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High Molecular Weight (HMW) Glutenin Subunit Composition of NS Wheat Cultivars Released in 1987-2008

Nikola Hristov • Novica Mladenov • Bojan Jocković • Veselinka Đurić • Ankica Kondić Špika • Dragana Obreht

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Summary: Gluten content, and more importantly its composition expressed through glutenin subunits, has great influence on the rheological and bread-making properties of wheat flour. Total of 168 winter wheat cultivars developed at the Institute of Field and Vegetable Crops, Novi Sad, Serbia in the period 1987-2008 were analysed for high molecular weight glutenin subunits (HMW-GS) composition using SDS-PAGE. Presence of twelve different alleles and nineteen different GS combinations was determined. The highest frequency was found for GS N at the locus Glu-A1 (46%), 7+9 (77%) at the locus Glu-B1 and 5+10 (72.7%) at the locus Glu-D1. The most frequent combination was 2*, 7+9, 5+10. Presence of several rare GS with positive effect (13+16 and 15+16) was determined, as well as high uniformity of the genetic material, considering small number of cultivars (4.2%) with different electrophoretic paths. Two modes of glutenin score (Glu-1 score) determination were applied, based on which differences in bread-making quality among individual cultivars can be determined more precisely.
Key words: Glu-1 loci, HMW glutenin subunits, NS wheat cultivars, SDS-PAGE, Triticum aestivum, wheat quality

Introduction

Wheat quality is chiefly determined by genetic quality potential and environmental factors (Graybosch et al. 1996, Mladenov et al. 2001). Individually, from the genetic aspect (Payne et al. 1981), and especially in the composition at different loci (*Glu-A1, Glu-B1* and *Glu-D1*), high molecular weight glutenin subunits (HMW-GS) affect the expression of the bread-making quality. Electrophoretic mobility of HMW-GS enables focusing on the composition of protein subunits, which represents the genetic structure of the cultivar (Tohver 2007). HMW-GS composition is conditioned by cultivar ideotype influenced by many factors: historical (Panin 1999), climatic (Graybosch et al. 1996, Mladenov et al. 2012), technological (Đurić et al. 2010), etc. Namely, the origin and the process of individual HMW-GS incorporation vary in wide geographical area. This was significantly aided by adaptation to local agroecological conditions and relation of specific subunits to certain stress factors (Dona et al. 2005, Al Jorf 2008). Thus, the area of northern Europe (Sweden, the Baltic countries) is characterised by the combinations HMW-GS, 2*, 6+8 or 7+9, and 2 + 12 (Johansson et al. 1995), and N or 1, 7+9 and 5+10 (Johansson et al. 2003), respectively. In Asian countries (China, Iran, India) there is the dominance of HMW-GS N, 7+8, 2+12 (Hua et al. 2009); 2*, 7 + 8, 2 + 12 (Shahnejat-Bushehri et al. 2006), and 2*, 7, 2+12 (Kalaiselvi & Reddy 2003), respectively. In France the characteristic combination is N, 7+8 or 6+8, 2+12 (Branlard et al. 2003), and in Russia N, 7+9, 5+10 (Morgunov et al. 1990; Zhenghui et al. 2009). According to many authors (Payne et al. 1987, Johansson et al.

N. Hristov* • N. Mladenov • B. Jocković • V. Đurić • A. Kondić Špika
Institute of Field and Vegetable Crops, 30 Maksima Gorkog, 21000 Novi Sad, Serbia
e-mail: nikola.hristov@ifvcns.ns.ac.rs

D. Obreht
University of Novi Sad, Faculty of Sciences, Department of Biology and Ecology, Trg Dositeja Obradovića 3, 21000 Novi Sad, Serbia

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1995, Rakszegi et al. 2005, Tohver 2007, Hristov et al. 2010a) the combination HMW-GS 2*, 7+9 and 5+10 contributes to the excellent quality in most cases, and at the same time represents the dominant combination for the area of south-eastern Europe (Denčić et al. 2008, Atanasova et al. 2009, Horvat et al. 2013). However, narrowing of genetic variability hampers further progress in quality improvement, so other HMW-GS with positive effect should be given a chance (Tohver 2007), especially at the *Glu-D1* locus. After Obreht et al. (2003), there are 30 different alleles at the locus *Glu-B1*, while such variability is much lower at the locus *Glu-D1* (11 alleles) but with profound individual effect.

The aim of this paper was to present and analyse the HMW-GS combination in NS wheat cultivars developed at the Institute of Field and Vegetable Crops, and in doing so facilitate a more efficient progress in breeding wheat for enhanced technological quality.

Materials and Methods

Total of 168 winter wheat cultivars developed in the period 1987-2008 were chosen from various breeding programmes of Small Grains Department of the Institute of Field and Vegetable Crops in Novi Sad and analysed for this research. The cultivars were conventionally grown (with optimal mineral nutrition and disease control) at the Experimental Field of the Institute at Rimski Šančevi site in 2011.

Twenty grains of each cultivar were analysed. Total reduced seed proteins were separated in order to define their HMW-GS composition by SDS-PAGE on 10% gel, in Tris-glycine buffer. After separation, the gels were stained with Commasie Brilliant Blue R-250 and fixed in 7% acetic acid. The standard system of designating glutenin loci, alleles and glutenin subunits (GS) was applied (Payne & Lawrence 1983).

Based on HMW-GS relative effect on gluten quality indices such as dough strength, which ranged from 3 to 10 (SDS-sedimentation) and 4 to 17 (alveograph W), the HMW-GS quality score was calculated according to Payne et al. (1987) and Pogna & Dal Belin Peruffo (1987), respectively.

Results and Discussion

In the course of 22 years (1987-2008) of intensive efforts at improving yield and quality of NS winter wheat cultivars, as the result of breeding and selection, the total of 168 cultivars with different genetic potential were developed. Climate change, intensive cultivation practices, contemporary machines and market demands resulted in the development of cultivars adapted to the new conditions of crop production. Besides grain yield as the basic economic element, special attention has been paid to the quality itself, as an inevitable parameter in the technological process of wheat processing. Large number of cultivars showed high yields (Mladenov et al. 2011) and excellent quality (Hristov et al. 2010), proving that these two parameters can be simultaneously incorporated in the same cultivar.

Based on the allele designation proposed by Payne & Lawrence (1983), at the locus *Glu-A1* alleles *a* and *b* were identified that control the synthesis of subunits 1, 2* and the so called null allele *c*, which does not form a visible protein band on the gel (N). Frequency of these alleles was 18.6, 35.4 and 46%, respectively (Tab. 1). In comparison with the results of Vapa (1989), who analysed Yugoslavian cultivars in the period 1967-1986, the same locus saw redistribution in favour of allele *c* in relation to *a*, while allele *b* kept approximately the same frequency. At the locus *Glu-B1* six alleles were found (*a, b, c, d, f* and *h*) that control subunits 7, 7+8, 7+9, 6+8, 13+16 and 14+15, respectively. Frequency of these alleles ranged between 0.6% and 77%. At this locus, a decreased variability was noted in relation to the 8 alleles analysed by Vapa (1989), where allele *c* kept the highest frequency, as established by Denčić & Vapa (1999) and Obreht et al. (2003). Even though all hexaploid wheats have six HMW subunit genes, only three, four or five subunits are expressed (Uthayakumaran et al. 2002). According to Rhazi et al. (2009), the variation in the number of alleles that control expression of individual GS is often caused by gene silencing, which had not sufficiently been explained. The research showed (Shewry et al. 1992) that allele variation is closely connected to the bread-making quality, especially at the locus *Glu-D1*. At this locus alleles *a, c* and *d* were found that control the synthesis of subunits 2+12, 4+12 and 5+10, respectively. Frequency of the allele *a* was 26.7, allele *b* 0.6, while the 72.7% frequency of allele *d* (Tab. 1) was in line with the results of Denčić & Vapa (1999) and significantly higher than the one reached by Vapa (1989). Among the most frequent GS, N has negative effect, 7+9 has both negative and positive effect (depending on the combination), while 5+10 has positive effect on the bread-making quality of the product (Payne et al. 1987). Nonetheless, due to high frequency of

Table 1. Frequency of HMW gluten alleles in the NS winter wheat cultivars (1987-2008)

No	Glu-A1 **loci**			Glu-B1 **loci**			Glu-D1 **loci**		
	Alleles	**NC***	**%**	**Alleles**	**NC**	**%**	**Alleles**	**NC**	**%**
1	a	30	18.6	a	12	7.5	a	43	26.7
2	b	57	35.4	b	18	11.2	c	1	0.6
3	c	74	46	c	124	77.0	d	117	72.7
4				d	5	3.1			
5				f	1	0.6			
6				h	1	0.6			
Total	**3**	**161**	**100**	**6**	**161**	**100**	**3**	**161**	**100**

*Number of cultivar

GS 1 and 2* (54%) that have positive effect and the domination of GS 5+10 at the locus *Glu D-1*, it can be concluded that quality has been improved compared to the previously analysed period, as established also by Hristov et al. (2010). Profound domination of GS 5+10 and high frequency of GS 2* in Serbian and Croatian cultivars have significantly contributed to the creation of new wheat cultivars with enhanced characteristics of gluten strength in the previous decade (Horvat et al. 2013).

Based on the given analysis, 161 cultivars with homogenous GS can be classified into XIX different groups according to the combination of HMW-GS (Tab. 2). The largest number of cultivars (30.4%) was found in group IV which is characterised by units 2*, 7+9, 5+10. Even though GS N was the most frequent, GS 2* was also found in the dominant combination as a consequence of four different combinations, whereas GS N was „scattered" throughout 7 combinations. Similar frequency was reported by Vapa (1989), Denčić & Vapa (1999) and Obreht et al. (2003), noting that this combination originates from the Russian cultivar Bezostaja 1, which most often appeared in the pedigree of this group's cultivars. The next one according to frequency was group X with 19.3% and combination of units N, 7+9, 5+10, and then group XVI with 15.5% and combination of units N, 7+9, 2+12. All of the remaining combinations were significantly less frequent, while groups III, IX, XV, XVII and XIX had only one cultivar. The domination of HMW glutenin combinations 2*, 7+9, 5+10 and N, 7+9, 5+10 in European winter wheat cultivars were reported by Denčić & Vapa (1999), Tohver (2007) and Atanasova et al. (2009).

The significance of correlations between different alleles with dough properties is expressed through the system of qualitative scoring HMW-GS, i.e. Payne's score (Payne et al. 1987), where GS 5+10, expressed in score 4, is connected with increased dough strength, while GS 2+12, expressed in score 2, is connected with dough weakness. Quality *Glu-1* score after the mentioned author ranged from 4 to 10, while the group XIX had no score due to GS 14+15 (Tab. 2). Maximum score 10 (groups I, II and III) was calculated for 10 cultivars with GS 1 or 2*; 7+8 or 13+16 and 5+10. Score 9 (groups IV and V) was calculated for 36% cultivars with GS 1 or 2*; 7+9 and 5+10 which is identical to Vapa (1989). It is interesting that the score 7 (groups X and XI) was calculated for 24.9% cultivars with GS N or 1; 7+9 and 2+12 or 5+10, indicating that selection pressure can be exerted at all loci aiming at optimal HMW-GS combination. Having in mind the average value of *Glu-1* score (7.3), it can be considered that the quality of cultivars has not altered, because Vapa (1989) calculated the same score. However, considering the fact that cultivars from other breeding centres were also analysed then, significant enhancement within the NS breeding programme can be observed. This was also confirmed by Hristov et al. (2010) who determined a special progress at the locus *Glu-D1* and more frequent presence of GS 5+10.

When *Glu-1* score was calculated after Pogna & Dal Belin Peruffo (1987), based on the alveograph values, cultivar ranking was somewhat different. Groups I, II and III (max Payne's score) did not have any value established, as well as groups VII, VIII, IX and XIX, primarily because GS 7+8, and 14+15, 13+16 had no established connection with the technological quality (Tab. 2). It can be observed that within the groups IV and V; VI, VII, VIII and IX; X and XI; XII, XIII, XIV and XV; as well as XVII and XVIII, which showed the same Payne's score, there was different scoring due to different points allocated to individual units. Thus, within Payne's score 6 there was gradation ranging from

Table 2. HMW-GS composition and *Glu-1* score of the NS winter wheat cultivars (1987-2008)

Group	Cultivar	Glu-1 **loci**			Glu-1 **score**		**Frequency**	
		A	**B**	**D**	**Payne**[2]	**Pogna**[3]	**NC**[4]	**%**
I	Jelica (1989)[1]; Novosadska 7 (1990); Ivanka (1999)	1	7+8	5+10	10	-	3	1.9
II	Neoplanta (1991); Dejana (1994); Sila (1995); Bajka (1997); Rapsodija, Arija (2003)	2*	7+8	5+10	10	-	6	3.7
II	Teodora (2006)	1	13+16	5+10	10	-	1	0.6
IV	Jednota, Poljana, Subotičanka (1987); Jadranka, Hlebna, Kosovka, Lozničanka, Rodna, Tanjugovka, Novosadska 6001 (1988); Novosadska 3205 (1989); Šančevka, Gradištanka, Krivaja, Lepa, Nera, Nova Jadranka, Pobeda, Rumenka (1990); Amajlija, Atarka, Duša, Novosadska rana 5, Novosadska 6864, Novosadska kasna, Varadinka, Žuta (1991); Bojana, Milica, Srna (1992); Čenejka, Sloga, Stepa (1993); Alfa (1994); Omega, Pesma, Tera (1995); Selekta (1997); Delta (1998); Sonja, Stamena, Sara (1999), Cipovka (2002); Balerina, Diva (2003); Oda (2004); Janja (2005); Srma, Angelina (2006)	2*	7+9	5+10	9	16	49	30.4
V	Crvenkapa, Novosadska 7000 (1988); Novosadska 7014 (1989); Grmuša (1991); Desa (1992); Tiha (1995); Sreća (1997); Gracija (1998); Isidora (2007)	1	7+9	5+10	9	14	9	5.6
VI	Novosadska 330 (1991); Silna (1995)	1	6+8	5+10	8	10	2	1.2
VII	Novosadska 5804, Senka (1988); Suvača (1994)	1	7+8	2+12	8	-	3	1.9
VIII	Lasta (1987); Košuta, Slavija (1992); Jarebica (1993); Sasanka (1994)	N	7+8	5+10	8	-	5	3.1
IX	Vera (1989)	2*	7+8	2+12	8	-	1	0.6
X	Pančevka, Viktorija (1987); Ibarka, Jedina, Panonka, Tamiš (1988); Avala, Belozrna, Pomurka, Rudničanka, Valjevka, Vukovarka (1989); Danica, Maja, Proteinka (1990); Rusija, Fortuna (1993); Stela, Neva, Renesansa (1994); Sofija (1998); Ljiljana (2000); Jefimija (2003); Donna, Bastijana, Lana (2005); Dama, Barbara, NS 40S, Etida (2006); Gordana (2008)	N	7+9	5+10	7	13	31	19.3
XI	Rana niska (1990); Zlatica (1992); Slava (1993); Prima (1995); Galija, Prva, Super rana, Zlatka (1997); Anastasija (1999)	1	7+9	2+12	7	10	9	5.6
XII	Stotka (1994); Dobra (1997)	1	7	5+10	6	11	2	1.2
XIII	Zora (1988); Nova rana (1989); Dična, Jovana (1992); Lira (1994); Mina (1997)	N	7	5+10	6	10	6	3.7
XIV	Dina (1994); Senica (1997)	N	6+8	5+10	6	9	2	1.2
XV	Novosadska 6439 (1990)	1	6+8	2+12	6	6	1	0.6
XVI	Nova Posavka (1987); Evropa, Francuska (1988); Italija, Sremka (1989); Evropa 90, Sremka 2 (1990); Kratka, Novosadska rana 6, Novosadska 6902 (1991); Draga (1992); Atina, Eva (1993); Divna, Struna (1994); Kremna, Laguna (1995); Milena (1998); Vila (2001); Dragana (2002); Balada, Simfonija, Simonida (2003); Helena (2004); Zvezdana (2005)	N	7+9	2+12	5	9	25	15.5
XVII	Palanka (1992);	N	7+9	4+12	4	8	1	0.6
XVIII	Novosadska 3183 (1988); Luna (1994); Sonata (2000); Astra (2003)	N	7	2+12	4	6	4	2.5
XIX	Sirena (1998)	2*	14+15	5+10	-	-	1	0.6
Average/Total					**7. 3**	**10.2**	**161**	**100**

[1]Year of release; [2]According to Payne et al. (1987); [3]According to Pogna & Dal Belin Peruffo (1987); [4]Number of cultivar

6 to 11 according to Pogna & Dal Belin Peruffo (1987). This can be of great importance for a more precise separation of cultivars according to quality indicators. Even though scoring after Payne et al. (1987) is generally accepted, it was noted that high or low score does not fully correspond to actual bread-making quality in some cultivars. It is well known that GS with positive effect predominantly result in flour with higher gluten strength. However, usually domesticated and widespread cultivars, famous for excellent quality, show poorer individual quality parameters. For example, cultivar Žitarka, the Croatian standard for quality but with unfavourable HMW-GS (N, 7+8, 2+12) and high GLI/GLU ratio, did not show any superior quality attributes (Horvat et al. 2012). This is understandable if higher selection pressure was exerted on the yield potential so that the expression of certain alleles was not fully realised. Bearing in mind that the realisation of quality potential does not solely depend on HMW-GS but also on LMW GS, the presence of 1BL/1RS translocation, and environmental factors and their interaction, research should be furthered towards the all-encompassing effect of different factors on bread-making quality.

According to Bekes et al. (2008) literature has witnessed certain disagreements regarding scoring of certain cultivars with GS 14+15 and 20 at the locus *Glu-B1*. Due to the close proximity of those bands while using *SDS-PAGE*, certain cultivars had incorrect scores calculated because it was common that GS 14+15 scores as GS 20. There were also various ways of scoring. In their results, certain authors (Johansson et al. 1993, Kuktaite et al. 2000, Tohver 2007) omit the score for cultivars with GS 14+15, while after Tohver (2007) and Johansson et al. (1995) the cultivars Dacke and Sport expressed significant effect of this GS with score 3, and the cultivar Troll with score 2, similarly to Johansson & Swensson (1999) for the cultivar Lavett, with score 2.

Within the analysed cultivars, the three stood out with specific GS which are not common in the NS wheat breeding programme: cultivar Sirena with GS 14+15 and Teodora with 13+16 at the locus *Glu-B1*, and cultivar Palanka with GS 4+12 at the locus *Glu-D1* (Tab. 2). After various authors (Deng et al. 2005, Liu et al. 2007, Rhazi et al. 2009) both of the mentioned GS at the locus *Glu-B1* have positive effect, while GS 4+12 has negative effect on the bread-making quality. Bekes et al. (2008) states that GS 14+15 at the locus *Glu-B1* is predominant in the Swedish cultivars but rare in the Finnish ones, which suggests possible northern origin. GS 13+16 originates from the Brazilian cultivars (Rabinovich et al. 2000) and is often found in spelt wheat, while its positive effect on the protein content and SDS-sedimentation value was found.

Incorporation of new and rare GS (13+16, 14+15, and 17+18) can largely increase variability in the breeding material (Tohver 2007). Significant improvement of wheat breeding is connected to the creation of new genotypes adapted to local agroecological conditions, essentially by using germplasm with wide genetic divergence. Increased variability of alleles at the locus *Glu-B1* enables widening and improvement of the genetic basis predominantly by adding GS with positive effects (Atanasova et al. 2009).

Wet gluten content and essentially its composition, expressed through HMW-GS, significantly affects indicators of wheat bread-making quality (Đurić et al. 2010). It was established that GS 2+12 and 5+10 are in a strong correlation with weak and strong gluten (Johansson et al. 1995). Up to now the positive effect on quality was noted with GS: 1, 2*, 7+8, 13+16, 14+15, 17+18 and 5+10, while GS: N, 7, 6+8 and 2+12 are related to the poorer quality (Rhazi et al. 2009). Uthayakumaran et al. (2002) point out that the presence of GS 5+10 at the locus *Glu-D1* has significantly higher positive effect on the dough properties as compared to GS 17+18 at the locus *Glu-B1*.

Genetic material is usually not fully homogenous, i.e. one cultivar sample can contain 1 to 4 different GS combinations (Vapa 1989). Only seven cultivars (or 4.2%) of the total analysed material have expressed heterogeneity in GS combination (Tab. 3). Three cultivars (Novosadska 6002, Novosadska 6389 and Kantata) had two electrophoretic paths each, which points to the achievement of uniformity in genetic material, considering the fact that Obreht et al. (2003) determined the presence of three paths for the first two cultivars. Cultivar Studena had three paths, and four paths were found in cultivars Novosadska 6238, Maka and Milijana. Changes occurred most often at the locus *Glu-A1*, and most rarely at the locus *Glu-D1*, which chiefly resulted from decreased variability at the locus *Glu-B1*, where generally large changes took place (Tohver 2007). Research on the Bulgarian breeding programme found that 26% out of all analysed wheat cultivars have two or more different combinations of GS (Atanasova et al. 2009),

Table 3. Frequency and type of heterogeneity of HMW-GS in the NS winter wheat cultivars

No	Cultivar	Year of release	Type	%	Glu-1 **loci**		
					A	**B**	**D**
1	Novosadska 6238	1988	A	45	N	7+9	5+10
			B	20	2*	7+9	5+10
			C	20	N	7+9	2+12
			D	15	N	7	2+12
2	Studena	1988	A	50	N	7+9	5+10
			B	30	2*	7+9	5+10
			C	20	1	7+9	5+10
3	Novosadska 6002	1988	A	70	1	7+8	2+12
			B	30	2*	7+8	2+12
4	Novosadska 6389	1989	A	60	N	7+8	5+10
			B	40	N	6+8	2+12
5	Maka	1991	A	45	2*	7+9	5+10
			B	35	N	7+9	5+10
			C	15	1	7+9	5+10
			D	5	2*	6+8	5+10
6	Kantata	2001	A	70	N	6+8	5+10
			B	30	N	7+9	2+12
7	Milijana	2004	A	45	N	7+9	5+10
			B	27	2*	7+9	5+10
			C	18	1	7+9	5+10
			D	10	N	6+8	5+10

while it is pointed out that these are different biotypes, created due to combination of parental subunits, cross-pollination or spontaneous mutations. Creation of biotypes is conditioned by the identical additional electrophoretic paths in seed samples from the same cultivar but from different locations (Vapa 1989). According to Knezevic et al. (1993), from the breeding aspect, heterogeneity in GS combinations can largely influence the increase in bread-making quality by the selection of biotypes whose GS combination is related to the positive effect on the quality.

Genetic variability of HMW-GS enables identification, description and assessment of homogeneity in different wheat cultivars (Bekes et al. 2008). Allele identification can also be used to predict technological and bread-making characteristics in the high-quality cultivars selection process, which will significantly contribute to more efficient breeding programmes.

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Kompozicija subjedinica glutenina velike molekulske mase kod NS sorti pšenice priznatih u periodu 1987-2008.

Nikola Hristov • Novica Mladenov • Bojan Jocković • Veselinka Đurić • Ankica Kondić Špika • Dragana Obreht

Sažetak: Sadržaj glutena, ali pre svega njegova kompozicija izražena kroz gluteninske subjedinice, značajno utiče na reološke i pekarske pokazatelje pšeničnog brašna. Kod ukupno 168 sorti ozime pšenice stvorenih u Institutu za ratartsvo i povrtartsvo u Novom Sadu, u periodu od 1987. do 2008. godine, analizirana je kompozicija subjedinica glutenina velike molekulske mase (HMW-GS) koristeći SDS-PAGE. Utvrđeno je prisustvo dvanaest različitih alela i devetnaest različitih kombinacija GS. Najveća učestalost uočena je kod GS N u lokusu Glu-A1 (46%), 7+9 (77%) u lokusu Glu-B1 i 5+10 (72,7%) u lokusu Glu-D1. Najzastupljenija kombinacija je bila 2*, 7+9, 5+10. Utvrđeno je prisustvo nekoliko retkih GS sa pozitivnim dejstvom (13+16 i 15+16) i visoka ujednačenost genetskog materijala, s obzirom na mali broj sorti (4.2%) sa različitim elektroforetskim putanjama. Primenjena su dva načina utvrđivanja gluteninskog (Glu-1) skora, na osnovu čega se mogu preciznije utvrditi razlike u krajnjem kvalitetu između pojedinih sorti.

Ključne reči: Glu-1 lokusi, kvalitet pšenice, NS sorte pšenice, SDS-PAGE, subjedinice glutenina velike molekulske mase, *Triticum aestivum*.