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ALLELIC COMPOSITION OF GLIADIN-CODING LOCI AS A 'PORTRAIT' IN SPRING SOFT WHEAT SELECTIONS OF RUSSIAN AND KAZAKH ORIGINS

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SUMMARY

The progressive study determined the gliadin 'profile' and genetic diversity based on allelic variations of gliadin-coding loci in spring soft wheat (*Triticum aestivum* L.) selection from Russian and Kazakh origins. A total of 139 samples obtained from a spring soft wheat collection consisting of 62 from Russia and 77 from Kazakhstan were studied. As a result of electrophoretic analysis in Russian wheat, the share of monomorphic gliadin cultivars was 63% and polymorphic was 37%. However, in the Kazakh wheat collection, the share of polymorphic gliadin cultivars was 26%. The alleles were mostly found among the Russian cultivars, i.e., *Gli-A1f* (46.9%), *Gli-B1e* (43.7%), *Gli-B1b* (30.8%), *Gli-D1a* (61.0%), *Gli-A2l* (17.0%), *Gli-A2m* (16.9%), *Gli-B2o* (16.1%), and *Gli-D2q* (19.8%). In wheat genotypes collected from Kazakhstan, the following alleles dominated, i.e., *Gli-A1f* (47.4%), *Gli-B1e* (72.0%), *Gli-D1a* (61.7%), *Gli-A2l* (25.3%), *Gli-A2s* (16.2%), *Gli-B2r* (25.7%), and *Gli-D2a* (40.3%). The study compiled the so-called 'ideal' electrophoretic spectrum of gliadin for several countries to visualize the 'portrait' of wheat, created based on common blocks of gliadin identified by the researchers at different times. It assumed that cultivars close to the 'ideal' spectrum in gliadin alleles should have a complex of economically valuable features. For example, the spectrum of Russian wheat consists of the blocks of components controlled by alleles, i.e., ***f, e, a, q, o, e***. As for the Kazakh wheat, its 'ideal' spectrum (***f, e, a, l, r, a***) coincides with the spectrum of Russian wheat at the loci *Gli-1*, as Russian cultivars were often taken as parental genotypes by the Kazakhstan breeders.

Keywords: spring soft wheat (*Triticum aestivum* L.), germplasm, breeding, gliadin, *Gli*-locus, polymorphism

Key findings: The concept of the 'ideal' electrophoretic spectrum of gliadin for specific climatic conditions is proposed, which implies that cultivars in which the spectrum of gliadin is close to 'ideal' can have a complex of economically valuable features.

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INTRODUCTION

For decades, scientists authenticated that wheat seed storage protein (gliadin) can be used to distinguish cultivars from one another (Autran *et al*., 1979; Metakovsky, 1991; Watry *et al*., 2020). Differences in gliadin spectra are associated with the allelic diversity localized in

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the chief loci, i.e., *Gli-A1, Gli-B1, Gli-D1, Gli-A2, Gli-B2,* and *Gli-D2*. The alleles at one locus control the synthesis of several components of gliadin, which are genetically linked in a composite form. Similarly, gliadin blocks may differ in intensity, electrophoretic mobility, and molecular weight of the components (Sozinov and Poperelya, 1980: Obukhova and Shumny, 2016). The use of buffer mixtures containing lactic (Bushuk and Zillman, 1978, Metakovsky *et al*., 1984: Branlard *et al*., 1990; Utebayev *et al*., 2019; Watry *et al*., 2020), formic (Kozub *et al*., 2009), and acetic (Clements, 1988; Konarev *et al*., 2005) acids determines the total gliadin by electrophoresis on a polyacrylamide gel.

Based on the study of the world wheat collection, allelic blocks of gliadin are identified and collected in catalogs for bread wheat (Metakovsky, 1991; Metakovsky *et al.*, 2018) and durum wheat (Melnikova *et al.*, 2012). Several studies also confirmed wheat cultivars created in certain climatic conditions could have similarities to each other for some alleles of gliadin-coding loci (Aguiriano *et al.*, 2008; Salavati *et al.*, 2008; Novoselskaya-Dragovich *et al.*, 2011; Hailegiorgis *et al.*, 2017; Utebayev *et al.*, 2019), although no distinct allele selections were fulfilled. The reason could probably be due to the linkage of these alleles to some genes that influence the crucial traits in wheat (Xynias *et al.*, 2006). Therefore, the common alleles of gliadin in specific climatic conditions can serve to identify other cultivars and as markers of valuable features of the breeding programs.

Currently, various DNA markers are widely used to identify the genotypic status of various crop plants (Shavrukov, 2016; Scheben *et al.*, 2017). The use of DNA markers made it possible to study the genes that control protein accumulation, gluten strength, and 1000 grains mass (Burridge *et al.*, 2018), hardness (Zhang *et al.*, 2018), the yield of flour during wheat grinding (Nirmal *et al.*, 2016), and quality of bread (Nirmal *et al.*, 2017). The newest technique was genome editing with the CRISPR/Cas9 system (Knott and Doudna, 2018), which helps create low-gluten wheat lines (Sánchez-León *et al.*, 2018), required for the nutrition of people with an allergic reaction—gluten enteropathy caused by certain fractions of gliadin (Palosuo *et al.*, 2001; Pastorello *et al.*, 2007).

Development and application of modern Omics- and DNA technologies (Goel *et al.*, 2020; Faryad *et al.*, 2021), used for the improvement of crop plants, made it possible to propose the so-called strategy '5Gs for crop genetic improvement', which include five areas, i.e., *1G* - genome, *2G* – germplasm or '*2G-hermaplasma*', *3G* - genes, *4G* - genomic selection, and *5G* - gene editing (Varshney *et al*., 2020). Relatedly, to implement the direction of *2G-hermaplasma*, it is necessary to use effective tools to study a large genetic array of crops. The use of modern molecular methods successfully solved the problems of identification and localization of certain genes and foreign translocations in the wheat collection (Tiwari *et al.*, 2014). The genotyping technique with SNP high-density markers has shown its effectiveness in identifying wheat cultivars (Shavrukov, 2016). The general trend toward plant research is probably an artificial creation of reference genomic variations of crops at the genus level (Alonge *et al.*, 2020; Liu *et al.*, 2020; Song *et al.*, 2020). However, with all the advantages of using DNA markers, several significant drawbacks also ensued, i.e., the high cost of equipment, consumables, and the creation of specific conditions, which limits the conduction of such research at this level.

Hence, using substances of protein origin, such as, enzymes and reserve proteins as genetic markers to implement the "*2G-hermaplasma*" process can serve as an effective alternative (Shewry and Halford, 2001; Al-Doss *et al*., 2010; Akhtariyeva *et al.*, 2019). Since protein synthesis is controlled by sections of genomic DNA, and the environment impacting biochemical and structural-functional features, the plant data based on protein polymorphism may not be inferior in informativeness of DNA markers. An additional advantage of using protein markers in identification and plant breeding is that inexpensive equipment makes analysis easy. In addition, the applied native and denaturing electrophoresis of prolamins is still used in the study of genetic control of reserve proteins synthesis in cereals (Pflüger *et al.*, 2001) and oats (Lyubimova *et al.*, 2020) and the identification of crop cultivars in alfalfa (Kakaei and Ahmadian, 2021).

Additionally, the studies on protein polymorphism may also provide the basis for a strategy for selecting wheat genotypes with a specific combination of gliadin alleles based on molecular methods. Consequently, the study of genetic resources, from various countries with different climatic conditions based on the polymorphism of wheat prolamins, will help identify and trace the selection criteria and establish the gliadin 'profile' of the wheat genotypes for specific conditions.

Thus, this study aims to: determine the gliadin 'profile' in the spring soft wheat

(*Triticum aestivum* L.) collection in the Russian and Kazakh regions, and determine genetic diversity through allelic variations in gliadin coding loci.

MATERIALS AND METHODS

A total of 139 samples obtained from a spring soft wheat collection comprising 62 from Russia (the Western Siberia region) and 77 samples from Kazakhstan (the regions of Central, Eastern, and Western Kazakhstan) were studied. The study followed the methodology proposed by Metakovsky and Novoselskaya (1991) in conducting the electrophoresis process of gliadin. Gliadins were extracted from individually milled seeds by adding 150 µL of 70% ethanol. Acrylamide polymerization was initiated using 50 µL of 3% H_2O_2 in 45 mL of gel solution. Electrophoresis was conducted at 520 V for 4 h. The experiment used 10% trichloroacetic acid supplied with 0.05% of Coomassie Brilliant Blue R-250 in ethanol (Sigma-Aldrich, USA) for gel fixation and staining. The identification of gliadins 'profile' was done as per the catalogue of alleles of gliadin-coding loci (Metakovsky, 1991). According to the wheat gene catalogue, the designation of gliadin loci were *Gli-A1, Gli-B1, Gli-D1, Gli-A2, Gli-B2*, and *Gli-D2* (McIntosh *et al.*, 2008). Alleles of loci were designated by letters of the Latin alphabet in sequence, i.e., for example, the genetic formula of the wheat cultivar, Chinese Spring: *Gli-A1a, Gli-B1a, Gli-D1a, Gli-A2a, Gli-B2a, Gli-D2a*, will have an abbreviated notation: *a, a, a, a, a, a*.

Statistical analysis

The data compilation and analysis were carried out based on previously published studies of gliadin-coding loci (Metakovsky *et al.*, 1993, 1994, 2000; Metakovsky and Branlard, 1998; Dobrotvorskaya *et al.*, 2009; Nikolaev *et al.*, 2009; Novoselskaya-Dragovich *et al.*, 2011, 2013; Utebayev *et al.*, 2016, 2019).

The formulation of intra-population diversity (μ), the proportion of rare alleles (h), the identity criterion (I), and the similarity index (r) was done according to Zhivotovsky (1979, 1991), and the degree of genetic diversity (H) was calculated according to Nei (1973) as follows:

$$H = 1 - \sum p_i^2$$

where:
p_i = is the allele frequency calculated by the formula,
$p = n/N$, where n is the number of alleles, and
N = is the sample volume.

RESULTS

In the spring soft wheat (*Triticum aestivum* L.) collection from Russia and Kazakhstan, Table 1 presents the alleles of identified loci *Gli-1* and *Gli-2*. Electrophoretic analysis of Russian wheat revealed that both monomorphic (63%, 39 out of 62 samples) and polymorphic (37%, 23 of 62 samples) can serve as gliadin samples. The analysis of the genetic formulas of gliadin showed that in the loci *Gli-A1, Gli-B1, Gli-D1*, the alleles *Gli-A1f* (46.9%), *Gli-B1e* (43.7%), *Gli-B1b* (30.8%), and *Gli-D1a* (61.0%) were most frequent. The loci *Gli-A2, Gli-B2,* and *Gli-D2* were dominated by the alleles *Gli-A2l* (17.0%), *Gli-A2m* (16.9%), *Gli-B2o* (16.1%), *Gli-B2r* (14.5%), *Gli-D2q* (19.8%), and *Gli-D2a* (17.7%). Around eight to 17 alleles have been identified for each locus (Figure 1).

The electrophoregram analysis of the Kazakh wheat collection showed that about 26.0% (20 out of 77) of the samples were polymorphic at the gliadin loci. The most common alleles of loci *Gli-1* of Kazakh wheat partially coincide with the frequencies of Russian wheat (Figure 1). The occurrence of the allele *Gli-A1f* in Kazakh wheat was 47.4%, whereas in Russian, it was 46.9%. The locus *Gli-B1* in Kazakh wheat was dominated by the allele *Gli-B1e* with a frequency of 72.0%, and in Russian wheat alleles, i.e., *b* (30.1%) and *e* (43.7%). The share of rare alleles (h), the degree of genetic diversity (H), and the intra-population diversity (μ) of the wheat collection from Kazakh and Russia were calculated based on allele frequencies (Table 2).

For both wheat groups, the indicators of intra-population and genetic diversities ranged from 0.45 (*Gli-B1*, Kazakhstan) to 0.91 (*Gli-B2*, Siberia) (Table 2). The greatest value of μ and H for both wheat groups was noted for the locus *Gli-B2*, which is due to the presence of the highest number of identified alleles. On average, the greatest diversity in gliadin-coding loci is recognized in Russian wheat samples. The indicator of the rare alleles proportion (h) characterizes the distribution of frequencies, which, when uneven, is always *h*

Table 1. Gliadin genetic formulas of bread wheat from Russia and Kazakhstan.

Cultivars/advanced lines	Gliadin-coding loci (*Gli*)					
	A1	*B1*	*D1*	*A2*	*B2*	*D2*
Bread wheat from Russia						
Aviada	*m*	*b*	*a*	*d*	*v*	*q*
Adelina	*l*	*a*	*g*	*a*	*a*	*l*
GAU 21-2018	*d+g+i*	*l*	*f*	*d+l*	*r*	*i*
GAU 6-2018	*f*	*e*	*b*	*l*	*a*	*q*
Zlatozara	*k*	*b*	*h**	*b*	*v*	*m*
Ikar	*l*	*n*	*a*	*b*	*b*	*o*
Il'inskaya	*f*	*f*	*a*	*m*	*d*	*p*
Latona	*f*	*e*	*a*	*m+q*	*d*	*q*
Line TGU-1	*f*	*l*	*g*	*f**	*r*	*a*
Lutescens 585	*f*	*e*	*a*	*f*	*o*	*a*
Lutescens 70	*f*	*f*	*b*	*q+f*	*b+k*	*b+m*
Rechka	*c*	*b*	*a*	*l+g*	*r+o*	*m+a*
Riks	*o*	*b*	*b*	*f*	*o*	*q*
Serebrina	*b+o*	*e*	*a*	*f*	*n*	*m*
SKENT-1	*f*	*b*	*a**	*f*	*m*	*q*
SKENT-3	*a*	*e*	*b*	*f*	*t*	*a*
Surenta - 3	*f*	*f*	*n+a*	*m+q*	*b*	*b*
Surenta - 4	*f+o*	*b+e*	*a*	*k+f*	*o+t*	*l+p*
Surenta - 5	*a*	*e*	*a*	*s*	*r*	*r*
Surenta - 6	*f*	*e*	*b*	*m+q*	*m+i*	*b+q*
Surenta -7	*f*	*e*	*b*	*m*	*l*	*q*
Turinskaya	*o*	*b*	*a*	*m*	*c*	*m*
Tyumenets 2	*i*	*e*	*a*	*a*	*p*	*k*
Tyumenochka	*c*	*l*	*h*	*l*	*r*	*q*
Tyumenskaya 25	*f*	*e*	*a*	*q*	*a*	*k*
Tyumenskaya 27	*f*	*e*	*a*	*f*	*o*	*a*
Tyumenskaya 29	*k+a+f*	*e*	*a*	*m+i*	*o*	*q*
Tyumenskaya 30	*f*	*f+e*	*f+h*	*m+s*	*m+a*	*q+o*
Tyumenskaya 31	*c*	*b*	*i*	*m*	*r*	*a*
Tyumenskaya 32	*m*	*b*	*f*	*m*	*t*	*j*
Tyumenskaya 33	*f*	*e*	*a*	*m*	*o*	*q*
Tyumenskaya 80	*k*	*b*	*f*	*k*	*r*	*n*
Tyumenskaya yubileynaya	*f*	*l+e*	*l+f*	*l+m*	*m+o*	*p+q*
Vesna	*j*	*e*	*a*	*k*	*c*	*e*
Duet	*f+k*	*b+e*	*a*	*d*	*g+f*	*m+a*
Izumrudnaya	*k*	*b*	*b*	*b*	*b*	*r*
Il'menskaya	*f*	*b*	*i*	*u*	*c*	*h*
Il'menskaya 2	*f*	*e*	*a*	*p*	*o*	*n*
Kvinta	*k*	*e*	*a*	*n*	*k*	*g*
Kukushka	*f*	*b*	*a*	*q*	*m*	*a*
Kukushka 12-6	*f+h*	*f+b+e*	*c+a*	*n+l*	*f+m+b*	*e+q+r*
Kukushka 14-6	*c*	*e*	*g*	*l*	*b*	*b*
Lutescens 23490	*f*	*e*	*a*	*p*	*b*	*b*
Milturum 12013	*k+o*	*m+e*	*f+c*	*b+l*	*t+g*	*l+j*
Rossiyanka	*f+k*	*e+b*	*a+b*	*l+m*	*t+r*	*b+a*
Silach	*c*	*l*	*a*	*k*	*n*	*e*
Uralochka	*f*	*b*	*a*	*m*	*j*	*q*
Ural'skaya 52	*m*	*e*	*a*	*q*	*c*	*i*
Ural'skaya kukushka	*a+i*	*b*	*a*	*l+n*	*g+o*	*d+l*
Fiton c-36	*f*	*e*	*a*	*s*	*m*	*a*
Chebarkul'skaya	*f*	*b*	*a*	*l+f*	*b*	*q+l*
Chelyaba	*f*	*l*	*a*	*l*	*d*	*p*
Chelyaba 2	*c+f+a*	*b+e*	*a*	*i+f+l*	*o+v+g*	*i+k+l*
Chelyaba 75	*i*	*e*	*a*	*p*	*k*	*a*
Chelyaba 80	*o*	*b*	*a*	*l+b*	*j*	*l+n*
Chelyaba ranna	*d*	*e*	*a*	*i*	*f*	*m*
Chelyaba stepnaya	*h*	*e+d*	*b*	*n*	*o*	*k*
Chelyaba yubileynaya	*f*	*l*	*f*	*l*	*r*	*a*
Chelyabinskaya 17	*g+c+f+h*	*b+a+e*	*a+f+b*	*b+i+q+l*	*g+o+b+v+f*	*j+l+s*
Erythrospermum 23390	*f+k*	*b+l*	*a*	*b+k*	*i+p*	*o*
Erythrospermum 24841	*f*	*e+l*	*a*	*b+l*	*o+g*	*l+a*

Table 1 (cont'd).

Cultivars/advanced lines	Gliadin-coding loci (*Gli*)					
	A1	*B1*	*D1*	*A2*	*B2*	*D2*
Erythrospermum 25787	*f*	*l*	*a*	*b*	*r*	*l*
Bread wheat from Kazakhstan						
Karagandinskaya 2	*h+f*	*b+e*	*g*	*q*	*f*	*k*
Karagandinskaya 21	*h*	*b**	*a*	*v*	*l*	*i*
Karagandinskaya 30	*f+h*	*e*	*f*	*e+l*	*t+m*	*a*
Karagandinskaya 31	*a*	*e*	*a*	*e*	*o*	*a*
Karagandinskaya 70	*f*	*e*	*g*	*l*	*f*	*a*
Karagandinskaya 93	*h*	*e*(new)*	*a*	*s*	*l*	*r*
Lutescens 1021	*k+f*	*e*	*g*	*l*	*p*	*i*
Lutescens 1022	*h*	*b*	*g+a*	*s*	*r*	*a*
Lutescens 1052	*f*	*e*(new)*	*g*	*s*	*?*	*i*
Lutescens 1098	*f*	*e*	*b*	*s*	*r*	*a*
Lutescens 1136	*h*	*e*	*f*	*l*	*r*	*q*
Lutescens 1153	*f*	*e*	*g+a*	*s*	*r*	*a*
Lutescens 1166	*c*	*b*	*a*	*t*	*r*	*m*
Lutescens 1192	*a*	*e*	*a*	*q*	*r*	*a*
Lutescens 1194	*f*	*e*	*a*	*s*	*r*	*o*
Lutescens 1212	*f*	*e*(new)*	*a+g*	*l*	*r*	*r*
Lutescens 1220	*f+a*	*e*	*a*	*l+s*	*t+a+r*	*a+r*
Lutescens 1221	*f*	*e*	*a*	*l*	*t*	*a*
Lutescens 1226	*f*	*e*	*a*	*l*	*r*	*a*
Lutescens 1228	*m*	*b*	*a*	*l*	*p*	*r*
Lutescens 1229	*f*	*e*	*a*	*l*	*t*	*a*
Lutescens 1235	*f*	*e*	*a*	*l*	*b*	*a*
Lutescens 1242	*m+k*	*e+b*	*a*	*e+l*	*r+r*+d*	*a+c*
Lutescens 1245	*h*	*e*	*b*	*s*	*a*	*a*
Lutescens 1272	*k*	*e*	*g*	*l*	*r*	*k*
Lutescens 1519	*h*	*e+b*	*a*	*s*	*d*	*i*
Lutescens 1541	*m+f*	*e*	*a+b*	*m+t*	*r+m*	*a*
Lutescens 1545	*f*	*e*	*a*	*t*	*r*	*a*
Lutescens 1558	*a*	*e*	*a*	*e*	*o*	*q*
Lutescens 1569	*o*	*b*	*b*	*l*	*r*	*a*
Lutescens 1614	*o*	*e*	*i*	*b*	*a*	*m*
Lutescens 1669	*f*	*e*	*a*	*t*	*f*	*a*
Lutescens 1764	*h*	*b*	*a*	*s*	*f*	*a*
Lutescens 1991	*i*	*e*	*f*	*e*	*r*	*q*
Lutescens 2028	*h+n*	*b*	*a*	*l*	*o*	*a*
Lutescens 2055	*f*	*e*	*a*	*i*	*b*	*a*
Lutescens 2102	*f*	*e*	*a*	*e*	*o*	*a*
Lutescens 2174	*f*	*b*	*a*	*s*	*b*	*q*
Lutescens 270	*k+f*	*e*	*a*	*q+g*	*t*	*r*
Lutescens 720	*i*	*e*	*a*	*q*	*k*	*m*
Lutescens 932	*f*	*e*	*a*	*l*	*f*	*i*
Lutescens 944	*c*	*e*	*a*	*l*	*d*	*i*
Sary-Arka	*f*	*e*	*a*	*l*	*o*	*a*
GVK - 2077-11	*f*	*e*	*a*	*c*	*r*	*p*
VK - 3488	*k*	*e*	*a*	*f*	*m*	*p*
VK - 3632	*f*	*e*	*a*	*x*	*i+v*	*r+g*
GVK - 1337/10	*f*	*e*	*a*	*m*	*r*	*s*
GVK - 1369-2	*f+d*	*e+l*	*a+f*	*e+k**	*l+r*	*a+l*
GVK - 1596/6	*f*	*e+l*	*g+a*	*k*	*f*	*i*
GVK - 1672/8	*c*	*l*	*f*	*j*	*g*	*a*
GVK - 1678/12	*f*	*e*	*a*	*h*	*k*	*a*
GVK - 1719/1	*f*	*e*	*a*	*m*	*b*	*g*
GVK - 1857-9	*d*	*l*	*a*	*b*	*r*	*a*
GVK - 1860-8	*f*	*e*	*a*	*n*	*r*	*a*
GVK - 2033/7	*c*	*l*	*b*	*m*	*g*	*p*
GVK - 2036-15	*f*	*e*	*g+a*	*f+i*	*m*	*a*+a*
GVK - 2055-1	*f*	*e*	*a*	*m*	*g*	*p*
GVK - 2097/14	*f*	*e*	*a*	*n*	*r*	*a*
GVK – 2127	*c*	*l*	*g*	*m*	*g*	*p*

Table 1 (cont'd).

Cultivars/advanced lines	Gliadin-coding loci (*Gli*)					
	A1	*B1*	*D1*	*A2*	*B2*	*D2*
GVK – 2161	*f+c*	*e+l*	*f+g*	*e+k+f*	*f+g*	*s+a*
GVK 2140/6	*d*	*l*	*f*	*b*	*e*	*q*
Zaul'binka	*f*	*e*	*g*	*m*	*a*	*p*
Zyryanovka	*c*	*e+b*	*a*	*l*	*d+n*	*k*
Lada	*f*	*e*	*a*	*m*	*m*	*e*
Lyazat	*o*	*e*	*b*	*m*	*t*	*i*
381 MC	*f*	*l*	*h*	*l*	*a*	*a*
424 MC	*k*	*e*	*g*	*i*	*t*	*g*
Aktobe 10	*a*	*b**	*f*	*s*	*n*	*m*
Aktobe 130	*r*	*g**	*f*	*p*	*e*	*b*
Aktobe 14	*f*	*e*	*a*	*q*	*b+f*	*q*
Aktobe 32	*i*	*e*	*a*	*t*	*i*	*s*
Aktobe 33	*m*	*b*	*f*	*r*	*p*	*s*
Aktobe 39	*f*	*e*	*a*	*l*	*k*	*a*
Aktobe 42	*k*	*f*	*g*	*d*	*n*	*j*
Aktyubinka	*c*	*e*	*f*	*s*	*k*	*m*
Stepnaya 1	*r*	*e*	*a*	*e*	*h*	*s*
Stepnaya 253	*f+m*	*e*	*a*	*q*	*t+p*	*r*

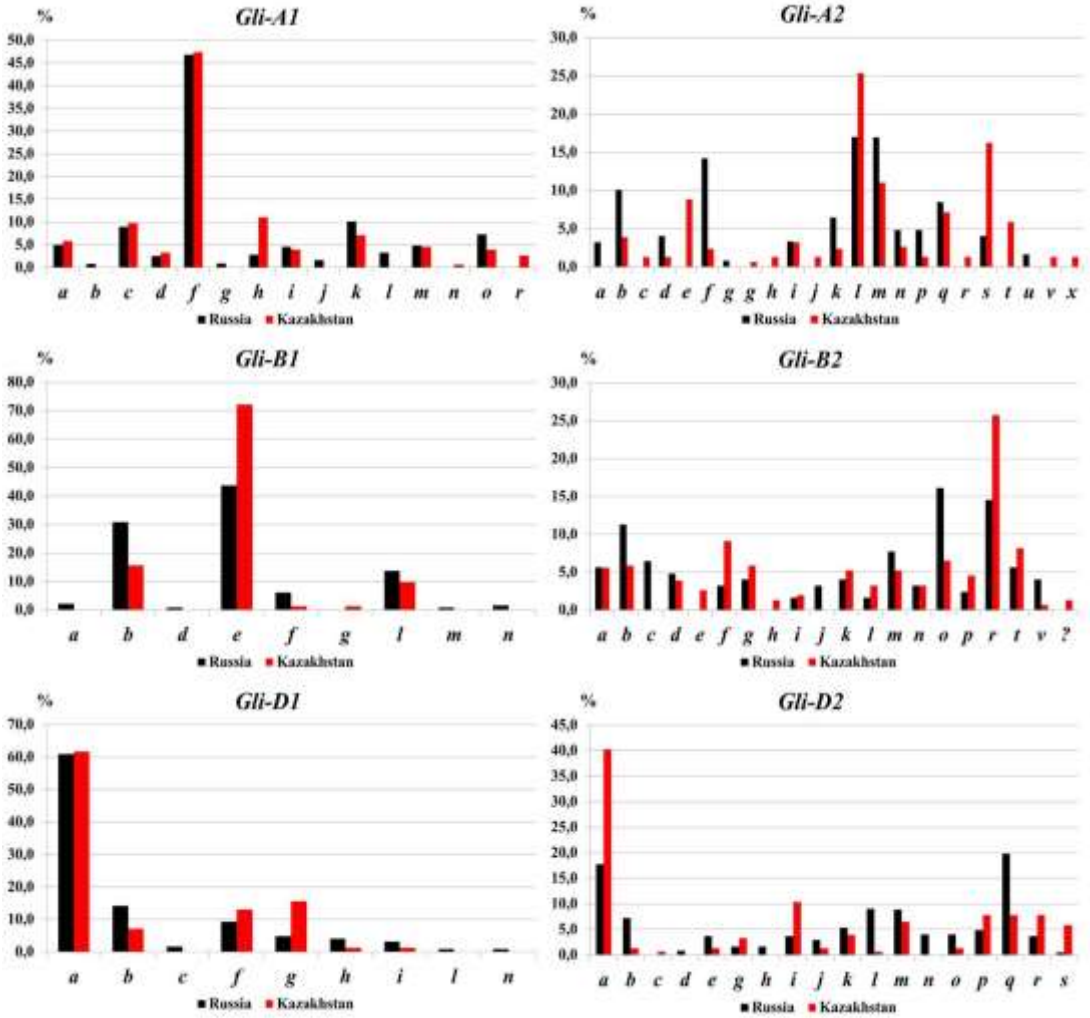

Figure 1. Allele frequencies (%) in *Gli* loci identified in the studied collection of 139 samples of spring soft wheat from Russia and Kazakhstan.

Table 2. Genetic diversity (*H*), intra-population diversity (μ), and frequencies of rare alleles (*h*) in 139 samples of spring soft wheat from Russia and Kazakhstan.

Diversity estimates	Country	Gliadin-coding loci (*Gli*)						Mean
		A1	*B1*	*D1*	*A2*	*B2*	*D2*	
H	Russia	0.75	0.69	0.59	0.89	0.91	0.89	0.79
	Kazakhstan	0.74	0.45	0.57	0.88	0.89	0.80	0.72
$\mu \pm S_\mu$	Russia	9.29±0.74	5.22±0.48	5.62±0.55	12.13±0.60	15.19±0.66	14.05±0.81	10.25±0.64
	Kazakhstan	8.25±0.54	3.18±0.27	4.14±0.32	15.07±0.98	15.52±0.74	10.79±0.77	9.49±0.60
$h \pm S_h$	Russia	0.28±0.05	0.34±0.06	0.37±0.06	0.13±0.04	0.10±0.03	0.17±0.04	0.23±0.05
	Kazakhstan	0.25±0.05	0.36±0.05	0.31±0.05	0.25±0.05	0.15±0.04	0.28±0.05	0.26±0.05

Table 3. Genetic similarity (*r*) and identity criterion (*I*) of groups of spring soft wheat from Russia and Kazakhstan according to the frequency of alleles of *Gli* loci.

Compared groups	Estimates	Gliadin-coding loci (*Gli*)					
		A1	*B1*	*D1*	*A2*	*B2*	*D2*
Russia – Kazakhstan	*r*	0.80 ± 0.02	0.90 ± 0.02	0.96 ± 0.01	0.88 ± 0.02	0.86 ± 0.02	0.88 ± 0.02
	I	68.60 (27.6)	34.30 (19.7)	13.72 (18.3)	41.16 (28.9)	48.02 (31.4)	41.16 (28.9)

Note: in brackets χ^2 for 5% significance level

> 0. In the latest study, this criterion ranged from 0.10 ± 0.03 (*Gli-B2*, Siberia) to 0.37 ± 0.06 (*Gli-D1*, Russia). Based on these findings in both groups, the loci *Gli-1* is characterized by an uneven ratio between the frequencies of rare and frequent alleles.

The comparison of the frequencies of alleles, according to the indicator of genetic similarity (*r*) and the criterion of identity (*I*), evaluated the degree of differences in the allelic composition of the gliadin-coding loci between Russian and Kazakh wheat, (Table 3). The genetic similarity (*r*) does not exceed unity but may be equal to one if the compared groups are identical in the number and frequency of alleles. If the obtained value exceeds the table value of χ^2 at a given level of significance, then a significant difference between the groups based on genetic similarity (*r*) exists, which defines the essence of criterion (*I*) (Zhivotovsky, 1979). The results also revealed that the values of the identity criterion (*I*) exceeded the table value of χ^2 (Table 3). Accordingly, the studied groups of spring soft wheat samples differ significantly from each other in gliadin-coding loci, except for the locus *Gli-D1*.

DISCUSSION

The study and comparison of genetic resources of different ecological and geographical origins is an important step in the creation of new wheat genotypes. With the wheat's earlier identification results, the conduct of comparative analyses of the obtained genetic formulas of gliadin revealed identical alleles at the loci *Gli-1*, whereas at the loci *Gli-2*, the allelic composition was different (Novoselskaya-Dragovich *et al.*, 2003; Utebayev *et al.*, 2019). The probable combination of alleles *Gli-A1f, Gli-B1e,* and *Gli-D1a* can be associated with some valuable characteristics.

The results made it possible to identify the preference of selection of the wheat genetic types with a combination of *Gli* loci alleles by Russian and Kazakh breeders, which is consistent with one of the directions of the *5G* strategy in the crop improvement (Varshney *et al.*, 2020). As a matter of fact, in certain environmental conditions, a specific 'portrait' of wheat cultivars is formed with a predominance of gliadin alleles associated with certain valuable features (Metakovsky *et al.,* 2019; Noma *et al.,* 2019). To visualize the said wheat 'portrait', the study compiled the so-called 'ideal' electrophoretic spectrum of gliadin for several countries (Figure 2), which is created based on common blocks of gliadin identified by the researchers at different times (Table 4).

The idea of describing the genetic diversity of wheat from gliadin-coding loci based on an 'ideal spectrum' was proposed by an analogy of creating an 'ideal plant architecture' (Guo *et al.,* 2020; Wang *et al.,* 2021). Therefore, the cultivars close to the 'ideal' spectrum in gliadin alleles should have a complex of economically valuable features. For this, the spectrum of Russian wheat that

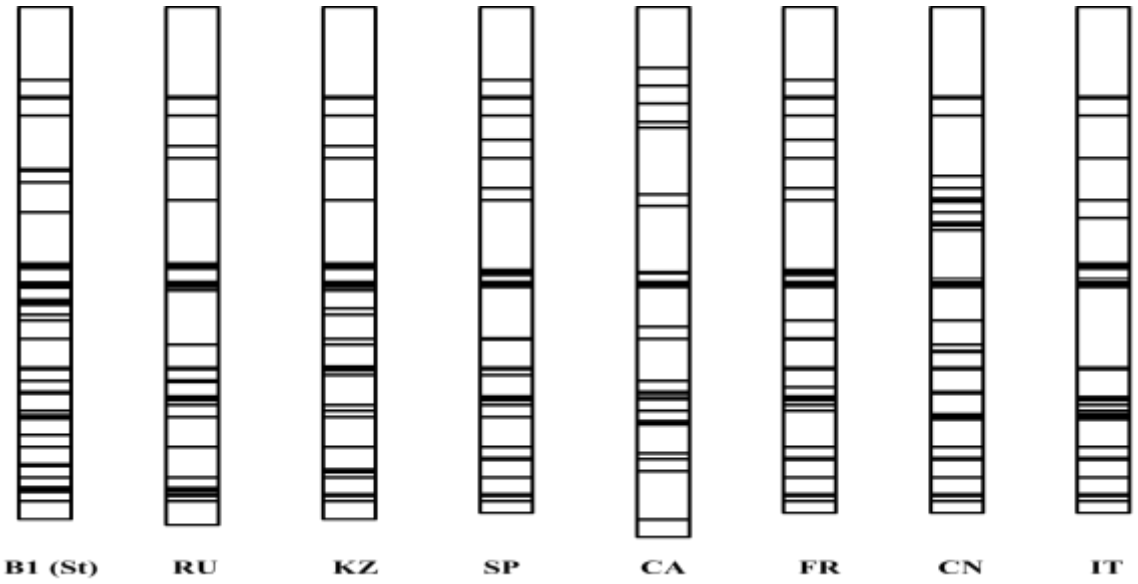

Figure 2. 'Ideal' Electrophoregrams of gliadin of the wheat from different countries: RU – Russia, KZ – Kazakhstan, SP – Spain, CA – Canada, FR – France, CN – China, IT – Italy, B1 (St) – standard, soft wheat cultivar Bezostaya 1.

Table 4. Variety of allele gliadin-coding loci in wheat of different origins

Countries	Gliadin-coding loci (*Gli*)						References
	A1	*B1*	*D1*	*A2*	*B2*	*D2*	
Canada	*m*	*d*	*j*	*m*	*c*	*h*	Metakovsky *et al*.,1993
China	*a*	*l*	*a*	*g*	*?*	*b*	Novoselskaya-Dragovich *et al*., 2011
France	*o*	*f*	*b*	*g*	*g*	*a*	Metakovsky and Branlard, 1998
Italy	*a*	*g*	*k*	*g*	*o*	*a*	Metakovsky *et al*.,1994
Kazakhstan	*f*	*e*	*a*	*l*	*r*	*a*	Utebayev *et al*., 2016; Utebayev *et al*., 2019; and current study
Russia	*f*	*e*	*a*	*q*	*o*	*e*	Dobrotvorskaya *et al*., 2009; Nikolaev *et al*., 2009; Novoselskaya-Dragovich *et al*., 2013; and current study
Spain	*o*	*f*	*b*	*g*	*o*	*a*	Metakovsky *et al*., 2000

consist of blocks of components controlled by alleles, i.e., *f, e, a, q, o,* and *e,* serves as an example (Figure 2). Moreover, it also concluded that the main pool of high-quality Russian wheat consists of the cultivars of Saratov and Omsk selection, which practically repeat the 'ideal' spectrum, except for the locus *Gli-B2* alleles (Bebyakin and Balabolina, 1980; Novoselskaya-Dragovich *et al.,* 2003, 2013).

As for Kazakh wheat, its 'ideal' spectrum coincides with the spectrum of Russian wheat at the loci *Gli-1*, as Kazakhstan breeders often take Russian cultivars as parental genotypes (Shavrukov *et al.*, 2014; Utebayev *et al.*, 2016, 2019). Moreover, the selection process to improve grain quality fully explains the similarity in the loci *Gli-1*, since the loci *Gli-1* alleles are more associated with the qualitative characteristics of the grain, while the loci *Gli-2* alleles are more related with the adaptability to external conditions (Li *et al.*, 2009; Novoselskaya-Dragovich *et al.*, 2013). However, few studies found that some alleles of the loci *Gli-2* can also affect positively (Noma *et al.*, 2019) and negatively (Li *et al.*, 2018) the quality of wheat grain.

Notably, the gliadin spectra of wheat in Italy, France, and Spain also have identical loci *Gli* alleles. The similarity of the 'ideal' spectra of wheat gliadin of Spain and France may be due to the use of the same set of parental types and the fairly close climatic conditions. Interestingly, the cultivar Cappelle Desprez, which is included in the genealogy of French cultivars, such as, Tobak, Rudi, Aiglon, and Trocadero (GRIS), needs further studying. The gliadin formula of Cappelle Desprez (*o, f, b, g,*

g, and *g*) (Metakovsky and Branlard, 1998) is close to the formula of the 'ideal' spectrum for Spain and France (Table 3). This cultivar is well-known to form a stable yield (Mesdag, 1985) and is highly resistant to striped rust (Pawar *et al.*, 2016). However, it is characterized by low resistance to drought (Fábián *et al.*, 2011) and classified as a cultivar with medium-baking properties (Burnouf and Bouriquet, 1980). The wheat cultivars viz., Ducat (*o, f, b, g, g, h*), Rudi (*o, h, b, g, a*), and Top (*o, f, b, g, g, a*) were included in the group with best- and average- baking properties and also close to the 'ideal' spectrum of gliadin (Burnouf and Bouriquet, 1980; Metakovsky and Branlard, 1998).

The alleles, *Gli-B1e, Gli-B1g*, and *Gli-B1f*, present in the cultivars of Russia, Kazakhstan, France, and Italy, also need checking. These alleles control the synthesis of gliadin blocks similar to each other in electrophoretic mobility, have a consonant nucleotide sequence (Chebotar *et al*., 2012), and likely have the same effect on grain quality. The conclusion suggested that if the electrophoretic spectrum of gliadin is close to the 'ideal' for these conditions, this can also guarantee the fabrication of productive, stress-resistant wheat types and cultivars with good baking properties. However, the increase in productivity decreases plant fitness and adaptability, such as, a decrease in plant growth and the formation of vertical root growth (Weiner, 2019). Moreover, the desire to bring the gliadin profile of wheat closer to the 'ideal' spectrum may reduce the 'selfishness' of the plant, i.e., some properties of individual plants may deteriorate, such as, adaptability to external stressors (Abbai *et al.*, 2020), which is a negative side in plant breeding. These negative phenomena can be avoided by taking into account the trade-offs between plant traits, such as, grain yield and quality (Pleijel and Uddling, 2012).

CONCLUSIONS

Based on the study results of gliadin electrophoresis of the spring soft wheat collection from Russia and Kazakhstan, an assessment of the allelic diversity of gliadin loci was done. Genetic formulas were compiled, and based on the frequency of occurrence, the predominant alleles of gliadin were identified in the studied wheat collection. In Russian cultivars with climatic conditions of Siberia, the alleles *Gli-A1f* (46.9%), *Gli-B1e* (43.7%), *Gli-B1b* (30.8%), *Gli-D1a* (61.0%), *Gli-A2l* (17.0%), *Gli-A2m* (16.9%), *Gli-B2o* (16.1%), and *Gli-D2q* (19.8%) were frequently observed. The wheat collection from the Central, Eastern, and Western regions of Kazakhstan was dominated by alleles *Gli-A1f* (47.4%), *Gli-B1e* (72.0%), *Gli-D1a* (61.7%), *Gli-A2l* (25.3%), *Gli-A2s* (16.2%), *Gli-B2r* (25.7%), and *Gli-D2a* (40.3%). Based on the proposed concept of the "ideal" electrophoretic spectrum, the study established the spectrum of Russian wheat consisting of the blocks of components controlled by alleles, i.e., *f, e, a, q, o, and e*. The 'ideal' spectrum wheat from Kazakhstan: *f, e, a, l, r, and a* matches with the spectrum of Russian wheat at the loci *Gli-1*, since Kazakhstan breeders often chose Russian cultivars as parental genotypes. The wheat cultivars with an electrophoretic spectrum close to the 'ideal' one are believed to have a complex of economically valuable features. Furthermore, the genotypes with such gliadin formula can serve as prospective breeding materials for elite grain quality and better adaptability to the environment of Russia (the Western Siberia region) and Kazakhstan (the regions of Central, Eastern, and Western Kazakhstan).

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REFERENCES

Abbai R, Singh VK, Snowdon RJ, Kumar A, Schnurbusch T (2020). Seeking crops with balanced parts for the ideal whole. *Trends Plant Sci*. 25(12): 1189-1193.

Aguiriano E, Ruiz M, Fité R, Carrillo JM (2008). Genetic variation for glutenin and gliadins associated with quality in durum wheat (*Triticum turgidum* L. ssp. turgidum) landraces from Spain. *Span. J. Agric. Res*. 6(4): 599-609.

Akhtariyeva MK, Kozelets YO, Filippova YM, Netsvetaev VP (2019). Beta-amylase

isozymes in spring common wheat and their role in the aggregation of grain proteins. *Cytol. Genet*. 53(4): 294-299.

Al-Doss AA, Al-Hazmi AS, Dawabah AAM, Abdel-Mawgood AA, Al-Rehiayani SM, Solaiman A, Moustafa KA, Motawei MI (2010). Impact of '*Cre'* and peroxidase genes of selected new wheat lines on cereal cyst nematode (*Heterodera avenae* woll) resistance. *Aust. J. Crop. Sci*. 4(9): 737-743.

Alonge M, Wang X, Benoit M, Soyk S, Pereira L, Zhang L, Suresh H, Ramakrishnan S, Maumus F, Ciren D, Levy Y, Hai-Harel T, Shalev-Schlosser G, Amsellem Z, Razifard H, Caicedo AL, Tieman DM, Klee H, Kirsche M, Aganezov S, Ranallo-Benavidez TR, Lemmon ZH, Kim J, Robitaille G, Kramer M, Goodwin S, McCombie WR, Hutton S, Eck JV, Gillis J, Eshed Y, Sedlazeck FJ, der Knaap E, Schatz MC, Lippman ZB (2020). Major impacts of widespread structural variation on gene expression and crop improvement in tomato. *Cell* 182(1): 145-161.e23.

Autran JC, Bushuk W, Wrigley CW, Zillman RR (1979). Wheat cultivar identification by gliadin electropherograms. IV. Comparison of international methods. *Cereal Foods World* 24(9): 471-475.

Bebyakin VM, Balabolina TG (1980). Gliadin component composition, its biochemical polymorphism, and flour quality in wheat. *Sel'skokhozyaistvennaya Biol*. 15(4): 549-555. (in Russian).

Branlard G, Picard B, Courvoisier C (1990). Electrophoresis of gliadins in long acrylamide gels: Method and nomenclature. *Electrophoresis* 11(4): 310-314.

Burnouf T, Bouriquet R (1980). Glutenin subunits of genetically related European hexaploid wheat cultivars: Their relation to bread-making quality. *Theor. Appl. Genet*. 58(3): 107-111.

Burridge AJ, Wilkinson PA, Winfield MO, Barker GL, Allen AM, Coghill JA, Waterfall C, Edwards KJ (2018). Conversion of array-based single nucleotide polymorphic markers for use in targeted genotyping by sequencing in hexaploid wheat (*Triticum aestivum* L.). *Plant Biotechnol. J.* 16(4): 867-876.

Bushuk W, Zillman RR (1978). Wheat cultivar identification by gliadin electropherograms. I. Apparatus, method and nomenclature. *Can. J. Plant Sci*. 58(2): 505-515.

Chebotar SV, Blagodarova EM, Kurakina EA, Semenyuk IV, Polishchuk AM, Kozub NA, Sozinov IA, Khokhlov AN, Ribalka AI, Sivolap YuM (2012). Genetic polymorphism of loci determining bread-making quality in Ukrainian wheat varieties. *Vavilov J. Genet. Breed.* 16(1): 87-98. (in Russian).

Clements RL (1988). A continuous acetic acid system for polyacrylamide gel electrophoresis of gliadins and other prolamines. *Electrophoresis* 9(2): 90-93.

Dobrotvorskaya TV, Dragovich AY, Martynov SP, Pukhal'skii VA (2009). Genealogical and statistical analyses of the inheritance of gliadin-coding alleles in a model set of common wheat *Triticum aestivum* L. cultivars. *Russ. J. Genet*. 45(6): 685-695.

Fábián A, Jäger K, Rakszegi M, Barnabás B (2011). Embryo and endosperm development in wheat (*Triticum aestivum* L.) kernels subjected to drought stress. *Plant Cell Rep*. 30(4): 551-563.

Faryad A, Aziz F, Tahir J, Kousar M, Qasim M, Shamim A (2021). Integration of OMICS technologies for crop improvement. *Protein Pept. Lett*. 28(8): 896-908.

Goel S, Singh K, Grewal S, Nath M (2020). Impact of "omics" in improving drought tolerance in wheat. *Crit. Rev. Plant Sci*. 39(3): 222-235.

GRIS - Genetic Resources Information System for Wheat and Triticale. database http://wheatpedigree.net/

Guo W, Chen L, Herrera-Estrella L, Cao D, Tran LSP (2020). Altering plant architecture to improve performance and resistance. *Trends Plant Sci*. 25(11): 1154-1170.

Hailegiorgis D, Lee CA, Yun SJ (2017) Allelic variation at the gliadin coding loci of improved Ethiopian durum wheat varieties. *J. Crop. Sci. Biotechnol*. 20(4): 287-293.

Kakaei M, Ahmadian S (2021). Genetic diversity study of some Iranian alfalfa genotypes based on seed storage protein patterns. *Iranian J. Sci. Technol. Trans. A: Sci*. 45(4): 1223-1228.

Knott GJ, Doudna JA (2018). CRISPR-Cas guides the future of genetic engineering. *Science* 361(6405): 866-869.

Konarev A, Gubareva N, Kornuchin D, Börner A (2005). Gliadin electrophoretic analysis of the genetic integrity of wheat (*Triticum aestivum* L.) accessions after frequent seed reproductions. *Genet. Resour. Crop Evol*. 52(5): 519-523.

Kozub NA, Sozinov IA, Sobko TA, Kolyuchii VT, Kuptsov SV, Sozinov AA (2009). Variation at storage protein loci in winter common wheat cultivars of the Central Forest-Steppe of Ukraine. *Cytol. Genet*. 43(1): 55-62.

Li D, Jin H, Zhang K, Wang Z, Wang F, Zhao Y, Huo N, Liu X, Gu YQ, Wang D, Dong L (2018). Analysis of the Gli-D2 locus identifies a genetic target for simultaneously improving the breadmaking and health-related traits of common wheat. *Plant J.* 95(3): 414-426.

Li Y, Song Y, Zhou R, Branlard G, Jia J (2009). Detection of QTLs for bread-making quality in wheat using a recombinant inbred line population. *Plant Breed*. 128: 235-243.

Liu Y, Du H, Li P, Shen Y, Peng H, Liu S, Zhou GA, Zhang H, Liu Z, Shi M, Huang X, Li Y, Zhang M, Wang Z, Zhu B, Han B, Liang C, Tian Z (2020). Pan-genome of wild and cultivated soybeans. *Cell* 182(1): 162-176.e13.

Lyubimova AV, Tobolova GV, Eremin DI, Loskutov IG (2020). Dynamics of the genetic diversity of oat varieties in the Tyumen region at

avenin-coding loci. *Vavilov J. Genet. Breed*. 24(2): 123-130.

McIntosh RA, Yamazaki Y, Devos KM, Dubkovsky J, Rogers J, Appels R (2008) MacGene 2003. Catalogue of Gene Symbols for Wheat. *In: Proc. 10th Int. Wheat Genet. Symp.* Paestum, Italy. Available: http://wheat.pw.usda.gov/ggpages/wgc/2003/.

Melnikova NV, Kudryavtseva AV, Kudryavtsev AM (2012) Catalogue of alleles of gliadin-coding loci in durum wheat (*Triticum durum* Desf.). *Biochimie* 94(2): 551-557.

Mesdag J (1985). Developments in breeding winter wheat for bread-baking quality in some north-western European countries. *Neth. J. Agri. Sci*. 33(3): 215-234.

Metakovsky E, Melnik V, Rodriguez-Quijano M, Upelniek V, Carrillo JM (2018). A catalog of gliadin alleles: Polymorphism of 20th-century common wheat germplasm. *Crop J*. 6(6): 628-641.

Metakovsky E, Melnik VA, Pascual L, Wrigley CW (2019). Gliadin genotypes worldwide for spring wheats (*Triticum aestivum* L.) 1. Genetic diversity and grain-quality gliadin alleles during the 20th century. *J Cer. Sci*. 87: 172-177.

Metakovsky EV (1991). Gliadin allele identification in common wheat. II. Catalogue of gliadin alleles in common wheat. *J. Genet. Breed*. 45(4): 325-344.

Metakovsky EV, Branlard G (1998). Genetic diversity of French common wheat germplasm based on gliadin alleles. *Theor. Appl. Genet*. 96(2): 209-218.

Metakovsky EV, Gomez M, Vazquez JF, Carrillo J M (2000). High genetic diversity of Spanish common wheats as judged from gliadin alleles. *Plant Breed*. 119(1): 37-42.

Metakovsky EV, Ng PKW, Chernakov VM, Pogna NE, Bushuk W (1993). Gliadin alleles in Canadian western red spring wheat cultivars: use of two different procedures of acid polyacrylamide gel electrophoresis for gliadin separation. *Genome* 36(4): 743-749.

Metakovsky EV, Novoselskaya AY, Kopus MM, Sobko TA, Sozinov AA (1984). Blocks of gliadin components in winter wheat detected by one-dimensional polyacrylamide gel electrophoresis. *Theor. Appl. Genet*. 67(6): 559-568.

Metakovsky EV, Novoselskaya AY (1991) Gliadin allele identification in common wheat. 1. Methodological aspects of the analysis of gliadin pattern by one-dimensional polyacrylamide - gel electrophoresis. *J. Genet Breed*. 45: 317-324.

Metakovsky EV, Pogna NE, Biancardi AM, Redaelli R (1994). Gliadin allele composition of common wheat cultivars grown in Italy. *J. Genet. Breed*. 48: 55-66.

Nei M (1973). Analysis of gene diversity in subdivided populations. *Proc. Nat. Acad. Sci. USA*. 70(12): 3321-3323.

Nikolaev AA, Pukhal'sky VA, Upelniek VP (2009). Genetic diversity of local spring bread wheats (*Triticum aestivum* L.) of West and East Siberia in gliadin genes. *Russ. J. Genet*. 45(2):189-197

Nirmal RC, Furtado A, Rangan P, Henry RJ (2017). Fasciclin-like arabinogalactan protein gene expression is associated with yield of flour in the milling of wheat. *Sci. Rep*. 7: 12539.

Nirmal RC, Furtado A, Wrigley C, Henry RJ (2016). Influence of gene expression on hardness in wheat. *PLoS One*. 11(10): e0164746.

Noma S, Hayakawa K, Abe C, Suzuki S, Kawaura K (2019). Contribution of α-gliadin alleles to the extensibility of flour dough in Japanese wheat cultivars. *J. Cereal Sci*. 86: 15-21.

Novoselskaya-Dragovich AY, Fisenko AV, Puhal'skii VA (2013). Genetic differentiation of common wheat cultivars using multiple alleles of gliadin-coding loci. *Russ J. Genet*. 49(5): 487-496.

Novoselskaya-Dragovich AY, Fisenko AV, Yankovsky NK, Kudryavtsev AM, Yang Q, Lu Z, Wang D (2011). Genetic diversity of storage protein genes in common wheat (*Triticum aestivum* L.) cultivars from China and its comparison with genetic diversity of cultivars from other countries. *Genet. Resour. Crop Evol*. 58(4): 533-543.

Novoselskaya-Dragovich AY, Krupnov VA, Saifulin RA, Pukhalskiy VA (2003). Dynamics of genetic variation at gliadin-coding loci in Saratov cultivars of common wheat *Triticum aestivum* L. over eight decades of scientific breeding. *Russ. J. Genet*. 39(10): 1130-1137.

Obukhova LV, Shumny VK (2016). The inheritance of endosperm storage proteins by the line of the Saratovskaya 29 cultivar of common wheat from its parental forms. *Russ. J. Genet*. 52(1): 49-55.

Palosuo K, Varjonen E, Kekki OM, Klemola T, Kalkkinen N, Alenius H, Reunala T (2001). Wheat ω-5 gliadin is a major allergen in children with immediate allergy to ingested wheat. *J. Allergy Clin. Immunol*. 108(4): 634-638.

Pastorello EA, Farioli L, Conti A, Pravettoni V, Bonomi S, Iametti S, Fortunato D, Scibilia J, Bindslev-Jensen C, Ballmer-Weber B, Robino AM, Ortolani C (2007) Wheat IgE-mediated food allergy in European patients: α-amylase inhibitors, lipid transfer proteins and low-molecular-weight glutenins. *Int. Arch. Allergy Immunol*. 144: 10-22.

Pawar SK, Sharma D, Duhan JS, Saharan MS, Tiwari R, Sharma I (2016). Mapping of stripe rust resistance QTL in Cappelle–Desprez × PBW343 RIL population effective in Northern wheat belt of India. *3 Biotech*. 6(1): 76.

Pflüger LA, Martín LM, Alvarez JB (2001). Variation in the HMW and LMW glutenin subunits from Spanish accessions of emmer wheat (*Triticum turgidum* ssp. dicoccum Schrank). *Theor. Appl. Genet*. 102(5): 767-772.

Pleijel H, Uddling J (2012). Yield vs. Quality trade-offs for wheat in response to carbon dioxide and ozone. *Glob. Chang Biol*. 18(2): 596-605.

Salavati A, Sameri H, Boushehri AAS, Yazdi-Samadi B (2008). Evaluation of genetic diversity in Iranian landrace wheat *Triticum aestivum* L. by using gliadin alleles. *Asian J. Plant Sci*. 7(5): 440-446.

Sánchez-León S, Gil-Humanes J, Ozuna CV, Giménez MJ, Sousa C, Voytas DF, Barro F (2018). Low-gluten, nontransgenic wheat engineered with CRISPR/Cas9. *Plant Biotechnol. J*. 16(4): 902-910.

Scheben A, Batley J, Edwards D (2017) Genotyping-by-sequencing approaches to characterize crop genomes: Choosing the right tool for the right application. *Plant Biotechnol. J*. 15(2): 149-161.

Shavrukov Y (2016). Comparison of SNP and CAPS markers application in genetic research in wheat and barley. *BMC Plant Biol*. 16(1): 47-51.

Shavrukov Y, Suchecki R, Eliby S, Abugalieva A, Kenebayev S, Langridge P (2014). Application of next-generation sequencing technology to study genetic diversity and identify unique SNP markers in bread wheat from Kazakhstan. *BMC Plant Biol*. 14(1): 1-13.

Shewry PR, Halford NG (2001) Cereal seed storage proteins: Structures, properties and role in grain utilization. *J. Exp. Bot*. 53(370): 947-958.

Song J-M, Guan Z, Hu J, Guo C, Yang Z, Wang S, Liu D, Wang B, Lu S, Zhou R, Xie WZ, Cheng Y, Zhang Y, Liu K, Yang QY, Chen LL, Guo L (2020). Eight high-quality genomes reveal pan-genome architecture and ecotype differentiation of *Brassica napus*. *Nat Plants*. 6: 34-45.

Sozinov AA, Poperelya FA (1980) Genetic classification of prolamins and its use for plant breeding. *Ann. Technol. Agric*. 29: 229-245.

Tiwari VK, Wang S, Sehgal S, Vrána J, Friebe B, Kubaláková M, Chhuneja P, Doležel J, Akhunov E, Kalia B, Sabir J, Gill BS (2014). SNP discovery for mapping alien introgressions in wheat. *BMC Genomics* 15: 273.

Utebayev M, Dashkevich S, Babkenov A, Shtefan G, Fahrudenova I, Bayahmetova S, Sharipova B, Kaskarbayev Z, Shavrukov Y (2016). Application of gliadin polymorphism for pedigree analysis in common wheat (*Triticum aestivum* L.) from Northern Kazakhstan. *Acta Physiol. Plant*. 38: 204.

Utebayev M, Dashkevich S, Bome N, Bulatova K, Shavrukov Y (2019). Genetic diversity of gliadin-coding alleles in bread wheat (*Triticum aestivum* L.) from Northern Kazakhstan. *Peer J.* 7: e7082.

Varshney RK, Sinha P, Singh VK, Kumar A, Zhang Q, Bennetzen JL (2020). 5Gs for crop genetic improvement. *Curr. Opin. Plant Biol*. 56: 190-196.

Wang X, Yu R, Li J (2021). Using genetic engineering techniques to develop banana cultivars with fusarium wilt resistance and ideal plant architecture. *Front. Plant Sci*. 11: 617528.

Watry H, Zerkle A, Laudencia-Chingcuanco D (2020). Modified acid-PAGE method for rapid screening and phenotyping of wheat gliadin mutant lines. *Methods X*. 7: 100858.

Weiner J (2019). Looking in the wrong direction for higher-yielding crop genotypes. *Trends Plant Sci*. 24(10): 927-933.

Xynias IN, Kozub NO, Sozinov IA (2006) Seed storage protein composition of Hellenic bread wheat cultivars. *Plant Breed*. 125(4): 408-410.

Zhang Y, Li D, Zhang D, Zhao X, Cao X, Dong L, Liu J, Chen K, Zhang H, Gao C, Wang D (2018). Analysis of the functions of TaGW2 homoeologs in wheat grain weight and protein content traits. *Plant J*. 94(5): 857-866.

Zhivotovsky LA (1979). Population similarity measure for polymorphic characters. *J. Gen. Biol*. 40(4): 587-602. [in Russian].

Zhivotovsky LA (1991). Population biometry. Moskow: Nauka. [in Russian].