Comparative-Genetic Analysis – a Base for Wheat Taxonomy Revision

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Abstract: Comparative-genetic analysis performed at the same time on cultivated wheat species and their wild relatives permits the definition of an introgressive hybridization strategy and reconstruction of the origin of the taxonomy important genes. The analysis also allows clarification of the origin of wheats and their differentiation into species, thereby proving a basis for a successful revision of *Triticum* L. genus system.

Keywords: *Triticum* genus; comparative-genetic analysis; taxonomy

The genus *Triticum* L. has a diphyletic origin (DOROFEEV & KOROVINA 1979). Its includes di- ($2n = 14$), tetra- ($2n = 28$) and hexaploid ($2n = 42$) species, with the phylogeny of most of them more or less clarified (TSUNEWAKI 1968). The main result of the wheat domestication process was the reconstruction of rachis and glumes, which has converted fragile spikes of the wild species into non-fragile, naked grain cultivated species. These traits underlie LINNAEUS (1753) classification of *Triticum*. His hexaploid wheat classification was exceptional in dividing such wheats into species based only on differences in awned-awnedlessness, but also in spring vs. winter growth habit. Later researchers have demonstrated that the traits underlying the classification of Linnaeus and his followers are controlled by a small number of oligogenes that lead to formation of their hexaploid wheat species. There are four such taxonomically important genes and, on their basis, hexaploid wheat genotypes may be listed as (SWAMINATHAN & RAO 1961):

T. spelta L. – *qq cc SS vv*
T. macha Dek. et Men. – *qq CC SS vv*
T. *vavilovii Jakubz.* – *qq cc SS VV*
T. compactum Host – *QQ CC SS vv*
T. aestivum L. – *QQ cc SS vv*
T. sphaerococcum Persiv. – *QQ CC ss vv.*

Random amplified polymorphic DNA analysis was used to assess the phylogenetic relationships among these five morphological groups of hexaploid wheat. These results are in agreement with those based on morphological classification (CAO *et al.* 2000). As to di- and tetraploid wheat species, no such genes controlling taxonomically important traits has been as yet identified and, accordingly taxonomists usually use a species "radical', in Vavilov's terms, i.e. use a trait set with so far unknown genetic determination. One taxonomically important gene *P* is found only in *T. polonicum*.

The poorly studied genetics of di- and tetraploid wheats is the main weakness in MACKEY (1989) genetic classification of *Triticum*. Despite this the idea of developing a genetic classification of the genus *Triticum* has not been abandoned. The goal of the current study was to disclose and identify genes providing taxonomic clues for the classification of *Triticum* species and to produce a revised classification.

MATERIALS AND METHODS

Accessions of di-, tetra- and hexaploid wheats from the Institute of Cytology and Genetics (Novosibirsk, Russia), the Vavilov Institute of Plant

Industry (St-Petersburg, Russian), the Small Grains Collection (Aberdeen, USA) and the Germplasm Plant Institute of Kyoto University (Japan) collections were used in the present investigation.

The segregation ratio for each cross was determined and compared with the expected segregation ratio using the chi-square test.

RESULTS AND DISCUSSION

The number of genes that control morphological traits, which are simultaneously localized in three wheat genomes, is small (Goncharov 2002). There are no complete genetic collections of the species for *Triticum* and *Aegilops* L. Nevertheless, genetic collections provide real opportunities for comparative-genetic investigations in the genus *Triticum*. They are also used for phylogenetic studies. The drawback of wheat phylogenetic schemes currently proposed consists in the absence of data on the character (type) of genetic control of the morphological traits that are identical in their phenotypic manifestation. These external morphological traits are very often arbitrary.

Extremely dense or compact spike. Naked grain and compact spike are the main traits used to distinguish *T. sinskajae* A. Filat. et Kurk. from *T. monococcum* L. The every traits is under the control of independent single recessive genes (Kondratenko 2005). As that time the compact spike character is controlled by differebt way – a pair complementary recessive genes, *sc1* and *sc2*, in tetraploid wheats (Goncharov 1997).

Compact spike is also the trait that distinguishes *T. compactum* Host from other hexaploid wheat species (Dorofeev & Korovina 1979). It is controlled by a single dominant gene, *C*, located on chromosome 2D. This gene is not present in the di- and tetraploid wheat genomes. The gene that controls compact spike in hexaploid wheats *T. sphaerococcum* and *T. antiquorum* is not allelic to the gene *C* of *T. compactum* (Table 1). We identify it as *C2*. The origin of the dominant genes *C* and *C2* in hexaploid wheats is unknown because compact spike accessions of *Ae. squarrosa*, the D genome donor of hexaploid wheats, have not been discovered (Goncharov *et al*. 2002). The *C* gene may be present in one of the subspecies of *T. macha*.

Elongated glume. Spike and flower glumes are very long in *Triticum polonicum* L. (about 30 mm, on the average); in durum wheats they are about 10 mm-long. It is a frequently studied trait because it is correlated with the valuable agronomic trait ‘long grains’. In *T. polonicum*, the long glumes are controlled by a single dominant gene (Table 2). This dominant gene *P* is localized on chromosome 7A. Other tetraploid wheat species *T. ipahanicum* Heslot possesses a non-allelic gene *P2*. Long glumes also occur in hexaploid wheat *T. petropavlovskyi* Udacz. et Migusch., but it is more weakly manifested than in

Table 1. Allelic test of genes controlling compact spike in *T.compactum*, *T.sphaerococcum* and *T.antiquorum*

Cross combinations	Segregation into spike shape in F_2 generation		χ^2 value for ratio*	
	Compact	Normal	3:1	15:1
Vakka *T.compactum* × K-20900 *T.aestivum*	47	19	0,51	57,22
Vakka *T.compactum* × K-56397 *T.antiquorum*	79	31	0,59	90,30
K-23790 *T.sphaerococcum* × CI 3090 *T.compactum*	105	17	7,97	1,86

*Values for significance of $P = 0.005$ is 3.84

Table 2. F_2 segregation for glume shape in *T.polonicum*

Cross combinations	Segregation into glume shape in F_2 generation		χ^2 value for ratio*	
	long glume	short glume	3:1	15:1
Gaza × *T. polonicum*	189	60	0,11	135,35
BS2E × K-39297 *T. polonicum*	63	30	2,61	107,36

*Values for significance of $P = 0.005$ is 3.84

Table 3. F_2 segregation for spelta in hexaploid wheat

Cross combinations	Segregation into spike shape in F_2 generation		χ^2 value for ratio*	
	Spelta	Norma	3:1	15:1
Triple Dirk D[1] × K-43376 *T. petropavlovskyi*	48	24	2.67	90.13
Triple Dirk B[1] × K-1731 *T. spelta*	59	28	2.40	90.86
Masljaninskaya[1] × K-1728 *T. spelta*	122	44	0.20	116.24
			3:1	13:3
K-152 × *T. spelta*	129	28	4.30	0.09

*Values for significance of $P = 0.005$ is 3.84; [1]*T. aestivum*; XW – Xinjiang Wheat

T. polonicum. Long glume was observed in offspring of a F_1BC_1 K-44126 *T. petropavlovskyi* × K-20538 *T. spelta* cross. The glume was long in 25 plants and short in 33, thereby proving that long glume is indeed under the control of single dominant gene. Watanabe and Imamura (2002) have demonstrated that genes controlling long glumes are allelic in *T. petropavlovskyi* and *T. polonicum*. *Triticum petropavlovskyi* shows no interspecific polymorphism for grain storage proteins (Watanabe *et al*. 2004). Thus, it appears very likely that *T. petropavlovskyi* is a man-made synthetic wheat.

Awnlessness. No awnless accessions are known for diploid *Triticum urartu* Thum. ex Gandil., *T. monococcum,* or *T. boeoticum* Boiss. (Dorofeev & Korovina 1979; Goncharov 2002). *Triticum sinskajae* is the sole diploid wheat species characterized by awnless spikes; the trait is controlled by a recessive gene (Kondratenko 2005). However, awnlessness is under the control of a dominant gene in the diploid species *Aegilops longissima* Schweinf. et Muschl. of sect. *Sitopsis* (Goncharov 2002).

There are no awnless accessions in tetraploid species of non-hybrid origin (Dorofeev & Korovina 1979; Goncharov 2002).

A new dominant gene *Hd2* that controls awnlessness has been detected in common wheat of Asian origin (Goncharov 2002).

Spelt. Despite frequent studies, spelt has not been accurately defined. In together spelt form of ear, the other correlated traits are inherited as a monogenic dominant addition characters, i.e. brittle rachis and hulled glumes. The results for studies on the spelt traits in a few wheat species are shown in Table 3. The trait is controlled by non-allelic genes in *T. petropavlovskyi* and *T. spelta*.

Spelt accessions have not been described in tetraploid wheats (Muramatsu 1986). However, Tsujimoto (2001) demonstrated that the wild tetraploid species *Triticum dicoccoides* Körn. has a dominant gene controlling spelt characters in this species.

Spelt accessions have not been described for diploid wheats. However, *Ae. speltoides* Tausch, the B (G) genome donor of polyploid wheat, possesses the spelt-gene. However, its inheritance cannot be studied, because non-spelt accessions are absent in the species.

CONCLUSION

Wheat classification reflects the presence of three ploidy levels in the genus. This fact was revealed at the beginning of the 20th century. Nevertheless, division of wheat species by their ploidy did not always underlie the assignment of the species to sections (see, for example, Dorofeev & Korovina 1979). Our idea was to identify wheat species according to the subordination principle inferred from their comparative value and genetic control pattern. A single or a few taxonomically important traits were assigned domination in the classification. Taken together, the results allowed to us assign the 29 wheat species to 5 sections (Goncharov 2002 with additions):

I. Sectio ***Monococcon*** Dum. includes 4 diploid ($2n = 14$) species, ***T. urartu*** Thum. ex Gandil., ***T. boeoticum*** Boiss., ***T. monococcum*** L. are hulled and ***T. sinskajae*** A. Filat. et Kurk. is naked;

II. Sectio ***Dicoccoides*** Flaksb. includes 10 tetraploid ($2n = 28$) species, ***T. dicoccoides*** (Körn. ex Aschers. et Graebn.) Schweinf., ***T. dicoccum*** (Schrank) Schuebl., ***T. karamyschevii*** Nevski, ***T. ispahanicum*** Heslot are hulled and ***T. turgidum*** L., ***T. durum*** Desf., ***T. turanicum*** Jakubz., ***T. polonicum*** L., ***T. aethiopicum*** Jakubz., ***T. carthlicum*** Nevski are naked;

III. Sectio ***Triticum*** includes 7 hexaploid (2*n* = 42) species, ***T. macha*** Dekapr. et Menabde, ***T. spelta*** L., ***T. vavilovii*** (Thum.) Jakubz. and man-made synthetic ***T. dimococcum*** Schieman et Staudt are hulled and ***T. compactum*** Host, ***T. aestivum*** L., ***T. sphaerococcum*** Perciv. are naked;

IV. Sectio ***Timopheevii*** A. Filat. et Dorof. includes 2 tetraploid (2*n* = 28) species, ***T. araraticum*** Jakubz. and ***T. timopheevii*** Zhuk. and hexaploid (2*n* = 42) species, ***T. zhukovskyi*** Menabde et Erizjan. All are hulled;

IV. Sectio ***Compositum*** N.Gontsch. includes tetraploid (2*n* = 28) species, ***T. erebuni*** Gandil. (syn. ***T. palmovae*** G. Ivanov), hexaploid (2*n* = 42) species, ***T. kiharae*** Dorof. et Migusch., 2 octoploid (2*n* = 56) species, ***T. soveticum*** Zhebrak, ***T. flaksbergeri*** Navr. and decaploid (2*n* = 70) species, *T. borisii* Zhebrak.

It is hoped that our revision proposed within the framework of classical taxonomic traditions has fewer drawbacks than the previous classifications. It is also hoped that the proposed revision would promote conservation of the man-made wheat synthetics in the world gene banks. Currently, the proposed classification is being checked by molecular genetic analysis.

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