobjective of this work was to evaluate the influence of HMW-GS and individual alleles of LMW-GS on elastic properties of intact kernels and sedimentation volume.

Materials and Methods

Plant materials

Twenty-six wheat lines were grown by CIMMYT in Sonora, Mexico during the crop cycle 2006–07. The SD-PAGE protocol described by Peña et al. (2004) was used to determine HMW-GS and LMW-GS composition. The wheat lines were classified into 14 different genotypic allelic groups according to their LMW-GS composition.

Physical and chemical properties of the various wheat groups

Moisture content was determined by Approved Method 44-15A (AACC International 2000). Protein content (N × 5.7) and sedimentation tests were carried out in accordance to Peña et al. (1990). Kernel thickness represented the highest point of the dorsal part of the grain was measured using a Mitutoyo model CD-6” CS digital caliper (Mitutoyo Corp., Japan). Analyses were done at least in duplicate.

Uniaxial compression test

A TA-XT2 Texture Analyzer (Texture Technologies Corporation, Stable Micro Systems, Surrey, England) was used to measure the kernel response to compressive loadings in the elastic regime of the material (modulus of elasticity) using parallel plates at 20°C by the method reported by Ponce-García et al. (2008).

Elastic and plastic wheat components from compression loading testing

The visco-elastic behaviour of the wheat kernels was calculated using compression experiments, specifically the work of compression from the loading/unloading curve (Ponce-García et al. 2008). The area under the loading curve gives the total work (WT) done by the loading device during compression. During unloading a portion of this work can be regained. This recoverable work or elastic contribution (WE) of the total work, can be obtained from the area under the unloading curve, and the work dissipated by the plastic deformation alone is the difference between WT–WE, i.e. WP = WT – WE (Gubicza et al. 1996). Analysis was performed in 10 wheat kernels per sample. Linear regressions were fitted to the experimental values of elastic modulus from each sample (10 kernels).

Statistical analysis

Analysis of variance (ANOVA) and least significant difference were conducted to each parameter using the SAS software program (SAS 2009). Linear regression curves were performed using PROC GLM and were considered significant at $P \leq 0.05$ (SAS 2009).

Results

Influence of kernel elasticity by the HMW and LMW glutenin subunits from wheat samples and their relationship to sedimentation volume

A kernel quality model is proposed in order to explain the influence of LMW-GS within specific allelic group on the SDSS behaviour where kernel elasticity and kernel size, as traits influenced by genetic and environmental factors. A plot of the modulus of elasticity versus kernel thickness would be a simple representation of the effect of LMW- and HMW-GS on SDSS values. Kernel elasticity was positively related to elastic work and SDSS ($r = 0.44$; $P < 0.05$) as well as to sedimentation index ($r = 0.53$; $P < 0.001$). Consequently, a high modulus of elasticity, combined with a high gradient (slope) of the modulus of elasticity versus kernel size regression curve, can be expected to indicate the best potential for overall kernel quality performance.

Kernel elasticity influenced by LMW glutenin subunits of the allelic group at locus Glu-A3 *of* T. aestivum *L.*

Glu-A3 b was found in 4 lines with different HMW-GS alleles (Fig. 1, Table 1). In general, *Glu-A3 b* allelic variants showed relatively high modulus of elasticity (averaging 200 MPa or higher) and SDSS. *Glu-A3 c* was found in 16 lines (Table 1) with different

Table 1. Physico-chemical characteristics of wheat with different composition of HMW and LMW glutenin subunits[a]

Lines	*Glu-A1*	*Glu-B1*	*Glu-D1*	*Glu-A3*	*Glu-B3*	*Glu-D3*	E (MPa)	Force (N)	Prot (%)	SDS (ml)	SDS index	WE N-mm	WP N-mm	EP ratio
1	1	17+18	5+10	*c*	*g*	*b*	202.2	76.75	13.4	21.0	1.7	13.02	1.70	7.66
2	null	7+8	2+12	*e*	*i*	*b*	149.6	63.86	13.5	13.5	1.1	9.29	2.99	3.10
3	2*	7+9	5+10	*c*	*h*	*b*	178.8	68.32	11.9	12.0	1.1	10.92	1.83	5.97
4	2*	13+16	5+10	*c*	*h*	*b*	171.9	71.26	12.6	17.5	1.5	11.73	1.73	6.78
5	2*	7+9	5+10	*c*	*h*	*b*	172.7	61.55	13.8	20.5	1.6	9.93	1.80	5.51
6	1	7+9	5+10	*c*	*h*	*b*	167.1	60.20	14.4	20.0	1.6	10.69	1.42	7.54
7	1	7+9	5+10	*c*	*h*	*b*	247.6	72.97	13.1	16.5	1.4	12.70	1.49	8.50
8	2*	7+9	5+10	*c*	*h*	*b*	200.1	72.00	12.8	16.0	1.3	12.44	1.49	8.35
9	1	7+9	5+10	*c*	*h,i*	*b*	195.6	64.98	12.3	18.5	1.6	10.02	2.13	4.70
10	1	7+9	5+10	*c*	*h*	*b*	237.1	70.09	11.9	18.0	1.7	12.00	1.58	7.58
11	1	7+9	5+10	*c*	*h*	*b*	216.1	71.92	12.3	18.0	1.6	11.62	1.75	6.63
12	2*	7+9	5+10	*c*	*h*	*b*	224.0	77.94	12.6	18.0	1.6	13.72	1.62	8.45
13	2*	7+9	5+10	*b*	*h*	*a*	226.3	77.34	12.6	20.0	1.7	13.20	1.53	8.64
14	2*	7+9	5+10	*e*	*i*	*b*	204.2	66.93	13.3	19.5	1.6	11.39	2.18	5.23
15	1	17+18	5+10	*e*	*f*	*c*	111.9	55.63	14.1	18.0	1.4	8.73	3.04	2.87
16	2*	7+9	5+10	*e*	*j*	*b*	158.2	65.11	13.5	15.0	1.3	10.41	3.42	3.04
17	2*	7	5+10	*c*	*h*	*b*	170.2	67.23	13.3	20.0	1.7	13.66	1.54	8.86
18	1	7+9	5+10	*c*	*d*	*b*	195.4	69.74	13.3	21.0	1.8	11.92	2.41	4.94
19	2*	7+9	5+10	*d*	*h*	*b*	222.6	74.72	13.1	23.0	1.9	12.95	2.35	5.51
20	2*	7+9	5+10	*b*	*h*	*a*	209.3	73.74	14.2	19.5	1.6	13.19	1.63	8.09
21	2*	13+16	5+10	*b*	*h*	*a*	211.0	76.65	13.3	20.0	1.7	14.30	1.11	12.88
22	2*	7+9	2+12	*b*	*d*	*a*	196.8	75.51	13.0	21.5	1.8	13.78	2.56	5.38
23	2*	17+18	5+10	*e*	*h*	*a*	157.8	68.30	13.4	21.0	1.8	11.65	2.11	5.52
24	2*	17+18	5+10	*c*	*i*	*a*	139.0	58.52	13.7	16.0	1.4	10.17	2.90	3.50
25	null	17+18	5+10	*c*	*d*	*d*	142.8	60.67	13.4	20.0	1.7	9.71	1.39	6.98
26	1	7+8	5+10	*c*	*d*	*b*	211.4	74.88	13.4	22.0	1.8	13.70	2.01	6.81
Least Significant Difference ($P < 0.05$)							36.5	7.5	1.8	0.9	0.2	1.9	0.6	2.2

[a] E = Modulus of elasticity; Force = peak force; Prot = kernel protein (12.5% mb); SDS = SDS sedimentation volume of flour; WE = area under the curve of elastic work N-mm; WP = area under the curve of plastic work N-mm; EP = WP/WP ratio. Protein and sedimentation were performed in duplicate. Elastic and plastic parameters were obtained from 10 kernels.

HMW-GS alleles. Regression lines at the top of the plot of modulus of elasticity versus kernel thickness (Fig. 1B) had higher modulus of elasticity and an overall trend to higher SDSS, compared to the lines at the bottom which presented poor SDSS. Two interesting cases are line 8 with relatively low SDSS (16 ml) due to low protein content (12.8%), but with modulus of elasticity relatively high (200.1 MPa); the other case is line 25 with good SDSS (20 ml) and low modulus of elasticity (142.8 MPa). The latter case agrees with the *Glu-A1* null allelic form. *Glu-A3 d* was present in line 19 which also had a high quality combination of HMW 2*, 7 + 9 and 5 + 10 subunits (Fig. 1C), the highest SDSS (23 ml) and excellent modulus of elasticity (average 222.6 MPa) (Table 1). The LMW-GS, although important for the rheological properties of the dough, appeared to have relatively less influence on modulus of elasticity and SDSS than the HMW-GS. A good example of this is presented in Fig. 1D where the *Glu-A3 e* indicates that not always the null or silent allelic form produces poor quality. For example, lines 14 and 23 showed excellent quality with SDSS of 19.5 and 21 ml, respectively. These samples showed HMW subunits 2*, 7 + 9 and 5 + 10 and 17 + 18 (Table 1) which are considered of good quality. The lower regression curve in Fig. 1D represent poor quality lines 15, 2 and 16 with SDSS of 18, 13.5 and 15 ml, respectively, and poor modulus of elasticity.

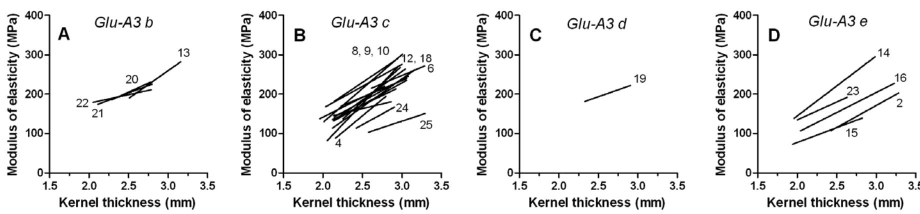

Figure 1. Regression trends showing the relationship between modulus of elasticity vs kernel size for allelic groups at locus *Glu-A3* of LMW-GS. *Glu-A3 b; Glu-A3 c; Glu-A3 d* and *Glu-A3 e* (null or silent). Each line represents 10 observations

Kernel elasticity influenced by LMW glutenin subunits of the allelic group at locus Glu-B3 *of* T. aestivum *L.*

The *Glu-B3* allelic groups *d, g* and *h* in general presented higher SDSS, except lines 3, 4, and 8 which had lower protein content, compared to the *Glu-B3 f, i* and *j* alleles that presented poor modulus of elasticity and SDSS (Fig. 2, Table 1). The *Glu-B3 d* and *g* were not as abundantly present as were *Glu-B3 h* in this set of lines. However, within the *Glu-B3 h* there are some lines located at top of the plot (20, 8, 10, 12, 13 and 6) with high elasticity and good SDSS. Other lines (3 and 4) within the *Glu-B3* h showed low elasticity as well as low SDSS.

Line 14 showed a poor *Glu-3*loci combination (*Glu-A3 e* and *Glu-B3 i,* Figs 1D and 2E) but good modulus of elasticity. The line 16 with *Glu-B3 j* allele present which possesses the wheat–rye translocation showed a tendency to a poor elastic modulus but high plastic area, and as expected a poor SDSS of 15 ml (Fig. 2F, Table 1).

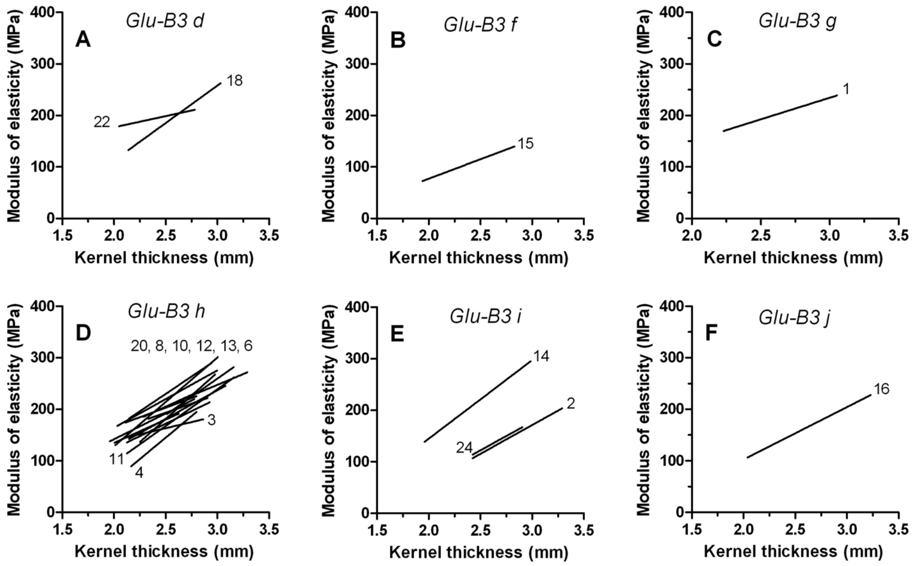

Figure 2. Regression trends showing the relationship between modulus of elasticity vs kernel size for allelic groups at locus *Glu-B3* of LMW-GS. *Glu-B3 d; Glu-B3 f; Glu-B3 h; Glu-B3 i* and *Glu-B3 j*. Each line represents 10 observations

Kernel elasticity influenced by the LMW glutenin subunits of the allelic group at locus Glu-D3 *of* T. aestivum *L.*

Figure 3 shows the regression trend for the 6 lines containing loci *Glu-D3 a* located at the top of the plot showing good SDSS, and lines located at the bottom of the plot and showing low SDSS, or modulus of elasticity mainly due to the presence of *Glu-B3* with *i* allelic form. The *Glu-A3 e* allelic form in line 23 can explain the poor modulus of elasticity and WP but the relatively good SDSS due to the good HMW background.

Glu-D3 b allele was present in the largest number of lines of this set (Fig. 3B). This indicates that breeding programs have selected wheat containing this allele related to good quality traits. However, there were some lines with poor combination of HMW-GS that showed low kernel modulus of elasticity and SDSS. The poor quality of lines such as 2 and 16 can be explained by the poor allelic combination in HMW-GS Glu-1 null, 7 + 8 and 2 + 12 and LMW-GS *Glu-3* with *e* (silent), and *j* (wheat–rye translocation) allelic variants, respectively. The low SDSS and average modulus of elasticity in lines 3 and 4 could be related to the relatively low protein content (11.9 and 12.6%, respectively). Other lines from Figure 3B showed good SDSS with the exception of line 8 which, as explained above, also presented low protein content (12.8%) but a good modulus of elasticity. Lines *Glu-D3 c* and *Glu-D3 d* with a poor genetic background of *Glu-A3 e* (silent) and *Glu-A1* null, respectively, presented a very poor modulus of elasticity, as expected, but regular SDSS which may be due to high protein content, especially in line 15 (14.1%).

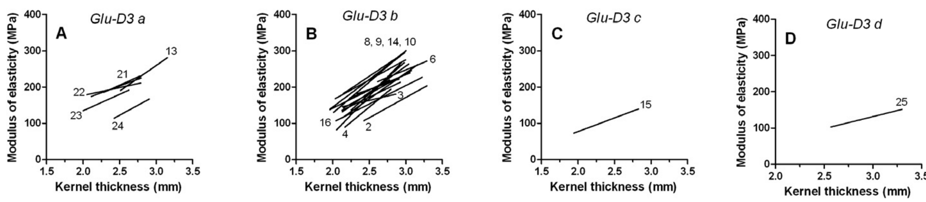

Figure 3. Regression trends showing the relationship between modulus of elasticity vs kernel size for allelic groups at locus *Glu-D3* of LMW-GS. *Glu-D3 a*; *Glu-D3 b Glu-D3 c* and *Glu-D3 d*. Each line represents 10 observations

Discussion

Most of the lines with good SDSS also represented a relatively high elastic work value (WE > 11.7 N-mm) along with a medium plastic work value (WP < 1.8 N-mm) and normal protein content (Table 1). Excessively high WE > 18.2 N-mm and low WP < 1.0 N-mm is found in durum wheat and should be avoided for good bread quality (Ponce-García et al. 2008). Figueroa et al. (2009) and Maucher et al. (2009) reported that the correlation of SDSS to elastic work was due to protein quality, partly by the presence of some specific HMW-GS. As indicated by Figueroa et al. (2009) for HMW-GS, and Maucher et al. (2009) for LMW-GS, the WE/WP ratio was significantly correlated with the alveograph P/L ratio and the WE/WP ratio is generally high in lines with good SDSS. The beneficial effects of good HMW-GS (high WE) and good LMW-GS (low WP) background seem to be additive, the presence of both types of glutenin allelic forms giving better elastic characteristic and SDSS than the presence of each one separately. Cornish et al. (2006) reported similar results where the predicted and actual Rmax of the world wheat set showed the highest correlation coefficients when the predictions were based on HMW-GS and LMW-GS together. However, the contribution of LMW-GS to variation in kernel WE and quality was lower than the positive influence on protein by a good HMW-GS background. Wheat types with HMW-GS of excellent quality *Glu-1* locus 1, 2*, 7 + 9 and 5 + 10 as those reported by Payne et al. (1980; 1987) and Tohver (2007) usually presented a high modulus of elasticity (Figueroa et al. 2009). On the contrary, those combined with HMW subunits null, 7 + 8 and 2 + 12 produced lower values.

The *Glu-A3* e in Fig. 1D indicates that not always the null or silent allelic form produces poor quality. As other researchers have shown, the quality depends on the combination of good LMW and HMW allelic forms (Gupta and MacRitchie 1994; Flæt and Uhlen 2003; Cornish et al. 2006; Maucher et al. 2009). Of the *Glu-3* loci, it was found that the *Glu-B3* locus made the largest contribution to Rmax score (Cornish et al. 2006). Figure 1D and Table 1 show that lines 14 and 23 of *Glu-A3 e* had high WP due to allelic variant *Glu A3 e* (silent), but they also had high WE that contributed to a medium to good quality performance mainly due to a good background of the HMW-GS Glu-1 2*, 7 + 9 or 17 + 18 and 5 + 10. However, if the HMW-GS and LMW-GS combination had regular to poor SDSS, as found in lines 15, 2 and 16 of *Glu-A3 e* (silent), the poor quality is mainly affected by a high WP and a low WE (Table 1, Fig. 1D). Similar behaviour was shown by the locus

Glu-D3 a allelic variant, where line 24, located at the bottom of the plot Figure 3A, presented poor quality with a SDSS of 16 ml and poor elastic performance compared to lines 13, 21 and 22 with SDSS of 20, 20 and 21.5 ml, respectively (Table 1). The combination of LMW-GS loci *Glu-B3 i* may explain the low SDSS volume due to an increment of WP (2.90 N-mm) and a relatively low WE (10.17 N-mm, line 24) compared to the other *Glu-D3* a lines 13, 22 and 21, which showed good SDSS as well as WE and WP values. Although *Glu-B3 i* showed poor performance, there are inconsistent reports in the literature on the influence of this allelic form. Luo et al. (2001) reported that the presence of *Glu-B3 i* gave good performance related to the dough strength, while poor performance was reported in the samples analyzed by Flæt and Uhlen (2003).

In general, *Glu-1* null HMW in the lines mainly decreased the elastic work. On the contrary, *Glu-A3 e* (silent) or null allelic LMW-GS increased the plastic work. This data also agrees with the studies of dough which suggest that rich in HMW-GS provide elastic properties, whereas fractions rich in LMW-GS impart viscous properties (Jood et al. 2000). high WE and low WP should be avoided for bread quality.

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