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Allelic Variation in *Glu-1* and *Glu-3* Loci of Bread Wheat (*Triticum aestivum* ssp. *aestivum* L. em. Thell.) Germplasm Cultivated in Algeria

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Wheat endosperm storage proteins are the major components of gluten. They play an important role in dough properties and in bread making quality in various wheat varieties. In the present study, the different alleles encoded at the 6 glutenin loci were identified from a set of 71 hexaploid wheat germplasm cultivated in Algeria using SDS-PAGE. At *Glu-A1, Glu-B1* and *Glu-D1,* encoding high molecular weight glutenin subunits (HMW-GS), 3, 6 and 5 alleles were observed, respectively. Low molecular weight glutenin subunits (LMW-GS) displayed similar polymorphism, as 4, 9 and 3 alleles were identified at loci *Glu-A3, Glu-B3* and *Glu-D3,* respectively. A total of 52 patterns resulted from the genetic combination of the alleles encoding at the six glutenin loci. This led to a significantly higher Nei coefficient of genetic variation in *Glu-1* and *Glu-3* loci (0.54). The Algerian hexaploid wheats exhibited allelic variation in HMW and LMW glutenin subunit composition and the variation differed from that of hexaploid wheats of other countries. The presence of high quality alleles in glutenin loci have led the Algerian wheat cultivars to be considered as an asset in breeding programs aimed for wheat quality.

Keywords: allelic variation, genetic diversity, glutenin subunits, polymorphism, *Triticum aestivum*

Introduction

In order to evaluate genetic diversity the study of biochemical and molecular markers, less affected by environmental factors, is more important than morphological traits. Seed storage proteins are the result of expression of genome and contain extensive genetic variation in wheat. Thus, they are taken as good criteria for genetic diversity studies (Proceddu et al. 1998). The major endosperm storage proteins are glutenin, which consists of polypeptides cross-linked by interpolypeptide disulfide bonds, and gliadins, a complex mixture of single polypeptides (Shewry and Tatham 1990). Using a reducing agent, the glutenins were divided into two groups: high molecular weight (HMW-GS, 80–120 KDa)

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and low molecular weight (LMW-GS, 30–50 KDa) glutenin subunits (Payne and Corfield 1979). The HMW-GS are encoded by the *Glu-1* loci located on the long arms of chromosomes 1A, 1B and 1D, each locus encoding one x-type gene and one y-type subunit gene (Payne 1987). However, gene silencing results in the presence of only three to five HMW-GS in hexaploid bread wheats. Allelic variation also results in differences in HMW-GS composition between varieties (Shewry et al. 2003). The main LMW-GS (named B-subunits) are controlled by genes called *Glu-A3, Glu-B3* and *Glu-D3,* located on the short arms of group 1 chromosomes (Payne et al. 1984). The allelic diversity found at these loci was first described by Jackson et al. (1983) and Gupta and Shepherd (1990). Storage proteins of hexaploid wheat (*Triticum aestivum* L.) are primarily important in bread making quality (Branlard and Dardevet 1985; Payne et al. 1987; Ng and Bushuk 1989). May other studies have shown that allelic variations in HMW-GS and LMW-GS are both associated with differences in the technological qualities of wheat flour (Autran et al. 1987; Gupta et al. 1989; Khelifi and Branlard 1992; Nieto-Taladriz et al. 1994). The aim of the present study is to describe the allelic variation of HMW and LMW glutenin subunits in the bread wheat germplasm cultivated in Algeria and to determine the genetic diversity at the *Glu-1* and *Glu-3* loci in these wheats.

Materials and Methods

Plant material

Seventy-one bread wheat genotypes (*Triticum aestivum* ssp. *aestivum* L. em. Thell.) were used to analyze the allelic diversity of glutenins (Table 1). This germplasm cultivated in Algeria, is obtained by the Technical Institute of Field Crops (ITGC) Constantine, Algeria. Some European bread wheats were used as standards to identify HMW-GS and LMW-GS alleles.

Glutenin extraction and SDS-PAGE

Proteins were extracts from individual grains using the sequential procedure of Singh et al. (1991). Electrophoresis of HMW-GS and LMW-GS was performed on vertical gel according to the SDS-PAGE protocol described by Singh et al. (1991).

Nomenclature

The identification of HMW-GS was based on the classification of Payne and Lawrence (1983) completed by Branlard et al. (2003). The LMW-GS were identified using the nomenclature proposed by Jackson et al. (1996) completed by Branlard et al. (2003).

Statistics

The genetic diversity at each locus was calculated according to Nei (1973) as follows: $H = 1 - \Sigma\, Pi^2$, where H is Nei's genetic variation index and *Pi* the frequency of a particular allele at that locus. Allelic frequencies were determined by summing the frequencies of alleles in the individual genotypes and then dividing this total by the number of genotypes.

Table 1. Allelic composition at the six HMW and LMW loci found in 71 bread wheat germplasm cultivated in Algeria

No.	Cultivars	HMW			LMW		
		Glu-A1	*Glu-B1*	*Glu-D1*	*Glu-A3*	*Glu-B3*	*Glu-D3*
1	PBW343	*a*	*a*	*h*	*a*	*j*	*b*
2	Ain Abid (AS)	*a*	*b*	*a*	*a*	*a*	*b*
3	Pastor//Site/MO/3/Chen/…	*a*	*b*	*d*	*a*	*h*	*b*
4	Cham-6	*a*	*c*	*a*	*a*	*b*	*b*
5	TUI	*a*	*c*	*b*	*a*	*i*	*b*
6	Sagitario	*a*	*c*	*b*	*a*	*b*	*b*
7	Ziad, Giza164, Choix/Star/3/HE 1/3* CNO79//2* Seri	*a*	*c*	*d*	*a*	*j*	*b*
8	Super Seri//2	*a*	*c*	*d*	*a*	*i*	*b*
9	Trident	*a*	*c*	*d*	*d*	*d*	*b*
10	Filin/2*Pastor	*a*	*c*	*d*	*d*	*b'*	*b*
11	BOW/Ures//2*WEA VER/3/BOW/ PRL//BUC	*a*	*c*	*d*	*a*	*f*	*b*
12	Falk*2/Bisu/3/Chen/…	*a*	*c*	*d*	*e/f*	*d*	*b*
13	Hidhab (HD1220)	*a*	*i*	*a*	*b*	*h*	*b*
14	Giza163	*a*	*i*	*a*	*b*	*j*	*b*
15	Super Seri//1	*a*	*i*	*a*	*d*	*b'*	*b*
16	Croc-1/*Ae.squarrosa*(224)//Opata/3/Pastor	*a*	*i*	*a*	*a*	*b*	*b*
17	HPO/TAN/VEE/3/2*PGO/4/Milan/5/Seri1	*a*	*i*	*a*	*a*	*h*	*b*
18	Jagger	*a*	*i*	*d*	*a*	*i*	*b*
19	Pastor, Pastor/BAV92, Gen*2//BUC/ FLK/3/2*Pastor	*a*	*i*	*d*	*a*	*b*	*b*
20	Oasis/Skanz//4*BCN*2/3/Pastor	*a*	*i*	*d*	*a*	*f*	*b*
21	WBU1*2/Tukuru	*a*	*i*	*d*	*a*	*h*	*b*
22	BOW/PRL//BUC/3/WH576	*b*	*a*	*d*	*a*	*h*	*b*
23	Arz	*b*	*b*	*a*	*e/f*	*j*	*c*
24	Nesser Dwarf	*b*	*b*	*a*	*a*	*b*	*b*
25	Sahel, Punjab96	*b*	*b*	*d*	*a*	*b*	*b*
26	Pinzon	*b*	*b*	*h*	*a*	*b*	*d*
27	Nesser Tall	*b*	*c*	*a*	*a*	*i*	*b*
28	PRL/SARA//TSI/VEE//5/3/Ducula	*b*	*c*	*a*	*b*	*f*	*b*
29	REH/Hare//2*BCN/3/Croc-1/ *Ae.squarrosa*213//PGO/4/Hnites	*b*	*c*	*a*	*b*	*j*	*b*
30	NAC/Thac//3*PRN/3/Mirlo/BNC/ 4/2*Pastor	*b*	*c*	*a*	*a*	*d*	*c*
31	Florence Aurore	*b*	*c*	*d*	*a*	*b*	*b*
32	WH542, Irena, Bacanora, Chen/ *Ae.squarrosa*(tous)//BCN/3/2*Kanz	*b*	*c*	*d*	*a*	*j*	*b*
33	Baviacora-M92	*b*	*c*	*d*	*a*	*i*	*b*
34	Chil/PRL, Kambi*2/Kukur	*b*	*c*	*d*	*a*	*h*	*b*
35	Milan/587230//Hnites	*b*	*c*	*d*	*b*	*j*	*b*
36	Milan/587230//Babax	*b*	*c*	*d*	*d*	*d*	*b*
37	Attila/3*BCN//BAV92/3/Tilhi	*b*	*c*	*d*	*b*	*b*	*c*
38	Chen/*Ae.squarrosa*(tous)//BCN/3/BAV92	*b*	*c*	*m*	*a*	*h*	*b*
39	Mahon Demias	*b*	*e*	*a*	*e/f*	*d*	*c*
40	Sakha69	*b*	*f*	*d*	*e/f*	*i*	*c*

Table 1 (cont.)

No.	Cultivars	HMW			LMW		
		Glu-A1	*Glu-B1*	*Glu-D1*	*Glu-A3*	*Glu-B3*	*Glu-D3*
41	Inqilab91, Mexipak	*b*	*i*	*a*	*a*	*b*	*b*
42	Cham-4	*b*	*i*	*a*	*d*	*b'*	*b*
43	PBW65/2*Pastor, BL1724	*b*	*i*	*a*	*b*	*j*	*b*
44	Kauz/Pastor, WEAVER/4/NAC/ TH.AC//3*PVN/3/Mirlo/BUC	*b*	*i*	*a*	*a*	*h*	*b*
45	Sonalika, Pavon Tall, Irena/Babax// Pastor, Wblli/Kambi//Pastor	*b*	*i*	*d*	*a*	*h*	*b*
46	WEA VER/Prinia	*b*	*i*	*d*	*b*	*b*	*c*
47	Ranz//Alta84/ACS/3/Milan/Kanz/4/ Hnites, Milan/Lotus//Attila/3*BCN	*b*	*i*	*d*	*a*	*f*	*b*
48	Anza	*c*	*b*	*a*	*a*	*b*	*b*
49	Dharwar Dry/Nesser	*c*	*b*	*a*	*e/f*	*g*	*b*
50	Benmabrouk	*c*	*b*	*a*	*a*	*d*	*b*
51	HXL7579/*2BAU	*c*	*c*	*a*	*e/f*	*h*	*c*
52	Sultan95	*c*	*i*	*a*	*a*	*b*	*b*

Overall quality scores of the HMW-GS (*Glu-1* quality scores) for a given variety could be obtained as the sum of the scores of individual subunits. HMW *Glu-1* scores were calculated and compared with the official bread making quality of the wheat varieties (Payne 1987). *Glu-3* quality classes were determined following Gupta et al. (1990).

Results

Allelic variation of HMW and LMW glutenin subunits

Thirty alleles were identified in total at the six loci *Glu-A1, Glu-B1, Glu-D1, Glu-A3, Glu-B3* and *Glu-D3*. On the basis of the genetic diversity found at the six loci, 52 patterns were established among the 71 bread wheat germplasm analyzed (Table 1). Forty-one patterns were specific to one cultivar each. Figure 1 shows some of the patterns found. Extensive variability was observed for the HMW glutenins. A total of 14 HMW subunits were revealed from the analysis of different Algerian bread wheats. The majority of the seventy-one cultivars possessed three to five bands and 22 types of patterns were determined (Table 1). Each combination was encountered in one to eleven cultivars, with the combination *Glu-A1b–Glu-B1C–Glu-D1d* being the most common (15.49%). Concerning B-LMW subunits, large variability in patterns was detected and 21 combinations were listed (Table 1). The number of cultivars for each combination of B-LMW subunits varied from one to sixteen. The most common combination was *Glu-A3a–Glu-B3b–Glu-D3b* (22.54%). A total of 16 LMW subunits were revealed from the analysis of bread wheat germplasm. The results shows that the greatest polymorphism of storage proteins in Algerian bread wheats was on chromosomes 1B with six and nine allelic forms at the *Glu-B1* and *Glu-B3* loci, respectively.

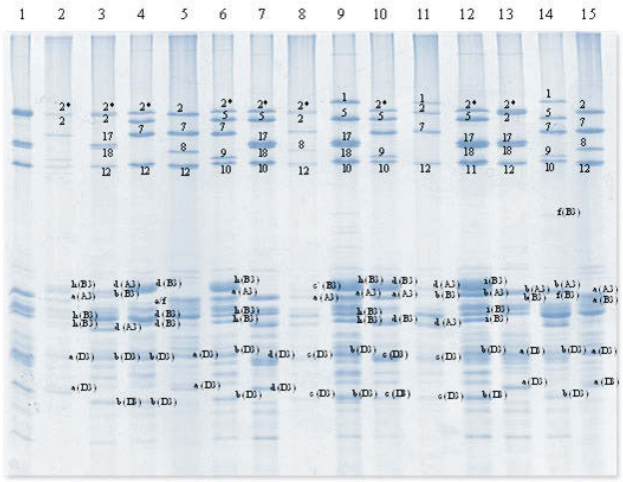

Figure 1. SDS-PAGE patterns of HMW and LMW glutenin subunits in some cultivars of bread wheat cultivated in Algeria. 1: 'PBW65/2*Pastor'; 2: 'Démocrat'; 3: 'Cham-4'; 4: 'BOW/PRL//BUC/3/WH576'; 5: 'Chinese Spring'; 6: 'Chil/PRL'; 7: 'WEA VER/Prinia'; 8: 'Courtout'; 9: 'Wbll1/Kamb1//Pastor'; 10: 'Milan/587230//Babax'; 11: 'Copain'; 12: 'Sonalika'; 13: 'BL 1724'; 14: 'Filin/2*Pastor'; 15: 'Chinese Spring' (lanes 2; 5; 8; 11 and 15 wheat checks)

Allelic frequencies and genetic diversity

The HMW-GS and LMW-GS composition and allelic frequencies in the 71 bread wheat germplasm cultivated in Algeria are shown in Table 2. Fourteen different *Glu-1* alleles were found, three at *Glu-A1*, six at *Glu-B1* and five at the *Glu-D1* locus. At the *Glu-A1* locus, allelic distribution among the 71 cultivars was 54.93% and 38.03% for the two alleles *b* and *a,* respectively, and lower for allele *c* with 7.04%. at the *Glu-B1* locus, alleles *a* encoding for subunit 7, *e* encoding for subunit 20 and *f* encoding for subunits 13+16 were rare at 2.82% and 1.41%, respectively. Otherwise, the most frequent alleles were *Glu-B1c* and *Glu-B1i* encoding for subunits 7+9 and 17+18 with 40.84% and 39.44%, respectively. Other allele occurring at a relatively high frequency (14.08%) was *Glu-B1b* encoding for subunits 7+8. At the *Glu-D1* locus, subunits 5+10 encoded by *Glu-D1d* and subunits 2+12 encoded by *Glu-D1a* were predominant (54.93% and 38.03%, respectively). The less frequent alleles were *Glu-D1b* (subunits 3+12), *Glu-D1h* (subunit 10), observed only in two cultivars each and *Glu-D1m* (subunit 11) was found only in one cultivar. Using the bread wheat nomenclature proposed by Branlard et al. (2003) for LMW glutenin subunits, we were able to identify 16 LMW subunits among the 71 cultivars. The *Glu-B3d*, *Glu-B3b*, *Glu-B3h* and *Glu-B3j* were frequent in the collection (26.76% and 21.13%, respectively). Otherwise, the less frequent alleles were the alleles *a* and *g* (1.41%), allele *b'* (4.23%) and alleles *f, d* and *i* (7.04% and 8.45%), respectively. Concerning the *Glu-A3* locus, 70.42% of the collection analyzed can be characterized by one allele, only *Glu-A3a*. Moreover *Glu-A3b* was found in ten cultivars (14.08%). The two other alleles *d* and *e/f* were less

common. For the *Glu-D3* locus, we observed two alleles at a low frequency, *Glu-D3c* found only in seven cultivars (9.86%) followed by *Glu-D3d* encoded only in one cultivar (1.41%). The most frequently observed allele was *Glu-D3b* (88.73%).

Table 2. Allele frequencies of HMW and LMW glutenin subunits and genetic index diversity at the *Glu-1* and *Glu-3* loci of bread wheat germplasm cultivated in Algeria

Locus	Allele	Subunit	Frequency (%)
Glu-A1	*a*	1	38.03
	b	2*	54.93
	c	null	7.04
	H index		**0.55**
Glu-B1	*a*	7	2.82
	b	7+8	14.08
	c	7+9	40.84
	e	20	1.41
	f	13+16	1.41
	i	17+18	39.44
	H index		0.66
Glu-D1	*a*	2+12	38.03
	b	3+12	2.82
	d	5+10	54.93
	h	10	2.82
	m	11	1.41
	H index	0.55	
Glu-A3	*a*		70.42
	b		14.08
	d		7.04
	e/f		8.45
	H index		0.47
Glu-B3	*a*		1.41
	b		26.76
	b'		4.23
	d		8.45
	f		7.04
	g		1.41
	h		21.13
	i		8.45
	j		21.13
	H index		0.82
Glu-D3	*b*		88.73
	c		9.86
	d		1.41
	H index		0.20

Table 3. Allelic variations in *Glu-1* and *Glu-3* loci, quality scores based on *Glu-1* loci and the quality classes based on the *Glu-3* loci of bread wheat germplasm cultivated in Algeria

Locus	Alleles	Number of varieties	Glu-1 quality scores	Locus	Alleles	Number of varieties	Glu-3 quality classes
Glu-A1,B1,D1	*a,a,h*	1	–	*Glu-A3,B3,D3*			
	a,b,a	1	8		*a,a,b*	1	moderate
	a,b,d	1	10		*a,b,b*	16	high
	a,c,a	1	7		*a,b,d*	1	high
	a,c,b	2	7		*a,d,b*	1	high
	a,c,d	8	9		*a,d,c*	1	moderate
	a,i,a	5	8		*a,f,b*	4	high
	a,i,d	8	10		*a,h,b*	13	high
	b,a,d	1	8		*a,i,b*	5	high
	b,b,a	2	8		*a,j,b*	8	moderate
	b,b,d	2	10		*b,b,c*	2	moderate
	b,b,h	1	–		*b,f,b*	1	high
	b,c,a	5	7		*b,h,b*	1	high
	b,c,d	11	9		*b,j,b*	6	moderate
	b,c,m	1	–		*d,b',b*	3	moderate
	b,e,a	1	6		*d,d,b*	2	high
	b,f,d	1	10		*e/f,d,b*	1	moderate
	b,i,a	7	8		*e/f,d,c*	1	low
	b,i,d	7	10		*e/f,g,b*	1	low
	c,b,a	3	6		*e/f,h,c*	1	low
	c,c,a	1	5		*e/f,i,c*	1	low
	c,i,a	1	6		*e/f,j,c*	1	low

The indices (H) of genetic variation at the *Glu-1* and *Glu-3* loci computed following Nei (1973) method are shown in Table 2. The mean index of genetic variation for the bread wheat germplasm analyzed was 0.54, ranging from 0.20 to 0.82. The lowest genetic variation index was at the *Glu-D3* locus and the highest at the *Glu-B3* locus. On an average, the genetic variability in *Glu-1* loci (0.58) was greater than that of *Glu-3* loci (0.49). the greater Nei's coefficient of genetic variation for *Glu-1* loci (as compared with that of *Glu-3* loci) indicates that the alleles in *Glu-1* loci are relatively more distributed amongst the cultivars and representing a bimodal or trimodal distribution whereas, the alleles in *Glu-3* loci are relatively less distributed and creating a unimodal distribution.

Quality scores and classes of Algerian bread wheats

Table 3 includes quality scores calculated over the subunits of *Glu-1* following Payne (1987) and quality classes for *Glu-3* after Gupta et al. (1990) of 71 varieties. *Glu-1* quality scores, range from 5 to 10. Quality scores for 3 cultivars with three subunit compositions (1, 7, 10; 2*, 7+8, 10 and 2*, 7+9, 11) were not determined because the effects rare subunits 10 and 11 on bread making quality are yet to be determined. It is evident from the present study that the 71 Algerian wheat germplasm varies widely in HMW glutenin subunits composition. The frequency of subunits related to good bread making quality, such as 5+10 controlled by the *Glu-D1d* allele on 1D chromosome is relatively high occurring in 39 varieties. The presence of high quality alleles in *Glu-A3, Glu-B3* and *Glu-D3* loci have led the Algerian wheat cultivars to be classified into medium or high quality classes (Table 3). The occurrence of this wide allelic polymorphism in our panel of cultivars can be considered as an asset in breeding programs aimed for wheat quality.

Discussion

In this study, we dissected the allelic variation of HMW and LMW glutenin loci in 71 hexaploid wheat germplasm cultivated in Algeria. The seeds were obtained from the Technical Institute of Field Crops (ITGC), Constantine, Algeria. The genetic diversity index of 0.54 was higher than that reported for other collections, but it was lower than the value 0.59 obtained in Saharan bread wheat from Algerian oases (Bellil et al. 2012) and in French bread wheat cultivars (Branlard et al. 2003). All the loci, except *Glu-D3,* displayed a genetic variability higher than 0.47, *Glu-B3* being the most polymorphic (Table 2). The number of alleles detected at the *Glu-1* and *Glu-3* loci was higher than that in other collections. The HMW-GS composition has been widely used to assess the genetic diversity and grain quality of wheat. The frequency of a number of subunits in the Algerian bread wheats differed considerably from that noted in the previous study. The allele *c* at *Glu-A1,* subunits 7, 20 and 13+16 at *Glu-B1* and subunits 3+12, 10 and 11 at *Glu-D1* appeared less frequently in this study while subunits 7+9 and 17+18 at *Glu-B1* were observed more frequently. The dominant alleles were the *Glu-A1b* (2*), *Glu-B1c* (subunits 7+9) and *Glu-D1d* (subunits 5+10), which are known for their favourable effect on dough properties (Payne et al. 1987). Alleles *Glu-B1d* (subunits 6+8) and *Glu-D1a* have a negative effect on dough strength. The *Glu-B1d* was absent in the collection analyzed and the

Glu-D1a was present in 38.03% of the varieties. A total of 14 alleles encoding HMW-GS were present in only 71 cultivars of Algerian bread wheat and this high level of diversity agrees with the results of Bellil et al. (2012). Major differences between Algerian bread wheats and other collections were observed in the frequency of subunit 7 controlled by *Glu-B1a* although Algerian bread wheats had not subunit pair 6+22 controlled by *Glu-B1o*. The effect of these subunits on wheat quality still remains unclear. No Algerian bread wheats possessed subunit pair 14+15 controlled by *Glu-B1h* which was in other collections. The seventy-one bread wheats analyzed had a somewhat rare subunit pair, 17+18 *(Glu-B1g)* present in 28 cultivars and subunit 20 *(Glu-B1e)* present in only one cultivar. It is thus clear that allelic variation among the germplasm analyzed is considerably at the *Glu-B1* locus. Subunit pair 5+10 at the *Glu-D1* allele is seen more frequently in our collection as that in European wheat cultivars (Payne et al. 1984) and in French bread wheat (Branlard et al. 2003), possibly owing to their correlation with good bread-making quality. The mean genetic variation index at *Glu-1* loci was 0.58. It was higher than that reported for other collections, showing that Algerian hexaploid wheats have relatively high genetic diversity. High diversity was found in the Algerian wheats for LMW-GS. The *Glu-A3a* allele was the most frequent as it was in French cultivars (Branlard et al. 2003) and in Saharan bread wheat from Algerian oases (Bellil et al. 2012). It has a positive effect on dough properties (strength and extensibility). The number of alleles detected at *Glu-B3* (9 alleles) was the same as that found by Bellil et al. (2012) in Saharan bread wheat, seven and eight of them were present in both collections, respectively. The most frequent allele was *Glu-B3b*.*Glu-B3g* which was less frequent in our collection was more frequent in other collections (Branlard et al. 2003; Bellil et al. 2012). The allele *b* was the most frequent at the *Glu-D3* locus as it was in Saharan bread wheats (Bellil et al. 2012).

Analysis of glutenins is known to be a powerful tool for the evaluation of genetic resources. The glutenin characteristics of the analyzed germplasm have a potential value in wheat breeding. The occurrence of this wide allelic polymorphism in our panel of cultivars can be considered as an asset in breeding programs aimed for wheat quality.

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