ISSN 1022-7954, Russian Journal of Genetics, 2011, Vol. 47, No. 7, pp. 799–812. © Pleiades Publishing, Inc., 2011.
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PLANT GENETICS

Analysis of Diversity of Russian and Ukrainian Bread Wheat (*Triticum aestivum* L.) Cultivars for High-Molecular-Weight Glutenin Subunits

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Received November 16, 2010

Abstract—The allelic diversity of high-moleculat-weght glutenin subunits (HMWGS) in Russian and Ukrainian bread wheat cultivars was analyzed. The diversity of spring wheat cultivars for alleles of the *Glu-1* loci is characterized by medium values of the polymorphism polymorphism information content (*PIC*), and in winter wheats it varies from high at the *Glu-A1* locus to low at the *Glu-D1* locus. The spring and winter cultivars differ significantly in the frequencies of alleles of the glutenin loci. The combination of the *Glu-A1b, Glu-B1c*, and *Glu-D1a* alleles prevails among the spring cultivars, and the combination of the *Glu-A1a, Glu-B1c*, and *Glu-D1d* alleles prevails among the winter cultivars. The distribution of the *Glu-1* alleles significantly depends on the moisture and heat supply in the region of origin of the cultivars. Drought resistance is associated with the *Glu-D1a* allele in the spring wheat and with the *Glu-B1b* allele in the winter wheat. The sources of the *Glu-1* alleles were identified in the spring and wheat cultivars. The analysis of independence of the distribution of the spring and winter cultivars by the market classes and by the alleles of the HMWGS loci showed a highly significant association of the alleles of three *Glu-1* loci with the market classes in foreign cultivars and independence or a weak association in the Russian and Ukrainian cultivars. This seems to be due to the absence of a statistically substantiated system of classification of the domestic cultivars on the basis of their quality.

DOI: 10.1134/S1022795411070052

INTRODUCTION

High-molecular-weight glutenin subunits (HMWGS) compose about 10% of endosperm storage proteins and are very important factors determining the bread-making quality. Multiple alleles of the HMGS loci *Glu-A1, Glu-B1*, and *Glu-D1* are localized in the long arms of chromosomes of the first group and can serve as effective genetic markers of a number of traits permitting monitoring of gene pool changes [1].

The only way to consolidate a vast scattered material collected in the GRIS database [2] are contingency tables. To analyze the HMWGS diversity in the cultivars, cross classification was used in the given work. The associated HMWGS diversity was assessed by means of constructing and analyzing dimeric tables.

The aims of the present work are to reveal regularities in the geographic distribution of the HMWGS alleles in bread wheat cultivars from Russia and Ukraine, to establish the sources of the HMWGS alleles using the genealogical and statistical analyses, and to evaluate the association of the *Glu-1* alleles with the growth habit and market classes.

MATERIALS AND METHODS

The objects of the study were bread wheat cultivars with identified alleles of the loci of high-molecular-weight glutenins [3–19] taken from the Genetic Resources Information and Analytical System (GRIS) [2]. Spring (282) and winter (323) cultivars from Russia and Ukraine were analyzed. The association of the HMWGS alleles with the growth habit, moisture and heat supply in the regions of origin of the cultivars, and with the market classes was studied by analyzing the contingency two-way tables. The gradations of entry 1 were alleles of the glutenin loci, and the gradations of entry 2 were groups of cultivars formed on the basis of the trait under study. Independence or contigency of the association of allelic distribution with the growth habit, moisture and heat supply, and with the market classes in the groups of cultivars was estimated using the χ^2 test [20]. To study the relationship between the alleles of the *Glu-A1, Glu-B1*, and *Glu-D1* loci and the original ancestors (landraces), the pedigree analysis was performed with the construction of the genealogical profiles with the aid of of GRIS program [2]. The relationship between the alleles and the original ancestors was determined using a two-factor analysis of variance of the contributions of the landraces for programm unorganized replications plan.

The factors studied were alleles of the glutenin loci (factor *A*) and the original ancestors (factor *B*). The replications were cultivars from the corresponding groups. To visualize the relationship between the alleles and the original ancestors, cluster analysis of the matrix of the genealogical profiles supplemented with vectors of the sign of the presence of different alleles was carried out. A two-step procedure of hierarchic clustering based on the UPGMA algorithm was used. The transmission of the alleles from the ancestors to the offsprings was traced from the developed pedigrees of the cultivars in GRIS [2]. Software packages AGROS 2.13 [21] (analysis of contingency tables, analysis of variance) and NTSYS 2.02c [22] (cluster analysis) were used for calculations.

RESULTS AND DISCUSSION

Frequencies of Alleles of the Glutenin Loci Glu-A1, Glu-B1, and Glu-D1 in Russian and Ukrainian Cultivars of Spring and Winter Bread Wheats

Among the Russian and Ukrainian spring wheat cultivars, 26.2% were heterogenous for one or more loci, and 45.5% were heterogenous among the winter cultivars. However, for individual loci the percentage of heterogenous cultivars was lower: 13.1 and 32.5% (*Glu-A1*), 13.5 and 21.4% (*Glu-B1*), 8.9 and 9.6% (*Glu-D1*) for the spring and winter cultivars, respectively.

The index of polymorphism (*PIC*) [23] for the loci of high-molecular-weight glutenins was calculated as

$$PIC_i = 1 - \sum_{j=1}^{a} P_{ij}^2,$$

where $P_{ij} = n_{ij} / \sum_{j=1}^{a} n_{ij}$ is the relative frequency of the *j*th allele at the *i*th locus, n_{ij} is the absolute frequency of the allele, *a* is the number of alleles at the locus. *PIC* values > 0.5 point to a high index of polymorphism, $0.5 > PIC > 0.25$ values correspond to the medium level, and $PIC \leq 0.25$ corresponds to a low index of polymorphism [24].

Table 1 presents *PIC* values for the group of homogeneous cultivars and for all cultivars examined study for each locus. In the group of winter cultivars, the highest *PIC* value was recorded at the *Glu-A1* locus, and the lowest one at the *Glu-D1* locus. In the group of spring cultivars, the medium value of *PIC* was shown for all three loci. Nevertheless, among the spring cultivars the *PIC* value for the *Glu-D1* locus is more than twofold higher than in the winter cultivars.

To check independence of the frequencies of alleles of the *Glu-A1, Glu-B1*, and *Glu-D1* loci on the growth habit, cultivars homogeneous for the glutenin alleles were analyzed (Table 2). In this group of cultivars, alleles *a, b*, and *c* of the *Glu-A1* locus were present. The *Glu-B1* locus had 13 alleles, but only four of them were analyzed, and their total frequency made up 98.4 and 99.6% in the spring and winter cultivars, respectively. Five alleles were found at the *Glu-D1* locus, of which two were analyzed and showed a total frequency of 100.0 and 99.6% in the winter and spring cultivars, respectively. The analysis was performed independently for each locus.

The χ^2 test showed a significant association between the distribution of alleles of the *Glu-A1, Glu-B1*, and *Glu-D1* loci and the growth habit. The frequency of presence of the *Glu-A1a, Glu-B1b*, and *Glu-D1d* alleles in the winter cultivars is higher than in the spring cultivars, and the frequencies of the *Glu-A1b* and *Glu-D1d* alleles in the spring cultivars are higher than in the winter cultivars (Table 2). Since the spring and winter cultivars differ significantly in the distribution of the glutenin alleles, further analysis was carried out separately in these groups of cultivars.

Association of the Frequencies of Alleles of the HMWGS Loci with the Moisture and Heat Supply in the Regions of Origin of the Cultivars

To reveal dependence of the distribution of the HMWGS alleles on the main agroclimatic characteristics of natural agricultural provinces [25], the latter were grouped in accordance with moisture and heat supply. Excessively humid, humid, and semihumid provinces formed one group (13 provinces). This group included the Moscow, Novosibirsk, Sverdlov, Kiev, and other oblasts of Russia and Ukraine. The second group included semiarid, arid, and very arid provinces of the steppe and dry-steppe zones (11 provinces): Saratov, Rostov, Odessa, Kherson oblasts, Krasnodar krai, and other regions. The same provinces were also grouped on the basis of heat supply. One group was formed of 18 provinces of the southern-taiga–forest and forest–steppe zones, and partially of the steppe zone with a medium, insufficient, or below-medium heat supply, and six provinces of the steppe and dry-steppe zones with a heat supply exceeding the medium level were included into the second group. Thus, contingency tables showing the association of the alleles of the *Glu-A1, Glu-B1*, and *Glu-D1* loci with moisture and heat supply in natural agricultural provinces were obtained (Tables 3 and 4).

The data in Table 3 demonstrate that in the spring wheat the distribution of alleles of the glutenin loci significantly depends on moisture and heat supply in natural agricultural provinces. An exception is the distribution of the *Glu-B1* alleles, which proved to be independent of heat supply. A statistically significant tendency to prevail is observed for the *Glu-A1b* and *Glu-B1c* alleles in the arid regions. Other alleles of the *Glu-A1* and *Glu-B1* loci are more frequent in the humid cool provinces. A particularly close association with moisture and heat supply is observed for the *Glu-D1* locus alleles (Yule's coefficient of association r_a = 0.32 and 0.37, respectively). The prevalence of the *Glu-D1a* allele, as compared to the theoretically expected frequency, is 27% in the arid provinces and

Table 1. The frequencies of alleles of the glutenin *Glu-1* loci in the Russian and Ukrainian spring and winter wheat cultivars

Locus	Allele	Spring cultivars			Winter cultivars		
		homogeneous	heterogenous	total	homogeneous	heterogenous	total
Glu-A1	*a*	39	22	61	118	83	201
	b	191	36	227	84	99	183
	c	15	17	32	16	33	49
Cultivars total		245 (86.9%)	37 (13.1%)	282	218 (67.5%)	105 (32.5%)	323
PIC		0.36		0.45	0.55		0.59
Glu-B1	*a*	0	1	1	2	2	4
	b	25	27	52	45	64	108
	c	194	33	227	203	66	267
	d	3	5	8	2	8	10
	e	0	0	0	0	1	1
	f	0	0	0	1	0	1
	i	9	8	17	0	2	2
	j	0	0	0	0	2	2
	u	12	3	15	0	1	1
	aj	1	0	1	0	1	1
	ah	0	1	1	0	0	0
	an	0	0	0	0	1	1
	au	0	0	0	1	0	1
Cultivars total		244 (86.5%)	38 (13.5%)	282	254 (78.6%)	69 (21.4%)	323
PIC		0.35		0.47	0.33		0.48
Glu-D1	*a*	132	25	157	17	29	46
	d	123	25	148	275	31	306
	e	0	0	0	0	1	1
	f	0	0	0	0	1	1
	s	1	0	1	0	0	0
Cultivars total		256 (91.1%)	25 (8.9%)	281	292 (90.4%)	31 (9.6%)	323
PIC		0.50		0.50	0.11		0.24

62% in the provinces with a heat supply exceeding the medium level. Hence, it can be assumed that the *Glu-D1a* allele is associated with drought and heat resistance. For example, of 44 cultivars from the Saratov oblast intended for the steppe and dry-steppe zones 38 cultivars (86.4%) carry the *Glu-D1a* allele, and only six (13.6%) carry the *D1d* allele. In contrast, the *Glu-D1d* allele prevails in the humid (37%) and cool provinces with a medium and lower heat supply (22%). For instance, of 13 cultivars from the Moscow oblast (southern-taiga–forest zone) ten cultivars (76.9%) have the *Glu-D1d* allele and three cultivars (23.1%) have the *Glu-D1a* allele. Hence, the cultivars carrying the *Glu-D1d* allele are, on the average, less adaptive to the climatic conditions, such as drought and heat. Analogous results for the *Glu-D1* locus alleles were also obtained by other authors [8, 12].

In the winter wheat cultivars, the distribution of the *Glu-A1* locus alleles is very weakly dependent on the agroclimatic factors, and the distribution of the *Glu-D1* alleles does not depend at all. Nervertheless, a highly significant association of the *Glu-B1* locus alleles with moisture and heat supply (Yule's coefficient of association r_a = 0.33 and 0.32, respectively) is observed. The frequency of the *Glu-B1b* allele is higher in the arid provinces with an elevated heat supply, while the widely spread allele *Glu-B1c* prevails in the humid and cool provinces. For example, of 55 winter wheat cultivars produced at the breeding stations in the Kiev oblast (forest–steppe and southern-taiga–forest zones) 53 cultivars (96.4%) have the *Glu-B1c* allele, and only two cultivars (3.6%) have the *Glu-B1b* allele. All analyzed cultivars from the Moscow oblast carry the *Glu-B1c* allele.

Table 2. Analysis of independence of the *Glu-1* allelic frequencies on the growth habit in the groups of Russian and Ukrainian wheat cultivars

Type of development	*Glu-A1*			*Glu-B1*				*Glu-D1*	
	a	*b*	*c*	*b*	*c*	*i*	*u*	*a*	*d*
Spring cultivars	39 (83)	191 (146)	15 (16)	25 (34)	194 (195)	9 (4)	12 (6)	132 (69)	123 (186)
Winter cultivars	118 (74)	84 (129)	16 (15)	45 (36)	203 (202)	0 (5)	0 (6)	17 (80)	275 (212)
	$\chi^2 = 80.11$* (*d.f.* = 2) *K* = 0.35			$\chi^2 = 26.79$* (*d.f.* = 3) *K* = 0.18				$\chi^2 = 142.66$* (*d.f.* = 1) *K* = 0.51	

* Significant at $P \leq 0.001$. K, Chuprov's coefficient of contingency. Hereafter theoretically expected frequencies rounded off to the whole number are shown in parentheses.

Comparison of Tables 3 and 4 shows that the patterns of distribution of the same alleles of the glutenin loci among natural agricultural provinces are not similar for the spring and winter wheats.

Relationship Between the Glu-1 Locus Alleles and Original Ancestors

Spring wheat. Of 282 cultivars with identified HMWGS alleles, 183 had pedigrees accessible for analysis and were homogeneous for the *Glu-A1* locus alleles, including 29 cultivars with the *Glu-A1a* allele, 143 cultivars with the *Glu-A1b* allele, and 11 cultivars with the *Glu-A1c* allele. There were 166 cultivars homogeneous for the *Glu-B1* locus: 20 cultivars with the *Glu-B1b* allele and 146 cultivars with the *Glu-B1c* allele. Homogeneous for the *Glu-D1* locus were 189 cultivars: 104 cultivars with the *Glu-D1a* allele and 85 cultivars with the *Glu-D1d* allele. The two-way analysis of variance for the *Glu-A1* locus included three alleles (factor *A*) and 60 landraces (factor *B*). For the *Glu-B1* and *Glu-D1* loci, factor *A* (alleles) had two gradations, factor *B* (landraces) had 68 and 54 gradations, respectively. The analysis of variance of the contributions of the landraces calculated with the use of the total Wright's path coefficients (Table 5) showed nonsignificant differences between the frequencies of the alleles (factor *A*), highly significant differences between the average contributions of the landraces (factor *B*), and significance of interaction (*A* × *B*). This points to a nonrandom distribution of the contributions of the landraces in the groups of cultivars with different alleles of three glutenin loci.

Table 3. Association of the HMW glutenin alleles of the Russian and Ukrainian spring bread wheats with moisture and heat supply in natural agricultural provinces

Allele	Characteristics of provinces			
	Moisture supply		Heat supply	
	humid	arid	medium and lower	above medium
Glu-A1a	26 (17)	11 (20)	35 (28)	2 (9)
Glu-A1b	64 (75)	104 (93)	117 (125)	45 (37)
Glu-A1c	8 (6)	6 (8)	12 (11)	2 (3)
	$\chi^2 = 13.63$* (*d.f.* = 2)		$\chi^2 = 9.15$* (*d.f.* = 2)	
Glu-B1b	18 (11)	7 (14)	21 (19)	4 (6)
Glu-B1c	69 (76)	104 (97)	130 (132)	43 (41)
	$\chi^2 = 7.89$* (*d.f.* = 1)		$\chi^2 = 0.52$*ns* (*d.f.* = 1)	
Glu-D1a	37 (55)	84 (66)	74 (92)	47 (29)
Glu-D1d	67 (49)	39 (57)	99 (81)	7 (25)
	$\chi^2 = 22.94$** (*d.f.* = 1)		$\chi^2 = 30.64$** (*d.f.* = 1)	

* , ** Significant at $P \leq 0.01$ and $P \leq 0.001$, respectively.

In the group of cultivars with the *Glu-A1a* allele, the landraces LV-Kremenchug (Artemovka) and Hard Red Calcutta are distinguished by the size of the ancestral contributions (Table 6). Pedigree analysis in this group of cultivars confirmed that the donor of the *Glu-A1a* allele could be either Mironovskaya 808 or the Canadian cultivars derived from Marquis (Selkirk, Kitchener, Hope, and others). In the first case, the source was the landrace LV-Kremenchug (for the cultivars Il'inskaya, Omskaya 17, Enita, and others); in the second case, the donor was Hard Red Calcutta or Red Fife (for the cultivars Voronezhskaya 10, Saratovskaya 758, Khar'kovskaya 24, and others).

In the group of cultivars carrying the *Glu-A1b* allele, significantly larger are the contributions of Poltavka, Selivanovskii Rusak, and Beloturka (Table 6). These landraces are the sources of the *Glu-A1b* allele for most (78%) cultivars of this group (Altaiskaya 92, Altaiskaya 100, Albidum 28, Albidum 29, Belyanka, and others). The pedigree analysis for the remaining cultivars of this group (Zhigulevskaya, Iren', Moskovskaya 21, Moskovskaya 35, and others) showed that another source could be the ancient cultivar Kanred selected from the landrace Crimean through the cultivars Bezenchukskaya 98, Bezostaya 1, or Thatcher.

Table 4. Association of the HMW glutenin alleles of the Russian and Ukrainian winter bread wheats with moisture and heat supply in natural agricultural provinces

Allele	Characteristics of provinces			
	Moisture supply		Heat supply	
	humid	arid	medium and lower	above medium
Glu-A1a	46 (45)	72 (73)	50 (48)	68 (70)
Glu-A1b	26 (32)	57 (51)	28 (34)	55 (49)
Glu-A1c	11 (6)	5 (10)	11 (7)	5 (9)
	$\chi^2 = 8.01^*$ (*d.f.* = 2)		$\chi^2 = 7.00^*$ (*d.f.* = 2)	
Glu-B1b	5 (20)	40 (25)	6 (20)	39 (25)
Glu-B1c	88 (73)	78 (93)	90 (76)	76 (90)
	$\chi^2 = 23.55^{**}$ (*d.f.* = 1)		$\chi^2 = 22.24^{**}$(*d.f.* = 1)	
Glu-D1a	9 (6)	7 (10)	10 (6)	6 (10)
Glu-D1d	97 (100)	178 (175)	102 (106)	173 (169)
	$\chi^2 = 2.04^{NS}$ (*d.f.* = 1)		$\chi^2 = 3.12^{NS}$ (*d.f.* = 1)	

* , ** Significant at $P \leq 0.05$ and $P \leq 0.0001$, respectively.

A small group of cultivars with the *Glu-A1c* allele (Irkutyanka 90, Mal'tsevskaya 110, Skala, and others) is characterized by large contributions of the landraces LV-Balaganskii (Balaganskii uezd, Irkutsk oblast) and LV-Kuitunskii (Kuitunskii raion) (Table 6). However, we failed to trace the sources of the *Glu-A1c* allele from the pedigrees for the lack of sufficient information on the HMWGS profiles in the ancestors.

In the group of cultivars carrying the *Glu-B1b* allele, the contributions of the landraces LV-Omskii (Omskii raion) through Lutescens 956, LV-Samara and LV-Yakutia through Lutescens 1487, and LV-Halland are most prominent (Table 6). They are the sources of this allele for a third part of the cultivars of this group (Dias 2, Tertsiya, Udacha, and others) through Novosibirskaya 67. The pedigree analysis for other cultivars (Botanicheskaya 3, Botanicheskaya 4, Priokskaya, Enita, and others) permitted other sources to be identified from the CIMMYT material—Mediterranean and Akakomugi through Penjamo 62, Norin 10, and Frontana. For some cultivars, the sources were not established because of the lack of correspondence between the alleles of the offspring and both parents (Omskaya 22, Leningradskaya 88) or because of insufficient information about the ancestors (Grekum 114, Uralochka, Saratovskaya 54, and others).

In the group of cultivars with the *Glu-B1c* allele, the most significant contributions were made by the landraces Poltavka, Selivanovskii Rusak, Beloturka, Banatka, Crimean, LV-Tarashchanskii (Tarashchanskii uezd, Cherkassk oblast), LV-Kuitunskii (line 1571-5) (Table 6). The tracing of detailed pedigrees showed that most (78%) of the cultivars (Albidum 28, Albidum 29, Boevchanka, Buryatskaya 79, and others) received this allele from Poltavka, 27% (Lyuba, Moskovskaya 35, Omskaya 24, and others) from the landraces of the cultivar Bezostaya 1 (Banatka, Crimean), for 16% of the cultivars (Vetluzhanka, Novosibirskaya 22, Omskaya 29, and others) the donor of this allele was the cultivar Skala and the source was the landrace Red Fife (Ostka Galicijska).

The most important ancestors for the cultivars with the *Glu-D1a* allele were Poltavka, Selivanovskii Rusak, and Beloturka (Table 6). The pedigree analysis showed that 80% of the cultivars (Albidum 28, Albidum 29, Boevchanka, Buryatskaya 79, and others) could receive this allele from Poltavka.

In the group of cultivars with the *Glu-D1d* allele, significantly larger were the contributions of the original ancestors of the Canadian spring cultivars (Hard Red Calcutta, Red Fife) and domestic winter cultivars (LV-Kremenchug, Banatka, LV-Tarashchanskii). The tracing of detailed pedigrees showed that 72% of the cultivars (Altaiskaya 50, Baganskaya 93, Voronezhskaya 10, Krest'yanka, and others) received this allele from the landrace Ostka Galicijska through Marquis and its derivatives, 29% (Voronezhskaya 12, Zhigulevskaya, Lyuba, Moskovskaya 35, and others) from the original ancestors of the cultivar Bezostaya 1 (Banatka, Crimean), 14% (Luganskaya 4, Khar'kovskaya 22, Enita, and others) from the original ancestor of the cultivar Mironovskaya 808 (LV-Kremenchug).

The pedigree analysis confirms on the whole the results of the analysis of variance. In some cases, with a low frequency of presence in the pedigrees or in small groups, the analysis of variance is not effective.

Table 5. Analysis of variance of the contributions of the original ancestors in the groups of spring wheat cultivars carrying the same alleles of the *Glu-1* loci

Source	*Glu-A1*			*Glu-B1*			*Glu-D1*		
	MS	*DF*	*F*	*MS*	*DF*	*F*	*MS*	*DF*	*F*
Alleles (*A*)	0.0006	2	0.58	0.0012	1	1.024	0.0017	1	1.38
Landraces (*B*)	0.1297	59	115.19*	0.1311	67	114.113*	0.1814	53	142.83*
Interaction ($A \times B$)	0.0185	118	16.41*	0.0046	67	4.016*	0.0241	53	18.94*
Error	0.0011	10800		0.0011	11152		0.0013	10098	

* Significant at $P \leq 0.01$.

Table 6. Average contributions of the landraces* in the Russian and Ukrainian spring wheat cultivars for groups with identical alleles of the *Glu-A1*, *Glu-B1*, and *Glu-D1* loci

Original ancestors	*Glu-A1*			*Glu-B1*		*Glu-D1*	
	a	*b*	*c*	*b*	*c*	*a*	*d*
Crimean	0.040*a*	0.038*a*	0.032*a*	0.019*a*	0.037*b*	0.033*a*	0.039*a*
Hard Red Calcutta	0.054*b*	0.043*ab*	0.035*a*	0.041*a*	0.044*a*	0.034*a*	0.051*b*
K-34291	0.019*a*	0.010*a*	0.017*a*	0.021*b*	0.011*a*	0.000*a*	0.023*b*
LV-Halland (Halland)	–	–	–	0.013*b*	0.002*a*	–	–
LV-Balaganskii Irkutsk oblast	0.001*a*	0.004*ab*	0.014*b*	0.000*a*	0.005*a*	0.003*a*	0.006*a*
LV-Kremenchug (Artemovka)	0.075*c*	0.017*b*	0.002*a*	0.021*a*	0.030*a*	0.021*a*	0.033*b*
LV-Kuitunskii (Line 1571-5)	0.003*a*	0.014*a*	0.055*b*	0.000*a*	0.016*b*	0.010*a*	0.021*b*
LV-Omskii (Lut. 956)	–	–	–	0.043*b*	0.010*a*	–	–
LV-Samara (Lut. 1487)	–	–	–	0.028*b*	0.003*a*	–	–
LV-Tarashchanskii Cherkassk oblast	0.013*a*	0.013*a*	0.020*a*	0.001*a*	0.014*b*	0.006*a*	0.018*b*
LV-Yakutia (Lut. 1487)	–	–	–	0.028*b*	0.003*a*	–	–
Red Fife (Ostka Galicijska)	0.060*a*	0.049*a*	0.047*a*	0.052*a*	0.051*a*	0.040*a*	0.059*b*
Banatka	0.014*a*	0.016*a*	0.020*a*	0.004*a*	0.018*b*	0.009*a*	0.020*b*
Beloturka	0.015*a*	0.032*b*	0.007*a*	0.011*a*	0.028*b*	0.038*b*	0.016*a*
Poltavka	0.138*b*	0.243*c*	0.086*a*	0.189*a*	0.231*b*	0.289*b*	0.141*a*
Selivanovskii Rusak	0.022*a*	0.039*b*	0.049*b*	0.017*a*	0.040*b*	0.050*b*	0.020*a*

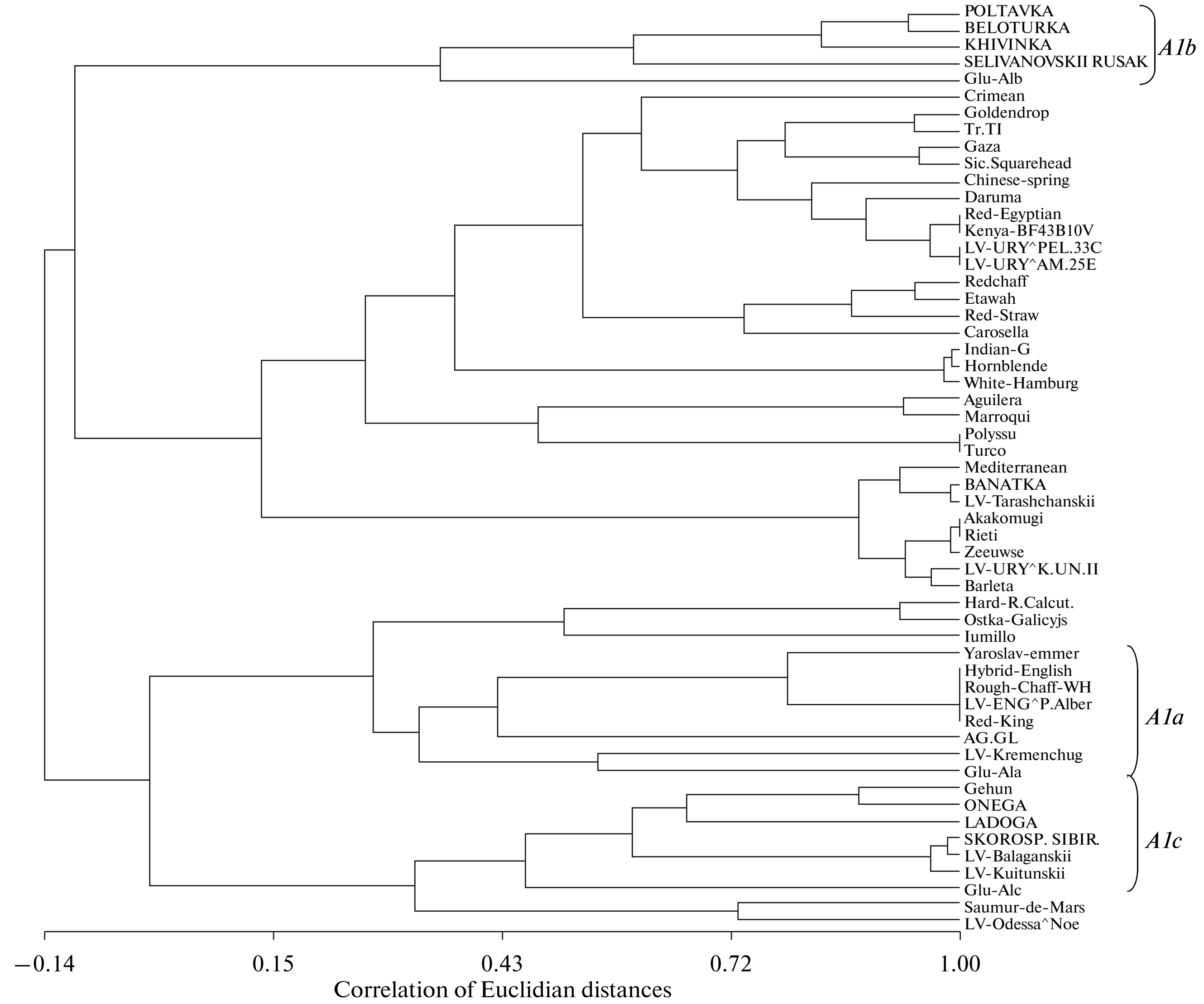
* The values accompanied by the same letters differ significantly by the Duncan's test for multiple comparisons.

On the other hand, in the absence of information on the *Glu-1* profiles in the original ancestors or in selections from them, the pedigree analysis does not allow the sources of the alleles to be established. Nevertheless, analysis of variance of the contributions of the ancestral landraces and pedigree analysis mutually complement each other.

The results obtained are supported on the whole by cluster analysis of the matrices of the genealogical profiles supplemented with vectors of the sign of the presence of the *Glu-1* alleles. As an example, a dendrogram of the cluster analysis of the original ancestors and *Glu-A1* alleles is presented in the figure.

Winter wheat. Of 323 cultivars, 203 had complete pedigrees and were homogeneous for the *Glu-A1* locus alleles. Among them, 111 cultivars carried the *Glu-A1a* allele, 78 carried the *Glu-A1b* allele, and 14 had the *Glu-A1c* allele. There were 228 cultivars homogeneous for the *Glu-B1* allele: 37 cultivars with the *Glu-B1b* allele and 191 cultivars with the *Glu-B1c* allele. The analysis also included 271 cultivars homogeneous for the *Glu-D1* locus: 14 cultivars carrying the *Glu-D1a* allele and 257 cultivars with the *Glu-D1d* allele. The two-way analysis variance for the *Glu-A1* locus included three alleles (factor *A*) and 76 landraces (factor *B*). For the loci *Glu-B1* and *Glu-D1* factor *A* (alleles) had two gradations, factor *B* (landraces) had 50 and 52 gradations, respectively. The analysis of variance of the contributions of the landraces (Table 7) showed highly significant differences between the average contributions of the landraces (factor *B*) and significance of interaction ($A \times B$). The latter points to differences in the distribution of the contributions of the landraces among the groups of cultivars with different alleles of three glutenin loci.

The comparison of the average contributions of the landraces between the cultivars grouped by the *Glu-A1* locus alleles (Table 8) shows that the groups differ significantly in the contributions of 17 landraces. The group for the *Glu-A1a* allele included 111 cultivars, half of them being derivatives of Mironovskaya 808 (Bazal't, Bezenchukskaya 380, Donskaya Bezostaya, and others), and the third part being derivatives of Odesskaya 16 (Al'batros Odesskii, Soratnitsa, Yunnat Odesskii, and others). This group of cultivars is distinguished by the sizes of the contributions of the ancestral landraces of the founder cultivars—LV-Kremenchug (Artemovka), LV-Odessa (Zemka), and Khar'kovskaya (Gostianum 237). It can be suggested that these landraces were the sources of the *a* allele. Nearly all cultivars with the *Glu-A1b* allele are derivatives of Bezostaya 1. Possible sources of the *Glu-A1b* allele are the landraces Banatka (Ukrainka) and LV- Tarashchanskii. Note that in the group of cultivars with the *Glu-A1b* allele half of the cultivars are also derivatives of Mironovskaya 808 (Kroshka, Levoberezhnaya 1, Naslednitsa), but the average contribution of the landrace LV-Kremenchug is



A dendrogram of the cluster analysis of the original ancestors and the *Glu-A1* locus alleles in the Russian and Ukrainian spring wheat cultivars. Clusters of the original ancestors associated with the alleles *a*, *b*, and *c* are shown.

more that two times lower. The landraces Khar'kovskaya and LV-Odessa (Zemka) heterogenous for the *Glu-A1* alleles have maximum contributions in this group and a maximum frequency of presence in the pedigrees. However, tracing of detailed pedigrees for the *Glu-A1b* allele shows that this allele from Khar'kovskaya through Gostianum 237 and from LV-Odessa through Zemka is blocked by the bottleneck of the cultivars Odesskaya 12 and Odesskaya 16 that carry the *Glu-A1a* allele. A comparatively rare null allele, *Glu-A1c*, associated with a poor grain quality could appear as a result of hybridization with a foreign material, for example, with Maris Huntsman (Oktava, Polesskaya 87), Carstens VIII (Mirhad, Rovenskaya 31), Siete Cerros 66 (Daha, Mirich), Geurumil (Uskoryanka). It may well be that the donors of the null allele were also the cultivars Avrora and Kavkaz (*Glu-A1c/b*) that are present in the pedigrees of Daha, Mirich, Mironovskaya 68 and other cultivars. In this case, the source of this allele could be the line Neuzucht 14-44 = Criewener 104/(*S. cereale*) Petkus. In four of 14 cultivars, both parents carry other alleles, for example, Rosinka Tarasovskaya (*Glu-A1c*) = Soratnitsa (*Glu-A1a*)/(*Glu-A1a*) Donshchina, Goryanka (*Glu-A1c*) = Olimpiya 2 (*Glu-A1b*)/(*Glu-A1b*) Massiv. The ancestral landraces of the foreign cultivars Indian-D, Sterling-B, and Wase Nibay have significantly larger contributions.

In the group of cultivars with the *Glu-B1b* allele, the most considerable contributions were made by the landraces LV-Odessa (Zemka) and Khar'kovskaya (Table 8) from which the cultivar Odesskaya was derived. The tracing of detailed pedigrees showed that for most (78%) cultivars of this group composed of Odesskaya 267, Prestizh, Ukrainka Odesskaya, and other cultivars the donors of

Table 7. Analysis of variance of the contributions of the original ancestors in the groups of winter wheat cultivars carrying identical alleles of the *Glu-1* loci

Source	*Glu-A1*			*Glu-B1*			*Glu-D1*		
	MS	*DF*	*F*	*MS*	*DF*	*F*	*MS*	*DF*	*F*
Alleles (*A*)	0.0003	2	0.6	0.0042	1	5.7*	0.0086	1	12.7**
Landraces (*B*)	0.0628	75	139.6**	0.0992	49	136.6**	0.1031	51	151.1**
Interaction (*A* × *B*)	0.0027	150	5.9**	0.0076	49	10.5**	0.0143	51	20.9**
Error	0.0004	15200		0.0007	11300		0.0007	13988	

* , ** Significant at $P \leq 0.05$ and $P \leq 0.01$, respectively.

Table 8. Average contributions of the landraces* in the Russian and Ukrainian winter wheat cultivars for groups with identical alleles of the *Glu-1* loci

Original ancestors**	*Glu-A1*			*Glu-B1*		*Glu-D1*	
	a	*b*	*c*	*b*	*c*	*a*	*d*
Akakomugi	0.027*a*	0.038*b*	0.034*b*	0.045*b*	0.034*a*	0.054*b*	0.034*a*
Barleta	0.020*a*	0.024*a*	0.017*a*	0.024*a*	0.022*a*	0.037*b*	0.021*a*
Crimean	0.065*a*	0.067*a*	0.060*a*	0.064*a*	0.069*a*	0.080*b*	0.063*a*
Hard Red Calcutta	0.009*a*	0.009*a*	0.010*a*	0.014*a*	0.008*a*	0.003*a*	0.010*b*
Indiana Swamp	0.013*b*	0.000*a*	0.004*a*	0.009*a*	0.007*a*	0.005*a*	0.007*a*
Indian-G	0.000*a*	0.000*a*	0.009*b*	0.000*a*	0.001*a*	0.000*a*	0.001*a*
LV-URY (Klein Universal-II)	0.018*a*	0.022*a*	0.016*a*	0.022*a*	0.021*a*	0.037*b*	0.019*a*
LV-Zolochevskii raion, Khar'kov oblast	0.011*b*	0.009*b*	0.000*a*	0.003*a*	0.014*b*	0.006*a*	0.011*a*
LV-Kremenchug (Artemovka)	0.104*c*	0.046*a*	0.055*b*	0.032*a*	0.086*b*	0.028*a*	0.080*b*
LV-Odessa (Zemka)	0.037*b*	0.043*b*	0.008*a*	0.068*b*	0.026*a*	0.002*a*	0.040*b*
LV-Tarashchanskii Cherkassk oblast	0.059*b*	0.073*c*	0.045*a*	0.060*a*	0.064*a*	0.044*a*	0.063*b*
Mediterranean	0.040*a*	0.055*b*	0.057*b*	0.050*a*	0.053*a*	0.089*b*	0.048*a*
Rieti	0.014*a*	0.024*b*	0.020*ab*	0.030*b*	0.018*a*	0.030*b*	0.020*a*
Sterling-B	0.000*a*	0.000*a*	0.009*b*	0.002*a*	0.005*a*	0.004*a*	0.004*a*
Wase Nibay	0.000*a*	0.000*a*	0.009*b*	0.002*a*	0.005*a*	0.004*a*	0.004*a*
Banatka	0.073*b*	0.076*b*	0.047*a*	0.073*a*	0.076*a*	0.044*a*	0.074*b*
Khar'kovskaya (Gostianum 237)	0.049*b*	0.058*c*	0.024*a*	0.074*b*	0.039*a*	0.007*a*	0.051*b*

Notes: * The values accompanied by the same letters differ significantly by the Duncan's test for multiple comparisons.
** LV-landrace.

Glu-B1b were most probably Odesskaya 16 and the CIMMYT cultivars (Red River 68, Pitic 62, Inia 66, and others). The cultivars Atkara and Levoberezhnaya 3 could receive the *Glu-B1b* allele from Albidum 114, but the source of this allele is unknown. In the cultivars with the *Glu-B1c* allele, the largest contribution belongs to the landrace LV-Kremenchug (Artemovka). This is due to the fact that in most (56%) cultivars of this group the donor of the *Glu-B1c* allele was Mironovskaya 808. The pedigree analysis showed that the remaining cultivars could receive the *Glu-B1c* allele from Bezostaya 1 (Donetskaya 46, Knyazhna, Lira, Polovchanka, and others), Ukrainka (Belotserkovskaya 198, Novoukrainka 83, and others), and from a number of selections from the landraces, for example, from Cheyenne (Priazovskaya Uluchshennaya), Gostianum 237 or Zemka (Odesskaya 12), Lutescens 329

Table 9. Analysis of independence of the frequencies of alleles of the glutenin loci and the market classes among the spring wheat cultivars from Russia and Ukraine

Class	*Glu-A1a*	*Glu-A1b*	*Glu-A1c*	*Glu-B1b*	*Glu-B1c*	*Glu-D1a*	*Glu-D1d*
Strong	17 (20)	76 (68)	5 (10)	16 (18)	82 (80)	51 (53)	52 (50)
Valuable	12 (12)	43 (41)	5 (6)	10 (11)	46 (46)	23 (30)	35 (28)
Fillers	33 (30)	90 (100)	22 (15)	25(22)	93 (96)	72 (63)	49 (58)
	$\chi^2 = 8.92$*ns* (*d.f.* = 4) $P > 0.06$			$\chi^2 = 0.97$*ns* (*d.f.* = 2) $P > 0.60$		$\chi^2 = 6.52$* (*d.f.* = 2) $0.01 < P \le 0.05$	

* Significant at $P \le 0.05$.

Table 10. Analysis of independence of the distribution of the spring cultivars by the market classes and by the alleles of the *Glu-1* loci in pairwise comparisons of the market classes according to the data in Table 9

Class	Valuable			Fillers		
	Glu-A1	*Glu-B1*	*Glu-D1*	*Glu-A1*	*Glu-B1*	*Glu-D1*
Strong	$\chi^2 = 0.93$*ns*, $P > 0.60$	$\chi^2 = 0.00$*ns*, $P > 0.95$	$\chi^2 = 1.08$*ns*, $P > 0.30$	$\chi^2 = 8.22$*, $0.01 < P \le 0.05$	$\chi^2 = 0.54$*ns*, $P > 0.40$	$\chi^2 = 1.86$*ns*, $P > 0.10$
Valuable	–	–	–	$\chi^2 = 2.26$*ns*, $P > 0.30$	$\chi^2 = 0.10$*ns*, $P > 0.75$	$\chi^2 = 5.43$*, $0.01 < P \le 0.05$

* Significant at $P \le 0.05$.

(Sibirskaya Niva). In the Russian and Ukrainian cultivars, the *Glu-B1c* allele is widely spread, and its sources could be a multitude of landraces or selections from them.

For the *Glu-D1* locus, the ancestral contributions of the landraces Mediterranean, Crimean, Akakomugi, LV-URY (Klein Universal-II), Barleta, and Rieti are significantly higher in the group of cultivars with the *Glu-D1a* allele. The pedigree analysis showed that the donors of the *Glu-D1a* allele, which is rare for the Russian and Ukrainian winter wheat cultivars, were foreign cultivars (Carstens VIII, Mara, Maris Huntsman, San Pastore, and others). In the group of cultivars with the *Glu-D1d* allele the largest contributions were from the landraces LV-Kremenchug (Artemovka), Banatka, LV-Tarashchanskii, Khar'kovskaya, and Hard Red Calcutta (Table 8). The pedigree analysis showed that the donors of the *Glu-D1d* allele were the founder cultivars Bezostaya 1, Mironovskaya 808, and Odesskaya 16. It can be suggested that the sources of the corresponding alleles are among the landraces distinguished by the largest sizes of the ancestral contribuions.

Association of the Frequencies of Alleles of the HMWGS Loci with Market Classes

In this work, the cultivars of spring and winter wheats from Russia and Ukraine were divided into three groups: (1) strong wheat cultivars, (2) cultivars valuable in quality, (3) cultivars with a medium breadmaking quality or fillers [26].

Spring wheat. Among cultivars with the known HMWGS compositions, 89 strong cultivars, 57 valuable cultivars, and 119 fillers were included in the analysis. The analysis of the frequencies of the *Glu-1* alleles in these groups (Table 9) demonstrates independence of the distributions of the cultivars by the market classes and by the alleles of the *Glu-A1* and *Glu-B1* loci. For the *Glu-D1* locus, the null hypothesis about independence is rejected at $P \le 0.05$. Analysis of independence by the χ^2 test with a pairwise comparison of the groups (Table 10) shows that the null hypothesis is rejected at $P = 0.05$ only for the *Glu-A1* locus in the case of comparison of the strong cultivars with the fillers and for the *Glu-D1* locus in the case of comparison of the valuable cultivars with the fillers. In all other cases, the distributions of the cultivars by the market classes and by the alleles of the glutenin loci are independent. Since the classes of strong and valuable cultivars showed independent distributions of the alleles of all three glutenin loci (Table 10), it was natural to compare the combined group of the strong and valuable cultivars with the fillers. The data in Table 11 show a significant prevalence of the *Glu-A1b* and *Glu-D1d* alleles in the combined group of strong and valuable cultivars.

Table 11. Estimation of independence of the distribution of the spring cultivars by the market classes and by the alleles of the *Glu-1* loci in comparisons of the combined group of strong and valuable cultivars with the fillers according to the data in Table 9

Class	*Glu-A1a*	*Glu-A1b*	*Glu-A1c*	*Glu-B1b*	*Glu-B1c*	*Glu-D1a*	*Glu-D1d*
Strong + valuable	29 (32)	119 (109)	10 (17)	26 (29)	128 (125)	74 (83)	87 (78)
Fillers	33 (30)	90 (100)	22 (15)	25 (22)	93 (96)	72 (55)	49 (52)
	$\chi^2 = 8.24$*, *d.f.* = 2			$\chi^2 = 0.55$*ns*, *d.f.* = 1		$\chi^2 = 4.55$*, *d.f.* = 1	

* Significant at $P \le 0.05$.

Table 12. Contingency table for the association between the market classes and the frequencies of the *Glu-1* alleles in the group of spring wheat cultivars from USA, Canada, and Australia

Class	*Glu-A1*			*Glu-B1*								*Glu-D1*	
	a	*b*	*c*	*a*	*b*	*c*	*d*	*e*	*f*	*i*	*u*	*a*	*d*
Hard-grain cultivars (HRS, HWS)	61 (64)	94 (84)	10 (17)	12 (10)	50 (41)	69 (55)	6 (6)	2 (18)	3 (6)	20 (27)	10 (9)	31 (55)	125 (101)
Soft-grain cultivars (SRS, SWS)	60 (57)	63 (73)	22 (15)	6 (8)	28 (37)	35 (49)	6 (6)	31 (15)	8 (5)	31 (24)	7 (8)	72 (48)	66 (90)
	$\chi^2 = 9.38$* (*d.f.* = 2) $P \le 0.01$			$\chi^2 = 48.93$* (*d.f.* = 7) $P \le 0.001$								$\chi^2 = 32.17$* (*d.f.* = 1) $P \le 0.001$	

* Significant at $P \le 0.01$.

For comparison, let us check independence of the distributions by the market classes and by the glutenin alleles among foreign spring wheat cultivars: in hard-grain (HRS, HWS) and soft-grain (SRS, SWS) cultivars from the United States, Canada, and Australia. The group of hard-grain wheats included 150 cultivars, and the group of soft-grain wheats included 125 cultivars (information from the GRIS database). Analysis with the χ^2 test showed a highly significant association between the distribution of alleles of all three HMWGS loci and the market classes (Table 12). The closest association was observed for the *Glu-D1* locus alleles (Yule's coefficient of association r_a = 0.33). In the class of hard-grain cultivars, the prevailing alleles are *Glu-A1b, Glu-B1b, Glu-B1c*, and *Glu-D1d*, and in the class of soft-grain cultivars the prevailing alleles are *Glu-A1c, Glu-B1e, Glu-B1i*, and *Glu-D1a*.

Analysis of independence of the distribution by the market classes and by the alleles of the glutenin loci among the domestic (Table 11) and foreign (Table 12) spring wheat cultivars showed different levels of association between the quality classes and high-molecular-weight glutenins. Nevertheless, in both cases a prevalence of the *Glu-A1b* and *Glu-D1d* alleles is observed both in the group of strong and valuable cultivars from Russia and Ukraine and in the group of hard-grain cultivars from the United States, Canada, and Australia. For the *Glu-B1* locus, the diversity in the foreign cultivars is much higher (*PIC* = 0.73) than in the domestic cultivars (*PIC* = 0.28) (it should be noted that the latter have an independent distribution of the alleles). The prevailing alleles in the hard-grain cultivars from the United States, Canada, and Australia are *Glu-B1b* and *Glu-B1c*.

In the Russian standard, the attribution of a cultivar to a market class depends on a wider range of characteristics than in the American one. Some parameters in the Russian and American standards are analogous. For instance, strong wheats, like hard-grain wheats, are genetically characterized by high bread-making qualities and by the ability to be improvers of weak wheats. Both standards take into account the grain nature and protein content. Yet, the Russian and American systems of classification differ in some parameters. For example, the American standard is based on the trait of grain hardness, while in the Russian standard this characteristic is absent. One of the most important characteristics in the Russian classification is the level and quality of gluten, but in the United States the analysis of gluten is not necessary in determining wheat classes. At the same time, most of the strong and valuable wheats of Russia and Ukraine are characterized by hard grain, and most of the American cultivars belong to the first group of gluten quality as the strong and valuable Russian and Ukrainian cultivars.

It can be assumed that the observed differences in the analysis of the domestic and foreign cultivars are

Table 13. Analysis of association of the frequencies of alleles of the glutenin loci with the market classes among the winter wheat cultivars from Russia and Ukraine

Class	*Glu-A1a*	*Glu-A1b*	*Glu-A1c*	*Glu-B1b*	*Glu-B1c*	*Glu-D1a*	*Glu-D1d*
Strong	60 (55)	55 (51)	5 (14)	41 (28)	62 (75)	8 (12)	86 (82)
Valuable	51 (50)	46 (46)	12 (12)	17 (27)	80 (70)	10 (12)	85 (83)
Fillers	79 (84)	74 (78)	30 (21)	40 (43)	116 (113)	25 (19)	127 (133)
	$\chi^2 = 10.77$* (*d.f.* = 4) $0.01 < P \leq 0.05$			$\chi^2 = 12.93$** (*d.f.* = 2) $P \leq 0.01$		$\chi^2 = 3.84$ *ns*, (*d.f.* = 2) $P > 0.20$	

* , ** Significant at $P \leq 0.05$ and $P \leq 0.01$, respectively.

Table 14. Analysis of independence of the distribution of the winter cultivars from Russia and Ukraine by the market classes and by the alleles of the *Glu-1* loci in pairwise comparisons of the market classes according to the data in Table 13

Class	Valuable			Fillers		
	Glu-A1	*Glu-B1*	*Glu-D1*	*Glu-A1*	*Glu-B1*	*Glu-D1*
Strong	$\chi^2 = 3.89$*ns*, $P > 0.10$	$\chi^2 = 10.99$**, $P \leq 0.01$	$\chi^2 = 0.05$*ns*, $P > 0.80$	$\chi^2 = 10.61$**, $P \leq 0.01$	$\chi^2 = 5.15$*, $0.01 < P \leq 0.05$	$\chi^2 = 2.50$*ns*, $P > 0.10$
Valuable	–	–	–	$\chi^2 = 1.63$*ns*, $P > 0.40$	$\chi^2 = 1.82$*ns*, $P > 0.10$	$\chi^2 = 1.23$*ns*, $P > 0.25$

* , ** Significant at $P \leq 0.05$ and $P \leq 0.01$, respectively.

determined by differences in the standards of classification by quality.

Winter wheat. Among cultivars with the known HMWGS compositions, 86 strong, 87 valuable, and 141 fillers were analyzed. In contrast to the spring wheats, 47 winter wheat cultivars carried the wheat–rye translocation 1BL.1RS, including one strong cultivar, 21 valuable cultivars, and 25 fillers. The translocation is known to deteriorate the bread-making quality [1]. Therefore, the analysis of the association of the HMWGS allelic frequencies with the market classes was carried out both for all cultivars and with the exclusion of cultivars carrying translocations.

The distribution of the most frequent alleles of the *Glu-1* loci in these groups of cultivars is presented in Table 13. The null hypothesis about independence of the distribution of the winter cultivars by the market classes and by the alleles of the high-molecular-weight glutenin loci *Glu-A1* and *Glu-B1* is rejected, while independence of the distribution is observed in the case of the *Glu-D1* locus (Table 13). The analysis of independence by the χ^2 test with a pairwise comparison of the groups (Table 14) showed a significant association between the market classes (strong and valuable cultivars) and the *Glu-B1* locus alleles and also between the strong cultivars and fillers and the alleles of the *Glu-A1* and *Glu-B1* loci. The comparison of the valuable cultivars and fillers showed independent distributions of the alleles of three glutenin loci.

Since the classes of valuable cultivars and fillers showed independence of the distribution for all three glutenin loci (Table 14), it was natural to compare the combined group of the valuable cultivars and fillers with the strong cultivars. It is seen from Table 15 that the *Glu-B1b* allele prevails in the strong cultivars, and in the combined group of valuable cultivars and fillers a significant prevalence of the *Glu-A1c* and *Glu-B1c* alleles is observed.

The exclusion from the analysis of cultivars with the 1BL.1RS translocation practically did not change the pattern of association between the frequencies of the HMWHS alleles and the market classes.

For comparison, let us check independence of the distributions by the market classes and by the HMWGS alleles among foreign winter wheats: in hard-grain (HRW, HWW) and soft-grain (SRW, SWW) cultivars from the United States and Canada. The group of hard-grain wheats included 282 cultivars (among them five cultivars with the 1BL.1RS translocation), and the group of soft-grain wheats included 168 cultivars without this translocation. The analysis of independence by the χ^2 test showed a highly significant ($P \leq 0.001$) association between the distribution of alleles of all three HMWGS loci and the market classes (Table 16). The prevailing alleles in the group of hard-grain cultivars are *Glu-A1b, Glu-B1c*, and *Glu-D1d*, and in the group of soft-grain cultivars the alleles *Glu-A1a, Glu-A1c, Glu-B1d*, and *Glu-D1a* prevail.

Table 15. Estimation of independence of the distribution of the winter cultivars by the market classes and by the alleles of the *Glu-1* loci in comparisons of the strong cultivars with the combined group of valuable cultivars and fillers according to the data in Table 13

Class	*Glu-A1a*	*Glu-A1b*	*Glu-A1c*	*Glu-B1b*	*Glu-B1c*	*Glu-D1a*	*Glu-D1d*
Strong	60 (55)	55 (51)	5 (14)	41 (28)	62 (75)	8 (12)	86 (82)
Valuable + fillers	130 (135)	120 (124)	42 (33)	57 (70)	196 (183)	35 (31)	212 (216)
	$\chi^2 = 8.79^*$ (*d.f.* = 2) $P \leq 0.05$			$\chi^2 = 10.10^{**}$ (*d.f.* = 1), $P \leq 0.01$		$\chi^2 = 1.50$*ns* (*d.f.* = 1) $P > 0.20$	

* , ** Significant at $P \leq 0.05$ and $P \leq 0.01$, respectively.|

Table 16. A contingency table for the association between the market classes and the frequencies of the *Glu-1* alleles in the group of winter wheat cultivars from USA and Canada

Class	*Glu-A1*			*Glu-B1*					*Glu-D1*		
	a	*b*	*c*	*a*	*b*	*c*	*d*	*f*	*a*	*b*	*d*
Hard-grain cultivars (HRW, HWW)	71 (99)	198 (159)	12 (24)	5 (17)	83 (84)	161 (137)	15 (23)	4 (7)	73 (111)	21 (23)	195 (155)
Soft-grain cultivars (SRW, SWW)	87 (59)	56 (95)	26 (14)	22 (10)	53 (52)	60 (84)	22 (14)	8 (5)	104 (66)	16 (14)	53 (93)
	$\chi^2 = 62.14^*$ (*d.f.* = 2)			$\chi^2 = 44.13^*$ (*d.f.* = 4)					$\chi^2 = 62.21^*$ (*d.f.* = 2)		

* Significant at $P \leq 0.001$.

Analysis of independence of the distribution by the market classes and by the alleles of the HMWGS loci among the domestic (Table 15) and North American winter wheat cultivars shows different levels of association between the market classes and high-molecular-weight glutenins. The prevailing alleles in the groups of the domestic and North American winter cultivars do not coincide.

Let us make another comparison using winter wheat cultivars from Western and Central Europe. The system of classification of wheats into market classes in the European countries differs from the standards in Russia, Ukraine, and North America. This is explained by different bread-making traditions. In the countries of Europe, the group of bread wheats includes three classes of quality: high or elite class (E) including cultivar-improvers, first (A) and second (B) classes. The group of wheats with unfit baking qualities includes soft-grain cultivars indended for confectionery production (C) and feed wheats (D).

Information about the cultivars from Western and Central Europe with the known HMWGS profiles and market classes was retrieved from the GRIS database. The cultivars were divided into two groups. The first group was represented by 131 cultivars of the elite and first classes (E and A) with 27 cultivars carrying the 1BL.1RS translocation; the second group included 146 soft-grain cultivars characterized by a mediim or poor bread-making quality (classes C and D) with 36 cultivars carrying the translocation. The cultivars with an intermediate quality (class B) were not taken in the analysis. The analysis of independence between the frequencies of the *Glu-1* alleles and the quality groups by the χ^2 test showed a highly significant association ($P \leq 0.001$) between the distribition of alleles of all three HMWGS loci and the market classes (Table 17). The coefficient of association between the *Glu-A1*, *Glu-B1*, and *Glu-D1* alleles and the quality groups is 0.34, 0.51, and 0.58, respectively. In the group of high-quality cultivars (classes E and A) the prevaling alleles are *Glu-A1a*, *Glu-A1b, Glu-B1c*, and *Glu-D1d*, and the *Glu-A1c, Glu-B1a, Glu-B1d*, *Glu-D1a*, and *Glu-D1b* alleles prevail in the groups of soft-grain and feed cultivars (classes C and D). The exclusion from the analysis of cultivars with the translocation practically did not change the degree of association of the HMWGS alleles with the market classes (results not shown).

It is seen from Tables 16 and 17 that the combination of the *Glu-A1b*/*a*, *Glu-B1c*, and *Glu-D1d* alleles characteristic of the European cultivars with a high bread-making quality is close to the combination of the *Glu-A1b, Glu-B1c,* and *Glu-D1d* alleles in the hard-grain North American cultivars. However, we failed to reveal a specific composition of alleles for the

Table 17. Contingency table for the association between the market classes and the frequencies of the *Glu-1* alleles in the group of winter wheat cultivars from the countries of Europe

Class	*Glu-A1*			*Glu-B1*				*Glu-D1*		
	a	*b*	*c*	*a*	*b*	*c*	*d*	*a*	*b*	*d*
E, A	41 (34)	48 (28)	52 (79)	9 (19)	15 (14)	95 (53)	10 (43)	27 (67)	0 (8)	109 (61)
C, D	29 (36)	11 (31)	113 (86)	32 (22)	15 (16)	16 (58)	81 (48)	112 (72)	16 (8)	17 (65)
	$\chi^2 = 47.40$* (*d.f.* = 2)			$\chi^2 = 124.07$* (*d.f.* = 3)				$\chi^2 = 135.00$* (*d.f.* = 2)		

* Significant at $P \leq 0.001$.

strong winter wheat cultivars from Russia and Ukraine (see Tables 13 and 15). Only one allele, *Glu-B1b*, significantly prevails in this group, which does not agree with the results of analysis of the foreign cultivars with a high bread-making quality. In the opinion of many authors, the *Glu-D1d* allele is associated with a high quality [1]. Yet, among the Russian and Ukrainian winter wheat cultivars, there are no significant differences between the strong wheats and fillers in the frequencies of the *Glu-D1* alleles, i. e., the *Glu-D1d* allele equally prevails in both these groups.

Thus, the analysis of HMWGS diversity in the Russian and Ukrainian bread wheat cultivars permits the following conclusions to be made.

(1) The diversity of the spring wheat cultivars for alleles of the *Glu-1* loci is characterized by intermediate values of the polymorphism index (*PIC* = 0.45–0.50). The allelic diversity in the winter cultivars varies from high at the *Glu-A1* locus (*PIC* = 0.59) and medium at the *Glu-B1* locus (*PIC* = 0.48) to low at the *Glu-D1* locus (*PIC* = 0.24). Loci with a large number of alleles and with *PIC* close to 1 are preferable to be used as markers. The estimates of bread wheat diversity show that the high-molecular-weight glutenin subunits cannot be good markers of commercial characteristics.

(2) The spring and winter cultivars are significantly different in the distribution of alleles of the glutenin loci. The frequency of presence of the *Glu-A1a*, *Glu-B1b*, and *Glu-D1d* alleles in the winter cultivars is higher than in the spring cultivars, and the frequencies of the *Glu-A1b* and *Glu-D1a* alleles in the spring cultivars are higher than in the winter cultivars. The *Glu-A1b*, *Glu-B1c*, *Glu-D1a* allelic composition prevails among the spring cultivars, and the *Glu-A1a*, *Glu-B1c*, *Glu-D1d* composition is most common in the winter cultivars.

(3) The distribution of the *Glu-1* alleles shows a significant association with moisture and heat supply in the regions of origin of the cultivars. The *Glu-D1a* allele in the spring wheat cultivars is associated with resistance to drought and heat, and cultivars with the *Glu-D1d* allele are less adaptive to climatic stresses. The *Glu-A1b* and *Glu-B1c* alleles display a statistically significant tendency to prevail in arid regions. The frequency of presence of the *Glu-B1b* allele in the winter wheat cultivars is significantly higher in arid provinces with an excessive heat supply, while the *Glu-B1c* allele prevails in humid and cool provinces.

(4) The glutenin profiles are associated with the original ancestors. In the spring cultivars, the source of the *Glu-A1b, Glu-B1c*, and *Glu-D1a* alleles is Poltavka, landrace from the Saratov oblast. Rather rare alleles, *Glu-A1a* and *Glu-B1b*, were received from the original ancestors of the cultivars Mironovskaya 808 and Novosibirskaya 67, respectively. Most of the cultivars with the *Glu-D1d* allele acquired it from the landrace Ostka Galicijska through Red Fife. The main sources among the Russian and Ukrainian cultivars were the original ancestors of the founder cultivars Mironovskaya 808, Bezostaya 1, and Odesskaya 16—LV-Kremenchug (*Glu-A1a, Glu-B1c, Glu-D1d*), Banatka, Crimean (*Glu-A1b, Glu-B1c, Glu-D1d*), Zemka, and Khar'kovskaya (*Glu-A1a, Glu-B1b, Glu-D1d*).

(5) The comparative analysis of independence of the distribution of the spring wheat cultivars by the market classes and by the alleles of the HMWGS loci showed independence (*Glu-A1*, *Glu-B1*) and a weak association (*Glu-D1*) in the Russian and Ukrainian cultivars and a highly significant association between the alleles of three *Glu-1* loci and the market classes in the foreign cultivars. An analogous comparison of the domestic winter wheat cultivars with the foreign cultivars also demonstrated a weak association (*Glu-A1*, *Glu-B1*) or independence (*Glu-D1*) in the domestic cultivars and a highly significant association between the alleles of three HMWGS loci and the market classes in the North American and European cultivars. It is probable that independence or a weak association between the distribution of the glutenin alleles and the market classes is due to the absence of a statistically substantiated system of classification of the domestic cultivars by their quality.

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