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Biodiversity of tetraploid wheats: taxonomy, studying, increasing and preservation

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Abstract. Tetraploid wheats have played a critical role in human history. They were the first polyploids domesticated by man. *Triticum durum* Desf. was bred nearly 2000 years ago and the last 70 years, breeders have been working with only this one agricultural important tetraploid wheat species. Related wheat species having preserved higher polymorphism than that of cultivated ones could be an additional source of increasing biodiversity. Solving the problems of effective utilization and preservation of the biodiversity of wheat related species is possible in four basic trends: arranging a scrupulous preliminary comparative-genetic studying of related species and generic gene pool, i.e., revising their biodiversity; aimed at usage of accessions with a preliminary established presence of gene(s) of interest for introgressive hybridisation or amphidiploidisation; obligatory cataloguing of accessions with introgression of genes or whole genomes in genebanks for their preservation; producing a new genus *Triticum* taxonomy including man-made species.

Keywords. Tetraploid wheat – Taxonomy – Biodiversity – Preservation.

Biodiversité des blés tétraploïdes : taxonomie, étude, augmentation et préservation

Résumé. Les blés tétraploïdes ont joué un rôle crucial dans l'histoire humaine. Ils ont été les premiers polyploïdes domestiqués par l'homme. *Triticum durum* Desf. a été sélectionné il y a environ 2000 ans et ces 70 dernières années, les obtenteurs ont travaillé seulement à cette espèce de blé tétraploïde importante du point de vue agricole. Les espèces de blé apparentées ayant conservé un polymorphisme plus élevé par rapport aux espèces cultivées pourraient constituer une source supplémentaire de biodiversité. Il est possible de résoudre les problèmes de l'utilisation efficace et de la conservation de la biodiversité des espèces de blé apparentées en suivant quatre approches : réaliser une étude préliminaire fine de génétique comparative sur les espèces apparentées et le pool génétique générique du blé, c'est-à-dire, reconsidérer leur biodiversité ; viser à utiliser des accessions chez lesquelles ont été identifiés des gènes d'intérêt pour une introgression ou une amphidiploïdisation ; répertorier obligatoirement les accessions avec introgression de gènes ou de génomes entiers dans des banques de gènes pour leur conservation ; produire la taxonomie d'un nouveau genre *Triticum* incluant les espèces obtenues par l'homme.

Mots-clés. Blé tétraploïde – Taxonomie – Biodiversité – Conservation.

I – Introduction

Searching for ways of increasing biodiversity and preservation is the key point in biology of the 21st century, whereas preservation of cultivated wheat species biodiversity is a strategic task of food security. Genus *Triticum* L. includes di- ($2n=14$), tetra- ($2n=28$) and hexaploid ($2n=42$) species. Tetraploid wheats are represented by 2 wild and 12 cultivated species including into two evolutionary lines (sections) – Emmer and Timopheevii (Goncharov, 2011; Hammer *et al.*, 2011). At present, only five of them, namely *Triticum durum* Desf., *T. turgidum* L., *T. dicoccum* (Schrank) Schuebl., *T. aethiopicum* Jakubz. and *T. turanicum* Udazch. are cultivated. Nowadays durum wheat is the primary wheat for pasta and semolina production and the second-most cultivated wheat after common (bread) wheat. Rivet, emmer and other tetraploid wheats practically disappeared from cultivation during the 20th century and its extinction was prevented only by inclusion of them accessions in germplasm bank collections. Collections of cultivated plant are traditionally regarded as the material used mainly for breeding purposes. However, they can also be used in genetic or botanical investigations. Rearrangement of huge germplasm bank collections is the taxonomy task.

II – Taxonomy

Traditionally, the taxonomy methods are based on revealing the affinity among organisms, determining the homology of their traits and common origin. At present, there is a tendency of juxtaposition of classical taxonomy, which had historically developed on the basis of comparative morphology, against modern taxonomy based on genetic and molecular-genetic investigations (see review Goncharov, 2011).

Swaminathan and Rao (1961) showed that differences in taxonomically important traits of hexaploid wheats are controlled by four pairs of nonallelic genes. taxonomically important traits are absent in tetraploid wheats. Unfortunately, tetraploid species do not possess such genes. The only exceptions are *P1* and *P2* y *T.policum* and *T. ispahanicum* (Watanabe, 1994), *Ta* – *T. carthlicum* (Haque *et al.*, 2011) and *Pp1* *T. aethiopicum* (Dobrovolskaya *et al.*, 2006; Khlestkina *et al.*, 2010).

Wheat taxonomy has a long history. The main goal of modern wheat taxonomy is to establish such a classification of wheat genera and species which would reflect both their phylogenetic relationships and genetic structure. Good and rigorous taxonomy is necessary for effective conservation and increasing cultivated plant biodiversity by introgressive hybridization. This is complicated by the lack of consensus concerning the taxonomy of tetraploid wheats and by unresolved questions regarding the domestication and spread of naked wheats. These knowledge gaps hinder crop diversity conservation efforts and plant breeding program (Nachit *et al.* 2001).

The classification that I have proposed (Goncharov, 2002; Goncharov *et al.*, 2009) follows in the Körnicke–Flaksberger–Dorofeev tradition and includes 29 species in five sections (Table 1). I do not divide the genus into subgenera and have instead designed sections (except for section *Compositum* N.P. Gontsch. which includes most of the artificial man-made species) based on ploidy levels, cytoplasm types and genome compositions. Traits were evaluated in terms of their variation and genetic control at the three different ploidy levels. Only experimental comparative-genetic studies will permit identification of individual ‘species-forming’ genera, determination of their allelism, and further evaluation of the species recognized. A detailed classification would permit easy identification of the material being stored and reproduced in genebanks (Filatenko and Hammer 1997).

Poor classifications are not just less useful, they are positively harmful. In the absence of acceptable criteria for distinguishing individual taxa, genebank staff cannot be expected to monitor the purity of their accessions, and important accessions may be eliminated because their significance is not appreciated. Indeed, failure to provide formal taxonomic, and hence nomenclatural, recognition of distinct entities may lead to what Dr. Michael Windham has referred to as “extinction by nomenclature.” Clearly, a classification that requires expertise in cytogenetic and/or molecular genetics will not be practical for many of those who work with *Triticum*. What is needed is a classification system that takes account of phylogenetic, cytogenetic, and molecular information but is accompanied by detailed morphological descriptions, workable keys, and correct nomenclature (Morrison 1995, 2001; Goncharov 2002).

The two examples illustrate the primary disadvantage of Mac Key’s (2005) approach to the classification of *Triticum* (Table 2). It overlooks and conceals many of the demonstrably distinct entities within the genus. This tends to result in the exclusion of these entities and the diversity they represent from research studies and may lead to the elimination of important accessions from the world’s genetic resources. It can also lead to problems with the identification of existing genetic resources. Examination of 576 accessions identified as *T. turgidum* and 1,189 accessions identified as *T. aestivum* in the International Center for Agricultural Research in the Dry Areas (ICARDA) and Uzbek Institute of Plant Industry genebank, respectively, revealed that about 5 and 8% did not belong to the designated taxon (Table 2).

Table 1. *Triticum* L. classification ((Goncharov, 2002) with additions according to: Goncharov *et al.* (2009)).

Section	Group of species	Species	2n	Genomes		
<i>Monococcon</i> Dum.	Hulled	<i>T. urartu</i> Thum. ex Gandil.	14	A ^u		
		<i>T. boeoticum</i> Boiss.	14	A ^b		
		<i>T. monococcum</i> L.	14	A ^b		
<i>Dicoccoides</i> Flaksb.	Naked	<i>T. sinskajae</i> A. Filat. et Kurk.	14	A ^b		
		Hulled	<i>T. dicoccoides</i> (Körn. ex Aschers et Graebn.) Schweinf.	28	BA ^u	
	tetraploids	<i>T. dicoccum</i> (Schrank) Schuebl. ^a	28	BA ^u		
		<i>T. karamyshevii</i> Nevski	28	BA ^u		
		<i>T. ispahanicum</i> Heslot	28	BA ^u		
		<i>T. turgidum</i> L.	28	BA ^u		
		<i>T. durum</i> Desf.	28	BA ^u		
		<i>T. turanicum</i> Jakubz.	28	BA ^u		
		<i>T. polonicum</i> L.	28	BA ^u		
		<i>T. aethiopicum</i> Jakubz.	28	BA ^u		
		<i>T. carthlicum</i> Nevski	28	BA ^u		
		<i>Triticum</i>	Hulled	<i>T. macha</i> Dekapr. et Menabde	42	BA ^u D
				<i>T. spelta</i> L.	42	BA ^u D
<i>T. vavilovii</i> (Thum.) Jakubz.	42			BA ^u D		
Naked hexaploids	<i>T. compactum</i> Host		42	BA ^u D		
	<i>T. aestivum</i> L.		42	BA ^u D		
	<i>T. sphaerococcum</i> Perciv.		42	BA ^u D		
<i>Timopheevii</i> A. Filat. et Dorof.	Hulled	<i>T. araraticum</i> Jakubz.	28	GA ^u		
		<i>T. timopheevii</i> (Zhuk.) Zhuk.	28	GA ^u		
		<i>T. zhukovskiyi</i> Menabde et Erizjan	42	GA ^u A ^b		
<i>Compositum</i> N.P. Gontsch.	Hulled	<i>T. palmovae</i> G. Ivanov	28	DA ^b (DA ^u)		
		<i>T. dimococcum</i> Schieman et Staudt	42	BA ^u A ^b		
		<i>T. kiharae</i> Dorof. et Migusch.	42	GA ^u D		
		<i>T. soveticum</i> Zhebrak	56	BA ^u GA ^u		
		<i>T. borisii</i> Zhebrak	70	BA ^u DGA ^u		
	Naked octoploid	<i>T. flaksbergeri</i> Navr.	56	GA ^u BA ^u		

^a In botanical literature there is a rule to Latinize Greek word ending. The noun "dicoccon" from Greek "χοχχον" (grain) when forming adjectives becomes 'dicoccus, -a, -um' in Latin. So there is no reason to change *T. dicoccon* for *T. dicoccon*. Moreover, Schrank used name '*T. dicoccon*' only 'for the time being' (for detail see review L.R. Morrison (1998)). Hence, his binominal proves to be only provisional name.

Table 2. Investigations into the authenticity of a collection of "tetraploid" wheats (*T. turgidum*) from West Asia and North Africa (WANA) country genebank (ICARDA), and a collection of hexaploid wheats (*T. aestivum*) from Uzbek Institute of Plant Industry wheat collections.

Species	No. of studied accessions	No. of misidentified accessions	Percent of non-conformity
<i>T. turgidum</i>	576	44 ^a	7,64
<i>T. aestivum</i>	1189	59 ^b	4,96

^a - Number of hexaploids;

^b - Number of accessions not corresponding to their passport botanical variety.

III – Biodiversity

Genetic resources provide the basic input to all plant breeding programs. Nowadays the genetic diversity and the population structure of tetraploid wheats has received a lot of attention (Li *et al.*, 2006; Yifru *et al.*, 2006; Moragues *et al.*, 2007; Oliveira *et al.*, 2012; Leigh *et al.*, 2013; among others). The first step of reasonable biodiversity preservation is drawing up a phenotypic identification and inventory and the second is its genetic analysis. Development of a database describing phenotypic and genetic collections is crucial for their goal-oriented biodiversity preservation (Goncharov and Shumny, 2008). Phenotypic collections contain accessions showing contrasting or alternative characters. Genetic collections contain accessions showing characters whose genetic control is known. The probability for biodiversity preservation is higher for accessions of genetically identifiable pure lines than for those reproduced as small populations, i.e., “native” populations. However, the question remains open of how many plants should be included in genebanks populations for preservation of gene pools of collected native populations. In fact, varieties compete, when maintained as small populations, and some varieties disappear, others show sharply altered gene frequencies in the course of reproduction.

Distribution areas of related wheat species are continuously reducing. So collecting, replenishing, reproducing, studying and maintaining those species living, being a constant supply for breeding are important to preserve biodiversity resources and future food security. It is obviously not feasible to gather again Vavilov’s or Kihara’s wheat biodiversity collections of tetraploid wheats, even after following the routes of their expeditions. Nature has not spared the biodiversity existing in their times, and this emphasizes the significance of reasonable maintenance of the maximally possible biodiversity presently stored in genebanks. The questions of how to preserve and of what to undertake so that biodiversity would not be subjected to erosion are more timely as ever. Reduction in the natural areas of wild endangered wheat species, as well as in their polymorphism due to their reproduction in small populations: in genebanks, decrease the potential biodiversity of cultivated tetraploid wheat species. To knowledgeably preserve gene pools maintained as small size populations, accessions should be fuller genetically characterised. This would allow goal-oriented preservation of the natural gene pool of the accessions.

Polymorphism of cultivated wheat species is inconsiderable in many traits (Boggini and Pogna, 1989; Pecetti and Annicchiarico, 1998). The wild and con-cultivated tetraploid species (fig.1) are still a valuable source of useful agronomic traits for the continued improvement of cultivated wheat species. Wide hybridization of cultivated wheats with wild ones, coupled with cytogenetic manipulation of the hybrid material, has been instrumental in the genetic improvement of durum and common wheats. What are the prospects of searching for polymorphic traits in wild related species? Let us demonstrate the statement using two types of traits – adaptive and neutral.

1. Adaptive trait

Low adaptability of cultivated tetraploid wheat *T. durum* complicates its successful cultivation in many agricultural areas and field experiments. Duration of vegetation period is one of the basic traits among those determining plant wheat adaptability to environments (Vavilov, 1935). Its cultivar character is the most important parameter in *T. durum* breeding programs. Despite considerable achievements in studying earliness, it remains so far the factor that limits agricultural cultivation on these or that regions. Earliness of tetraploid wheats is a complicated trait controlled by genes with different interaction effects. Basic differences in its manifestation are determined by *Vrn* genes controlling growth habit (spring vs. winter) and *Ppd* genes controlling photoperiod sensitivity (Wilhelm *et al.*, 2009). It is shown that *Vrn* genes control not only one of the cardinal ways of developmental switch to spring or winter growth habit but also determine maturity rate. By the way, different dominant *Vrn* genes condition basic distinctions in earliness in spring common wheat cultivars (Kato *et al.*, 1997).

Although the length of vegetation period in tetraploid wheats is controlled only by two not four dominant *Vrn* genes just like in common wheat, the expressiveness of character in studied cultivars of *T. durum* in Kazakhstan doesn't differ from the one in common wheat cultivars (fig.2).

2. Neutral trait

Neutral trait, i.e. the trait whose spreading in populations proceeds without the effect of natural and/or artificial selection - glucose-phosphate-isomerase (EC 5.3.1.9). Using a relatively 'neutral' trait allows us to estimate some formal-genetic parameters: level of polymorphism, degree of heterozygosity, relative genetic distance of those or that forms from each other, degree of isolation among close-related species, overlapping of close species gene-pools, parameters of reproduction systems (obligatory self-pollination and the presence of this or that degree of intraspecific cross-pollination).

a b c d e f

Figure1. The spikes of *T. durum* (a), *T. carthlicum* (b), *T. dicoccum* (c), *T. dicoccoides* (d), *T. turgidum* (e), *T. polonicum* (f).

Polymorphism on locus *Gpi-1*(glucose-phosphate-isomerase) was described in a genera *Triticum* and *Aegilops*. Its presence was shown in all donors of elementary genomes – *T.boeoticum*, *T.urartu*, *Ae.speltoides* and *Ae.aucheri*. However, it is worth noticing that frequencies of accessions with 'rare' variants are small. For example, analysis of 207 *T. urartu* accessions from Small Grain and VIR collections allowed to find out 9 of such variants with GPI mobility, different from the rest 199 studied (Table 3). It complicates their wide use for introgressive hybridization. No polymorphism was detected at locus *Gpi* in tetraploid species belonging to *Dicoccoides* section (Goncharov *et al.*, 1998).

Figure 2. Distribution of Kazakhstan common and durum wheat cultivars according length of vegetation period (Almaty, field).

The obtained results are presented in Table 3. Some diploids of *Triticum* produce a monomorphic *GPI-1* band while others display composite and polymorphic patterns at locus *Gpi-1*. The heterozygotes present in the samples have most likely resulted from cross-pollination.

Therefore, the task of related wheat species genepool preservation is simplest when solved first with an aimful collection, inventorisation and further their preservation in genebanks; second, by means of including their genepool in the genepool of cultivated species and making up gene storage, i.e. those of disease resistance; adaptivity; induces of grain quality, etc., also those controlling the morphological traits untypical for cultivated wheat species.

IV – Increasing biodiversity

Involving tetraploid species related to wheat and nowadays non-cultivated wheat tetraploids in interspecific hybridisation for introgression of genes and/or their alleles into cultivated species (especially *T. durum*) could be one of the ways to solve the problem of increasing genetic diversity source for durum wheat. These problems require an urgent solution for increasing *T. durum* biodiversity, hopefully, will enable us not to decrease grain presently and in the future. BA-genome species, except for part of *T. dicoccoides*, are easily crossed with each other producing fertile hybrids. Related tetraploid wheat species having preserved higher polymorphism than that of cultivated *T. durum* could be an additional source of increasing biodiversity. It is not complicated to obtain the hybrids between tetra- and hexa-, tetra- and diploid wheat species.

Table 3. Genetic distinctions on locus *Gpi-1* in wheat species having *A^b* genome.

Species	Genome	Number of found <i>Gpi-1</i> genotypes					Total
		$\beta\beta$	$\beta\delta$	$\delta\delta$	$\epsilon\xi$	2β	
<i>T. boeoticum</i>	A^bA^b	1 ^a	1 ^a	26			27
<i>T. monococcum</i>	A^bA^b	2		142			144
<i>T. sinskajae</i>	A^bA^b	1					1
<i>T. urartu</i>	A^uA^u	6			196	3	207
<i>T. araraticum</i>	GGA^uA^u		3+19+2 ^b		6+14+2 ^b		44 ^b
<i>T. timopheevii</i>	GGA^uA^u		10		4	11	25

a – polymorphic accessions are presented in different columns; *b* – heterozygotes of two types.

Searching for not only agronomic traits, but also marker-genes of these or other traits in wild related species of cultivated plants with their further introgression into genomes of improved cvs is an effective base to increase cultivated species biodiversity.

- 1) Characters on which a taxonomy of tetraploid wheats are based, namely:
 - a. branched spike from *T.turgidum*;
 - b. purple seed from *T.aethiopicum*;
 - c. the presence of awns at the same time with flower and awn glume from *T.carthlicum*;
 - d. elongated glume from *T.policum* and *T.ispahanicum*.
- 2) Characters appearing as a result of intraspecific hybridization in tetraploids:
 - a. the semicompactoid (semiclub) spike;
 - b. absence of nuclear organizer on chromosome 1B (lines Friebe 256/8/5 produced by Dr. Ponga from *durum* with *S. cereale* L).
- 3) *T. durum* mute collections.
- 4) Tetraploid wheat characters with the same genetic control as at hexaploid wheat (Table 4).

Table 4. List of tetraploid wheat genetic collection.

Phenotypes	Gene symbols	No. of genes and their chromosome localization	Accession with	
			Dominant genes	Recessive genes
Growth habit	<i>Vrn</i>	2 (5A, 5B)	BS1E, Bs2E	BWE
Hairy glume	<i>Hg</i>	1 (1AS)	Bs1E	Angara
Black glume	<i>Bg</i>	1 (1AS)	BS1E	Beloturka
Red grain	<i>R</i>	2 (3AL, 3BL)	tetraCS	K-43766
Awedness	<i>B</i>	2 (5A, 6B)	Sharik, tetraCS	BWE
Hybrid dwarfness	<i>D2</i>	1 (2BL)	Loro	BWE
Hybrid necrosis	<i>Ne1, Ne2</i>	2 (5BL, 2BS)	Gaza, K-35116	BWE
Glaucousness (waxlessness)	<i>W</i>	1 (2BS)	Gaza, Nursit	Angara
- " -	<i>w</i>	1 (2bS)	-	BS1Ew
Hairy peduncle	<i>Hp</i>	1 (5A)	BS1Ehp	Angara
Hairy node	<i>Hn</i>	1 (5A)	tetraCS	TetraThatcher
Hairy leaf	<i>Hl</i>	2 (4A, 5A)	K-47759	tetraCS
Hairy leaf sheath	<i>Hs</i>	1	K-20403	Beloturka
Lack of ligules	<i>Ig</i>	2	Mavroullos	Vroullos
Red coleoptiles	<i>Rc</i>	2 (7A, 7B)	K-29145	K-18999
Semicompactoid	<i>sc</i>	2	Angara	BWE, tetraThatcher
Chocolate color of glume		7BS	cv. Langdon mute	Beloturka
Purple pericarpe	<i>Pp3, Pp1</i>	2AL, 7BS	GAW 414	BWE
Branch sp ke	<i>bh</i>	2AS	branch line	BS1E
Tetraauricle	<i>ta</i>	5A	<i>T.carthlicum</i>	BS1E

BWE – Black Winter Emmer.

Availability of genetic collections of tetraploid wheats would allow us to:

- transfer genes from a wheat species at one ploidy level to another wheat species at a ploidy level different from it and *vice versa* with the expectation to increase the biodiversity of wheat species at any ploidy level;
- study the effect of ploidy level on the expression of wheat characters;
- study the effect of different kinds of wheat cytoplasm on gene expression;
- map characters that could not be introgressed to another ploidy level;
- investigate the effect of different cytoplasm on the traits expression;

- produce comparative gene mapping at different ploidy levels;
- obtain a model to study trait inheritance controlled polymerically - simplify models for studying the inheritance of characters under polygenic control.

We hope that maintenance and use of phenetic and genetic collections of di- and tetraploid wheat species are also a good strategy for biodiversity preservation.

V – Preservation

The two ways of preserving biodiversity are its to increase the long-term storage of the seeds.. The first way to do this was mentioned above.

The analysis of various methods of long-term storage of genetic resources was carried out. The conclusion was that the optimal method was cryopreservation method in a layer of permafrost in North-East Russia provided the following criteria has been made: 1) the maximal economic profitability and biological efficiency, 2) reliability and security from various natural and technogenic accidents, and 3) minimization of expenditures on labour. The project of creation of International cryobank for genetic resources with the use of «free and reliable natural cold» of permafrost is offered and directions of its activity are formulated (Kershengolts *et al.*, 2012). So in addition to the one created in Norway at the Svalbard Global Seed (Qvenild, 2008), one more is being built in Yakut region of Russia in the permafrost. To destroy the layer of permafrost in Yakutsk the general thaw of Earth to 20° C is necessary.

VI – Conclusion

Existing germplasm collections are not being effectively used in agricultural science and breeding programs. The effective use of wheat biodiversity in breeding programs is dependent on a sound conservation strategy for sources of biodiversity, and on appropriate techniques of incorporation into modern cultivars. Studying the genetics of tetraploid wheat genome species donor showed the presence of polymorphism in them on very different traits. Therefore, at present both the task of collection, preservation, and study and the problem of introgression of part of related species genes into the genepool of cultivated tetraploid species having lost wide polymorphism during breeding and multi-centennial cultivation are topical.

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