Review

SPIKE MORPHOLOGY GENES IN WHEAT SPECIES (*TRITICUM* L.)

Irina Konopatskaia, Valeriya Vavilova, Alexandr Blinov, and Nikolay P. Goncharov[#]

The Federal Research Center Institute of Cytology and Genetics SB RAS, Prospekt Lavrentyeva, 10, Novosibirsk, 630090, RUSSIAN FEDERATION

[#] Corresponding author: Nikolay P. Goncharov, e-mail: gonch@bionet.nsc.ru

Contributed by Nikolay P. Goncharov

The review examines the state of knowledge on genes that control the architectonics of wheat plant (spike morphology). It is shown that molecular genetic studies, which have been recently started, allow to find both the orthologous genes from relative species of wheat (barley, rye, etc.) and genes that were not previously used for breeding. Use of these genes for further breeding allows to produce modern wheat commercial cultivars.

Key words: *spike morphology, plant architecture, gene, wheat species,* Triticum.

INTRODUCTION

Wheat species of the genus *Triticum* L. are members of the *Triticeae* Dum. tribe of the Poaceae Barn. family and represent the world's most important monocotyledenous cereals (Anonymous, 2015). The genus *Triticum* consists of 29 species divided into five sections *Monococcon* Dum., *Dicoccoides* Flaksb., *Timopheevii* A. Filat. et. Dorof., *Triticum* L. and *Compositum* N. P. Gontsch. (Goncharov, 2011). The first four sections listed above were based on the species ploidy level, cytoplasm type and genome composition, while the *Compositum* section includes man-made species. Depending on the level of ploidy, the natural *Triticum* species are diploids ($2n = 14$, haploid genome: A), tetraploids ($2n = 28$, haploid genome: BA or GA), hexaploids ($2n = 42$, haploid genome: BAD or GAD) or octoploids ($2n = 56$, haploid genome: BAGA or GABA) (Kimber and Sears, 1987; Goncharov *et al.*, 2007a).

Presently, one diploid, three tetraploid, and two hexaploid species are cultivated under different climate conditions (Tadesse *et al.*, 2016). Wheat is the oldest and most widely grown grain crop, which occupies about 17% of the crop acreage worldwide and provides 19% of the calories to the world's population (Anonymous, 2015). At present, wheat is the main food for about 40% of the world population, and the future demand for wheat is estimated to increase significantly. Bread (common) wheat *Triticum aestivum* L. has been commonly used for the production of bread, durum wheat *T. durum* Desf. for macaroni and semolina, while *T. monococcum* L., *T. dicoccum* (Schrank) Schuebl. and *T. spelta* L. are groat crops.

The modern cultivated crops represent the result of domestication of wild ancestors by early farmers followed by the diversification and improvement for more than ten thousands of years (Gross and Olsen, 2010). Domestication is the process of genetic adaptation of wild species to human needs, typically including changes in appearance and lifestyle (Lenser and Theißen, 2013). According to archaeological data, the domestication of most cereals started 10–12 000 years ago and was completed about 3000–4000 years ago (Lev-Yadun *et al.*, 2000; Doebley *et al.*, 2006). The domestication of wheat started in the Fertile Crescent, the region partially covering the modern territory of Israel, Turkey, and Iraq (Glémin and Bataillon, 2009).

During the domestication and subsequent cultivation of wheat, new and improved cultivars were developed by selection in order to meet human demands: taste, yield, cultivation and harvest storage methods (Gepts, 2004). The set of traits acquired by species during the domestication was called the "domestication syndrome" (Hammer, 1984) and includes the reduction or loss of the ability of natural dispersal, the development towards compact growth habit, early maturity, reduction or loss of toxic compounds and other (for review see: Gross and Olsen, 2010) i.e. domestication alters the plant architecture. The improvement and diversification traits include selection for grain quality, color, shape, etc. (for review see: Gross and Olsen, 2010). There are no clear divisions between domestication, diversification and improvement traits and genes involved in their control. For example, *Rc* gene of rice is considered as both a domestication gene and an improvement gene (Gu *et al.*, 2004; Sweeney, 2006).

The modern cultivated wheats differ from their wild relatives and progenitors by a set of morphological and physiological features including traits related to spike morphology, such as spike shape, treshability, and shattering. In this pa-

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per, we present current knowledge of the agronomically important spike morphology traits in wheat (subtribe *Frumentaceae* Dum., tribe Triticeae) and explore some of the recent findings in the area of identification of the genes underlying the spike morphology traits.

SPIKE MORPHOLOGY TRAITS IN WHEAT SPECIES

The spike is one of the most important parts of a wheat plant. It includes the reproductive organs, produces the seeds, and ensures dispersal of the mature grains. Spike morphology greatly affects breeding, harvest procedures and the yield. Spikes of wheat species differ in several morphological characteristics, including threshability, the presence or absence of awns, spike shape, spike shattering, spike branching and supernumerary spikelets spike (Fig. 1).

Threshability. Easy threshing ability is mainly dependent on the tenacity of the glumes covering the grains. The wild species possess hulled grains (syn. non free-threshing), which are covered by a tough glume that remains adhered to the grain after the threshing (Dorofeev and Korovina, 1979). Naked or free-threshing seeds of cultivated wheat
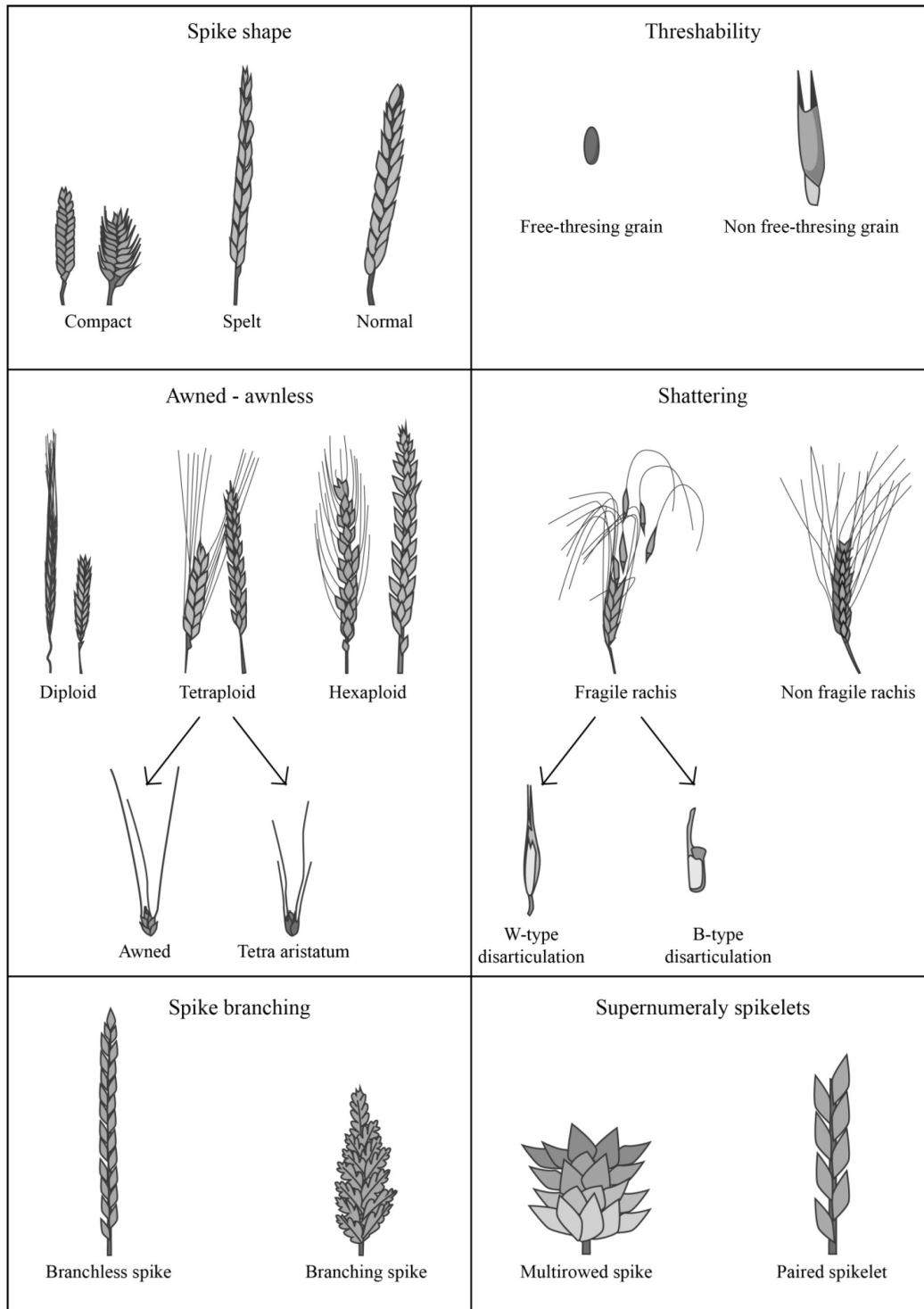

Fig. 1. Spike morphology traits in wheat species. *, for each ploidy level the awned (left spike) and awnless (right spike) phenotypes are presented.

species are rounded by soft glumes which release during threshing (Fig. 1). Wheat varieties with free-threshing seeds appeared during domestication and significantly advanced the efficiency of the threshing process and led to wheat becoming a major crop all over the world (Zhang *et al.*, 2011).

The presence or absence of awns. Awns are the threadlike extensions of the lemma. They have photosynthetic function, increase the assimilation of water, and may promote high yield of wheat grown under water-limited conditions (Reynolds and Tuberosa, 2008; Maydup *et al.*, 2010) (Fig. 1). Several comparative studies of the grain yield advantage in awned and awnless lines gave conflicting results. The comprehensive investigation of Rebetzke *et al.* (2016) showed that awned near-isogenic lines are characterised by slightly greater grain yield due to increased kernel size and reduced screening. It was also demonstrated that awnless wheats with acceptable yield and quality have provide advantage in more favourable environments and future changing climates.

In diploid wheat species *T. urartu* Thum. ex Gandil., *T. monococcum,* and *T. boeoticum* Boiss., only awned spikes have been identified to date, but only *T. sinskajae* A. Filat. et Kurk. has awnless spikes (Dorofeev and Korovina, 1979). Among tetraploid wheat species, all except *T. aethiopicum* Jakubz. awnless forms were obtained by hybridisation with *T. aestivum*. Both awned and awnless forms occur among hexaploid wheat species (Dorofeev and Korovina, 1979). Some accessions of *T. carthlicum* Nevski possess awns and awn-like appendages on the glume; these spikes were named tetraaristatum (four-awned) (Haque *et al.*, 2011) (Fig. 1). In the case of *T. aestivum*, breeders prefer to produce awnless cultivars. No commercial awnless cultivars of tetraploid wheat species were produced until now, because tetraploid wheat species with awnless spikes are characterised by reduced grain quality.

Spike shattering. Disintegration of the mature spike (disarticulation) allows seed dispersal of wheat species in the field. Two types of spikelet disarticulation have been described for the genus *Triticum*: barrel (B or *Aegilops tauschii* Coss. type) and wedge-shaped (W or *T. spelta* L. type) (Watkins, 1930). The B-type disarticulation is characteristic for hexaploid wheats and results in breakage at the lower side of the junction between the rachis and spikelet base, and the spike disarticulates into individual spikelets with a rachis fragment attached behind each spikelet (Kimber and Feldman, 1987) (Fig. 1). In the case of W-type disarticulation the breakages occurred at the upper side of the junction between the rachis and spikelet base and the spike disarticulates into individual spikelets with rachis attached below each spikelet. W-type disarticulation occurrs in di- and polyploidy wheat species (Kimber and Feldman, 1987) (Fig. 1). Spikes that undergo W- or B-type disarticulation are fragile, while the spikes that do not break easily are non-fragile (tough). Species of *T. monococcum, T. dicoccum* and *T. timopheevii* (Zhuk.) Zhuk. possess a specific type of brittle (fragile) rachis that disarticulates with the slightest mechanical pressure when mature (Dorofeev

and Korovina, 1979). The rachis of these species is less brittle compared to wild relatives with a fragile rachis. Transition from natural seed dispersal through shattering to obligate dispersal by humans is a key event in the domestication and evolution of cereals.

Spike shape. Spikes of wheat species can be attributed to one of the three morphological variants of spike shape:

• normal (relatively short square headed parallel-sided spike);

• spelt (pyramidal spikes featuring an elongated rachis and tenacious glumes);

• compact (short, dense spike with fewer spikelets per spike) (Fig. 1) (Dorofeev and Korovina, 1979).

The normal spike shape is widespread among the cultivated wheat species (*T. durum, T. aestivum* among other) (Dorofeev and Korovina, 1979). Spelt spikes were described for the tetraploid species *T. spelta, T. dicoccum, T. dicoccoides* (Körn. ex Aschers. et Graebn.) Schweinf. and speltoid mutants of *T. aestivum* (Dorofeev and Korovina, 1979). The compact spike shape was identified in diploid species *T. sinskajae* and two hexaploid species, *T. compactum* Host and *T. sphaerococcum* Perciv. (Dorofeev and Korovina, 1979). No accessions with compact spikes have been identified in tetraploid wheat species, while mutants of them (Kosuge *et al.*, 2008) and hybrids between varieties of *T. dicoccoides* and *T. dicoccum* possess less dense spikes (compactoid), in comparison to compact spikes of hexaploid accessions (Malinowski, 1914; Goncharov, 1997).

Spike branching. Normally the wheat spike (branchless spike) is composed of spikelets arranged in two opposite rows along the rachis. In contrast, in branching spikes, spikelets are replaced by lateral branch-like structures resembling small-sized secondary spikes (Fig. 1). This trait is important, because the branch formation produces significantly more grains per spike and thus increases grain yield (Poursarebani *et al.*, 2015). Branching spikes occur in *T. vavilovii* (Thum.) Jakubz. and some varieties of *T. turgidum* L. Diploid wheat species possess only branchless spikes (Lebedeva and Rigin, 1994).

Number and arrangement of spikelets: supernumerary spikelets. Normal wheat spikes bear one spikelet per rachis node (wild type), while some wheat accessions are characterised by an abnormal phenotype with additional spikelets per rachis node (supernumerary spikelets phenotype) (Pennell and Halloran, 1983) (Fig. 1). Several variants of the supernumerary spikelets phenotype have been identified, such as:

• multirow spike (MRS) with a cluster of spikelets at a rachis node;

• horizontal spikelets (HSs) with three spikelets (triple spikelet) and two spikelets in horizontal positions at a rachis node (Fig. 1).

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Some investigators define the branching spike as a variant of a ramified spike of a supernumerary spikelets phenotype (RS) (Dobrovolskaya *et al*., 2015).

Wheat accessions with the normal number of spikelets per rachis node prevail on the accessions with supernumerary spikelet spikes. Accessions with supernumerary spikelet spikes have been identified for *T. turgidum*, *T. durum* and *T. polonicum* L. (Klindworth *et al*., 1990; Lyapunova, p.c.; Goncharov, p.c.). The accessions with supernumerary spikelets represent the promising type for breeding to increase wheat grains yield and to satisfy human demand. It was proposed that wheat grain production must increase at an annual rate of 2%, without any additional land to become available for this crop (Gill *et al*., 2004).

GENES UNDERLYING SPIKE MORPHOLOGY IN DIFFERENT WHEAT SPECIES

Free-threshing vs. non free-threshing grains. Several major genes and loci related to threshability have been previously identified and include the spelt factor gene (*Q*), *tenacious glumes* locus (*Tg*), *tenacious glume 2* locus (*Tg2*) and the soft glume locus (*sog*) (Kerber and Rowland, 1974; Simonetti *et al*., 1999; Faris and Gill, 2002; Faris *et al*., 2003; Sood *et al*., 2009) (Table 1).

Q gene (synonyms: *WAP2*, wheat AP2) represents a transcription factor that regulates the threshability in polyploidy wheat species and has a pleiotropic effect on several other important traits, including spike shape, rachis fragility, plant height, and flowering time (Muramatsu, 1963; Kato *et al*., 1999; Faris and Gill, 2002; Faris *et al*., 2003; Simons *et al*., 2006; Zhang *et al*., 2011). Spelt factor gene was found to be located on the long arm of chromosome 5A and has been molecularly cloned for a number of wheat species (Faris and Gill, 2002; Faris *et al*., 2003; Simons *et al*., 2006; Sormacheva *et al*., 2015). Polyploid wheat species has an additional homoeologous loci for *Q* gene on chromosomes 5B and 5D. Analysis of *5AQ*, *5Bq* and *5Dq* showed that: (1) *5AQ* plays a major role in control of domestication-related traits; (2) *5Bq* is a pseudogene that does not encode a full-length q protein, but participates in the regulation of expression of *5AQ* and *5Dq*; and (3) a combination of the *5AQ*, *5Bq* and *5Dq* loci is important for the formation of free-threshing spikes (Simons *et al*., 2006; Zhang *et al*., 2011). The Q^m gene sequences have been identified for diploids and the spike phenotype was predicted to be regulated by the *Sog* gene in these species (see below).

Q gene encodes a floral homeotic protein, a member of the AP2 subfamily of plant-specific transcription factors (AP2/ERF family) (Simons *et al*., 2006). Two different alleles of this gene, *Q* and *q* in the A genome, were identified and associated with a particular spike phenotype. The *q* allele is presented among wild wheat species with non free-threshing grains and fragile speltoid spikes, while *Q* allele occurs in wild and cultivated species with free-threshing grains and non fragile not speltoid spikes (Simons *et al*.,

2006; Zhang *et al*., 2011; Sormacheva *et al*., 2015). The sequences of *q* and *Q* alleles have two main differences: presence of the amino acid substitution in the position 329 (Val/Ile) and the SNP in the binding site of miRNA172 within the exon 10 (T/C). However, all sequences of B and D genomes have Leu in position 329 and 418TTC triplet in the miR172 binding site.

Two mechanisms have been proposed to explain the increased transcription level of *Q* allele in compare to *q* in the A genomes. The presence of 329Ile is predicted to increase the formation of Q homodimers, which could lead to self up-regulation of *5AQ* transcription (Simons *et al*., 2006). The regulation of *Q* gene expression can occur through miRNA, as was shown for several other members of the AP2 family (Chen, 2004; Simons *et al*., 2006; Chuck *et al*., 2007).

Another locus (*Tg*) was described for hexaploid wheat species, which is localized on the short arm of the chromosome 2D (Kerber and Rowland, 1974; Rowland and Kerber, 1974; Jantasuriyarat *et al*., 2004; Sood *et al*., 2009) (Table 1). It was suggested that *Tg* has a more pronounced effect on threshability than *Q* gene (Kerber and Rowland, 1974). In tetraploid wheat species, an additional gene that influences the threshability trait (*Tg2*) is located on chromosome 2BS (Simonetti *et al*., 1999) (Table 1). Thus, the free-threshing trait in tetraploid wheat species is complex and *Q*, *Tg2* and several minor genes are predicted to be involved in its formation.

T. sinskajae is the only free-threshing diploid wheat species, but no difference among Q^m gene sequences from various diploid wheats are known (Simons *et al*., 2006; Sormacheva *et al*., 2015). In diploid wheat species the *Sog* locus is located on the short arm of the chromosome $2A^m$ (Taenzler *et al*., 2002) (Table 1). The spike type of *T. monococcum* is dominant (Goncharov *et al*., 2007b). The recessive gene *sog* controls soft glume formation in *T. sinskajae* and is responsible for the free-threshing character (Amagai *et al*., 2014). Moreover, free-threshing and soft glume traits display a linkage inheritance together with the specific compact shape in *T. sinskajae* (Goncharov *et al*., 2007b). Sood *et al*., (2009) suggested that *sog* and *Tg* are not true orthologues and that they apparently originated differently.

Awned vs. awnless spikes. Watkins and Ellerton (1940) established that the awnless spike phenotype is controlled by three non allelic genes *Hd* (*hooded*), *B1* (*tipped 1*) and *B2* (*tipped 2*), localised on chromosomes 4AS, 5AL and 6BL, respectively (Rao, 1981; Sears, 1954; Sears, 1966) (Table 1).

In hexaploid wheat species, the dominant gene *B1* plays a major role in awnless spike formation (Goncharov, 2012). The only exceptions are several accessions of *T. aestivum* from China and India, in which the dominant genes *B2* and *Hd* determine the spikes with specific types of awns (Goncharov, 2012). Goncharov (2012) proposed monogenic control of the awnless phenotype in *T. aestivum* Pamir

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Table 1

LIST OF THE GENES UNDERLING SPIKE MORPHOLOGY IN WHEAT

Gene symbol	Gene (locus) name	Chromosome location	Controlled trait	Species	Differences between alleles on the molecular level	References
Q	spelt factor gene	5AL, 5BL, 5DL	spike shape, rachis fragility, threshability	polyploid wheat species	Val to Ile substitution in the position 329, SNP in miRNA172 binding site within the exon 10	Faris *et al*., 2003
Tg	*tenacious glume*	2DS	glume toughness	hexaploid wheat species	Not molecularly cloned	Sood *et al*. 2009
$Tg2$	*tenacious glume 2*	2BS	glume toughness	tetraploid wheat species	Not molecularly cloned	Simonetti *et al*., 1999
sog	*soft glume* gene	2A^{m}S	compactoid spike shape, threshability	diploid wheat species *T. sinskajae*	Not molecularly cloned	Taenzler *et al*., 2002; Sood *et al*., 2009
Hd	*Hooded*	4AS	awned vs. awnless phenotype	hexaploid wheat species *T. aestivum*	Not molecularly cloned	Rao, 1981
B1	*Tipped 1*	5AL	awned vs. awnless phenotype	polyploid wheat species	Not molecularly cloned	Sears, 1954
B2	*Tipped 2*	6BL	awned vs. awnless phenotype	hexaploid wheat species *T. aestivum*	Not molecularly cloned	Sears, 1954; Sears, 1966
awn1	*awnless*	3B	awned vs. awnless phenotype	tetraploid wheat species *T. aethiopicum*	Not molecularly cloned	Goncharov *et al*., 2003
awn^S	*awnless*	2A^{m}S	awned vs. awnless phenotype	diploid wheat species *T. sinskajae*	Not molecularly cloned	Goncharov *et al*., 2007b
t	*tetraaristatum*	5AL	four-awned spike	tetraploid wheat species *T. carthlicum*	Not molecularly cloned	Haque *et al*., 2011
C	Club spike shape	2DL	compact spike shape	hehaploid wheat species *T. compactum*	Not molecularly cloned	Unrau, 1950; Rao, 1972; Johnson *et al*., 2008
C2	-	-	compact spike shape	hehaploid wheat species *T. sphaerococcum, T. antiquorum*	Not molecularly cloned	Goncharov and Gaidalenok, 2005
Br3	*brittle rachis 3*	3AS	rachis brittleness	tetraploid wheat species	Not molecularly cloned	Watanabe *et al*., 2002; Li and Gill, 2006
Br2	*brittle rachis 2*	3BS	rachis brittleness	tetraploid wheat species	Not molecularly cloned	Watanabe *et al*., 2002
Br1	*brittle rachis 1*	3DS	rachis brittleness	hehaploid wheat species	Not molecularly cloned	Chen *et al*., 1998
bh^m	*branched head*	2A^{m}S	spike branching	diploid wheat species	Not molecularly cloned	Amagai *et al*., 2014
bh^t	*branched head*	2AS	spike branching	tetraploid wheat species	Not molecularly cloned	Klindworth *et al*., 1997; Poursarebani *et al*., 2015
mrs1	*monstrosum spike*	2DS	supernumerary spikelet trait	hexaploid wheat species *T. aestivum*	Not molecularly cloned	Dobrovolskaya *et al*., 2009
WFZP	wheat *FRIZZY PANICLE*	2AS, 2BS, 2DS	supernumerary spikelet trait	hexaploid wheat species *T. aestivum*	Recessive alleles of *WFZP-D:* mutations close to the AP2/ERF functional domain. Recessive allele of *WFZP-A:* deletion that cause the framshift.	Dobrovolskaya *et al*., 2015
Ppd-D1	*Photoperiod-D1*	2D	inflorescence architecture, paired spikelet trait	hexaploid wheat species	-	Boden *et al*., 2015

landraces 'Babilo' and 'Kilyak' by the dominant gene designated as *Hd2*. Recently, locus *T* controlling awn formation on the glume in *T. carthlicum* (tetraaristatum) has been found to be localised on the long arm of chromosome 5A (Haque *et al*., 2011) (Table 1).

Using genome substitution lines, it was shown that in the only tetraploid species *T. aethiopicum* with awnless forms*,* this trait is under monogenic control by the recessive gene *awn1* located on chromosome 3B (Goncharov *et al*., 2003; Antonyuk *et al*., 2012). Goncharov *et al*. (2007) found that the recessive gene awn^S was localized on the short arm chromosome 2A of *T. sinskajae*.

Genes underlying the presence or absence of awns in wheat are poorly investigated. The localisation of *Hd2* and *awn1* genes has not been determined. None of the genes involved in awn development or formation of awnless spikes in wheat species have been molecular cloned so far.

Fragile vs. non-fragile rachis. In addition to the *Q* gene, three loci *Br1*, *Br2,* and *Br3* located on the homoeologous group 3 chromosomes control the rachis character (Chen *et al*., 1998; Watanabe and Ikebata, 2000; Watanabe *et al*., 2002; Li and Gill, 2006; Nalam *et al*., 2006) (Table 1). The recessive alleles of these loci determine the rashis that undergoes one of the disarticulation types described above.

The *Br* locus is localized on the short arm of chromosome 3D of Tibetan landraces of common wheat and the short arm of chromosomes 3A in *T. timopheevii* (Chen *et al*., 1998; Li and Gill, 2006). Recessive alleles of *Br2* and *Br3* located on 3AS and 3BS determine non-brittle rachis in tetraploids. No alleles of *Br1*, *Br2* and *Br3* have been molecularly cloned and no ortologs of these genes are known in cereals.

Spelt vs. normal or compact spike shape. Three main genes/loci are involved in spike shape control in wheat species: *Q, C, C2* (Unrau, 1950; Rao, 1972; Goncharov and Gaidalenok, 2005; Simons *et al*., 2006; Johnson *et al*., 2008; Zhang *et al*., 2011; Sormacheva *et al*., 2015) (Table 1). The alleles of *5AQ* gene, which determines the normal and spelt spike shape in different wheat species, are described above. Homologous *5Dq* and *5Bq* also contribute to the suppression of the spelt phenotype (Zhang *et al*., 2011).

In the hexaploid wheat species *T. compactum* the compact spike shape is controlled by gene *C*, which is located on the long arm of chromosome 2D (Rao, 1972). Mutation giving rise to the dominant allele *C* resulted in the origin of club wheat, thus the investigation of this gene is important for the taxonomy of wheat species (Johnson *et al*., 2008). *C2* gene controlling the compact spike characteristic in *T. sphaerococcum* is not allelic to gene *C* of *T. compactum* (Goncharov and Gaidalenok, 2005). The genome localisation of gene *C2* remains unknown. The compactoid spike shape trait in tetraploids is controlled by two nonallelic recessive genes, named *sc1* and *sc2* (Goncharov, 1997). The gene *sc1* alone is responsible for the semicompactoid spike, while together with gene *sc2*, leads to compactoid spike formation in tetraploid wheat. Sequences of the genes *C*, *C2*, *sc1* and *sc2* have not been molecularly cloned.

Supernumerary spikelets vs. normal number of spikelets. Some investigators define the branched spikes in which the additional spikelets number increases due to growth of the secondary spike rachis as a variant of supernumerary spikelets spikes (SS). The branched spike phenotype is common in tetraploid species *T. turgidum* and a single major locus *bh^t* (*branched head*) located on the short arm of the chromosome 2A is predicted to control this trait (Haque *et al*., 2012) (Table 1). Recently it was shown that the branched phenotype in *T. sinskajae* is under control of a recessive allele at a single locus and that this locus *bh^m* is located on the 2A^mS (Amagai *et al*., 2014) (Table 1).

In wheat species, the supernumerary spikelet trait is recessive. *WFZP* (wheat *FRIZZY PANICLE*) and *mrs1* (*monstrosum spike*) are the loci that control the formation of spikes with supernumerary spikelets in *T. aestivum* species (Dobrovolskaya *et al*., 2009; Dobrovolskaya *et al*., 2015) (Table 1). The *mrs1* gene mapped on chromosome 2DS is a predicted ortholog of *bh* loci. *WFZP-A*, *WFZP-B* and *WFZP-D* are located on homoeologous group 2 chromosomes (Dobrovolskaya *et al*., 2015). *WFZP* gene encodes an APETALA2/ERF transcription factor that probably inhibits SS phenotype formation. qRT-PCR and comparative se-

quence analysis showed that *WFZP-D* is the main contributor to the SS phenotype in bread wheat, while *WFZP-B* is non functional and possess the miniature inverted-repeat TEs inserted within the promoter region (Dobrovolskaya *et al*., 2015). For *WFZP-D*, two recessive alleles are associated with SS phenotypes: *wfzp-D.1* with the G-A substitution within the GCC-box binding site of the AP2/ERF functional domain and *wfzp-D.2* with C-T substitution in AP2/ERF. The recessive allele of the *WFZP-A* (*wfzp-A.1*) possesses a deletion 14 bp in length close to the functional AP2/ERF domain, which causes the frameshift (Dobrovolskaya *et al*., 2015). Different combinations of the alleles described above cause the differences in the phenotypic manifestations of the SS trait in *T. aestivum*.

Recently, in a comprehensive study, the influence of *Ppd-D1* gene on inflorescence architecture and paired spikelet development in hexaploid wheat species was described (Boden *et al*., 2015).

ORTHOLOGS OF SPIKE MORPHOLOGY GENES IN TRITICEAE TRIBE

A number of genes influence spike morphology in other species of subtribe *Frumentaceae,* namely in barley and rye. Only eight genes from barley, including *INT-C*, *Nud*, *vrs1*, *Vrs4*, *Btr1*, *Btr2*, *Bkn3* and *HvAP2,* have been molecularly cloned (Takahashi and Hayashi, 1964; Muller *et al*., 1995; Franckowiack and Konishi, 1997; Komatsuda and Mano, 2002; Santi *et al*., 2003; Komatsuda *et al*., 2007; Taketa *et al*., 2008; Ramsay *et al*., 2011; Houston *et al*., 2013; Koppolu *et al*., 2013; Taketa *et al*., 2013; Pourkheirandish *et al*., 2015; Yu *et al*., 2016). No genes related to spike morphology in rye have been cloned so far.

The sequences of eight genes involved in the regulation of grass inflorescence architecture in barley have been used for BLAST search against the NCBI databases. Homological sequences have been found in wheat, *Brachypodium distachyon* (L.) P. Beauv., rice, sorghum, and maize for four of them: *Vrs1*, *Vrs4*, *Nud,* and *HvAP2*. Homological sequences of two genes (*Btr*1 and *Btr*2) have been found in wheat only, while genes *INT-C* and *Bkn3* showed no homological sequences in the cereal genomes. All isolated sequences were aligned and used for the phylogenetic analysis. Multiple DNA alignments were performed by ClustalW (Thompson *et al*., 1994) with improvements by the MUSCLE algorithm in UGENE Results software (Okonechnikov *et al*., 2012). Phylogenetic analyses were performed using the neighbour-joining (NJ) method in MEGA7 software (Tamura *et al*., 2011). Statistical support for the NJ tree was evaluated by bootstrapping (1000 replications) (Felsenstein, 1985).

***Vrs1*-like genes.** *Vrs1* is a member of the HD-ZIP class of transcription factors, and encodes a transcription factor that includes a homeodomain with a closely linked leucine zipper motif. HD-Zip-encoding genes have been isolated from a wide variety of plants and grouped into four families
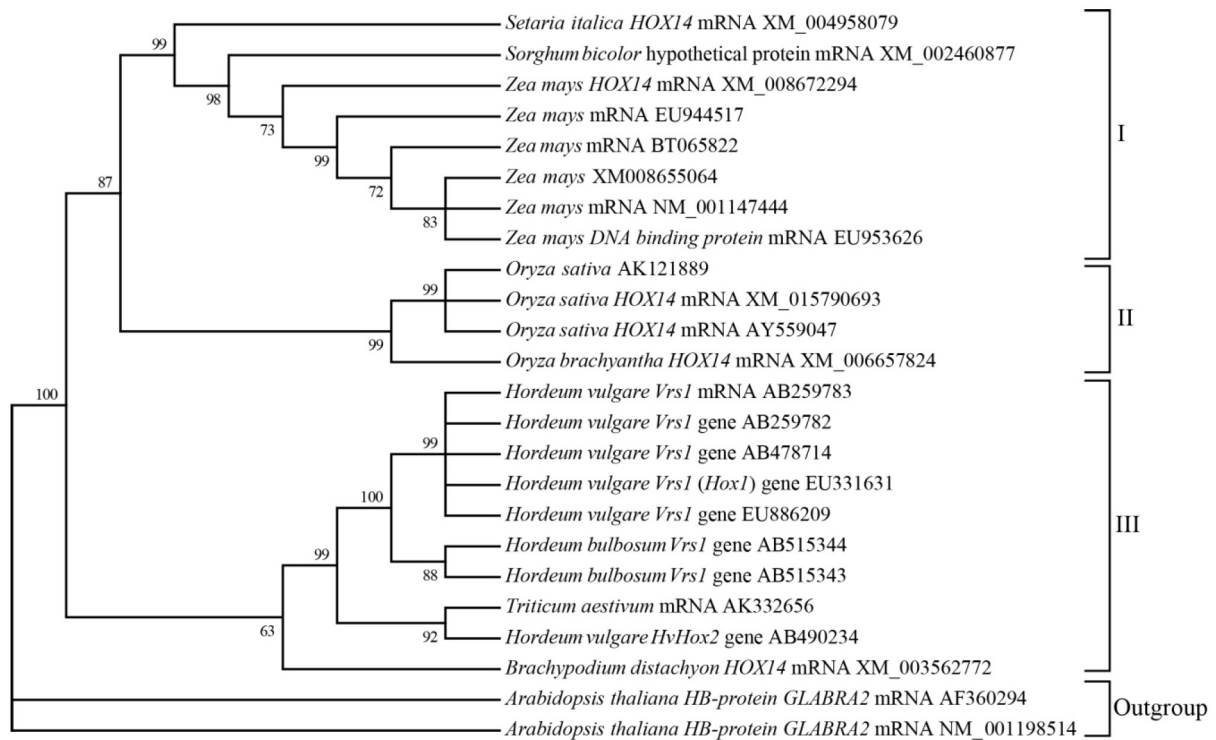
Fig. 2. Neighbour-joining (NJ) phylogenetic tree based on the coding region of *Vrs1* genes from various cereal species and their homologs identified from GenBank. Statistical support was evaluated by bootstrapping (1000 replications); nodes with bootstrap values over 50% are indicated. Sequences from *Arabidopsis thaliana* that were homological to the *Vrs1* gene were used as outgroups.

(I–IV) (Sessa *et al*. 1994, Ariel *et al*., 2007). The barley VRS1 gene belongs to family I (Sakuma *et al*., 2010). Expression of *Vrs1* is localised in the lateral-spikelet primordia of immature spikes, suggesting that the VRS1 protein suppresses development of the lateral rows. Homological sequences to the VRS1 sequences were selected by BLAST search in the NCBI databases against wheat, *B. distachyon*, rice, sorghum, and maize. The resulting phylogenetic tree is shown in Fig. 2. Three branches, in addition to the outgroup, are present in the phylogenetic tree. The first branch includes the homeobox-leucine zipper genes HOX14-like, mainly predicted, from three specimens: *Zea mays* L., *Sorghum bicolor* (L.) Moench**,** and *Setaria italic* (L.) P. Beauv. The second branch is monophyletic and consists of the genes that encode homeobox-leucine zipper protein HOX14 in rice (*Oryza sativa* L.). Finally, the third branch mainly is formed by *Vrs1* sequences of barley (*Hordeum vulgare* L. and *Hordeum bulbosum* L.), but two predicted *Vrs1* sequences of *T. aestivum* and *Brachipodium distachyon* are also placed in this branch.

***Vrs4* (*RAMOSA2*).** *Vrs4* is a barley ortholog of the maize inflorescence architecture gene *RAMOSA2* (*RA2*) (Koppolu *et al*., 2013). This group of transcriptional factors plays a significant role in the control of inflorescence development in grasses. Therefore, these transcriptional factors are present in all cereals. The evolutionary relationships of the *RA2* genes are shown in Fig. 3. The *R2* tree contains the same three branches as the previous tree: *Zea mays, Sorghum bicolor*, and *Setaria italic* (branch I); *Oryza sativa* (branch II); and two *Hordeum* species, two *Triticum* species, and *Brachipodium distachyon* (branch III).

***Q* gene (*APETALA2*-like genes).** The *APETALA2*-like genes (*AP2*) form a large multi-gene family of transcription factors, including *Q* gene described for wheat. The *APETALA2*-like proteins play an important role during the plant life cycle, being key regulators of many developmental processes. Phylogenetic analysis showed that the phylogenetic relationships of the *APETALA2*-like genes from cereals are similar to both the *Vrs1*-like and *RA2* genes described above (Fig. 4). The same three branches are present in the *APETALA2*-like tree: *Zea mays, Sorghum bicolor*, and *Setaria italic* (branch II); *O. sativa* (branch III); and *H. vulgare*, *Triticum* species, *Ae. tauscii*, and *B. distachyon* (branch I). Additionally, two other branches are present in the tree. Both branch V and branch IV include sequences of the AP2-like ethylene-responsive transcription factor TOE3 from *Z. mays* and *O. brachyantha* A. Chev. & Roehr. plus *B. distachyon,* correspondingly.

***Nud* (*WIN1*-like genes).** The gene for naked caryopsis, *nud*, has been described for barley only. No other crops in the tribe Triticeae show such a differentiation in grain type (Taketa *et al*., 2004). Our phylogenetic analysis showed that the *nud* gene from *Hordeum vulgare* is the most closely related to the ethylene-responsive transcription factor *WIN1* (Fig. 5). Three of four branches in the tree (I, II, III) are the same as in the other first trees. The branch IV includes *WIN1* sequences from three different species. We can suggest that this group of genes may be different from the transcription factor *WIN1*.

Finally, two genes, *Btr1* and *Btr2*, which had been described as transcriptional factors for the *Hordeum vulgare*
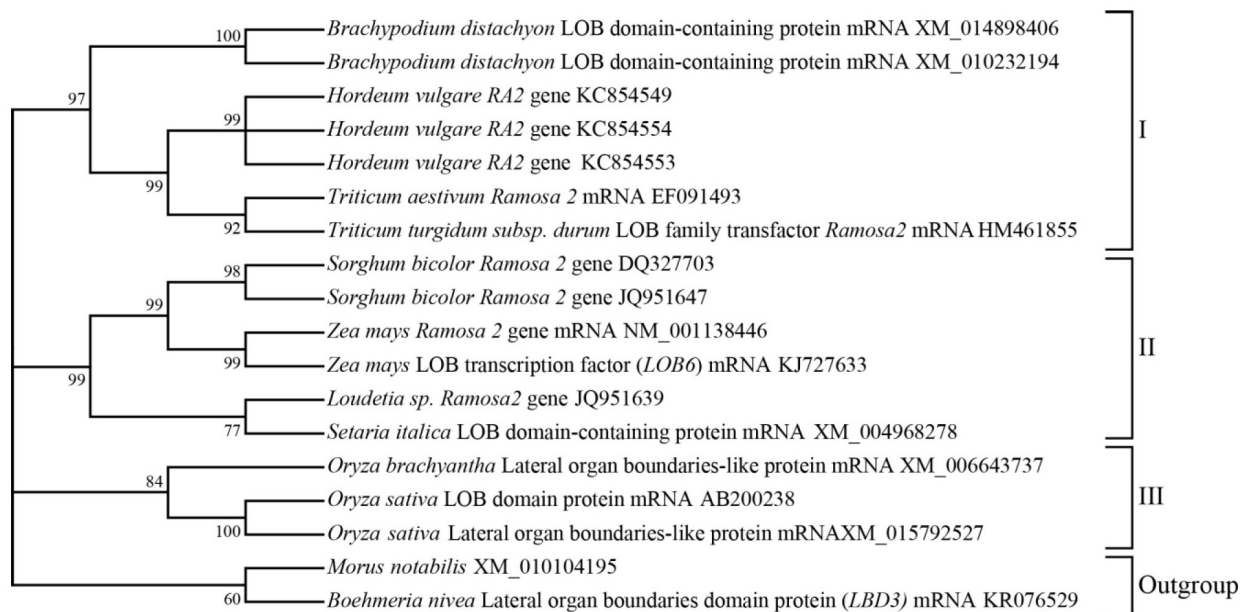
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Fig. 3. Neighbour-joining (NJ) phylogenetic tree based on the coding region of *Vrs4* genes from various cereal species and their homologues identified from GenBank. Statistical support was evaluated by bootstrapping (1000 replications); nodes with bootstrap values over 50% are indicated. Sequences from *Morus notabilis* and *Boehmeria nivea* that were homological to the *Vrs4* gene were used as outgroups.

Fig. 4. Neighbour-joining (NJ) phylogenetic tree based on the coding region of *Q* genes from various cereal species and their homologues identified from GenBank. Statistical support was evaluated by bootstrapping (1000 replications); nodes with bootstrap values over 50% are indicated. *APETAL2* gene sequences from *Arabidopsis* spp. were used as outgroups.

genome (Komatsuda and Mano, 2002), were not found in the tested cereal genomes, except for two *Triticum* species in which the homologous nucleotide sequences to both *Btr1* and *Btr2* have been found (GenBank Ac. N. HG670306 and KR813812).

CONCLUSIONS

Plant genomes can be modified by several techniques. In the present review we described genes commonly used in

standard breeding practice and several genes that control the wheat trait and could increase the biodiversity of commercial cultivars of modern wheat. During domestication and following cultivation, some genes underlying agronomically important traits were excluded from traditional breeding. A common drawback of the knowledge in the field of spike morphology genes in wheat is insufficient from the viewpoint of molecular biology and accurate description of the cultivar's phenotypes. Comprehensive studies, which combine the analysis of wheat genes and orthologous genes of related wheat species, such as barley and rye, are required
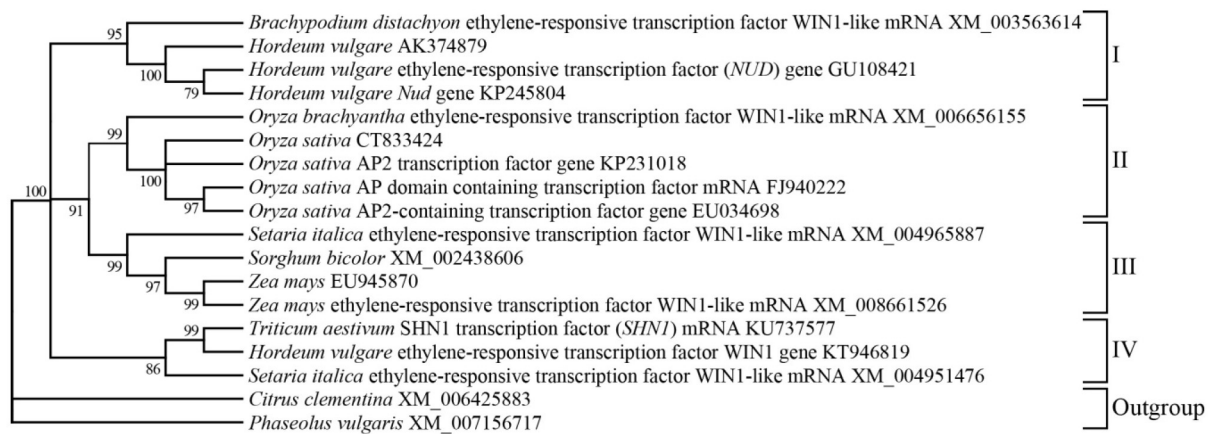
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Fig. 5. Neighbour-joining (NJ) phylogenetic tree based on the coding region of *Nud* genes from various cereal species and their homologues identified from GenBank. Statistical support was evaluated by bootstrapping (1000 replications); nodes with bootstrap values over 50% are indicated. Sequences from *Citrus elemtina* and *Phaseolus vulgaris* that were homological to the *Nud* gene were used as outgroups.

to eliminate this drawback. At present, it is clear that only the combination of comparative genetic and molecular biological studies will provide the reliable modern tools that could change the architectonic structure of cultivated wheat.

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KVIEŠU SUGU (*TRITICUM* L.) VĀRPU MORFOLOĢIJU NOSAKOŠIE GĒNI

Rakstā apkopota informācija par gēniem, kuri nosaka kviešu vārpu morfoloģiju. Parādīts, ka mūsdienu molekulārās ģenētikas pētījumi dod iespēju noteikt gēnus ortologus kviešu radniecīgām sugām (mieži, rudzi u.tml.) un atrast tādus gēnus, kuri līdz šim nav tikuši izmantoti selekcijā. Šo gēnu iesaistīšana varētu efektīvi sekmēt jaunu kviešu šķirņu izveidošanu.

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