Review

Taxonomy and molecular phylogeny of natural and artificial wheat species

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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. Producing artificial wheat amphiploids using genomes of related species is an effective way to increase the available gene pool. However, artificial amphiploids should be given botanic names and positions within genus *Triticum* classification to ensure effective collection and preservation in gene banks. In this review, an attempt to integrate the results of molecular-genetic analyses of natural and artificial wheats with their taxonomy has been made. The correspondence of earlier evolutionary and taxonomic specifications to phylogenetic relationships within *Triticum* has been estimated using chloroplast and nuclear DNA sequence data. The results indicated close relationships between all artificial and natural species. Based on the data, all wild and cultivated diploid wheat species were united in a separate section, *Monococcon*. Different variants of nuclear *Acc-1*, *Pgk-1*, and *Vrn-1* genes have been detected in diploid A genome species. Detailed analysis of the genes showed that one of these variants was a progenitor for all A genomes of polyploid wheats except for that in *Triticum zhukovskyi* and some of the artificial amphiploids.

Key Words: *Triticum*, artificial and natural species, biodiversity, taxonomy, molecular analysis.

Introduction

A key challenge facing biologists in the twenty-first century is the preservation of biodiversity. Worldwide, areas of biodiversity containing close relatives of the cultivated wheat species, i.e. wild wheats and *Aegilops* species, as the donors of wheat's plasmon, B and D genomes, are diminishing. The collection, study, replenishment and maintenance of those species still in existence as a source of pre-breeding material is of fundamental importance for preserving our food resources and security.

Existing germplasm collections are not being effectively used in agricultural science and development programs. There are three ways to improve ability of researchers to use the biodiversity present in wheat-related species: 1) Collection, identification, genetic characterization, and preservation of the cultivated wheats and their relatives; 2) Generation and preservation of artificial amphiploids among these taxa; and 3) Deposition of the artificial amphiploids and all accessions generated from working with them in gene banks and revision of *Triticum* L. taxonomy to include artificial species.

Each of these actions will contribute to progress in breeding and the possibility for increasing cultivated wheat's ag-

ricultural potential by introducing additional variability for selection. According to Migushova (1975, p. 3 [translated by authors]), "... nature used the genetic potential of genera *Triticum* L. and *Aegilops* L. in "developing" common wheat not taking care of matching qualitative initial forms (donor species)". At present, researchers are able to correct this 'mistake of nature' by producing *de novo* hexaploid wheat species. However, wheat, unlike many other crops, has not been precisely described. Hence, for effective preservation and use of their biodiversity we must produce 'good taxonomy'.

Wheat taxonomy

Wheat taxonomy has a long history. The first classification of *Triticum* was made by Linnaeus (1753). It was based on a number of clearly discernable characters, including spring growth habit (*Triticum aestivum* L.), winter growth habit (*T. hybernum* L.) and the 'spelt morphology' (*T. spelta* L.). Morphological characters also formed the basis of Körnicke (1885) later classification. Today, the taxonomy of *Triticum* is almost, although not completely, indisputable. Researchers use two main wheat classifications: Mac Key's classification (Mac Key 1966, 1989), as modified by van Slageren (1994), and Dorofeev *et al.* (1979) or revision of the latter carried out on the basis of comparative-genetic analysis by Goncharov (2002, 2005). The former system is mostly used in the Western scientific community, while the latter is now

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accepted in the East. The existence of different wheat classifications and the use of illegitimate species names continue to cause confusion amongst the global research community. Mac Key (1966, 1989) classification, even as modified by van Slageren (1994), has not been a very successful strategy. It is not satisfactory that one wild species, *T. dicoccoides* (Körn. ex Aschers. et Graebn.) Schweinf. and nine cultivated tetraploid wheat species *T. turgidum* L., *T. dicoccum* (Schränk) Schuebl., *T. karamyshevii* Nevski, *T. ispahanicum* Heslot, *T. durum* Desf., *T. turanicum* Jakubz., *T. polonicum* L., *T. aethiopicum* Jakubz., *T. carthlicum* Nevski are effectively 'hidden' by being included in *T. turgidum* L. This example illustrates the main drawback of the classification, namely that a multitude of criteria are used to divide species, subspecies and varieties, and maintaining collections based on this classification will lead to insufficient representation of the genetic diversity that must be preserved. Evolutionarily younger species, such as *T. turgidum* and *T. timopheevii* (Zhuk.) Zhuk., often include the older ones in the classification. This tends to impede appropriate adequate sampling of the genus in phylogenetic and other research, that need to sample as much of genetic diversity as possible. The species *T. araraticum* Jakubz. and *T. timopheevii*, with genomes *GGAA*, provide a second example. Although they can not be crossed with each other to produce a fertile progeny, the frequently cited as being necessary for recognition as species, they are treated as a single species in Mac Key's classification.

A lot of artificial amphiploids have been produced to obtain new plants which combine the agronomic characters of existing cultivated wheats with those from related species (von Tschermak and Bleier 1926, von Tschermak 1930, Zhukovsky 1944). Kostov (1936) proposed using synthetic amphiploids for introgressing genes from diploid wheat species into hexaploid ones. The amphiploids can be a valuable source of genes for disease resistance (Zarubailo and Tavrín 1972) and other agronomically important characters (eg. Lage *et al.* 2006). Some of the existing artificial amphiploids were produced 80 years ago, yet little work has been done to highlight potential contamination and/or genetic changes during their conservation (Goncharov *et al.* 2007). Furthermore, little information is available regarding the nature and the extent of genetic variability within artificial amphiploids.

Amphiploids produced by von Tschermak (see von Tschermak and Bleier 1926), Tavrín (see Zarubailo and Tavrín 1972) and some other researchers have been almost completely lost. It is therefore a matter of urgency to incorporate the preservation of such amphiploids in gene banks. Linnaeus, the founder of modern plant taxonomy, believed that: "If the names are unknown the knowledge of things also perishes (Linnaeus 1753, translated by Stafleu 1971, p. 143). We believe that it is necessary to formalize the naming of all artificial wheat amphiploids and their inclusion in a new section, *Compositum* N.Gontsch., within *Triticum* L. (Goncharov 2002) (Table 1).

Triticum sect. *Compositum* N.P. Gontsch. sect. nov.—

Glumae rigida, rachis infragilis, semen corticatum. Rigid glumes, non-fragile spike, non-naked grains.—Typus: *T. ×soveticum* Zhebrak.

In revising *Triticum* taxonomy, we believe that there are no objective reasons for including only one man-made wheat species, *T. kiharae* Dorof. et Migusch. (Dorofeev *et al.* 1979), while disregarding all others that have been produced.

T. ×soveticum was produced by Zhebrak (1939) earlier than *T. fungicidum*. According to our results (Fig. 1) the latter was produced also in cross combination BBAA on GGAA genome wheats just like *T. soveticum*.

Triticum soveticum ssp. *fungicidum* comb. et stat. nov. (Zhuk.) N.P. Gontsch.—*Triticum fungicidum* Zhuk., 1944, Trudi Mosk. Sel'sk.-khoz. Acad. im. Timiryazeva. 6: 10.

To accommodate synthetic wheats, Goncharov's classification has 29 species, including 6 synthetic species (Table 1).

There is a problem with the position in the *Triticeae* Dum. of some intergeneric amphiploids with non-typical genome for wheats, i.e. *×Triticale*, *×Haynaticum*, *×Tritordeum*, *×Aegilotriticum* and so on.

A rigorous and logical classification of the *Triticum* genus will be very important not only for understanding the origins of wheat and its phylogeny, but also for collecting further variants and estimating the extent of biodiversity preservation (Waines and Barnhart 1990, Goncharov 2002). Development of a detailed generic classification of *Triticum* is also very important in breeding practice, firstly for matching crossing parents, and secondly for prediction of success in gene introgression and in certification of new accessions and commercial cultivars.

The potential for using Goncharov's classification of *Triticum* for identifying and collecting wheat accessions for molecular-biological and phylogenetic investigations, is discussed below.

Molecular phylogeny of wheat species: evidence from chloroplast and nuclear data

Different genes from nuclear and chloroplast genomes have been useful for deducing the phylogenetic relationships of plant species. Our investigations of phylogenetic relationships within *Triticum* consisted of two principal parts: cpDNA sequences of wheats and their related species were analyzed; followed by nuclear genome analyses. The study included all known species of *Triticum*.

Chloroplast data sets

Our phylogenetic reconstruction was based on chloroplast *matK* gene comparisons of 45 accessions of the *Triticum*, *Aegilops* and other closely related species along with *trnL* (tRNA-Leu) intron sequences of a number of species (Fig. 1). We included both natural and artificial species in the analysis to investigate their relatedness. Studying artificial wheats provides information about pathways (hybridization schemes) that were used to produce them.

Table 1. *Triticum* classification (Goncharov 2002 with additions)

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
	Naked	<i>T. sinskajae</i> A.Filat. et Kurk.	14	A^b
<i>Dicoccoides</i> Flaksb.	Hulled	<i>T. dicoccoides</i> (Körn. ex Aschers. et Graebn.) Schweinf.	28	BA^u
		<i>T. dicoccum</i> (Schränk) Schuebl. ^a	28	BA^u
		<i>T. karamyshevii</i> Nevski	28	BA^u
		<i>T. ispahanicum</i> Heslot	28	BA^u
	Naked	<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	<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.)	28	GA^u
		<i>T. zhukovskyi</i> Menabde et Erizjan	42	$GA^u A^b$
<i>Compositum</i> N. Gontsch.	Hulled	<i>T. palmovae</i> G. Ivanov (syn. <i>T. erebuni</i> Gandil.)	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	<i>T. flaksbergi</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 “δοχχον” (grain) when forming adjectives becomes ‘dicoccus, -a, -um’ in Latin. So there is no reason to change *T. dicoccum* 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.

While it is known that the inheritance of cytoplasmic genomes is not universally maternal (Birky 1995, Korpelainen 2004), the phylogenetic tree developed in this study showed strictly maternal plastid inheritance in all of the included artificial species (Golovnina *et al.* 2007). Moreover, based on our results, it is proposed that one *Ae. speltoides* Tausch ancestor was involved in the first polyploidization event leading to the development of hexaploid wheat (Fig. 1, Clade II). It is likely that there were two ancestral forms of *Ae. speltoides* involved in a two-step hybridization, i.e. independent events took place in the Emmer and Timopheevii groups. These two forms were the donors of different but closely related plastomes and genomes to the polyploid wheat species (Tsunewaki *et al.* 1976). The high degree of intra-specific variation observed among *Ae. speltoides* accessions, support this hypothesis (Golovnina *et al.* 2007, Killian *et al.* 2007). All diploid wheats can be robustly delineated from *Aegilops* species, Clades III and IV, but stay closely related to each other (Fig. 1). The relationships among the A genome diploids were unresolved and all diploid wheat species

were included in a separate section, *Monococcon* Dum. (Table 1)

Nuclear data sets

The presence of four different nuclear wheat genomes (A, B, D and G), whose various combinations form three groups of *Triticum* species based on ploidy (di-, tetra-, hexa- and rarely octoploid), is well known. The origin of polyploid wheat genomes has been a subject for discussion for more than seven decades. The A genome is found only in *Triticum* species and is further subdivided as A^u and A^b , to reflect the origin of the genome—the wild diploid wheat species *T. urartu* Thum. ex Gandil. or *T. boeoticum* Boiss., respectively.

Polyploidy of many of the *Triticum* species complicates phylogenetics studies made on the basis of nuclear sequences. Additional cloning procedures and knowledge of the specific characteristics of each genome are often necessary to separate sequences of different genomes. Also, information about different indel events and nucleotide substitutions in each genome may assist in designing genome-specific PCR-

Fig. 1. Neighbour-Joining phylogenetic tree based on the comparison of *matK* sequences (from Golovnina *et al.* 2007 with addition). Four observed clades (I, II, III, IV) are shown by solid lines on the right. The genome composition is given for each species. Synthetic wheats are represented in bold letters. A complete list of the investigated species belonging to the Emmer group (24 representatives in Clade I) is given in Golovnina *et al.* (2007, Table 1). Based on the indel event in the *trnL* intron sequence of some analyzed species, representatives with observed insertions are marked in solid and the remainder in dashed boxes. Asterisks denote species from which the *matK* sequence was obtained from GenBank. Numbers at the branch splitters depict statistical bootstrapping value (Felsenstein 1985).

based markers. In our study, available sequences of *Acc-1* (plastid acetyl-CoA carboxylase) and *Pgk-1* (plastid 3-phosphoglycerate kinase) genes and promoter sequences of the *Vrn-1* (MADS-box transcription factor, vernalization gene) gene belonging to different genomes and wheat species were compiled from GenBank and aligned. A number of B, G, and A genome-specific primers pairs were developed based on genome-specific indels (Golovnina *et al.* 2007, 2009, Goncharov *et al.* 2008). One of the A genome-specific primer pairs, Acc-1T(2T) sense/Acc-2T antisense, and the annealing sites are represented in Fig. 2A.

All of the A genomes of the polyploid wheat species we examined contained a 46 bp deletion in the *Acc-1* gene. However, we identified a polymorphism at this site amongst

the diploid wheat species (Fig. 2). So in contrast to the polyploid *Triticum* species, which contained definite genome-specific indels, three of the four diploid A genome wheat species (*T. urartu*, *T. boeoticum* and *T. monococcum* L.) produced unexpected results. PCR amplification with non-A genome-specific primers successfully amplified the 'A genome' fragments in these species and, *vice versa*, PCR using A genome-specific primers was negative. Sequencing of the corresponding regions in the genes *Acc-1* and *Pgk-1* indicated the presence of two different *Acc-1* gene variants and three *Pgk-1* gene variants in diploid wheat species (Fig. 2 and Fig. 3). A polymorphism in the *Vrn-1* promoter region was also observed. On the basis of the presence of an 8 bp specific indel, diploid species were divided into two groups,

A

B

Fig. 2. Heterogeneous PCR amplification of diploid species using A genome-specific primers. (A) Annealing sites for an A genome-specific primer pair (Acc1T(2T) sense/Acc2T antisense), and PCR amplification of part of the *Acc-1* gene using the A genome-specific primers. The primers were designed based on unique indels and nucleotide substitutions. (B) Alignment of *Acc-1* gene sequences. Only significant variable sites are shown. Letters at the left indicate different genomes of the polyploid species. Numbers I and II depict two different A genome variants within the diploid species.

while the A genomes of polyploid species contained no polymorphisms at this site (Golovkina, pers. comm.). Three different variants of the investigated genes have been detected in diploid A genome species. This detailed analysis showed that one of the variants was a progenitor for all A genomes of the polyploid *Triticum* species except for the hexaploid Timopheevii group species, *T. zhukovskyi* Menabde et Erizjan, and some of the artificial ones.

Diploid species are the most ancient representatives of *Triticum*. They are characterized by the presence of the A genome, which was later inherited by all polyploids. To determine phylogenetic relationships among di- and poly-

ploid wheat species, it is necessary to ascertain the donor species of the three elementary diploid genomes as well as to study species-specific genomes. Based on the variability of the studied regions of nuclear genes, obvious differences in elementary genomes (*T. boeoticum*, *T. urartu* and *T. monococcum*) were discovered. However, almost no polymorphisms were observed within the corresponding genome of polyploid wheats. It was discovered that only *T. urartu* has the genome variant that is identical to the A genomes of the polyploid wheat species. Unfortunately, a single molecular marker suitable for distinguishing each of the diploid species was not found. An investigation of the inheritance of

Fig. 3. Alignment of the *Pgi-1* gene sequences (from Golovkina *et al.* 2009). Only significant variable sites are shown. Genome-specific sites or sites specific for diploid species are indicated in colored letters: green for A genome-specific; blue for B genome-specific; red for D genome-specific; black for G genome, and purple specific for a diploid species variant. Numbers I, II and III depicted three different A genome variants found among the diploid species.

morphological traits also failed to identify species-specific characters in the three diploid wheats (Golovkina *et al.* 2009), except for hairy leaf type which has been previously described (Dorofeev *et al.* 1979).

Conclusion

Early advances achieved in cereal development resulted from domestication by farmers practising primitive breeding. All of the natural wheat species were domesticated between 6 and 12 thousand years ago (Nesbitt 2002). Classical plant breeding over the last hundred years and, more recently, genetic engineering, have made spectacular advances by comparison with early domestication (Gepts 2002). In the 1960s, Norman Borlaug (1968) harnessed several important agronomic characters to launch the Green Revolution, although this was largely a result of re-combination within a single wheat genotype. Subsequently, cultivated wheat germplasm was enriched with genes for resistance to fungal pathogens and other pests (Knott 1987). Future improvements in wheat productivity are limited by the relatively small gene pool existing in commercial wheat varieties. The possibility of widening the gene pool of cultivated varieties by directly using germplasm from related species is difficult, and it is more expedient to use human-made (synthetic) amphiploids for this purpose. In this context, a robust and detailed *Triticum* taxonomic classification is very important not only for understanding the origins of wheat phylogeny (Fig. 1) but also for collecting and estimating wheat biodiversity and for development of future breeding programs. Hence, the aim of modern taxonomy is to produce a classification system showing correct phylogeny that will be suitable for use by geneticists, botanists and breeders.

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