

Quality of triticale cultivars suitable for growing and bread-making in northern conditions

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Abstract

Rye and wheat are the major cereals consumed by people of northern and eastern Europe. However, it has become important to widen the use of cereal products. Attempts have been done to adapt western triticale cultivars to northern growing conditions. Serious investigations of triticale bread commenced as late as in 1997 in Estonia. The first attempts to grow the triticale cultivars Modus, Dato, Presto, SV 92280 in Estonian conditions have been successful. They are productive, resistant to leaf and stem rust, powdery mildew, and with good grain quality.

The aim of this work was to investigate the bread-making quality of western winter triticale cultivars grown in Estonia. The following grain quality parameters were estimated: grain protein content, SDS-sedimentation, falling number, water absorption, bread loaf volume.

HMW glutenin subunit composition, which was used to predict the baking quality, was determined by sodium dodecyl sulphate–polyacrylamide gel electrophoresis (SDS–PAGE). Seven different alleles were revealed in the set of 12 triticale cultivars. The best cultivars had HMW glutenin subunits 2* encoded by the *Glu-A1* locus, 7+26 and 7+19 encoded by the *Glu-B1* locus.

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1. Introduction

The hexaploid triticale (\times *Triticosecale* Wittmack) (AABBRR) created by crossing species of wheat (*Triticum*) (AABB) and rye (*Secale*) (RR) combines the properties of both parental cereals. Triticale has the high yield potential and grain quality of wheat and the resistance to pathogens of rye. When compared to wheats, modern hexaploid winter triticale cultivars show higher yields and good adaptation to northern environments. Their flour is rich in proteins (average 14–15%), suggesting a promising use for the production of human foods (Täht et al., 1998; Varughese, Pfeiffer, & Peña, 1996).

The good growing areas for triticale are Middle and South Europe – Germany, the Czech Republic, Poland,

Austria, Portugal (Igrejas, Guedes-Pinto, Carnide, & Branlard, 1999; Lafferty & Lelley, 2001; Šašek et al., 1988; Weipert, 1996; Wolski, 1986), USA (Varughese et al., 1996), Canada (Bushuk & Larter, 1980), Australia (Cooper, 1986), and Greece (Doxastakis, Zafiriadis, Irakli, Marlani, & Tananaki, 2002).

Estonia belongs to northern countries where it is still possible to cultivate rye, wheat, and triticale. The problems are caused by Estonian climate (cool, moist, rainy) – crops have unstable yields and low quality. Systematic investigation of triticale as a perspective food-fodder and technical culture was initiated in Estonia by the Estonian Agricultural University and Tallinn Technical University in 1995 (Laur, Jaama, Kasearu, & Vooremäe, 1997). In 1996 and 1997 a field trial with cultivars originated from Germany and Sweden was carried out at the Jõgeva Plant Breeding Institute with the cultivars Modus, SV 92280, Dato and Vision, and 9 breeding lines (Tupits & Kukk, 1999). The trials showed that the cultivars of triticale had yielding capacity exceeding that of wheat and rye ones,

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and medium winter hardness in Estonian climatic conditions.

The quality of kernel is a complex of physical and chemical characteristics whose expression depends on their genetic nature and influence of environment (Johansson, 2002; Johansson & Svensson, 1998). Methods of predicting genetically better cultivars and breeding lines are of great importance. The investigation of storage proteins of cereals by methods of electrophoresis is a useful tool for these purposes. Various allelic variants of the genes for the high-molecular-weight subunits of glutenin are particularly important for determining wheat gluten and dough elasticity (Payne, 1987; Shewry, Popineau, Lafiandra, & Belton, 2001) using for these purposes only half a kernel and being as predictors of grain quality. The verified correlations between bread-making quality and occurrence of specific HMW subunits of glutenin have been taken advantage of by wheat breeders, using SDS-PAGE of proteins as screening test for bread-making quality (Johansson, Svensson, & Heneen, 1995). The variation in high-molecular-weight glutenin subunit composition has been reported to account for up to 70% of the variation in breadmaking quality of European wheats (Branlard & Dardevet, 1985).

In hexaploid wheat (*Triticum aestivum* L.) the HMW glutenin subunits are encoded by genes located on chromosomes 1A, 1B, and 1D, in hexaploid triticale - on chromosomes 1A, 1B, and 2R. In the investigation of the *Glu-1* alleles (Brzezinski & Lukaszewski, 1998) it was shown that the gene pool of hexaploid winter triticale contains relatively high proportion of the *Glu-1* alleles, which correlates well with good bread-making quality.

During the mixing of wheat or other cereal flour with water to make dough, proteins form gluten that is the basis of dough functionality. Gluten can be divided into two groups – gliadins and glutenins, which together confer the properties of elasticity (strength) and extensibility (viscosity) (Kasarda, 1989). These unique properties of wheat gluten are the basis of the wide range of wheat-derived food products. Since the wheat parent of hexaploid triticale originates from tetraploid wheat and does not contain the D-genome, it also lacks the bread-making quality of hexaploid wheat (Lafferty & Lelley, 2001).

Because of influence of pentosans and α -amylase, the baking quality of rye is lower than that of wheat. As the genome of triticale contains the chromosomes of rye, the secalins encoded by rye chromosomes have a noticeable influence on the bread quality of triticale. The presence of the 1RS segment in triticale is responsible for significant reduction in rheological properties and overall gluten strength, and significant increase in dough stickiness (Peña & Amaya, 1992).

The contribution of the seed storage protein groups to dough properties of wheat flour has been studied extensively (Branlard & Dardevet, 1985; Branlard, Dardevet, Saccomano, Lagoutte, & Gourdon, 2001;

Gupta & Mac Ritchie, 1994; Hamer, Weegels, & Marseille, 1992; Payne, 1987; Sontag-Strohm & Juuti, 1997; Uhlen, 1990). The functional properties of triticale proteins, such as water absorption, viscosity, gelation, which influenced by agronomic factors, and storage, composition and processing of bread have been neglected (Dervas, Doxastakis, Hadjisavva-Zinoviadi, & Triantafyllakos, 1999).

The aim of the present study was: (1) to find the most suitable triticale cultivars to be used in local brown and white bread industry; (2) to study the influence of the alleles at *Glu-1* loci on bread-making quality.

2. Materials and methods

2.1. Materials

Seed samples of 12 hexaploid triticale cultivars were obtained from the Jõgeva Plant Breeding Institute, Viljandi Control Centre of Plant Production (Estonia), and Svalöf (Sweden). Among them the cultivars Lasko, Prego, Pinokio, Dagro, Tewo, Presto are originated from Poland, SW 98578 and SV 92280 – from Sweden, Dato, Vision, Modus – from Germany, Moreno – from the USA.

The cultivars were grown in Estonia since 1995, and the biochemical and baking investigations were performed in 1999–2001. The experiments were carried out at Tallinn Technical University (gluten content, baking), at the Institute of Experimental Biology of the Estonian Agricultural University (HMW glutenin subunit composition), and at Estonian Control Centre of Plant Production (protein and moisture content, falling number, Zeleny sedimentation test, water absorption).

2.2. Chemical analyses

Grains were milled in PERTEN instruments mill 3170 and QC-109 Labhim mill to pass a 0.8 mm screen.

Nitrogen content was determined by using Kjeltac 1015 digester and Kjeltac Auto 1030 Analyser on wholemeal flour and is presented on a dry weight basis (Tecator Application Note, 1987). Nitrogen content was multiplied by a factor of 5.7 to determine protein content in wheat and triticale and 6.25 (ICC Draft Standard No. 167) to determine protein content in rye. All the determinations were expressed on a dry weight basis. Moisture content was determined by drying the samples at 105 °C to constant weight.

Crude gluten in the flour was determined by ICC standard No. 137/1982 using a Glutomatic 2200 instrument on white flour milled on a Brabender Quadromat Junior which gave extraction rates of 55–65%. A dough was prepared from a flour sample by adding a buffered 2% sodium chloride solution. Gluten washing was carried out

by Glutomatic 2200 using a solution of 2% sodium chloride. The residual water adherent to the gluten was removed by centrifugation and the remainder weighed.

2.3. Zeleny sedimentation test

For Zeleny sedimentation test the grains were milled on a special Brabender OHG Duisburg mill which gave extraction rates of 8–10%. The test was performed according to the procedure of EVS 765:2000 (the standard of the Estonian Republic; ICC, 1972, 1982). 3.2 g flour was weighed and placed in a 100 ml cylinder, and mixed for 5 min. 25 ml of test solution (180 ml of lactic acid and 200 ml isopropanol) was added to obtain a final concentration of the solution 3.5% of lactic acid and 17.5% of isopropanol. The cylinder was shaken for 10 min, and 5 min later the volume of the sediment was measured.

2.4. Falling number

Falling number which represents the activity of α -amylase was estimated with Falling Number 1800 according to the procedure of EVS 654:1999 (the standard of the Estonian Republic; ICC Standard No. 107/1). The method is based on the rapid gelatinisation of a suspension of flour in a boiling water bath and the subsequent measurement of the liquefaction of starch by alpha amylase present in the sample.

The grains were milled with a special PERTEN instruments mill for falling number. The flour and water suspension (7 ± 0.05 g flour and 25 ml water) was placed in viscometer tube into a boiling water bath. The time in seconds needed by the stirrer of viscometer to drop down is falling number.

2.5. Electrophoresis

Total proteins were extracted from individually ground grains in a mortar with a pestle until a fine powder was obtained. Reduced protein extracts were obtained by incubating the samples in SDS–Tris–HCl buffer pH 6.8 containing 0.125 M Tris, 2.75% sodium dodecyl sulphate (SDS), 10% (v/v) glycerol, 1% (w/v) DTT, and 0.005% bromophenol blue for 1 h at 70 °C. After centrifugation (14,000 rpm, 10 min), 20 μ l of supernatant was used for electrophoresis. HMW glutenin subunits were separated in the presence of SDS at pH 8.3 for 22 h at 10 mA on 10% polyacrylamide gel. The running buffer contained 0.2 M glycine, 0.05 M Tris pH 8.3 and 0.1% SDS. After electrophoresis the gels were stained overnight with 0.05% Coomassie Brilliant Blue R-250 in water–methanol–glacial acetic acid (53:40:7) and destained in the solution of the same components (68:25:7), and photographed (D'Ovidio, Lafiandra, & Porceddu, 1996; Tohver, Täht, Kann, & Rahnu, 2000; Tohver, Kann, Täht, & Mihhalevski, 2001). The desig-

nation of triticale bands was performed on the basis of wheat genome, and HMW glutenin subunit bands were analysed according to the nomenclature of Payne and Lawrence (1983), UPOV (1994), and Brzezinski and Lukaszewski (1998).

2.6. Baking test

The baking formula was a typical wheat bread formula, but the wheat whole-grain flour was mixed with 10–70% triticale wholegrain flour (Table 1). Emulsifiers DRIV (E 471, E 260, E 262), Lecimax (E 472, E 300) and Balt (E 263, E 300) were also included in the bread formulas. The mix used was composed of non-fat milk powder, margarine, sugar, salt and baking yeast. Baking was performed using an automatic Panasonic™ baker's oven (Täht et al., 1998).

Spring wheat cultivar Heta was used in baking experiments (protein, 13.2%; FN, 376 s; Wac, 83.0%). Triticale flour was substituted for wheat flour up to 70% (Table 4). Flour (or flour blends) were stirred for 1 min in the bowl before adding the other ingredients (salt and yeast). Yeast was activated by warm water and sugar. The dough was mixed up to homogeneous consistency and then put into a fermentation cabinet at 31 ± 1 °C for 175 min at a relative humidity of 85%. The dough was scaled at 550 g, moulded, placed in a baking pan and returned to the fermentation cabinet, and proofed for 35 min at 35 ± 1 °C. After proofing the doughs of pan and round bread were baked in the oven for 40 min at 230 °C and for 30 min at 250 °C, respectively. The amount of water to be used was determined by the absorption value. Water absorption (Wac) was determined by centrifugation method (AOAC, 1984).

2.7. Bread volume

The loaf volumes were measured after baking using the rapeseed displacement method (AACC, 1983).

2.8. Statistical analysis

Statistical calculations (correlation coefficients and SD) were made using of MS Excel statistical package.

Table 1
Recipe of experimental breads (30% of triticale in wheat-triticale breads)

Ingredient	Amount (g)
Wheat flour	210
Triticale flour	90
Sugar	15
Milk powder	12
Margarin	10
Salt	5
Yeast	9
Water	210

3. Results and discussion

3.1. Grain protein and gluten content

Data describing the properties of triticale flour, dough, and the allelic variants of HMW gluten subunits for 13 cultivars are presented in Tables 2 and 3.

Protein content of flour is extremely important because almost all flour properties (gluten content, water absorption, mixing requirement, loaf volume) are highly correlated with protein content (Pomeranz, 1985). In 1999–2001 the protein content in the investigated cultivars varied from 9.7–14.5% with the average of 11.8% and with SD of 1.44. Protein content was higher in genotypes with HMW glutenin subunits 2* coded by the locus *Glu-A1*, and 7+19 and 7+26 coded by the *Glu-B1* (Table 3). Influence of environmental factors is dem-

onstrated on the examples of the cultivar Tewo (Table 2). Tewo 1 and Tewo 2 are the same cultivar, grown up in a different environment. Tewo 2 had a higher protein content and falling number, lower bread volume and Zeleny number. In Estonia where the summer climate is variable, the lower protein content and falling number for Tewo 1 could be related with the different weather conditions in northern and southern Estonia. Tewo 1 was grown in southern and Tewo 2 in northern Estonia. Northern Estonia differs from southern area in the average of summer temperatures and in amount of rainfalls.

Gluten content was generally low, and in some cases was not detectable. The absence of gluten shows that triticale protein behaves as that of rye, and is too low to yield good quality bread. Correlation between protein content and volume of bread was positively significant

Table 2
The properties of dough and gluten of triticale cultivars

Cultivar	<i>Glu-A1</i>	<i>Glu-B1</i>	Gluten (%)	GPC (%)	FN (s)	VB (%)	Zeleny (ml)	Wac (%)
Lasko	2*	7+19	0	12.8	240	96.8	–	–
Prego	N	7+8	0	11.2	357	73.0	–	–
Pinokio	2*	13+16	4.2	10.4	200	73.0	–	–
Dagro	N	7+19	0	9.7	62	75.8	–	–
Presto	2*	7+26	26.5	13.7	180	97.0	17.3	55.5
Tewo 1	2*	7+19	0	12.6	88	109.8	21.0	56.1
Tewo 2	2*	7+19	0	14.5	195	94.4	17.3	65.0
Vision	2*	7+19	0	11.6	89	–	10.5	90.3
Dato	2*	7+19	19.0	12.5	128	90.1	17.0	90.3
	N	6+8						
Modus	N	7+26	16.0	11.0	–	88.3	–	87.5
SW 98578	N	13+16	0	9.7	62	75.8	–	–
SV 92280	2*	6+8	8.0	12.3	182	88.6	–	87.5
Moreno	2*	6+8	0	11.8	240	104.2	21.0	61.9
		7+26						
Average of columns				11.83	168.58	88.9	17.35	74.26
SD				1.44	87.85	12.36	3.84	15.97

GPC, grain protein content; FN, falling number; VB, volume of triticale bread with 30% of wheat flour – % from control wheat bread; Wac, water absorption; N, null allele; –, not determined; 0, not detectable. The data are the averages of three repetitions.

Table 3
Dough and gluten properties of allelic variants of triticale

Genotype	<i>n</i>	GPC (%)	Wac (%)	Zeleny (ml)	FN (s)	VB (%)	
<i>Glu-A1</i>	<i>Glu-B1</i>						
2*	6+8	2	12.1	74.7	21.0	211	96.4
2*	7+19	5	12.8	75.4	16.4	149	97.8
2*	7+26	1	13.7	55.5	17.3	180	97.0
2*	13+16	1	10.4	–	–	131	74.4
N	13+16	1	9.7	–	–	62	75.8
N	7+8	1	11.2	–	–	357	73.0
N	7+19	1	9.7	–	–	62	75.8
N	7+26	1	11.0	87.5	–	–	88.3
Average			11.37	73.25	18.23	164.57	84.81
SD			1.45	13.22	2.43	101.52	11.17

GPC, grain protein content; Wac, water absorption; FN, falling number; VB, volume of bread – % from control wheat bread; *n*, number of cultivars.

($r = +0.696 \pm 0.228$), significantly negative between water absorption ($r = -0.559 \pm 0.339$), positive, but not significant between Zeleny number ($r = 0.177 \pm 0.492$). The rye proteins are not able to form gluten because of the structure of proteins, high content of pentosans, and high activity of alpha amylase (Weipert, 1996). In the cases of HMW glutenin subunits 2*, 7+19 and 7+26, gluten content was somewhat higher.

3.2. Falling number

The falling number influences the dough characteristics and bread properties, and shows also the preharvest sprouting. Preharvest sprouting is considered to be the main argument against using triticale for bread-making in regions with a moist climate. Investigating a large number of triticale cultivars enables to select the cultivars with satisfying quality. The viscoelastic properties of dough, as well as its ability to hold gas during fermentation and maintain the loaf shape, are found to be affected by the values of falling number. An extensive starch degradation prevents the formation of a sticky dough (Lafferty & Lelley, 2001). Flour with the optimum falling number is required to produce an optimum dough and optimum bread. Quite satisfactory baking performance showed flours with falling numbers 220–250 s, but poor results were obtained using flours with falling numbers below 120 s (Ingver & Koppel, 1998; Veskus & Kann, 1997). The falling numbers of investigated triticale cultivars varied from very low (62 s for SW 98578 and Dagro) and accordingly low volume of bread (75.8% from control wheat bread) to too high (357 s for Prego). Triticale flour with low falling number gives a soft dough which may be too fluid to bake into bread. Flour with high (more than 300 s) falling number yields a relatively stable dough, but the bread structure will be dense and its consistency hard. Volume of bread was satisfying in the case of cultivars Lasko, Presto, Tewo1 and Moreno (falling numbers 245, 180, 109.8 and 240, respectively). Although the falling number is considered as a varietal property, weather conditions have a marked effect on this grain quality characteristic (Tewo 1 and Tewo 2, Table 2).

3.3. Zeleny number

The Zeleny sedimentation value (SDS-sedimentation) was determined as one of the parameters for bread-making quality. The SDS-sedimentation values of the tested triticale cultivars varied from 10.5 to 21.0 ml, and were comparable to data for triticale cultivars found by Brzezinski and Lukaszewski (1998). These values are too low for good bread-making quality. The cultivars differing in *Glu-B1* alleles showed a slightly, though not significantly, higher sedimentation value in the presence of subunits 7+19 and 7+26. In these cases the volume of

bread was highest. Earlier it was shown that subunits 1 and 2* encoded by chromosome 1A, and 6+8, 7+8 and 7+9 encoded by chromosome 1B do not correlate with strong gluten (Payne, Nightingale, Krattinger, & Holt, 1987; Uhlen, 1990). Other authors (Johansson et al., 1995) demonstrated that subunit 2* had a fairly good quality score showing a slight positive correlation with the Zeleny sedimentation volume. This agrees with the findings of the present work. Correlation between Zeleny number and volume of bread was significantly positive ($r = +0.931 \pm 0.216$), negative correlation was estimated between Zeleny number and water absorption ($r = -0.723 \pm 0.346$). As the falling and Zeleny numbers were low, the triticale breads were baked with an addition of wheat flour.

3.4. Baking

The results of the baking test are presented in Tables 2 and 4. Water absorption and dough consistency are important in relation to mixing, dividing, panning and proofing steps (Kasearu et al., 1997). For optimum development the dough must attain a balance between elastic and viscous properties. The dough should be neither too elastic nor too extensible. Water absorption is considered to be good if it remains in the range of 55–65% (Kasearu et al., 1997). In this investigation water absorption level was negatively correlated with loaf volume ($r = -0.831 \pm 0.249$) and protein content ($r = -0.559 \pm 0.339$). Table 2 demonstrates that Wac of the cultivars Vision, Dato, Modus and SV 92280 are too high for good bread. The loaf volume which is generally regarded as an important quality criterion is biggest for bread baked from flour of 12.6% protein content, of 21 ml Zeleny number, falling number of 88 s and Wac of 56.1%. The flour from the cultivar Moreno gave a good volume of bread with protein content of 12.7%, Zeleny number of 21 ml, falling number of 240 and Wac of 61.9%. It is in good accordance with the results concerning water absorption and protein content, however, falling number 88 s was too low for good bread. Therefore, experiments were carried out to bake breads with wheat additions. Loaf volumes of wheat breads prepared with triticale additions of 30%, 50% and 70% were comparable with that of 100% wheat bread (Table 4).

Table 4
Volume of bread (% from control wheat bread)

Cultivar	% of triticale flour		
	30%	50%	70%
Tewo1	109.8	104.9	101.4
Tewo 2	94.4	97.2	88.7
Moreno	104.2	99.3	102.8
Presto	97.9	94.4	91.6
Average	96.13	98.95	96.13
SD	6.81	4.44	7.02

This agrees with the data reported by Doxastakis et al. (2002), and Peña and Amaya (1992), that the triticale flour blends (up to 50%) with wheat flours produce breads with quality similar to that of breads made from wheat flours only. Sensory evaluation studies indicate that triticale can be used satisfactorily as a good ingredient in bread-making. All the loaves baked from flour of different cultivars of triticale mixed with wheat flour proved to be of acceptable quality and fit for human consumption. All the loaves had a pleasant yellow colour, a fresh and pleasant smell and taste (Tohver et al., 2000; Täht et al., 1998).

3.5. HMW glutenin subunits and baking quality

It is now well established that the glutenin fraction is the most important fraction related to bread-making quality (Branlard et al., 2001; Mac Ritchie, Du Cross, & Wrigley, 1990; Shewry et al., 2001). The high-molecular-weight (HMW) subunits of glutenin are considered to be most important for baking quality (Branlard & Dardevet, 1985; Gupta & Mac Ritchie, 1994; Kasarda, 1989) because the composition of gluten proteins is genetically determined and environmentally stable. Separation of HMW glutenin subunits is shown in Fig. 1 and Table 2.

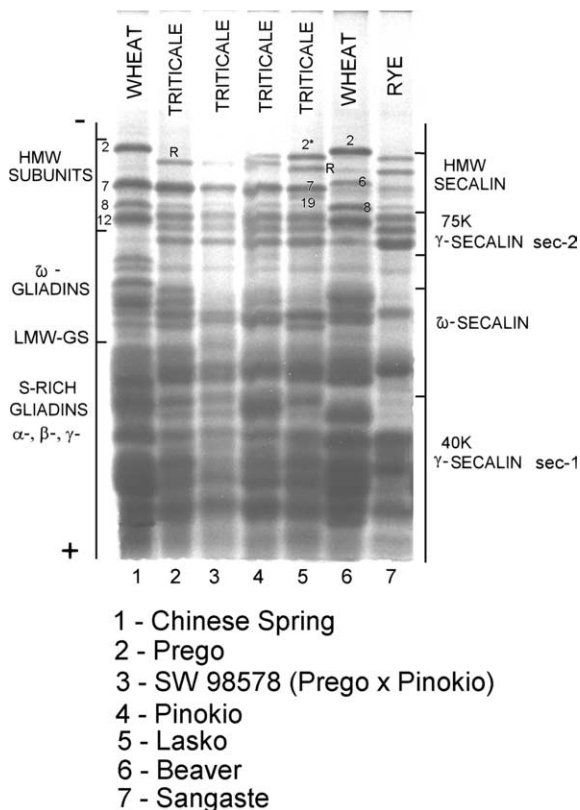


Fig. 1. SDS-PAGE of total protein fractions extracted from single seeds of wheat, rye and triticale cultivars. 1. Chinese Spring, 2. Prego, 3. SW 98578, 4. Pinokia, 5. Lasko, 6. Beaver, 7. Sangaste.

The comparison of the electrophoregram patterns of triticale cultivars with those of rye and wheat showed that most of the rye and wheat bands can be found in triticale patterns. The glutenin patterns of the cultivars Dato, Prego, and SW 98578 are more similar to the glutenin pattern of rye, whereas the glutenin pattern of Modus is closer to that of wheat.

Seven different alleles were revealed in the sample of 12 triticale cultivars: two at the *Glu-A1* locus, five at *Glu-B1*. Most frequent HMW glutenin subunits were 2* at the *Glu-A1* locus, and 7+19 at the *Glu-B1*. The genetic diversity resulting from two loci analysed enabled to distinguish 9 different patterns from 12 cultivars of triticale grown in Estonia. Most of the cultivars were uniform in their SDS electrophoretic patterns, some were heterogeneous having different alleles at the *Glu-I* locus: two variations were found for the Moreno (bands 6+8 and 7+26 at *Glu-B1*) and for Dato (bands 6+8 and 7+19 at *Glu-B1*, and N and 2* at *Glu-A1*). Polymorphism to be true for amphiploids if one of the parental species (rye) is characteristically an open-pollinating type (Virdi & Larter, 1984).

It was demonstrated that subunit 2* had a fairly good quality score, showing a slight positive correlation with the Zeleny sedimentation volume (Johansson et al., 1995). Other authors showed that subunits 1 and 2* encoded by chromosome 1A, and 6+8, 7+8 and 7+9 encoded by 1B did not correlate with strong gluten (Johansson et al., 1995; Payne et al., 1987; Uhlen, 1990). In the present investigation subunit 2* encoded by *Glu-A1*, and subunits 7+19 and 7+26 encoded by *Glu-B1* (Tables 2 and 3) were positively correlated with gluten and protein content, water absorption and bread volume. Using much more cultivars, the influence of the high-molecular-weight glutenin subunits on the technological qualities and the baking quality of triticale become clearer.

4. Conclusions

1. The baking test has shown that many cultivars of hexaploid triticale can be used in bread-making, mixing the wheat flour with up to 70% triticale amount.
2. Considering the allelic composition, the best cultivars would be Lasko, Pinokio, Prego, Dagro, Moreno, Presto, Tewo, Vision, Dato. Considering the indices characterising the bread-making properties (falling number, protein content, Zeleny number, water absorption capacity, and bread volume), Moreno, Presto, Tewo, Dato and SV 92280 were the best cultivars. This was in good accordance with the data about HMW glutenin subunit composition.
3. The baking quality of triticale cultivars was higher with HMW glutenin subunits 2* coded by the locus *Glu-A1*, and 7+26 and 7+19 coded by the locus *Glu-B1*.

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