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RESEARCH ARTICLE

Allelic variation and distribution of HMW glutenin subunit 1Ay in *Triticum* species

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Abstract The allelic variation and distribution of high-molecular-weight (HMW) glutenin subunit 1Ay in 814 *Triticum* lines were investigated by sodium dodecyl sulfate polyacrylamide-gel electrophoresis (SDS–PAGE). 1Ay subunit existed in 13 out of analyzed 21 species. The four species *T. turgidum* L., *T. polonicum* L., *T. turanicum* Jakubz. and *T. zhukovskyi* Men. et Er. were firstly discovered with expressed 1Ay subunit. The distribution frequencies for diploid, tetraploid and hexaploid wheats were at 87.89, 20.31 and 1.79%, respectively. Among the observed eight 1Ay alleles, three with the electrophoretic mobilities similar to 1Bx6, 1By8, and between 1By8 and 1Dy10 were firstly observed. Five had the mobilities similar to 1Bx6, 1Bx7, 1By8, 1Dy10, and 1Dy12 in *Glu-1B* and *Glu-1D* loci of hexaploid wheat. It is very difficult to distinguish these 1Ay alleles in *Glu-1Ay* from those in hexaploid wheat. The predominant 1Ay alleles were those with the mobilities similar to 1Bx7, 1By8, 1Dy10 and 1Dy12, and faster than 1Dy12. Comparison results of 1Ay alleles in different species indicated that multiple diploid lines were involved in the evolution process of tetraploid wheat. The 1Ay allelic variations and genetic resources might be useful in the quality improvement of common wheat.

Keywords Distribution · 1Ay subunit · Evolvement · Genetic resources · *Triticum* · Variation

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Introduction

Glutenins and gliadins are the major storage proteins determining end-use quality of wheat flours (Payne 1987; Shewry et al. 1992). Glutenins can be divided into two distinct groups: high and low molecular weight glutenin subunits (HMW-GS and LMW-GS) by SDS polyacrylamide-gel electrophoresis (SDS–PAGE) (Payne et al. 1981) and size exclusion high performance liquid chromatography (SE–HPLC) (Batey et al. 1991). The genes encoding HMW-GS at the *Glu-1* loci are located on the long arm of chromosomes 1A, 1B and 1D. Each *Glu-1* loci consists of two tightly linked genes encoding one larger *x*-type and one smaller *y*-type subunits. The variations, structures and function of HMW-GS genes

from wheat and its related species have been considerably studied due to HMW-GS being associated with the elasticity of wheat dough (Payne 1987; Shewry et al. 1992).

Hexaploid wheat contains six HMW-GS genes. However, not all genes are expressed and thus resulted in the variations on the number of HMW-GSs among genotypes (Payne et al. 1981; Payne and Lawrence 1983). The 1Ay subunit encoded by the *y*-type gene at *Glu-1A* locus has been deemed to be always silent in hexaploid wheat (Forde et al. 1985; Halford et al. 1989) with the exception of two Swedish bread wheat lines (Margiotta et al. 1996). However, 1Ay subunit can express in some wild diploid (AA, $2n = 2x = 14$) (Ciaffi et al. 1998; Ma et al. 2007; Hu et al. 2008) and tetraploid wheat lines (AABB, $2n = 4x = 28$) (Levy and Feldman 1988; Ciaffi et al. 1991; Ciaffi et al. 1993; Wan et al. 2002; Jiang et al. 2009; Xu et al. 2009). Some durum lines containing 1Ay subunit transferred from *T. dicoccoides* Körn. ex Asch. et Graebn.) Schweinf. showed very promising gluten properties (Ciaffi et al. 1991). Likewise, the introduction of 1Ay subunit from diploid *T. boeoticum* Boiss. ssp. *thaoudar* (Reut. ex Hausskn.) Grossh. (AA, $2n = 2x = 14$) into hexaploid wheat increased the gluten strength (Rogers et al. 1997). Several expressed 1Ay genes have been cloned and sequenced, even heterogenously expressed (Wan et al. 2002; Bai et al. 2004; Jiang et al. 2009; Hu et al. 2010). Recently, a 1Ay faster than 1Dy12 in electrophoretic mobility was transferred into common wheat by transgenic technology (Bai et al. 2004; Ma et al. 2008).

The information on genetic variation and distribution of 1Ay subunit among different *Triticum* species with A genome is important to further understand its evolution and to better use it in wheat quality improvement. The objectives of this study are to investigate the distribution of 1Ay subunit and its allelic variation in 814 *Triticum* lines with different ploidies and genomes, which might provide more extensive 1Ay genetic resources for quality improvement of bread wheat.

Materials and methods

Plant materials

A total of *Triticum* 814 lines including five groups with different genome constitutes and belonging to diploid, tetraploid, or hexaploid wheat were used in this study (Table 1). Of which, 300 were provided by Triticeae Research Institute, Sichuan Agricultural University, China, and the remainders were kindly provided by USDA-ARS, National Small Grains Collection (http://www.ars-grin.gov).

Tetraploid wheat Langdon (LDN) (Null, 1Bx6 + 1By8) and hexaploid wheat Chinese Spring (CS) (Null, 1Bx7 + 1By8, 1Dx2 + 1Dy12), Chuanyu12 (CY12) (1Ax1, 1Bx7 + 1By8, 1Dx5 + 1Dy10), and Xiaoyan6 (XY6) (1Ax1, 1Bx14 + 1By15, 1Dx2 + 1Dy11), were used as checks. HMW-GSs were identified according to Payne and Lawrence (1983) and Ciaffi et al. (1993).

Protein extraction and SDS–PAGE analysis

The HMW glutenin protein was extracted by two kinds of methods. One general method of extraction was used as described by Wan et al. (2000). The other for selective precipitating the HMW glutenin protein was adopted as reported by Hu et al. (2010).

HMW glutenin subunits were separated by SDS–PAGE with 10% (w/v) separating and 3% (w/v) stacking gels. Electrophoresis was performed at a constant 20 mA for about 2.5 h. Then, the gels were stained overnight with 0.001% (w/v) Coomassie Brilliant Blue R-250, in 25% (v/v) isopropanol and 10% (v/v) acetic acid. De-staining was carried out with tap water.

Results

Distribution of 1Ay subunit

The expression of 1Ay subunit showed distinct difference among the five groups (Table 1). The four groups with genomes AA, AABB, AAGG, and AAAAGG showed the frequencies with 1Ay subunit of 87.89, 19.41, 26.09, and 40.00%, respectively. Expressed 1Ay subunit in the group with genome AABBDD was not observed.

The expression of 1Ay subunit also showed distinct difference among different ploidies of *Triticum*. In the analyzed 190 diploid wheats, 167 had 1Ay subunit with the highest frequency of 87.89%. In the 512 tetraploid and 112 hexaploid wheats, 20.31 and 1.79% of lines expressed 1Ay subunit, respectively.

Table 1 The 1Ay distribution in different groups and species of *Triticum*

Groups	No. of lines analyzed	Frequency with 1Ay subunit (%)	Species	No. of lines analyzed	Frequency with 1Ay subunit (%)
Diploid with genome AA ($2n = 2x = 14$)	190	87.89	*T. monococcum* L.	60	96.67
			T. boeoticum Boiss.	68	95.59
			T. urartu Tum.	62	70.97
Tetraploid with genome AABB ($2n = 4x = 28$)	443	19.41	*T. dicoccoides* Körn.	108	57.41
			T. turgidum L.	106	14.15
			T. polonicum L.	43	6.98
			T. dicoccon Schrank	55	5.45
			T. turanicum Jakubz.	40	2.50
			T. carthlicum Nevski	30	3.33
			T. durum Desf.	51	1.96
			T. ispahanicum Heslot	7	0.00
			T. karamyschevii Nevski (syn. *T. palaeocolchicum* Men.)	3	0.00
Tetraploid with genome AAGG ($2n = 4x = 28$)	69	26.09	*T. araraticum* Jakubz.	54	22.22
			T. timopheevii Zhuk.	15	40.00
Hexaploid with genome AABBDD ($2n = 6x = 42$)	107	0.00	*T. compactum* Host	15	0.00
			T. spelta L.	15	0.00
			T. macha Dek. et Men.	15	0.00
			T. sphaerococcum Perc.	15	0.00
			T. vavilovi Jakubz.	3	0.00
			T. aestivum L.[a]	44	0.00
Hexaploid with genome AAAAGG ($2n = 6x = 42$)	5	40.00	*T. zhukovskyi* Men. et Er.	5	40.00

[a] The 44 *T. aestivum* L. lines including 26 Tibetan weedrace, 5 Xingjiang rice and 13 Yunnan hulled wheats

Among 21 species of *Triticum*, the expressed 1Ay subunit was observed in 13 species with the distribution frequencies ranging from 1.96% for *T. durum* Desf. to 96.67% for *T. monococcum* L. (Table 1). No 1Ay subunit was observed in the two tetraploid species *T. ispahanicum* Heslot and *T. karamyschevii* Nevski (syn. *T. palaeocolchicum* Men.) with genome AABB, and all the hexaploid species *T. compactum* Host., *T. spelta* L., *T. macha* Dek. et Men., *T. sphaerococcum* Perc., *T. aestivum* L. and *T. vavilovi* Jakubz. with genome AABBDD.

Variation of 1Ay alleles in diploid wheat

In the analyzed 814 *Triticum* lines, eight 1Ay alleles were identified based on their electrophoretic mobilities in SDS–PAGE gel (Table 2, Fig. 1). Of which, six were observed in diploid wheats with genome AA (Fig. 1a, b). The 1Ay allele with the similar mobility to 1By8 was firstly discovered in all the three diploid species *T. urartu* Tum., *T. boeoticum* Boiss. and *T. monococcum* (Tu1, Tb1, Tm5). The 1Ay allele with similar mobility to 1Bx6 was also firstly discovered in *T. boeoticum* and *T. monococcum* lines (Tb4, Tm4). The 1Ay alleles faster than 1Dy12 (Tu2, Tm2), similar to 1Bx7 (Tb3, Tm1), and between 1Bx7 and 1By8 (Tb2, Tm3) existed in both of three species. However, the 1Ay allele similar to 1Dy12 was only found in *T. urartu* lines with a frequency of 72.73% (Tu3). The results revealed that diploid wheat conserved extensive variations of 1Ay alleles. The predominant 1Ay alleles in *T. urartu*, *T. boeoticum,* and *T. monococcum* were those with the mobilities similar to 1Dy12, 1By8 and 1Bx7, with the

Table 2 The 1Ay alleles in different *Triticum* species

Species	No. of lines with 1Ay subunit	Mobility of 1Ay subunit	No.	Frequency (%)
T. urartu	44	Similar to 1By8	1	2.27
		Similar to 1Dy12	32	72.73
		Faster than 1Dy12	11	25.00
T. boeoticum	65	Similar to 1Bx6	4	6.15
		Similar to 1Bx7	7	10.77
		Between 1Bx7 and 1By8	7	10.77
		Similar to 1By8	47	72.31
T. monococcum	58	Similar to 1Bx6	2	3.45
		Similar to 1Bx7	46	79.31
		Between 1Bx7 and 1By8	5	8.62
		Similar to 1By8	2	3.45
		Faster than 1Dy12	3	5.17
T. dicoccoides	62	Similar to 1Dy10	32	51.61
		Similar to 1Dy12	7	11.29
		Between 1By8 and 1Dy10	15	24.19
		Faster than 1Dy12	8	12.90
T. turgidum	15	Similar to 1Dy12	14	93.33
		Similar to 1Dy10	1	6.67
T. polonicum	3	Similar to 1Dy12	2	66.67
		Similar to 1Dy10	1	33.33
T. dicoccon	3	Faster than 1Dy12	2	66.67
		Similar to 1Dy12	1	33.33
T. carthlicum	1	Similar to 1Dy10	1	100.00
T. turanicum	1	Similar to 1Dy10	1	100.00
T. durum	1	Faster than 1Dy12	1	100.00
T. araraticum	12	Similar to 1Bx7	5	41.67
		Similar to 1By8	4	33.33
		Faster than 1Dy12	3	25.00
T. timopheevii	6	Faster than 1Dy12	6	100.00
T. zhukovskyi	2	Similar to 1Dy12	1	50.00
		Faster than 1Dy12	1	50.00

frequencies of 72.73, 72.31, and 79.31%, respectively. These results indicated the different distribution of 1Ay alleles among the three diploid species.

Variation of 1Ay alleles in tetraploid and hexaploid wheat

Six 1Ay alleles were found in tetraploid wheat (Table 2, Fig. 1c–e). The 1Ay alleles similar to 1Dy10, 1Dy12, and faster than 1Dy12 were observed in the five, four, and three tetraploid speices with genome AABB. The firstly observed 1Ay allele between 1By8 and 1Dy10 was only found in 24.19% *T. dicoccoides* lines (Td2). *T. dicoccoides* possessed all the four 1Ay alleles existed in other tetraploid wheat with genome AABB (Fig. 1c, Td1, Td2, Td3, Td4). Of which, the preponderant 1Ay allele similar to 1Dy10 accounted for 51.61%. Three 1Ay alleles, faster than 1Dy12, similar to 1By8 and 1Bx7, were identified in *T. araraticum* Jakubz. (Fig. 1d, Ta1, Ta2, Ta3). Of which, the allele similar to 1By8 was not found in other tetraploid wheats while it existed in diploid wheats *T. boeoticum* and *T. monococcum*.

Among the analyzed hexaploid wheat, only two 1Ay alleles were firstly observed in *T. zhukovskyi* (Fig. 1e, Tz1, Tz2).

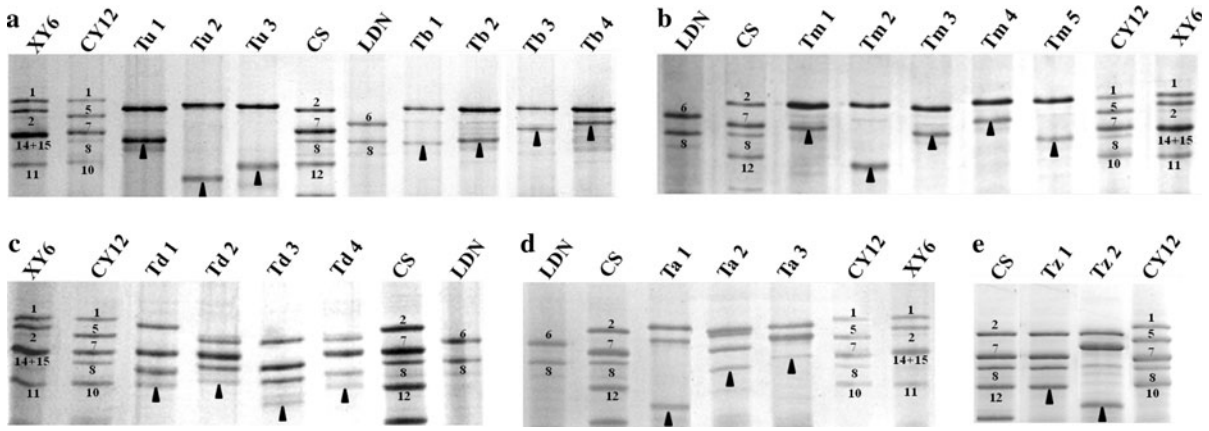

Fig. 1 SDS-PAGE analysis of 1Ay alleles in *Titicum* species. Tu, *T. urartu*; Tb, *T. boeoticum*; Tm, *T. monococcum*; Td, *T. dicoccoides*; Ta, *T. araraticum*; Tz, *T. zhukovskyi*; LDN, Langdon; CS, Chinese Spring; CY12, Chuanyu12; XY6, Xiaoyan6; 1Ay subunit was marked by solid arrow. **a** the 1Ay alleles with the mobilities similar to 1By8 (*Lanes Tu1* and *Tb1*), faster than and similar to 1Dy12 (*Lanes Tu2* and *Tu3*), between 1Bx7 and 1By8 (*Lane Tb2*), similar to 1Bx7 and 1Bx6 (*Lanes Tb3* and *Tb4*); **b** the 1Ay alleles with the mobilities similar to 1Bx7, 1Bx6 and 1By8 (*lanes Tm1*, *Tm4* and *Tm5*), faster than 1Dy12 (*Lane Tm2*), between 1Bx7 and 1By8 (*Lane Tm3*); **c** the 1Ay alleles with the mobilities similar to 1Dy10 (*lane Td1*), between 1By8 and 1Dy10 (*Lane Td2*), faster than and similar to 1Dy12 (*Lanes Td3 and Td4*); **d** the 1Ay alleles with the mobilities faster than 1Dy12 (*Lane Ta1*), similar to 1By8 and 1Bx7 (*Lanes Ta2* and *Ta3*); **e** the 1Ay alleles with the mobilities similar to and faster than 1Dy12 (*Lanes Tz1* and *Tz2*)

Discussion

Besides in the diploid *T. urartu*, *T. boeoticum* and *T. monococcum* (Ciaffi et al. 1998; Ma et al. 2007; Hu et al. 2008), and the tetraploid *T. dicoccoides* (Levy and Feldman 1988; Ciaffi et al. 1993), *T. carthlicum* Nevski (Xu et al. 2009), *T. durum* (Ciaffi et al. 1991), *T. dicoccon* (Jiang et al. 2009) and *T. timopheevii* Zhuk. (Wan et al. 2002), the present study found that 1Ay subunit also existed in the tetraploids *T. turgidum*, *T. polonicum* and *T. turanicum*, and in the hexaploid *T. zhukovskyi* (Table 1). Eight 1Ay alleles were detected in this study (Table 2). Of them, the three 1Ay alleles with electrophoretic mobilities similar to 1Bx6, 1By8, and between 1By8 and 1Dy10 were firstly observed. As a result, there were abundant 1Ay allelic variations and genetic resources in *Triticum* species.

Among the eight observed 1Ay alleles, only two similar to and faster than 1Dy12 were common in diploid, tetraploid and hexaploid wheat with genome AAAAGG. And, the successful transfer of 1Ay allele faster than 1Dy12, from diploid wheats *T. boeoticum* ssp. *thaoudar* (AA, $2n = 2x = 14$) into common wheats with genome AABBDD (Rogers et al. 1997) further proved active 1Ay origin of polyploidy wheat. In addition, the 1Ay allele similar to 1Dy10 was in both diploid wheat (Ma et al. 2007) and tetraploid wheat with genome AABB (Table 2). These suggested diploid wheats with these active 1Ay alleles participated in the evolution of tetraploid wheat with genome AABB. Similarity, the diploid wheat with 1Ay alleles similar to 1Bx7, 1By8, and faster than 1Dy12, participated in the evolution of tetraploid wheat with genome AAGG. The 1Ay variations in *T. zhukovskyi* also indicated that different diploids were involved. The results indicated multiple diploid lines were involved in the evolution process of wheat.

Genetic diploidization process, which may cause gene inactivation that have been involved in the evolution of allopolyploid wheat under wild and cultivation, may be responsible for the reduction in the number or activity of duplicated genes (Ciaffi et al. 1993). Xu et al. (2009) considered that HMW-GS alleles must be lost during the evolution from diploid to polyploid wheats. And, HMW glutenin gene inactivation, following diploidization, affected mainly the A genome (Galili et al. 1988). In the present research, the tested diploid, tetraploid and hexaploid wheats had 1Ay subunit at 87.89, 20.31 and 1.79%, respectively, revealing the gradual decrease of 1Ay subunit from diploidization to tetraploidization then to hexaploidization processes. And, all the four 1Ay alleles similar to 1Bx6, 1Bx7,

1By8, and between 1Bx7 and 1By8 existed in diploid wheats, were not discovered in tetraploid wheats with AABB genome and hexaploid wheats. In the tetraploid wheats with genome AABB, *T. dicoccoides*, which is the most age-old species of emmer (Feldman et al. 1995; Chantret et al. 2005), possessed both the highest distribution frequency of 1Ay subunit at 57.41% and the most 1Ay alleles including those similar to 1Dy10 and 1Dy12, and faster than 1Dy12 and the exclusive allele between 1By8 and 1Dy10, while the cultivated wheat *T. dicoccon* was with 1Ay subunit only for 5.45% and without the 1Ay allele similar to 1Dy10 existing in *T. dicoccoides* at a high frequency of 51.61% (Tables 1, 2), indicating that a lot of active 1Ay alleles in *T. dicoccoides* were reduced during the domestication. Similarly, in the tetraploid wheats with genome AAGG, the wild *T. araraticum* (Kimber and Feldman 1987; Kilian et al. 2006) had the three 1Ay alleles similar to 1Bx7 and 1By8, and faster than 1Dy12, while its domesticated wheat *T. timopheevii* (Kimber and Feldman 1987) had only the allele faster than 1Dy12. Accordingly, that 1Ay bands were absent in hexaploid wheat with genome AABBDD might be resulted from the fierce reduction and variation of 1Ay alleles in the two processes, including the first domestication from *T. dicoccoides* to *T. dicoccon*, then the evolution to hexaploid wheat (Feldman et al. 1995; Allaby et al. 1999; Eckardt 2001; Huang et al. 2002; Chantret et al. 2005).

Additionally, *T. urartu* is widely considered as the A genome progenitor of tetraploid and hexaploid wheats (Dvořák et al. 1993). The present research further corroborated that *T. urartu* is relatively distant from *T. boeoticum* and its domesticated *T. monococcum* (Takumi et al. 1993; Feldman et al. 1995; Eckardt 2001), because it had lower 1Ay subunit distribution frequencies and less 1Ay alleles while the latter both were with alike higher frequencies about 96% and the identical alleles similar to 1Bx6, 1Bx7 and 1By8, and between 1Bx7 and 1By8 (Tables 1, 2). Several researches also found that quarter of 155 and 18% of 150 *T. urartu* lines were without expressed 1Ay subunit (Waines and Payne 1987; Ciaffi et al. 1998). Consequently, the tetraploid and hexaploid wheat lines lacking 1Ay subunit might be evolved from the *T. urartu* lines with inactive 1Ay gene (Xu et al. 2009). On the other hand, 1Ay subunit usually had the mobilities situated between 1Bx and 1Dy (Ciaffi et al. 1998). The present study found that five 1Ay alleles had mobilities similar to 1Bx6, 1Bx7, 1By8, 1Dy10, and 1Dy12 in *Glu-1B* and *Glu-1D* loci of hexaploid wheat. It is very difficult to distinguish these 1Ay alleles in *Glu-1Ay* from those in hexaploid wheats because of their similar electrophoretic mobilities. Therefore, it is also possible that 1Ay subunit exists in some hexploid wheats but we can not 'see' it. Maybe, the tetraploid wheats with B genome or hexaploid wheats with both B and D genomes without these 1Ay alleles (Table 2), was associated with the mixture/covering/confusion between 1Ay and those HMW-GSs in *Glu-1B* and *Glu-1D* loci, which might also make the 1Ay distribution frequency to be decreased from diploid to tetraploid then to hexaploid wheat (Table 1). These might result in the viewpoint that 1Ay subunit is always slient in hexaploid wheat (Forde et al. 1985; D'Ovidio et al. 1996).

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