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SPECIFICITY OF WEST PAMIR WHEAT LANDRACES AND THEIR ALLELIC VARIATIONS AT THE VERNALIZATION RESPONSE (*VRN-1*), PHOTOPERIOD SENSITIVITY (*PPD-1*), AND *GLU-1* GENES

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SUMMARY

The article presents data reflecting the uniqueness and adaptive traits of landrace wheat varieties of the Western Pamir, continuously cultivated in highland small farms at altitudes of more than 2000 masl. For the important traits, like lodging resistance and quality, the bread wheat (*Triticum aestivum* L.) varietal improvement is possible. Protein labeling showed the significant polymorphism and distinctiveness in varietal samples within all α, β, γ, and ω subfractions of storage seed proteins – gliadins, which is the specificity of wheat cultivars of Tajik Badakhshan on *Gli-B1* locus. Most of the local bread wheat cultivars had the composition of high molecular weight glutenin subunits, i.e., null (*Glu-1A*), 7+8 (*Glu-B1*), and 2+12 (*Glu-D1*). Genetic diversity analysis of West Pamir landraces by the alleles of *VRN-A1* and *VRN-D1* vernalization genes showed their identity that all cultivars had recessive (*vrn-A1*) and dominant allele (*Vrn-D1*). For *PPD-1* genes, the allelic composition of the wheat cultivars revealed a representation of an allele of insensitivity to day length (*Ppd-A1a*) and two alleles (*Ppd-B1b* and *Ppd-D1b*) providing sensitivity to the photoperiod.

Keywords: Local bread wheat (*T. aestivum* L.), West Pamir, molecular markers, diversity of *VRN-1*, *PPD-1, Glu-1* genes, polymorphism, quality traits

Key findings: The combination of recessive allele (*vrn-A1*) and dominant allele (*Vrn-D1*) with the main genes of sensitivity to photoperiod (*Ppd-1D, Ppd-1B*) promotes the adaptation of Western Pamir bread wheat (*T. aestivum* L.) landraces to conditions of the highlands.

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INTRODUCTION

Climate aridization and population growth are critical challenges to countries' food security. In this regard, developing crop cultivars and hybrids exceeding current breeding achievements by yield is a priority task of agricultural science. However, the solution of these problems and success depends on the initial base material's diversity and genetic variability, the available gene sources able to adapt to changing climatic and growing conditions, and economical traits of the cultivar.

Ancient and landrace cultivars of crops, long-cultivated in specific environmental conditions of the highlands, drought, and unfavorable wintering conditions, are the reserve of unused genetic diversity. They are a source of valuable genes, and their introduction in breeding allows the development of new generation cultivars able to overcome stress factors with significant yields. The cultivation of landrace cultivars of grain crops still continues in unpretentious conditions due to their adaptability and represents a valuable genetic source for improving resistance to biotic and abiotic stress factors through modern breeding (Marone *et al.,* 2021).

The identification of bread wheat (*Triticum aestivum* L.) landraces collection and tracking their genetic diversity is highly crucial. The genetic diversity of Afghan wheat landraces' assessment gave increased content of biofortification elements through breeding (Manickavelu *et al.,* 2017). In this regard, the seed's protein profiles, prolamins, and glutenins are the stable markers of varietal affiliation and transfer of genetic material during breeding involving landraces (Chegdali *et al.,* 2020; López-Fernández *et al.,* 2021; Visioli *et al.,* 2021; Palombieri *et al.,* 2024).

The potential of landraces has insufficient exploration through modern plant breeding techniques (Langridge and Waugh*,* 2019). The landraces preservation should not only be in the collection pool and by the farming community who still grow them in their fields. These landraces also need conservation in breeding programs, with the help of advances in molecular biology and transferring valuable genes into improved cultivars capable of ensuring high yields in an increasingly arid climate (Tehseen *et al.,* 2022).

Drought affects the wheat crop at all growth stages; however, these effects are most prominent during the heading and grain filling periods, leading to significant yield losses in wheat (Yu *et al.,* 2018; Baloch *et al.,* 2024). The heading time of di-, tetra-, and hexaploid wheat depends on the combination of *Vrn* and *Ppd* genes (Smolenskaya and Goncharov*,* 2023). Generally, in wheat, combining *Vrn* and *Ppd* alleles significantly influences the rate of plant development, crop yield formation, frost, and winter hardiness, the need for vernalization, drought resistance, resilience in high summer temperatures, and resistance to diseases (Stelmakh, 1998).

Regarding this, studying characteristics of genes' allelic state for vernalization and sensitivity to photoperiod of landraces and combining with similar wheat cultivars' alleles from other regions can develop new and high-yielding genotypes adapted to changing climatic conditions (Plotnikov *et al.,* 2024). Therefore, based on the above discussion, the presented research aimed to study the features of the genetic diversity of Western Pamir bread wheat landraces for genes determining their regional adaptability. Likewise, the research will assess the specificity of the composition of storage proteins and plan marker selection of the allele combinations.

MATERIALS AND METHODS

The research object, represented by the bread wheat (*T. aestivum* L.) landraces, have long been cultivated in the Western Pamir's high-mountain conditions (Table 1). Characteristics and growing conditions of local wheat cultivars came from the following sources, i.e., Baranov *et al.* (1964), FAO (2015), and Husenov *et al.* (2021).

Protein marking engaged the electrophoresis of wheat grain storage proteins, viz., gliadins and glutenins, according to the standard ST RK 3323-2018 and

Table 1. Bread wheat landraces of the Western Pamir.

Varieties	Origin	Growth habit	Characteristics, growing conditions
Safedak Ishkashimskiy	Local, from Tajik Badakhshan	Spring (Facultative)	Introduced in 1935 in Ishkashim, *Var. graecum* (Koern.) Mansf., as the most common high-yielding local spring variety
Surkhusha	Local, from Tajik Badakhshan	Spring	The second most common high-yielding local spring variety
Bobilo	Local, from Tajik Badakhshan	Spring	Early maturing, cold-resistant, cultivated at altitudes from 2000 to 3250 masl, undemanding to moisture
Kilyak bartangskiy	Local, from Tajik Badakhshan	Spring	It forms the main background of crops in the Bartang Valley at 2060–3200 m altitudes
Dzhaldak	Local, from Tajik Badakhshan	Spring	Var. *kabulicum* (Vav.) Mansf, early maturing wheat from Pamir
Pandaki	Local, from Tajik Badakhshan	Spring	Recommended and widely implemented in farms of the Wakhan and Shakhdara valleys of GBAO at altitudes of 2000–3000 masl
Sadiras belokolosiy	Local, from Tajik Badakhshan	Spring	Cultivated at 2600 masl in Tajik and 2500 m in Afghan Badakhshan; the grain yield exceeds the standard by
Sadiras krasnokolosiy	Local, from Tajik Badakhshan	Spring	0.61–0.76 t/ha and has high resistance (9 points) to yellow rust
Bludon	Unknown	Winter (facultative)	Recommended and implemented in a number of farms in the Darvoz, Rushan, and Ishkoshim districts at altitudes of 1150–3000 masl

recommendations of UPOV (2017). Genomic DNA isolation resulted from finely ground seeds for molecular screening (Dellaporta *et al.,* 1983). Allelic variants of *Glu-1, VRN-1*, and *PPD-1* loci were carried out using PCR markers recommended by Yan *et al.* (2004), Hanocq *et al.* (2007), Liu *et al.* (2008), and Nishida *et al.* (2013) (Table 2). The PCR analysis ran in the iCycler 'BIORAD' thermal cycler.

Electrophoresis of the amplification products transpired in a polyacrylamide gel (8% acrylamide, 1× Tris-borate buffer). The amplification products' were detected with ethidium bromide. The obtained electropherograms recording used the Quantum ST4 gel documentation system, with the product dimensions determined using the Quantum Capt, image analysis computer program relative to the DNA fragment length markers. Hierarchical cluster analysis ensued following Ward's method in R (version 4.3.3) and applying the Euclidean distance metric (Murtagh and Legendre, 2014).

RESULTS

Western Pamir landraces with growing conditions

In Gorno-Badakhshan, Eastern Tajikistan, in the total area of GBAO, the arable land area is only 2.6%. All the rest are mountains, screes, desert pastures, and valleys located at altitudes of 3,600 masl and even higher. Figure 1 showed the GBAO districts growing the studied landraces in small farms and in the Pamir stationary at altitudes of 2,000 masl, under low-temperature conditions.

Evaluation of local grain cultivars, including wheat in Badakhshan, Tajikistan, showed these genotypes are less demanding of nutrients versus other cultivars of foreign selection and produce good grain yield on low-fertility soils of mountain slopes. The grain yield of cultivars from foreign origin on rocky soils of slopes drops sharply. The disadvantages of local wheat cultivars are their low resistance to lodging, various diseases, and low baking quality.

Table 2. Primers used for detecting *VRN-1*, *PPD-1, Glu-1* gene alleles

Alleles	Primer pairs	Primer sequence	Amplicon (bp)	Reference
Vrn-A1a	*VRN1AF*	GAAAGGAAAAATTCTGCTCG	965+876	Yan *et al*. (2004)
Vrn-A1b	*VRN1-INT1R*	GCAGGAAATCGAAATCGAAG	714	
Vrn-A1			734	
VrnB1	*Intr1/B/F*	CAAGTGGAACGGTTAGGACA	709	Yan *et al*. (2004)
vrnb1	*Intr1/B/R3*	CTCATGCCAAAAATTGAAGATGA	1149	
	Intr1/B/R4	CAAATGAAAAGGAATGAGAGCA		
VrnD1	*Intr1/D/F*	GTTGTCTGCCTCATCAAATCC	1671	Yan *et al*. (2004)
vrnd1	*Intr1/D/R3*	GGTCACTGGTGGTCTGTGC	997	
	Intr1/D/R4	AAATGAAAAGGAACGAGAGCG		
Ppd-A1a	*TaPpd-A1-F1*	CGTACTCCCTCCGTTTCTTT	338	Nishida *et al*. (2013)
Ppd-A1b	*TaPpd-A1-R3*	AATTTACGGGGACCAAATACC	299	
	TaPpd-A1-R2	GTTGGGGTCGTTTGGTGGTG		
Ppd-B1a	*Xgwm148*	GTGAGGCAGCAAGAGAGAAA	167	Hanocq *et al*. (2007)
Ppd-B1b		CAAAGCTTGACTCAGACCAAA		
Ppd-D1a	*Ppd-D1-F1*	ACGCCTCCCACTACACTG	288	Beales *et al*. (2007)
Ppd-D1b	*Ppd-D1-R1*	CACTGGTGGTAGCTGAGATT	414	
	Ppd-D1-R2	GTTGGTTCAAACAGAGAGC		
Glu-A1	*UMN 19*	GGAGACAATATGAGCAGCAAG	344	Liu *et al*. (2008)
		CTGCCATGGAGAAGTTGGA	362	
Glu-D1	*UMN25*	GGGACAATACGAGCAGCAAA	299	Liu *et al*. (2008)
		CTTGTTCCGGTTGTTGCCA	281	
Glu-D1	*UMN26*	CGCAAGACAATATGAGCAAACT	397	Liu *et al*. (2008)
		TTGCCTTTGTCCTGTGTGTGC	415	

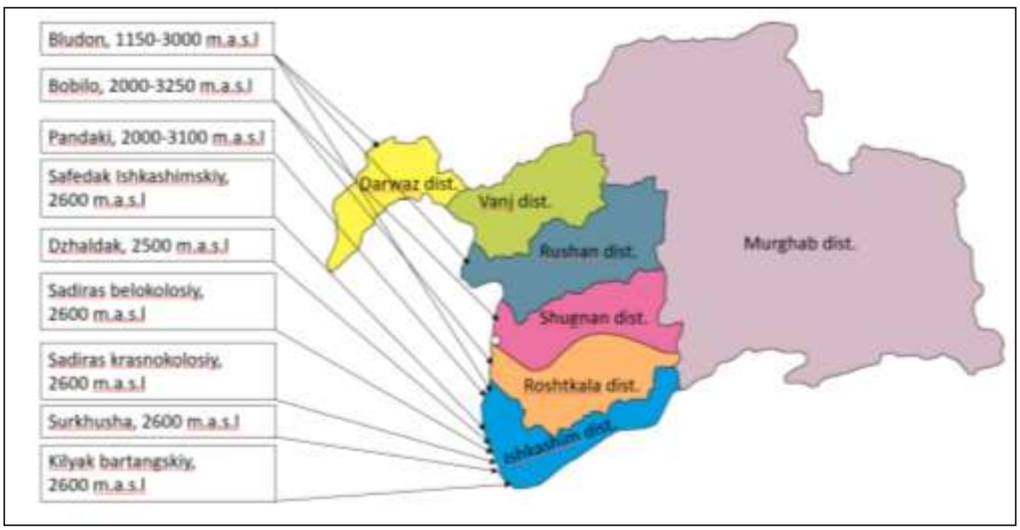

Figure 1. Cultivated areas of landraces in GBAO.

Regarding plant height in the highlands of the Pamir, the most low-growing cultivars include Surkhusha, Bobilo, and Bludon. Similar variations in the plant stature were also visible in spring bread wheat cultivars in the Kazakhstan selection. It is typical for plant height as one of the traits considerably correlating with lodging resistance (Khobra *et al.,* 2019; Rabieyan *et al.,* 2023).

A comparison of plant height in Western Pamir wheat landraces and cultivars of the Kazakh selection under the conditions of Kazakh Research Institute of Agriculture and Plant Growing, Kazakhstan, occurred. It showed the cultivar Safedak Ishkashimskiy, with a plant height of 93.6 cm, displayed poor lodging resistance, while the wheat cultivars Lutescens-32 and Kazakhstanskaya-3 were resistant (Figure 2).

Landraces identification based on seed storage proteins

Identification of landraces by the spectra of seed storage proteins–gliadins–showed significant polymorphism and distinctiveness of the landrace samples within α, β, γ, and ω subfractions (Figure 3). However, four out of five bread wheat landraces from Tajik Badakhshan exhibited characteristics of specific components of the γ zone (marked with an arrow), which were not evident in the spectra of the wheat landraces of Afghan Badakhshan. The presence of such a composition of various components in this zone is infrequent for the bread wheat cultivars developed by breeding institutions in Kazakhstan and approved for cultivation in the country.

Thus, only two cultivars, Kazakhstanskaya-4 and Nadezhda with pedigree from Kazakhstanskaya-4, also showed features by the same composition of the γ zone components of Safedak Ishkashimskiy, Bobilo, Kilyak bartangskiy, and one of the biotypes of the Dzhaldak varieties. These bread wheat cultivars were distinct with drought resistance and intended for cultivation under rainfed conditions (Collection of domestic cultivars and hybrids of agricultural crops used in the Republic of Kazakhstan, Nur-Sultan, 2022).

Using the wheat cultivar Bezostaya-1 as a standard further allowed us to use the catalog of Metakovsky *et al.* (2018). The assumption that the component of the γ zone of landraces of Tajik Badakhshan (marked with an arrow) bears control from the *Gli-B1* locus can refer to the group of alleles indicated in the catalog. These are *Gli-B1o, Gli-B1m, Gli-B1k, Gli-B1i, Gli-B1r, Gli-B1p*, or a new, previously unseen allele of this locus. The frequency of these alleles was very low among more than 1,000 bread wheat cultivars studied by the researchers.

Cluster analysis of the data on the relative electrophoretic mobility of prolamin components confirmed the similarity of the wheat cultivars Safedak Ishkashimskiy, Bobilo, Kilyak bartangskiy, and one of the biotypes of the Dzhaldak variety, grouped together in one cluster (Figure 3a).

Vernalization (*VRN-1*) and photoperiod sensitivity (*PPD-1*) genes with allelic variation

Genetic diversity analysis of the wheat landraces cultivated in small farms of Western Pamir showed their identity by the alleles of *VRN-A1* and *VRN-D1* locus. All the cultivar samples had recessive allele (*vrn-A1*) and dominant allele (*Vrn-D1*) (Table 3). Polymorphism revealed the locus *VRN-B1* for the three cultivars, Safedak Ishkashimskiy, Kilyak bartangskiy, and Bludon, with the characteristic of dominant allele (*Vrn B1*). Meanwhile, the five wheat cultivars Surkhusha, Bobilo, Dzhaldak, Pandaki, Sadiras belokolosiy, and Sadiras krasnkolosiy contain a recessive allele (*vrnB1*).

The comparison of data provided on spring wheat cultivars of the Kazakhstan selection (Kazakhstanskaya-3 and Lutescens-32), revealed a dominant allele of the *Vrn-A1* locus in their genome, and the winter bread wheat cultivar Bezostaya-1 carries a recessive allele at the same locus.

All the analyzed samples of Western Pamir bread wheat landraces were homogeneous in *PPD-1* genes. The allelic composition displays a representation of one gene of insensitivity to day length (*Ppd-A1a*) and two genes providing sensitivity to photoperiod (*Ppd-B1b and Ppd-D1b*). The cultivars Lutescens-32 and Bezostaya-1 studied for comparison had the similar alleles at these loci, while the cultivar Kazakhstanskaya-3 was the carrier of the photoperiod insensitivity allele of the *PPD-B1* locus.

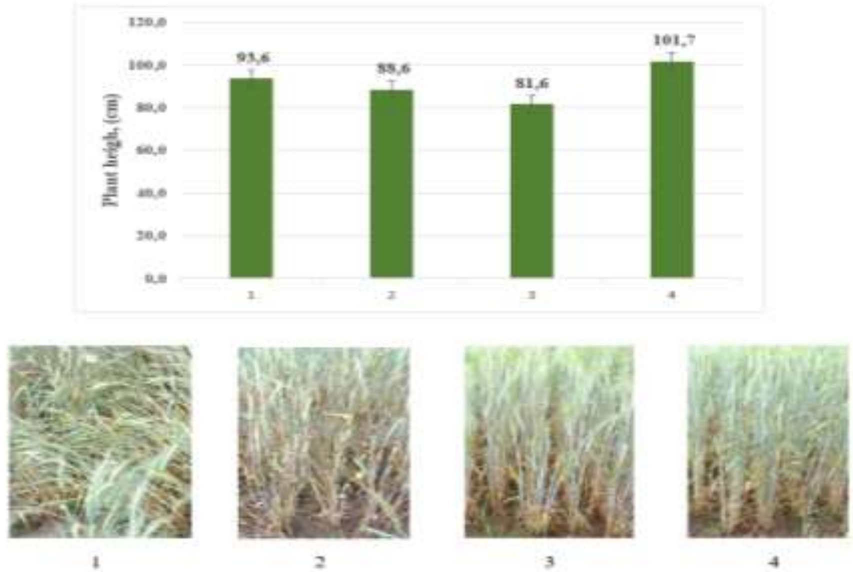

Figure 2. Plant height and lodging resistance of the Western Pamir landraces in comparison with cultivars of Kazakhstan selection. 1 - Safedak Ishkashimskiy, 2 - Bobilo, 3 - Kazakhstanskaya-3, 4 - Lutescens-32.

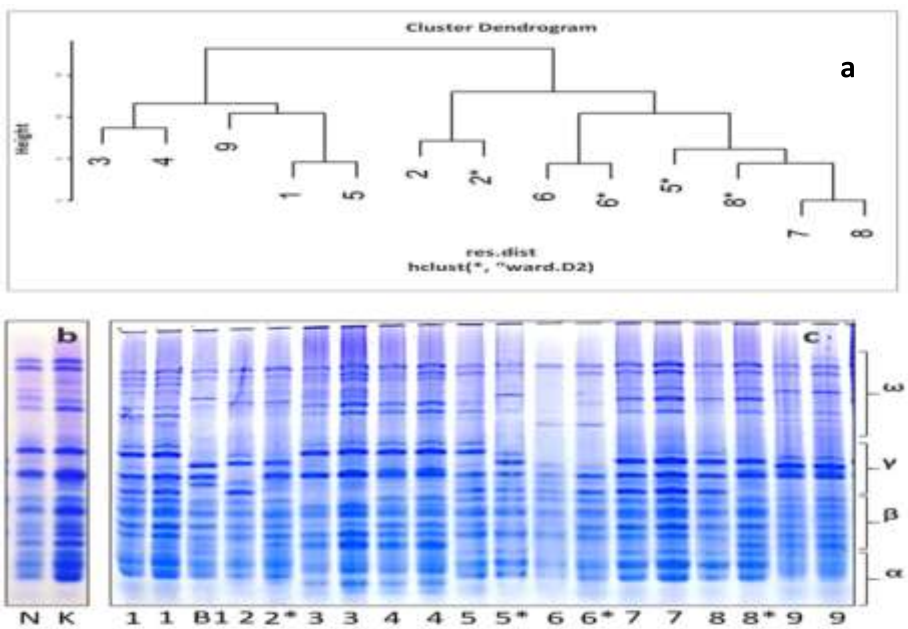

Figure 3. Specificity of landrace wheat cultivars on prolamin composition: (a) a cluster dendrogram based on the relative electrophoretic mobility of prolamin components; (b) spectra of Nadezhda and Kazakhstanskaya 4; (c) spectra of landraces. N - Nadezhda; K - Kazakhstanskaya 4; 1 - Safedak ishkashimskiy; 2&2* -Surkhusha; 3 - Bobilo; 4 - Kilyak bartangskiy; 5&5*- Dzhaldak; 6&6*- Pandaki; 7 - Sadiras belokolosiy; 8&8*-Sadiras krasnokolosiy; and 9 - Bludon. B1-Bezostaya-1.

Table 3. Genetic diversity of Western Pamir landraces for *VRN-1* and *PPD-1* genes.

Varieties	*VRN-A1*	*VRN-B1*	*VRN-D1*	*PPD- A1*	*PPD-B1*	*PPD-D1*
Safedak Ishkashimskiy	*vrn-A1*	*Vrn B1*	*Vrn-D1*	*Ppd-A1a*	*Ppd-B1b*	*Ppd-D1b*
Surkhusha	*vrn-A1*	*vrnB1*	*Vrn-D1*	*Ppd-A1a*	*Ppd-B1b*	*Ppd-D1b*
Bobilo	*vrn-A1*	*vrnB1*	*Vrn-D1*	*Ppd-A1a*	*Ppd-B1b*	*Ppd-D1b*
Kilyak bartangskiy	*vrn-A1*	*Vrn B1*	*Vrn-D1*	*Ppd-A1a*	*Ppd-B1b*	*Ppd-D1b*
Dzhaldak	*vrn-A1*	*vrnB1*	*Vrn-D1*	*Ppd-A1a*	*Ppd-B1b*	*Ppd-D1b*
Pandaki	*vrn-A1*	*vrnB1*	*Vrn-D1*	*Ppd-A1a*	*Ppd-B1b*	*Ppd-D1b*
Sadiras belokolosiy	*vrn-A1*	*vrnB1*	*Vrn-D1*	*Ppd-A1a*	*Ppd-B1b*	*Ppd-D1b*
Sadiras krasnokolosiy	*vrn-A1*	*vrnB1*	*Vrn-D1*	*Ppd-A1a*	*Ppd-B1b*	*Ppd-D1b*
Bludon	*vrn-A1*	*Vrn B1*	*vrn D1*	*Ppd-A1a*	*Ppd-B1b*	*Ppd-D1b*
Kazakhstanskaya-3	*Vrn-A1a*	*vrnB1*	*Vrn-D1*	*Ppd-A1a*	*Ppd-B1a*	*Ppd-D1b*
Lutescens-32	*Vrn-A1a*	*Vrn B1*	*vrn D1*	*Ppd-A1a*	*Ppd-B1b*	*Ppd-D1b*
Bezostaya-1	*vrnA1*	*vrnB1*	*vrn D1*	*Ppd-A1a*	*Ppd-B1b*	*Ppd-D1b*

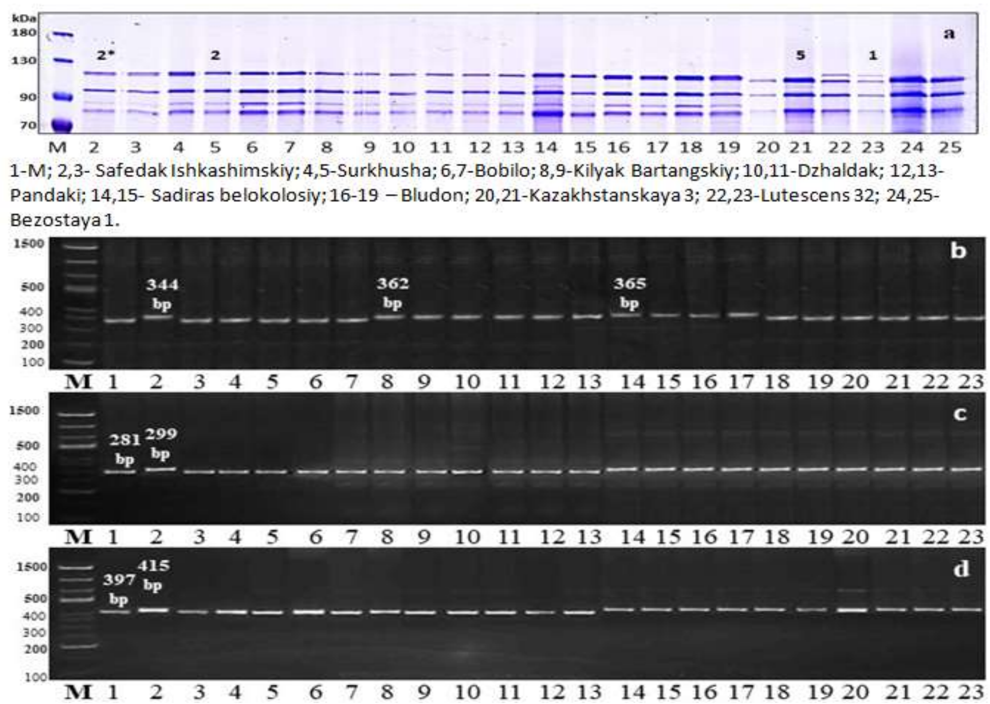

Figure 4. Identification of landrace wheat cultivars of the Western Pamir by the composition of high molecular weight glutenin subunits (a) electrophoresis; SSR markers, (b) *UMN 19,* (c) *UMN 25, (d) UMN 26.* M-Marker Step100 plus; 1- Pavon; 2- Pitic; 3-Bezostaya 1; 4-7- Kazakhstanskaya 3; 8-13-Lutescens 32; 14-17- Bobilo; 18-23 –Safedak Ishkashimskiy.

Genetic diversity on *Glu-1* loci

The composition of high-molecular-weight glutenin subunits (HMW-GSs) succeeded detection by the electrophoresis of total proteins isolated from wheat grains (Figure 4a). In some cases, subunits 2* and 2 can merge and appear as one intense band. Therefore, it was also challenging to determine the absence of the high-molecular subunit 2*, controlled by the *Glu 1A* locus. Using the SSR markers *UMN 19, UMN 25* and *UMN 26* helped accurately identify the *x* subunits of the *Glu-A1* and *Glu-D1* loci (Liu, 2010). The spectrum of amplified DNA fragments of two highland bread wheat cultivars, Safedak Ishkashimskiy and

Table 4. Composition of HMW-GS of landrace cultivars from Western Pamir.

Varieties	Loci		
	Glu-A1	*Glu-B1*	*Glu-D1*
Safedak Ishkashimskiy	2*	7+8	2+12
Surkhusha	0/2*	7+8	2+12
Bobilo	0	7+8	2+12
Kilyak bartangskiy	0	7+8	2+12
Dzhaldak	0	7+8	2+12
Pandaki	0	7+8	2+12
Sadiras belokolosiy	0	7+8	2+12
Sadiras krasnokolosiy	0	7+8	2+12
Bludon	2*	7+8	2+12
Bezostaya-1	2*	7+9	5+10
Kazakhstanskaya-3	2*	7+9	5+10
Lutescens-32	1	7+9	5+10

Bobilo, and two cultivars of Kazakhstan selection (Kazakhstanskaya-3 and Lutescens-32) appear in Figures 4b, c, and d. It should also be noteworthy that the markers of the HMW-GS 1 encoded by the *Glu-A1* locus (allele 'a') and the null allele (c) of this locus (Payne *et al.,* 1987) differed in size, hence, the marker designation of the allele 'c' with a length of 365 bp.

In Western Pamir bread wheat landraces, the high-molecular-weight glutenin subunits (HMW-GS) composition was highly uniform. All the cultivars carried the '*a*' allele of the *Glu-D1* locus and the '*b*' allele of the *Glu-B1* locus, which controlled the subunits 2+12 and 7+8, respectively. A difference was only evident for the *Glu-A1* locus of the most widely cultivated cultivar Safedak Ishkashimskiy. It accounts for approximately 70% of wheat crops at the altitudes of 2,000–3,200 m in Badakhshan and has subunit 2* in its high-molecular subunits, associated with high baking quality. A similar subunit appeared in the storage proteins of the cultivar Bludon, the origin of which is unknown and could receive a modern variety classification. The cultivar Surkhusha is heterogeneous and consists of the genotypes with different alleles at this locus. The wheat cultivars Bobilo, Kilyak bartangskiy, Dzhaldak, Pandaki, and Sadiras belokolosiy lack the high-molecular glutenin subunits encoded by the *Glu-A1* locus. Almost all the cultivars of winter and spring bread wheat grown in Kazakhstan comprised the characteristic of a high-molecular glutenin subunits composition associated with high baking quality. Table 4 detailed the subunit composition of two spring (Kazakhstanskaya-3 and Lutescens-32) and one winter (Bezostaya-1) cultivars, with the seeds analyzed together with ancient cultivars of the Western Pamir, Tajikistan.

DISCUSSION

Tajik bread wheat landraces evaluation in Turkish conditions (Konya, 2017–2019) for key agronomic traits showed a longer period of their development than with cultivars usually cultivated under rainfed conditions (Husenov *et al.,* 2021). Researchers concluded wheat landraces were adaptive to the cold summer of the highlands, since most landraces were of spring/facultative wheat. This can be due to the adaptation mechanism allowing their sowing in a wide range of time (from autumn to spring). Many of those landraces were unstable to leaf and yellow rust pathogens and lodged regardless of plant height.

Most landraces of Afghanistan has primitive morphology, low bread quality, and low genetic diversity, and at first glance, were not valuable genetic resources (Terasawa *et al.*, 2009). However, the breeders believe since these genotypes have a long-time cultivation under the same conditions and adapted to the existing environment, these cultivars may contain original endemic genetic traits requiring investigation for adaptability. Specific alleles of gliadin-coding loci in bread wheat can also be beneficial as resistance markers to adverse environmental conditions (Utebayev *et al.,* 2019).

Landraces of Tajikistan have the features of rare alleles of the gliadin-coding locus *Gli-B1*, which can serve as markers of adaptability to growing conditions. Therefore, a more detailed study of their carriers for resistance to drought and low temperature is necessary. The analyzed landraces of the wheat cultivars from the Pamir highlands, in most cases, except for the cultivars Safedak Ishkashimsky and Bludon, consist of high-molecular glutenin subunits Null (*Glu-1A*), 7+8 (*Glu-B1*), and 2+12 (*Glu-D1*). An analysis of 116 bread wheat landraces from the various geographical regions of Turkey indicated the highest frequencies were apparent for the alleles *Glu-A1c* (65.11%), *Glu-B1b* (54.30%), and *Glu-D1a* (58.30%). These control biosynthesis of null, 7+8, and 2+12 subunits (Temizgul and Akbulut*,* 2020) and the low frequency of the *Glu-D1d* allele, which regulates the 5+10 subunit pair, providing the highest contribution to quality (Morgounov *et al*., 2021).

Analysis of the allelic diversity of Chinese landraces at the *Glu-1* locus also revealed the predominant ones among them were the carriers of genes controlling the composition of the HMW-GS, i.e., Null, 7+8, and 2+12 (Wang *et al.,* 2022). The uniformity of wheat landraces in loci alleles implied association with quality and has apparent relation with the priority importance of wheat yield for the local population. The adaptability of cereals, including wheat, to climatic conditions of cultivation is mainly notable in the duration of the vegetative development of its interphase periods. The main genes determining the timing of the onset of development stages are *VRN-1* and *PPD-1*, which determine the need of plants for vernalization and the sensitivity of plants to the length of daylight.

The bread wheat landraces of the Western Pamir highlands presently studied displayed the fact that these genotypes had a recessive allele of *the VRN-A1* locus, usually found in winter-type cultivars. In contrast, most of the spring cultivars of soft wheat were the carriers of the dominant allele. The low frequency of dominant alleles of the *VRN-A1* gene suggests even local spring cultivars require medium-moderate vernalization (Kalybekova, 2019). Analysis of the vernalization genes of Afghan wheat cultivars exhibited the absence of dominant allele *Vrn-A1* and *Vrn-B1* and the presence of only the dominant gene *Vrn-D1*, which determines the spring type of development (Dragovich *et al.,* 2021).

Molecular markers' assessment for *VRN-A1* loci ensued in a set of 142 genotypes of spring bread wheat from breeding institutions in Kazakhstan and Siberia (Russian Federation). The analysis of their relationship with maturation time and grain yield detailed the dominant allele of the *VRN-A1* gene accelerated heading by two days (5.6%) and was in 80% of the germplasm. The gene's recessive (*vrn-A1*) allele significantly enhanced the grain yield by 2.7% (Morgounov *et al.,* 2024). The studies reported the frequency of this allele was very high (95%) among the wheat samples obtained from the breeding program of East Kazakhstan.

Breeders can utilize the combinations of *VRN-1* and *PPD-1* allelic variants to modify the crop phenology, so that, the sensitive developmental phases take place in more optimal conditions (Amo *et al.,* 2022). All the studied cultivars of the Tajik and Afghan Badakhshan landrace had the genes of sensitivity to photoperiod at the *PPD–B1* and *PPD-D1* loci. However, at the *PPD-A1* locus, these genotypes were the carriers of *Ppd-A1a* allele. Given that *Ppd-D1a* generally exhibits the most substantial effect, followed by *Ppd-B1a* and *Ppd-A1a* (Makhoul *et al.,* 2024).

Most local Afghan cultivars (97%) were photoperiod-sensitive (*Ppd-D1b* carriers), with a distribution throughout the country without much dependence on agroecological zones (Kalybekova, 2019). Based on the studied bread wheat cultivar samples, one can assume the unique allelic composition of the *VRN-1* and *PPD-1* genes of the cultivars of Western Pamir landrace contributed in the adaptation to growing conditions. This happened by adjusting the most stress-sensitive phases of development to periods favorable for precipitation and temperature (Ammar *et al*., 2023; Buronov *et al*., 2023; Anwar *et al*., 2024).

CONCLUSIONS

The combination of recessive allele of *VRN-A1* gene and dominant allele of *VRN-D1* gene with the main genes of sensitivity to photoperiod (*PPD-1D, PPD-1B*) characterized the landrace cultivars of spring bread wheat cultivated in the Western Pamir, Tajikistan highlands. According to the HMW-GS composition, the Western Pamir wheat landraces emerged highly uniform. All the bread wheat cultivars carried the *'a'* allele of the *Glu-D1* locus and the '*b*' allele of the *Glu-B1* locus, which controlled the subunits 2+12 and 7+8, respectively.

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