Review

SPIKE MORPHOLOGY GENES IN WHEAT SPECIES (TRITICUM L.)

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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-
per, we present current knowledge of the agronomically im-
portant 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 mor-
phological characteristics, including threshability, the pres-
ence 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.](image-url)
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 wheat 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 occurs 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 (compaktoid), 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).
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 accesses with supernumerary spikelet spikes. Accessions with supernumerary spikelet spikes have been identified for T. durum, T. durum and T. polonicum L. (Klindworth et al., 1990; Lyapunova, p.c.; Goncharov, p.c.). The accesses 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 (Muramoto, 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 et al., 2002) (Table 1). The spike type of T. monococcum is the only free-threshing diploid wheat species, in which the dominant genes controlling soft glume formation in T. aestivum and several minor genes are predicted to be involved in its formation.

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 Qm 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 (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 mono- genic control of the awnless phenotype in T. aestivum Pamir...
**Table 1**

<table>
<thead>
<tr>
<th>Gene symbol</th>
<th>Gene (locus) name</th>
<th>Chromosome location</th>
<th>Controlled trait</th>
<th>Species</th>
<th>Differences between alleles on the molecular level</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Q</td>
<td>spelt factor gene</td>
<td>5AL, 5BL, 5DL</td>
<td>spike shape, rachis fragility, threshability</td>
<td>polyplod wheats species</td>
<td>Val to Ile substitution in the position 329, SNP in miRNA172 binding site within the exon 10</td>
<td>Faris et al., 2003</td>
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<td>Tg</td>
<td>tenacious glume</td>
<td>2DS</td>
<td>glume toughness</td>
<td>hexaploid wheats species</td>
<td>Not molecularly cloned</td>
<td>Sood et al., 2009</td>
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<tr>
<td>Tg2</td>
<td>tenacious glume 2</td>
<td>2BS</td>
<td>glume toughness</td>
<td>tetraploid wheats species</td>
<td>Not molecularly cloned</td>
<td>Simonetti et al., 1999</td>
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<tr>
<td>sog</td>
<td>soft glume gene</td>
<td>2A&lt;sup&gt;3&lt;/sup&gt;S</td>
<td>compactoid spike shape, threshability</td>
<td>diploid wheats species T. siskaiaj</td>
<td>Not molecularly cloned</td>
<td>Taenzler et al., 2002; Sood et al., 2009</td>
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<td>Hd</td>
<td>Hooded</td>
<td>4AS</td>
<td>awned vs. awnless phenotype</td>
<td>hexaploid wheats species T. aestivum</td>
<td>Not molecularly cloned</td>
<td>Rao, 1981</td>
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<td>Br1</td>
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<td>5AL</td>
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<td>Sears, 1954</td>
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<tr>
<td>Br2</td>
<td>Tipped 2</td>
<td>6BL</td>
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<td>Not molecularly cloned</td>
<td>Sears, 1954; Sears, 1966</td>
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<tr>
<td>awn&lt;sup&gt;1&lt;/sup&gt;</td>
<td>awnless</td>
<td>3B</td>
<td>awned vs. awnless phenotype</td>
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<td>Not molecularly cloned</td>
<td>Goncharov et al., 2003</td>
</tr>
<tr>
<td>awn&lt;sup&gt;5&lt;/sup&gt;</td>
<td>awnless</td>
<td>2A&lt;sup&gt;3&lt;/sup&gt;S</td>
<td>awned vs. awnless phenotype</td>
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<td>Not molecularly cloned</td>
<td>Goncharov et al., 2007b</td>
</tr>
<tr>
<td>t</td>
<td>tetraaristatum</td>
<td>5AL</td>
<td>four-awned spike</td>
<td>tetraploid wheats species T. carthlicum</td>
<td>Not molecularly cloned</td>
<td>Haque et al., 2011</td>
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<td>C</td>
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<td>2DL</td>
<td>compact spike shape</td>
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<td>Unrau, 1950; Rao, 1972; Johnson et al., 2008</td>
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<td>-</td>
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<td>Chen et al., 1998</td>
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<td>2A&lt;sup&gt;3&lt;/sup&gt;S</td>
<td>spike branching</td>
<td>diploid wheats species</td>
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<td>branched head</td>
<td>2AS</td>
<td>spike branching</td>
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<td>Not molecularly cloned</td>
<td>Kindworth et al., 1997; Poursarebani et al., 2015</td>
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<td>2DS</td>
<td>supernumerary spikelet trait</td>
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<td>Not molecularly cloned</td>
<td>Dobrovolskaya et al., 2009</td>
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<td>2AS, 2BS, 2DS</td>
<td>supernumerary spikelet trait</td>
<td>hehaploid wheats species T. aestivum</td>
<td>Recessive alleles of WFZP-D: mutations close to the AP2/ERF functional domain. Recessive allele of WFZP-A: deletion that cause the framshift.</td>
<td>Dobrovolskaya et al., 2015</td>
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<td>2D</td>
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<td>-</td>
<td>Boden et al., 2015</td>
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</table>

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 inawn development or formation of awnless spikes in wheat species have been molecularly 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 rachis 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 orthologs 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, 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 localization 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 semicomactoid 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 (SS). The branched spike phenotype is common in tetraploid species T. turgidum and a single major locus bh1 (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. sinskajaе is under control of a recessive allele at a single locus and that this locus bh”m is located on the 2A5S (Amagai et al., 2014) (Table 1).

In wheat species, the supernumerary spikelet trait is recessive. WFZP (wheat FRIZZY PANICLE) and mrs1 (MONOSTROSUM 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 bb 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 sequence 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 TE 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; Franckowiak 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. Homologous sequences have been found in wheat, Brachypodium distachyon (L.) P. Beauv., rice, sorghum, and maize for four of them: Vrs1, Vrs4, Nud, and HvAP2. Homologous sequences of two genes (Btr1 and Btr2) have been found in wheat only, while genes INT-C and Bkn3 showed no homologous 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.
(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 Brachypodium 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 Brachypodium 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. tauschii, 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
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.
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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REFERENCES


