AGRICULTURAL BIOLOGY,
2019, V. 54, № 5, pp. 920-933
(SEL'SKOKHOZYAISTVENNAYA BIOLOGIYA)

ISSN 2412-0324 (English ed. Online)
ISSN 0131-6397 (Russian ed. Print)
ISSN 2313-4836 (Russian ed. Online)

Triticale

UDC 633.1:581.14:577.21

doi: 10.15389/agrobiology.2019.5.920eng
doi: 10.15389/agrobiology.2019.5.920rus

EFFECTS OF DWARFING WHEAT (*Triticum aestivum* L.) AND RYE (*Secale cereale* L.) GENES IN SPRING TRITICALE SEGREGATING POPULATION AS STUDIED IN POT TRIALS

P.Yu. KROUPIN[1, 2], A.G. CHERNOOK[1, 2], G.I. KARLOV[1, 2], A.A. SOLOV'EV[1], A.D. KORSHUNOVA[2], M.G. DIVASHUK[1, 2]

[1]*All-Russian Research Institute of Agricultural Biotechnology,* 42, ul. Timiryazevskaya, Moscow, 127550 Russia, e-mail pavelkroupin1985@gmail.com (✉ corresponding author), irbis-sibri@ya.ru, karlov@iab.ac.ru, a.soloviev70@gmail.com, divashuk@gmail.com;
[2]*Timiryazev Russian State Agrarian University—Moscow Agrarian Academy,* 49, ul. Timiryazevskaya, Moscow, 127550 Russia, e-mail korshunova.ad88@gmail.com
ORCID:
Kroupin P.Yu. orcid.org/0000-0001-6858-3941
Chernook A.G. orcid.org/0000-0002-8793-1742
Karlov G.I. orcid.org/0000-0002-9016-103X
Solov'ev A.A. orcid.org/0000-0003-4480-8776
Korshunova A.D. orci.dorg/0000-0002-8651-8286
Divashuk M.G. orcid.org/0000-0001-6221-3659
The authors declare no conflict of interests
Acknowledgements:
Supported financially by Russian Science Foundation (grant No. 17-76-20023)
Received April 25, 2018

Abstract

The urgent problem of triticale lodging may be reliably overcome by introgression of dwarfing genes into triticale cultivars. Notable, both wheat and rye dwarfing genes can reduce the height of triticale plants. Therefore, a single contribution of various dwarfing genes and their additive effects in triticale which is an intergeneric hybrid still remain intriguing in fundamental aspects and important for breeding practice. In our study, rye dwarfing gene *Ddw1* has been transferred into spring triticale. Then we have hybridized winter triticale cv. Avanguard (*Ddw1 Ddw1 Rht-B1a Rht-B1a*) with spring triticale cv. Solovei Kharkovskii (*ddw1 ddw1 Rht-B1b Rht-B1b*) and used F_2 seeds to reveal the mechanism of inheritance of the studied dwarfing genes *Ddw1* and *Rht-B1b* and to determine the effect of the dwarfing alleles on economically valuable traits in the segregating population of spring triticale. Under the greenhouse conditions, 273 plants of the spring type of the segregating population F_2 were grown to individually estimate plant height, the number and length of internodes, spikelet length and number per spike, spike density, grain weight, grain number and 1000-grain weight per the main spike. Each plant was also genotyped by PCR using the markers of the *Ddw1* and *Rht-B1* allelic state. To investigate inheritance patterns, the dominant and additive effects of genes were calculated. The second task was achieved by comparing plants homozygous for wild-type alleles (*ddw1* and *Rht-B1a*) and short-stem alleles (*Ddw1* and *Rht-B1b*) with estimation of both independent effect of each genes and their interlocus interaction. Using statistical methods (Fisher *F*-criterion, Mann-Whitney *U*-test, and Spearman rank correlation coefficient ρ), we found the significance of the differences and associations between phenotypic traits and genotype. Our studies have shown that the effects of the *Ddw1* and *Rht-B1b* are somewhat different from those in wheat. The *Ddw1* statistically significant affects plant height (by reducing up to 40 %, $p = 0.05$), manifesting itself as a partially dominant allele. The *Rht-B1b* results in a decrease in the spring triticale plant height but less than the *Ddw1* gene does (only up to 20 %, $p = 0.05$). Hence, the *Rht-B1b* allele is proven to be partially recessive. In the presence of gene *Rht-B1b* a kernel weight increases from 1.4 g to 1.7 g (by 21.4 %) due to higher spike density and fertility. The *Ddw1* gene introgression leads to a 16.7 % decrease ($p = 0.05$) in the total grain weight per spike (from 1.8 g to 1.5 g) due to a 9.6 % decrease ($p = 0.05$) in the 1000-grain weight (from 45.7 g до 41.3 g). In general, the *Ddw1* and *Rht-B1b* genes affect the studied traits as antagonists. In summary, a combination of two dwarfing genes, *Ddw1* from rye and *Rht-B1b* from wheat, makes it possible to maximize yield of dwarf spring triticale plants and is promising for breeding.

Keywords: spring triticale, *Rht-B1b*, *Ddw1*, structural analysis, dwarfing genes, DNA markers, breeding

The main idea behind creation of triticale was to combine positive traits of

rye *Secale cereale* L. (resistance to hostile conditions) and wheat *Triticum aestivum* L. (suitability for diversified use in food industry). The global production of triticale maintains stable growth and reached 15 million tons in 2016 with total crop acres equal to 4.2 million hectares [1[, whereas the culture has both forage and food value [2, 3]. Lodging is among the drawbacks of triticale, limiting its wider spread during crop cultivation. Treatment with growth retardants is used to fight lodging; however, this makes the products more expensive and increases chemical load on the environment. The other approach to solving this problem is selective improvement of triticale and creation of varieties resistant to lodging. High correlation between resistance of triticale plants to lodging and plant height has been observed [4, 5]. Losert et al. [5] analyzed a collection consisting of 199 winter and 2 spring triticale crops and demonstrated that during the last 30 years a tendency of significant triticale plant height reduction has been observed (by 0.38 cm per year) and reduced lodging tendency as a result of selection, which is due to close interconnection of these two features (shorter plants, as a rule, are more resistant to lodging) [4, 6].

Plant height is a complex quantitative trait (7, 8). In hexaploid triticales (BBAARR) combining wheat (BBAA) and rye (RR) genomes the dwarfing can be ensured by wheat, rye genes and/or their combination genes.

At this time, common wheat bears 24 dwarfing genes [9, 10]. *Rht-B1b* (=*Rht1*), *Rht-D1b* (=*Rht2*), *Rht-8c*, *Rht-B1e* (=*Rht11*) genes gained the biggest widespread in commercial wheat varieties. They are also effective at high dosages of fertilizers and possess pleiotropic effect on many agronomic characters [11-13]. In wheat, plant height is reduced by 10-15% on the average as compared to the height of *Rht-B1a* [14-16] wild type allele carrier when *Rht-B1b*, *Rht-D1b*, *Rht-B1e* dwarfing genes insensitive to gibberellin are present. In terms of impact on stalk growth these genes manifest themselves as recessive or partially recessive. The height of rye is also controlled by numerous genetic factors [17, 18]. A total of 14 different rye dwarfing genes [19-21] are already known, among which three are dominant genes, and *Ddw1* is of the highest selective value. In presence of *Ddw1* dominant gene the dwarfing of plants is up to 40%, for diploid rye and up to 55 % for tetraploid rye [22]. About 80% of rye varieties of Russian selection were created using *Ddw1* gene carriers and donors, which on the average allowed an increase in crop yield of winter rye by 12-15 % [23[. *Ddw1* gene was successfully transferred into winter triticale (Debo and Dalo varieties) [24, 25] and a number of dwarf varieties of winter triticale [26, 27] were created with this gene in Poland and Romania.

Various wheat dwarf genes and *Ddw1* rye dwarf gene are widely spread among commercial varieties of winter triticale. In spring triticale, dwarf genes are engaged not so actively. For instance, Korshunova et al. [28] by analyzing 86 samples of spring triticale identified *Rht-B1b* gene in 76 samples, whereas all of them belong to commercial varieties. However, *Ddw1* gene was not found in any samples of spring triticale. Therefore, at this time, the diversity of dwarf genes in spring triticale is very limited [28]. The 2R/2D chromosome substitution, which also dwarfs plants, is not encountered among commercial varieties of spring triticale [29, 30]. It is typical for wheat and winter triticale to have a large diversity of dwarfing genes, and in various varieties the reduction of plant height is ensured by various genes or their combinations. The spring triticale does not display such diversity, and no focused efforts to introduce other dwarfing genes in its genome have taken place. The introgressions of additional dwarfing genes from winter triticale and/or wheat in genomic pool of spring triticale can help solve the height problem of this culture and give a new impetus to its develop-

ment due to pleiotropic action of dwarfing genes to many agronomic characters. Furthermore, it has to be taken into account that mechanisms of action of dwarfing genes of plant height are complex, as a rule, it is implemented via involvement of response to phytohormones in various ways [31] and depends, inter alia, on gene dosage in the genome. The effects of different dwarfing genes in triticale genome, where genomes that are far apart are combined as a result of bigeneric crossing, arouse interest due to knowledge of specifics of interlocus interaction of genes and practical selection, and still have not been properly studied.

In this study, we showed that the effects of *Ddw1* dwarfing genes of rye origin and *Rht-B1b* dwarfing genes of wheat origin in spring triticale vary insignificantly from those in rye and wheat. The studied genes had different impact on height of triticale plants and acted as antagonists in terms of impact on productivity elements.

Our goal was to assess the impact of *Ddw1* and *Rht-B1b* genes and their effect of their interaction on plant height and other agronomic characters in spring triticale in the context of greenhouse studies in F_2 segregating population.

Techniques. We selected those varieties that carry contrast combinations of dwarfing wheat and rye alleles as seed parents, i.e. winter triticale Avanguard variety (*Ddw1 Ddw1 Rht-B1a Rht-B1a* genotype; female parent) and Solovei Kharkovskii spring triticale variety (*ddw1 ddw1 Rht-B1b Rht-B1b* genotype; male parent). Hybridization of parent plants was performed by substitution method (a greenhouse of the Center of Molecular Biotechnology, Russian State Agrarian University—Timiryazev Moscow Agricultural Academy, 2014) to obtain F_1 plants. The seeds of Avanguard parent variety were sown, 10 seeds per pot. During the tillering stage the plants were placed in vernalization chamber for 2 months at 5 °C. After vernalization (during the paniculation stage) the plants were again moved to the greenhouse; during the ligule stage the head was castrated and placed under an isolator made of parchment paper. A head of a cut male parent plant was placed under the isolator during blooming, whereas the stalk was placed in a vessel with water to maintain viability.

From the seeds of F_2 generation sown in pots, 10 psc. per each, plants were grown at identical lighting conditions with dosed irrigation and equal fertilizer dosages (a greenhouse of the Center of Molecular Biotechnology, Russian State Agrarian University—Timiryazev Moscow Agricultural Academy). A total of 273 F_2 plants were obtained. Because of a winter parent variety, F_2 segregating population had several winter forms, which were rejected based on phenotype.

Height, number of joints, length of each joint, main head length (MHL), number of seeds per the main head (SNH), number of ears per the main head (ENH), main head seed weight (SWH) were analyzed individually in each plant. Furthermore, head density (HD) and 1000-seed weight (W_{1000}) were calculated as per [1] and [2], respectively:

$$HD = \frac{ENH}{MHL} 10, \quad (1)$$

$$W_{1000} = \frac{SWH}{SNH} 1000. \quad (2)$$

Molecular markers were used to determine *Ddw1* and *Rht-B1* allele profiles in each F_2 plant individually.

CTAB (cetyltrimethylammonium bromide) method was used for genome DNA extraction from each F_1 and F_2 plants to further evaluate the hybridity and the combinations of analyzed alleles [32].

The alleles of *Rht-B1* and *Ddw1* genes in F_1 and F_2 plants were determined in polymerase chain reaction (PCR) using molecular markers (primer synthesis was performed at Syntol LLC, Russia). Primers BF, MR1 and WR1In were used to identify *Rht-B1a* alleles (wild type) and *Rht-B1b*; PCR was per-

formed as recommended [33]. PCR products were separated in a 2 % agarose gel electrophoresis (TBE buffer; molecular weight marker GeneRuler 100 bp DNA Ladder, Thermo Fisher Scientific, USA) and stained with ethidium bromide for UV-visualization. Presence of *Ddw1* gene was determined with the primers for amplification of REMS1218 microsatellite loci sequence closely linked to this gene [34] as per the PCR protocol described by the authors of the molecular marker with fragment analysis (3130xl Genetic Analyzer, Applied Biosystems, USA). Dominant *Ddw1 Ddw1* homozygote produces two fragments of 317 bps and 321 bps with identical peak height, whereas *Ddw1 ddw1* heterozygote has two fragments with different peak height, of 317 bps (high) and 321 bps (low). One 317 bps fragment is detected in *ddw1 ddw1* recessive homozygote.

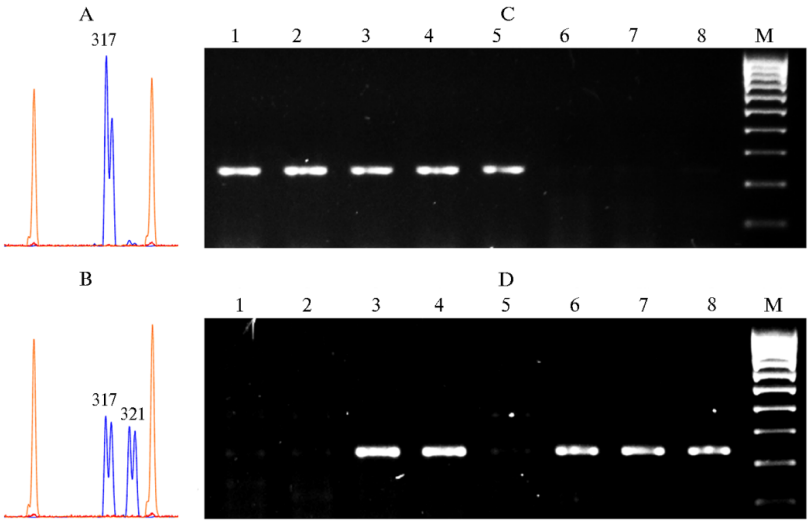
The pattern of allele inheritance was assessed based on genetic effects according to Smiryaev and Kilchevsky [35]. The additive (a) and dominant (d) effects were calculated regarding the average for the entire population. If $d = 0$ the inheritance is additive; if $d = a$, the allele is dominant, if $d = -a$, the allele is recessive; if $0 < |d| < |a|$, the allele is partially dominant (for identical, positive or negative, sings of d and a) or partially recessive (for different sings of d and a); if $|d| > |a|$, heterozygote displays overdominance for the analyzed trait (heterosis).

The impact of dwarf alleles on traits in question was determined in two ways based on comparison of their manifestation in dwarf and wild type allele homozygotes. To evaluate the effects of each gene separately (independent analysis), the average population values were compared for homozygotes with wheat genes (*Rht-B1a* or *Rht-B1b*) only, i.e. without the impact of rye genotype, or for homozygotes with rye gene (*Ddw1* or *ddw1*) only, i.e. without the impact of wheat genotype. To evaluate the combined effect of rye (*Ddw1*) and wheat (*Rht-B1*) genotypes, the impact of wheat gene was estimated depending on the rye gene allele status, and vice versa (interlocus interaction).

Distribution of quantitative parameters was tested for normality by Shapiro-Wilk *W* test. The arithmetical mean (*M*) and standard deviation (±SD) were determined. The significance of variance between homozygotes with wild type alleles (*ddw1* or *Rht-B1a*) and dwarf alleles (*Ddw1* or *Rht-B1b*) was determined as follows. Nonparametric Mann-Whitney *U*-test was used to evaluate the differences between the two groups. Analysis of Spearman's rank correlation coefficient (Spearman's ρ) was used to summarize the strength and direction (negative or positive) of a relationship between compared values. Differences were considered statistically significant at $p \leq 0.05$. To reveal reliable differences between the means, dispersion analysis and the least significant differences at the 5% level of significance ($p = 0.05$; LSD_{05}) were used. Statistical analysis was performed with Statistica 10.0 software (StatSoft Inc., USA).

Results. In order to determine the mode of inheritance and impact of dwarfing genes on spring triticale agronomic characters in the greenhouse we used seeds of F_2 generation from crossing Avanguard winter triticale variety (*Ddw1 Ddw1 Rht-B1a Rht-B1a* genotype) and Solovei Kharkovskii spring triticale variety (*ddw1 ddw1 Rht-B1b Rht-B1b* genotype). Avanguard combines high crop productivity with resistance to lodging, high winter- and cold resistance and good bread-baking qualities [36-38]. The second parent form, Solovei Kharkovskii, is grown for bread, technical and feed grain, possesses good bread-baking qualities, optimal height of culm (95-110 cm) which is robust and resistant to lodging [39].

The genotype of each F_2 plant was determined in terms of dwarfing gene allele profiles (Fig.) and main agronomic characters.



Identification of alleles of *Ddw1 genes* (A and B) **and *Rht-B1 genes*** (C and D) **in plants of spring triticale F_2 (Avanguard × Solovei Kharkovskii).** Electropherogram of PCR products amplified with the primers to REMS1218 microsatellite locus (fragment analysis): A — homozygote for *ddw1* allele, 317 bps; B — homozygote for *Ddw1* allele, 317 bps and 321 bps. Electropherogram of PCR products amplified with BF + WR1 primers (C, *Rht-B1a* identification, 237 bps) and BF + MR1 (D, *Rht-B1b* identification, 237 bps): 1, 2, 5 — *Rht-B1a Rht-B1a* homozygotes; 6, 7, 8 — *Rht-B1b Rht-B1b* homozygotes; 3, 4 —*Rht-B1a Rht-B1b* heterozygotes; M — molecular weight markers (GeneRuler 100 bp DNA Ladder (Thermo Fisher Scientific, USA).

Plant height. Statistical analysis revealed that *Ddw1* shows incomplete dominance in triticale, *Rht-B1b* allele is a partially recessive, and both genes significantly affect plant height in greenhouse conditions (Table 1).

Identification of *Ddw1* and *Rht-B1b* gene effects showed that in the resulting spring triticale segregating population of F_2 *Ddw1* dwarf allele has additive effect in case of height reduction by 20.9 cm on average and dominant effect when height is reduced by 11.7 cm ($d < a$). The *Ddw1* homozygotes and heterozygotes varied statistically significantly ($p = 0.05$). Thence, in terms of general impact on plant height this allele displays incomplete dominance. *Rht-B1b* allele turned out to be partially recessive, its additive effect amounted to 7.1 cm with dominant effect of +2.3 cm ($0 < |d| < |a|$) (homozygotes and heterozygotes *Rht-B1b* without *Ddw1* vary significantly, $p = 0.05$). Other authors also described *Rht-B1b* allele as a partially recessive [40-43].

1. Statistical analysis of *Rht-B1 and Ddw1* genes impact on plant height in F_2 segregating population of spring triticale hybrid (Avanguard × Solovei Kharkovskii; a greenhouse study)

Genotype for *Ddw1* alleles	Height, cm	Genotype for *Rht-B1*			Difference between homozygotes *Rht-B1b* and *Rht-B1a*, cm
		Rht-B1b Rht-B1b	*Rht-B1a Rht-B1b*	*Rht-B1a Rht-B1a*	
		height, cm			
		88.4±22.2[a] §	92.6±23.6[a] §	97.5±30.9[b] §	–9.1* (–9.3 %)
Ddw1 Ddw1	76.3±13.8[a] §	74.7±13.7	77.9±14.2	75.3±13.9	–0.6 (–0.8 %)
Ddw1 ddw1	84.3±18.7[a] §	84.5±19.6	84.3±16.1	84.0±22.0	
ddw1 ddw1	116.3±23.5[b] §	102.8±23.0	118.6±19.4	130.8±20.1	–28.0* (–21.4 %)
Difference between homozygotes *Ddw1* and *ddw1*, cm		–40.0* (–34.4 %)	–28.1* (–27.3 %)	–55.5* (–42.4%)	

N o t e. The table shows mean values with standard deviation (M±SD); § — the results of independent analysis of allele effect; $F(Ddw1) = 111.2 > F_{0.05} = 3.0$; $F(Rht\text{-}B1) = 5.0 > F_{0.05} = 3.0$; $F(Ddw1 \times Rht\text{-}B1) = 5.2 > F_{0.05} = 2.4$.
* The differences between homozygotes are essential at the 95% level of confidence probability ($p = 0.05$). Identical letters designate mean values identified in independent analysis for each gene, which did and differ statistically significantly at 95% level of confidence probability ($p = 0.05$).

When analyzing the effect of *Rht-B1b* allele without consideration of *Ddw1* gene (see Table 1) the difference between homozygotes *Rht-B1b Rht-B1b* and *Rht-B1a Rht-B1a* was statistically significant and constituted 9 cm or 9.1 % ($p = 0.05$). Furthermore, independent analysis of *Ddw1* effect identified that *Ddw1 Ddw1* and *ddw1 ddw1* homozygotes varied statistically significantly in terms of plant height (by an average of 40 cm or 34.4 %, $p = 0.05$).

When studying the interlocus interaction, the difference between *Rht-B1b Rht-B1b* and *Rht-B1a Rht-B1a* homozygotes in absence of *Ddw1* allele also turned out significant and constituted 28 cm or 21.0 % ($p = 0.05$) (see Table 1). The reduction of soft wheat plant height with *Rht-B1b* allele as compared to carriers of wild type *Rht-B1a* allele can be up to 17 % [42, 44]. In presence of *Ddw1* allele the differences between homozygotes and heterozygotes for *Rht-B1b* allele were statistically insignificant, which, possibly, can be explained by the masking effect of *Ddw1* gene, i.e. the reduction of height on account of *Ddw1* significantly exceeds such reduction due to presence of *Rht-B1b*.

The height difference between *Ddw1 Ddw1* and *ddw1ddw1* homozygote plants that do not carry wheat *Rht-B1b* was significant ($p = 0.05$) and constituted –55.5 cm (–42.4 %), and with those carrying *Rht-B1b* allele the difference amounted to 28.1 cm (–27.3 %) (see Table 1). Lower difference between homozygotes for *Ddw1* depending on presence of *Rht-B1b* can be explained by the fact that the *Ddw1* gene reduces the height of plants for which the height has already been reduced due to *Rht-B1b*. The differences between *Ddw1 Ddw1* homozygotes with and without *Rht-B1b* allele are statistically insignificant. Reportedly [22], the reduction of height of rye plants on account of *Ddw1* allele amounts to 40-55%.

According to the data that we obtained in the greenhouse study, during statistical analysis of spring triticale for each of the analyzed dwarfing genes their effects are similar to those in wheat and rye. In spring triticale genome the effect of *Ddw1* rye dwarf gene significantly exceeds the effect of *Rht-B1b* wheat dwarf gene. However, there is no cumulative effect of reducing plant height when both genes are present. In contrast [45, 46], when *Rht-B1b* and *Rht-D1b* or *Rht-B1b/Rht-B1e/Rht-D1b* and *Rht-8* dwarfing genes are simultaneously present in wheat, plant height is reduced much more significantly than under the effect of only one gene. Therefore, if the goal of the selection process consists of reducing the height of triticale plants, the combination of two dwarfing genes (*Ddw1* and *Rht-B1b*) will hardly prove more effective than introgression of one of the genes. Furthermore, it has to be taken into account that introduction of *Ddw1* gene in spring triticale genome will allow reducing the height of plants to a larger extent than using *Rht-B1b* gene which is currently prevalent in commercial varieties of this culture.

Joint quantity and length. In the course of independent analysis we observed no impact of *Rht-B1b* wheat gene on the number and length of joints in spring triticale population. The presence of *Ddw1* rye allele regardless of the *Rht-B1* wheat gene alleles reduces the number of joints on the average by 0.2 joints ($p = 0.05$); the reliable reduction of length on account of *Ddw1* was observed for all joints, whereas reduction was the highest for the upper 1st and 2nd joints (by 32.7 and 37.5 %, respectively, $p = 0.05$, Table 2).

During analysis of interlocus interaction in F_2 segregating population we failed to observe *Rht-B1b* allele effect with regard to the number of joints both in the presence and absence of *Ddw1* allele. Whereas *Ddw1* allele masks the effect of *Rht-B1b* on plant height in spring triticale, we have studied the consequences of presence of *Rht-B1b* allele on change of interlocus length only in plants that

2. *Rht-B1* and *Ddw1* gene effects on plant joint length in F_2 spring triticale segregating population (Avanguard × Solovei Kharkovskii; a greenhouse study)

Genotype	*Rht-B1* without *Ddw1*				*Ddw1*§				*Ddw1* without *Rht-B1b*				*Ddw1* with *Rht-B1b*			
	1LJ	3UL	2UJ	1UJ	1LJ§	3UL§	2UL§	1UL§	1LJ	3UL	2UL	1UL	1LJ	3UL	2UL	1UL
2	5.3±3.8^a	17.6±4.2^a	27.4±5.7^a	34.7±8.7^a	4.8±2.6^b	12.5±3.5^b	17.8±6.4^c	26.8±6.3^b	5.4±3.3	12.6±4.2	18.0±5.0	25.9±6.4	4.0±1.9^a	12.58±3.8^b	16.2±4.3^b	24.4±5.0^b
1	5.5±3.2^a	19.2±4.6^a	28.8±6.0^a	40.6±9.3^b	4.7±2.4^b	13.1±3.3^b	19.9±5.8^b	28.0±7.4^b	4.3±2.0	12.6±3.2	21.5±7.8	29.1±7.8	5.2±2.8^a	13.36±3.4^b	18.8±5.0^{ab}	26.1±8.4^b
0	7.0±3.8^a	18.2±3.6^a	32.6±6.5^a	44.2±10.0^a	5.9±3.6^a	17.8±4.3^a	28.5±6.3^a	39.8±9.9^a	7.0±3.8	18.2±3.7	31.0±6.5	44.4±10.0	5.3±3.8^a	16.30±4.2^a	26.0±5.7^a	35.1±8.7^a
Difference between homozygotes, cm (%)	–1.7 (–23.0 %)	–2.0 (–10.0 %)	–5.2 (–16.0 %)	–9.5* (–22.0 %)	1.1* (18.6 %)	5.3* (29.6 %)	10.7* (37.5 %)	13.0* (32.7 %)	–1.6 (23.0 %)	5.6* (31.0 %)	–13.0* (42.0 %)	–18.5* (42.0 %)	–1.3 (25.0 %)	–3.7* (23.0 %)	–9.8* (38.0 %)	–10.6* (30.0 %)

N o t e. The table shows mean values with standard deviation (*M*±SD); 0 — homozygote for wild type allele (*Rht-B1a Rht-B1a* or *ddw1 ddw1*), 1 — heterozygote (*Rht-B1a Rht-B1b* or *Ddw1 ddw1*), 2 — homozygote for dwarf allele (*Rht-B1b Rht-B1b* or *Ddw1 Ddw1*); 1LJ — 1st lower joint, 1UJ —1st upper joint, 2UJ — 2nd lower joint, 3UJ − 3rd upper joint; § — the results of independent *Ddw1* effect analysis.

* The differences between homozygotes are statistically significant at 95% level of confidence probability (p = 0.05). Identical letters designate mean values identified in independent analysis for each gene (or gene combinations) which did not differ at 95% level of confidence probability (p = 0.05).

do not carry *Ddw1* allele (see Table 2). The statistically significant reduction of length on account of *Rht-B1b* occurred for the 1st upper joint and amounted to 9.5 cm (–22.0%, $p = 0.05$). An overall dwarfing tendency was observed for all joints on account of *Rht-B1b*. According to the published data, joint height is reduced unevenly in various wheat populations due to presence of *Rht-B1b*. For instance, Liu et al. [4] report 17, 21 and 24% distribution by joints (the 1st, 2nd and 3rd joint from the top, respectively); whereas Hu [47] reports joint distribution of 23, 14 and 28%. According to other papers [4, 47] and results we obtained, the biggest contribution to plant height reduction in the presence of *Rht-B1b* is ensured specifically on account of length reduction of the 1st joint.

The analysis of the first interlocus interaction showed that in presence of *Rht-B1b* wheat dwarf allele the 1st upper joint is shortened under the impact of *Ddw1* allele on the average by 18.5 cm (42.0 %), and due to *Rht-B1b* allele by 10.6 cm (30.0%); in both cases the statistically significant height reduction ($p = 0.05$) was in three upper joints (see Table 2). The *Ddw1* impact on joint length depending on presence/absence of *Rht-B1b* is due to the fact that in absence of *Rht-B1b* the 1st joint is already dwarfed due to wheat dwarf gene effect.

Head length. *Rht-B1b* allele did not display sufficient impact on head length. Statistically significant differences (at $p = 0.04$) were identified in independent analysis of impact of *Ddw1* rye dwarf gene on head length using non-parametric Mann-Whitney *U*-test (distribution deviated from normal). Furthermore, statistically significant correlation between head length and *Ddw1* in plant genome ($\rho = –0.15$; $p = 0.05$) was identified using Spearman rank correlation test. Therefore, greenhouse study showed that *Ddw1* rye gene statistically significantly reduced head length by 1 cm on the average.

We have not observed any statistically significant effect of interlocus interaction of two genes on main head length in spring triticale in F_2 segregating population in question. The average head length of plants was 10.3 cm without dwarfing genes, 9.3 cm with *Ddw1* gene, 8.9 cm with *Rht-B1b* gene and 9.5 cm with two genes (Table 3).

Number of ears. We have not observed statistically significant impact of two analyzed genes on the number of ears of main head in spring triticale in F_2 segregating population in question either in the course of independent analysis or during analysis of interlocus interaction (see Table 3); however, we can identify certain tendency in this trait change. For instance, in the presence of *Ddw1* rye dwarf gene *Rht-B1b* wheat dwarf gene increased the number of ears on the main head and a reverse effect was observed in absence of the rye gene (see Table 3).

Head density. In independent gene analysis (see Table 3) we identified statistically significant impact of *Rht-B1b* gene (Mann-Whitney *U*-test, $p = 0.02$) on head density increase. When using Spearman rank correlation analysis we also observed statistically significant correlation ($\rho = 0.19$, $p = 0.05$). The higher head density in this case was due to an increase in ears. In the course of independent analysis *Ddw1* allele did not display any statistically reliable impact on head density of spring triticale. This is presumably connected with unidirectional nature of head length reduction tendencies and with the number of ears. Furthermore, we have not observed any statistically significant impact of genes in terms of this criterion in spring triticale in F_2 segregating population.

Number of grains in the main head. Analysis of the *Rht-B1* gene inheritance showed its reliable additive impact on the number of grains in the main head (+3.3 grains or 9.2 %, $p = 0.05$); furthermore, *Rht-B1b* allele manifested itself as dominant, i.e. *Rht-B1b* heterozygotes and homozygotes did not

vary significantly (see Table 3). These data are comparable with the impact of *Rht-B1b* gene on the number of grains in soft wheat. As reported [42, 44, 48, 49], this gene increases the number of ears, their fertility, and, consequently, the number of grains in soft wheat.

We have not identified the impact of *Ddw1* gene on the number of grains per main head, although we observed the tendency to reduction of this parameter in absence of *Rht-B1b* dwarf allele. Furthermore, we have not observed any statistically significant impact of these two genes on the number of grains per main head in spring triticale in F_2 segregating population in question (see Table 3).

Grain weight per main head. In independent analysis of each gene individual effect under greenhouse conditions we identified the following patterns (see Table 3). The presence of *Rht-B1b* wheat dwarf allele resulted in statistically significant increase of main head grain weight (Mann-Whitney *U*-test $p = 0.04$) from 1.4 to 1.7 g (by 21.4 %). Furthermore, these parameters reliable correlate ($r = 0.15$; $p = 0.05$). The presence of *Ddw1* rye dwarf gene statistically significantly reduced the grain weight per main head (Mann-Whitney *U*-test $p = 0.02$) from 1.8 to 1.5 g (by 16.7 %) where $r = -0.18$ ($p = 0.05$).

3. *Rht-B1* and *Ddw1* gene effects on head and grain parameters in F_2 spring triticale segregating population (*M*±SD; Avanguard × Solovei Kharkovskii; a greenhouse study)

Genotype for *Ddw1*	Genotype for *Rht-B1*		
	Rht-B1b Rht-B1b	*Rht-B1a Rht-B1b*	*Rht-B1a Rht-B1a*
Main head length			
$F(Ddw1) = 0.8 < F_{0.05} = 3.1$; $F(Rht\text{-}B1) = 0.1 < F_{0.05} = 3.1$; $F(Ddw1 \times Rht\text{-}B1) = 0.7 < F_{0.05} = 2.4$			
Ddw1 Ddw1	9.5±3.4	8.5±1.8	9.3±2.9
Ddw1 ddw1	10.1±2.5	9.8±1.5	10.0±2.0
ddw1 ddw1	8.9±2.1	10.2±2.1	10.3±1.8
Number of ears per main head			
$F(Ddw1) = 2.0 < F_{0.05} = 3.1$; $F(Rht\text{-}B1) = 2.0 < F_{0.05} = 3.1$; $F(Ddw1 \times Rht\text{-}B1) = 1.8 < F_{0.05} = 2.4$			
Ddw1 Ddw1	24.0±5.5	23.4±3.5	21.1±5.2
Ddw1 ddw1	25.4±4.2	23.7±3.4	22.1±4.1
ddw1 ddw1	23.5±4.1	25.2±3.6	25.1±3.2
Main head density			
$F(Ddw1) = 2.0 < F_{0.05} = 3.1$; $F(Rht\text{-}B1) = 0.5 < F_{0.05} = 3.1$; $F(Ddw1 \times Rht\text{-}B1) = 1.2 < F_{0.05} = 2.4$			
Ddw1 Ddw1	25.1±7.0	26.6±3.2	23.2±4.5
Ddw1 ddw1	25.5±4.7	24.6±4.0	22.6±4.1
ddw1 ddw1	27.4±5.3	25.5±5.6	25.4±6.1
Grain number per main head			
$F(Ddw1) = 0.7 < F_{0.05} = 3.0$; $F(Rht\text{-}B1) = 2.5 < F_{0.05} = 3.0$; $F(Ddw1 \times Rht\text{-}B1) = 0.9 < F_{0.05} = 2.4$			
Ddw1 Ddw1	38.3±10.7	38.3±11.3	28.5±13.7
Ddw1 ddw1	36.4±17.8	36.2±12.5	32.2±15.8
ddw1 ddw1	34.2±18.0	42.1±15.6	37.4±7.9
Grain weight per main head			
$F(Ddw1) = 1.9 < F_{0.05} = 3.1$; $F(Rht\text{-}B1) = 3.5 > F_{0.05} = 3.1$; $F(Ddw1 \times Rht\text{-}B1) = 0.5 < F_{0.05} = 2.4$			
Ddw1 Ddw1	1.70±0.45	1.67±0.66	1.27±0.69
Ddw1 ddw1	1.56±0.87	1.64±0.72	1.27±0.77
ddw1 ddw1	1.61±0.92	2.01±0.80	1.66±0.40
1000-grain weight			
$F(Ddw1) = 1.6 < F_{0.05} = 3.1$; $F(Rht\text{-}B1) = 1.9 < F_{0.05} = 3.1$; $F(Ddw1 \times Rht\text{-}B1) = 0.5 < F_{0.05} = 2.4$			
Ddw1 Ddw1	45.6±9.7	42.8±9.0	40.7±14.2
Ddw1 ddw1	41.6±9.5	45.6±17.1	37.5±12.9
ddw1 ddw1	45.0±11.5	48.1±7.8	44.5±9.2

When studying the interlocus interaction in the population, the statistically significant dominant effect of *Rht-B1b* allele with regard to main head grain weight was +0.28 g (16.0 %), i.e. this allele increases main head grain weight in heterozygotes (see Table 3). There were no statistically significant differences during interaction of two genes; however, a tendency for head grain weight increase was observed in presence of *Rht-B1b* and for head grain weight reduction in presence of *Ddw1*. Generally speaking, we can assume there is a tendency of mutual compensation of gene effects in the studied segregating population of spring triticales for the analyzed trait (reduction of head grain weight under the

influence of *Ddw1* gene and increase of head grain weight under the influence of *Rht-B1b* gene).

1000-grain weight. When analyzing F_2 segregating population for each gene individually (see Table 3) it turned out that presence of *Rht-B1b* wheat dwarf allele does not have any statistically significant impact on the weight of 1000 grains. The presence of *Ddw1* rye dwarf gene statistically significantly reduced the 1000-grain weight for main head (Mann-Whitney *U*-test $p = 0.02$) from 45.7 to 41.3 g (by 9.6 %) under greenhouse comditions. Furthermore, there was a statistically significant correlation between the analyzed parameters $r = -0.17$ ($p = 0.05$). Consequently, the overall reduction of main head grain weight in presence of *Ddw1* rye dwarf gene is primarily attributable to the reduction of caryopsis weight and not reduction of their quantity. When analyzing the mode of inheritance, we observed an insignificant dominant effect of *Rht-B1b* gene with regard to the 1000-grain weight, which is expressed in the increase of this characteristic in heterozygotes on the average by 4.2 g (10.1%). The insignificant additive effect of *Ddw1* allele consisted in the 1000-grains weight reduction on the average by 2.0 g (4.5 %), whereas *Ddw1* manifested itself as dominant allele by revealing itself in homozygotes and heterozygotes.

This and the other patterns we identified require additional study on other populations of spring triticale and in field conditions.

To summarize, a greenhouse study we conducted on F_2 spring triticale hybrid segregating population showed that effects of *Ddw1* dwarfing genes of rye origin and *Rht-B1b* of wheat origin are slightly different from the effects on rye and wheat. *Ddw1* gene has statistically significant impact on plant height (its reduction reached 40%). However, potentially negative effects are observed in addition to that, which can backfire on crop yield of spring triticale. The presence of *Ddw1* gene resultes in reduction of overall head grain weight due to a decrease in 1000-grais weight. Furthermore, *Ddw1* gene, which in rye increases head size and grains per head, did not have this effect in our test on spring triticale. *Rht-B1b* gene also reduces plant height of spring triticale plant, but to a much smaller degree than *Ddw1* gene (to 20%), and does not affect this trait at all in presence of *Ddw1* gene. At the same time presence of *Rht-B1b* gene increased grain weight per head due to increase in head density, number of ears and fertility. In general, the dwarf genes in question (*Ddw1* of rye origin and *Rht-B1b* of wheat origin) were antagonists in terms of their impact on grain productivity parameters. However, their combination in spring triticale, although it does not result in additional reduction of plant height relative to *Ddw1* homozygotes, is promising for breeding due to potential of increasing crop yield on account of creation of dwarf forms.

REFERENCES

1. *FAOSTAT. Data*. Available http://www.fao.org/faostat/en/#data. Accessed 20.04.2018.
2. Goryanina T.A. *Izvestiya Orenburgskogo gosudarstvennogo agrarnogo universiteta*, 2017, 5(67): 42-44 (in Russ.).
3. McGoverin C.M., Snyders F., Muller N., Botes W., Fox G., Manley M. A review of triticale uses and the effect of growth environment on grain quality. *Journal of the Science of Food and Agriculture*, 2011, 91(7): 1155-1165 (doi: 10.1002/jsfa.4338).
4. Liu W., Leiser W.L., Maurer H.P., Li J., Weissmann S., Hahn V., Würschum T. Evaluation of genomic approaches for marker-based improvement of lodging tolerance in triticale. *Plant Breeding*, 2015, 134(4): 416-422 (doi: 10.1111/pbr.12284).
5. Losert D., Maurer H.P., Marulanda J.J., Würschum T. Phenotypic and genotypic analyses of diversity and breeding progress in European triticale (× *Triticosecale* Wittmack). *Plant Breeding*, 2017, 136(1): 18-27 (doi: 10.1111/pbr.12433).
6. Navabi A., Iqbal M., Strenzke K., Spaner D. The relationship between lodging and plant height

in a diverse wheat population. *Canadian Journal of Plant Science*, 2006, 86(3): 723-726 (doi: 10.4141/p05-144).
7. Würschum T., Liu W., Busemeyer L., Tucker M., Reif J., Weissmann E., Hahn V., Ruckelshausen A., Maurer H. Mapping dynamic QTL for plant height in triticale. *BMC Genetics*, 2014, 15(1): 59 (doi: 10.1186/1471-2156-15-59).
8. Miedaner T., Hübner M., Korzun V., Schmiedchen B., Bauer E., Haseneyer G., Wilde P., Reif J.C. Genetic architecture of complex agronomic traits examined in two testcross populations of rye (*Secale cereale* L.). *BMC Genomics*, 2012, 13(1): 706 (doi: 10.1186/1471-2164-13-706).
9. McIntosh R.A., Yamazaki Y., Dubcovsky J., Rogers J., Morris C., Appels R., Xia X.C. *Catalogue of gene symbols for wheat, 2013*. Available https://shigen.nig.ac.jp/wheat/komugi/genes/macgene/2013/GeneSymbol.pdf. Accessed 20.04.2018.
10. McIntosh R.A., Dubcovsky J., Rogers W.J., Morris C., Xia X.C. *Catalogue of gene symbols for wheat, 2017*. Available https://shigen.nig.ac.jp/wheat/komugi/genes/macgene/supplement2017.pdf. Accessed 20.04.2018.
11. Mo Y., Vanzetti L., Hale I., Spagnolo E., Guidobaldi F., Al-Oboudi J., Odle N., Pearce S., Helguera M., Dubcovsky J. Identification and characterization of *Rht25*, a locus on chromosome arm 6AS affecting wheat plant height, heading time, and spike development. *Theoretical and Applied Genetics*, 2018, 131(10): 2021-2035 (doi: 10.1007/s00122-018-3130-6).
12. Jobson E., Martin J., Schneider T., Giroux M. The impact of the *Rht-B1b*, *Rht-D1b*, and *Rht-8* wheat semi-dwarfing genes on flour milling, baking, and micronutrients. *Cereal Chemistry*, 2018, 95(6): 770-778 (doi: 10.1002/cche.10091).
13. Zhao K., Xiao J., Liu Y., Chen S., Yuan C., Cao A., You F., Yang D., An S., Wang H., Wang X. *Rht23* (5Dq′) likely encodes a *Q* homeologue with pleiotropic effects on plant height and spike compactness. *Theoretical and Applied Genetics*, 2018, 131(9): 1825-1834 (doi: 10.1007/s00122-018-3115-5).
14. Rebetzke G.J., Bonnett D.G., Ellis M.H. Combining gibberellic acid-sensitive and insensitive dwarfing genes in breeding of higher-yielding, sesqui-dwarf wheats. *Field Crops Research*, 2012, 127: 17-25 (doi: 10.1016/j.fcr.2011.11.003).
15. Divashuk M., Vasilyev A., Bespalova L., Karlov G. Identity of the *Rht-11 and Rht-B1e* reduced plant height genes. *Russian Journal of Genetics*, 2012, 48(7): 761-763 (doi: 10.1134/S1022795412050055).
16. Divashuk M.G., Fesenko I.A., Karlov G.I., Bespalova L.A., Vasilyev A.V., Puzyrnaya O.Y. Reduced height genes and their importance in winter wheat cultivars grown in southern Russia. *Euphytica*, 2013, 190(1): 137-144 (doi: 10.1007/s10681-012-0789-7).
17. Mahone G.S., Frisch M., Bauer E., Haseneyer G., Miedaner T., Falke K.C. Detection of donor effects in a rye introgression population with genome-wide prediction. *Plant Breeding*, 2015, 134(4): 406-415 (doi: 10.1111/pbr.12283).
18. Alheit K., Busemeyer L., Liu W., Maurer H., Gowda M., Hahn V., Weissmann S., Ruckelshausen A., Reif J., Würschum T. Multiple-line cross QTL mapping for biomass yield and plant height in triticale (× *Triticosecale* Wittmack). *Theoretical and Applied Genetics*, 2013, 127(1): 251-260 (doi: 10.1007/s00122-013-2214-6).
19. Börner A., Plaschke J., Korzun V., Worland A. The relationships between the dwarfing genes of wheat and rye. *Euphytica*, 1996, 89(1): 69-75 (doi: 10.1007/bf00015721).
20. Kobylyanskii V.D. *Materialy II Vavilovskoi mezhdunarodnoi konferentsii «Geneticheskie resursy kul'turnykh rastenii v XXI veke. Sostoyanie, problemy, perspektivy»* [Proc. II Vavilov Int. Conf. «Genetic resources of cultivated plants in the XXI century. Status, problems, prospects»]. St. Petersburg, 2007: 476-477 (in Russ.).
21. Stojałowski S., Myskow B., Hanek M. Phenotypic effect and chromosomal localization of *Ddw3*, the dominant dwarfing gene in rye (*Secale cereale* L.). *Euphytica*, 2015, 201(1): 43-52 (doi: 10.1007/s10681-014-1173-6).
22. Hackauf B., Goldfisch M., Musmann D., Melz G., Wehling P. Evaluation of the dominant dwarfing gene *Ddw1* with respect to its use in hybrid rye breeding. *Tagung der Vereinigung der Pflanzenzüchter und Saatgutkaufleute Österreichs*, 2013, 63: 41-42.
23. Kobylyanskii V.D., Solodukhina O.V. *Trudy po prikladnoi botanike, genetike i selektsii*, 2012, 169: 53-64 (in Russ.).
24. Wolski T., Gryka J. Semidwarf winter triticale. *Triticale today and tomorrow*. H. Guedes-Pinto, N. Darvey, V.P. Carnide (eds.). Kluwer Academic Publishers, Dordrecht Boston London, 1996: 581-588.
25. Pojmaj M.S., Wolski T. *Breeding strategies for improving lodging resistance in winter triticale in connection with heterosis*. CIMMYT, 1991. Available http://agris.fao.org/agris-search/search.do?recordID=QY9200132. No date.
26. Ittu G., Saulescu N.N., Ittu M., Mustatea P. Introduction of short straw genes in Romanian triticale germplasm. *Romanian Agricultural Research*, 2007, 24: 7-10.
27. Banaszak Z. Breeding of triticale in DANKO. *Tagung der Vereinigung der Pflanzenzüchter und Saatgutkaufleute Österreichs*, 2010, 61: 65-68.

28. Korshunova A.D., Divashuk M.G., Soloviev A.A., Karlov G.I. Analysis of wheat and rye semidwarfing gene distribution in spring hexaploid triticale (*Triticosecale* Wittm.) cultivars and breeding lines. *Russian Journal of Genetics*, 2015, 51(3): 272-277 (doi: 10.1134/s1022795415030072).
29. Korshunova A.D., Divashuk M.G., Karlov G.I., Solov'ev A.A. *Izvestiya TSKHA*, 2014, 6: 5-14 (in Russ.).
30. Bazhenov M.S., Divashuk M.G., Krupin P.Yu., Pylnev V.V., Karlov G.I. The effect of 2D (2R) substitution on the agronomical traits of winter triticale in early generations of two connected crosses. *Cereal Research Communications*, 2015, 43(3): 504-514 (doi: 10.1556/0806.43.2015.002).
31. Thomas S.G. Novel *Rht-1* dwarfing genes: tools for wheat breeding and dissecting the function of DELLA proteins. *Journal of Experimental Botany*, 2017, 68(3): 354-358 (doi: 10.1093/jxb/erw509).
32. Bernatzky R., Tanksley S.D. Genetics of actin-related sequences in tomato. *Theoretical and Applied Genetics*, 1986, 72(3): 314-321 (doi: 10.1007/BF00288567).
33. Ellis M., Spielmeyer W., Gale K., Rebetzke G., Richards R. "Perfect" markers for the *Rht-B1b* and *RhtD1b* dwarfing genes in wheat. *Theoretical and Applied Genetics*, 2002, 105: 1038-1042 (doi: 10.1007/s00122-002-1048-4).
34. Tenhola-Roininen T., Tanhuanpää P. Tagging the dwarfing gene *Ddw1* in a rye population derived from doubled haploid parents. *Euphytica*, 2010, 172(3): 303-312 (doi: 10.1007/s10681-009-9982-8).
35. Smiryaev A.V., Kil'chevskii A.V. *Genetika populyatsii i kolichestvennykh priznakov* [Genetics of populations and quantitative traits]. Moscow, 2007 (in Russ.).
36. Kovtunenko V.Ya., Timofeev V.B., Dudka L.F., Panchenko V.V. *Selektsiya i nasinnitstvo*, 2008, 96: 89-97 (in Russ.).
37. Pinkal' A.V. *Omskii nauchnyi vestnik*, 2012, 2 (114): 167-172 (in Russ.).
38. Gol'dvarg B.A., Gritsienko V.G., Boraeva L.N. *Sbornik nauchnykh trudov Vserossiiskogo nauchno-issledovatel'skogo instituta ovtsevodstva i kozovodstva*, 2007, 2(2-2): 124-128 (in Russ.).
39. *Innovatsionnye sorta i tekhnologii vozdelyvaniya yarovogo tritikale: kollektivnaya monografiya* [Innovative varieties and technologies for spring triticale cultivation: a collective monograph]. Vladimir, 2017 (in Russ.).
40. Gale M.D., Salter A.M., Angus F.J. The effect of dwarfing genes on the expression of heterosis for grain yield in F_1 hybrid wheat. In: *Current options for cereal improvement*. M. Maluszynski (ed.). Kluwer Academic, Dordrecht, 1989: 49-62.
41. Keyes G., Sorrells M. *Rht1* and *Rht2* semidwarf genes effect on hybrid vigor and agronomic traits of wheat. *Crop Science*, 1989, 29: 1442-1447 (doi: 10.2135/cropsci1989.0011183X002900060023x).
42. Flintham E., Borner A., Worland A., Gale M. Optimizing wheat grain yield effects of *Rht* (gibberellin-insensitive) dwarfing genes. *The Journal of Agricultural Science*, 1997, 128: 11-25 (doi: 10.1017/S0021859696003942).
43. Flintham J.E., Gale M.D. Plant height and yield components of inbred isogenic and F_1 hybrid dwarf wheat. *Journal of Applied Genetics*, 1998, 39: 73-83.
44. Gale M.D., Youssefian S. Dwarfing genes in wheat. In: *Progress in plant breeding*. G.E. Russel (ed.). Butterworths and Co., London, 1985, V. 1: 1-35.
45. Li X., Lan S., Liu Y., Gale M., Worland T. Effects of different Rht-B1b, Rht-D1b and Rht-B1c dwarfing genes on agronomic characteristics in wheat. *Cereal Research Communications*, 2006, 34(2-3): 919-924 (doi: 10.1556/CRC.34.2006.2-3.220).
46. Chebotar G., Motsnyy I., Chebotar S., Sivolap Y. Effects of dwarfing genes on the genetic background of wheat varieties in Southern Ukraine. *Cytology and Genetics*, 2012, 46(6): 366-372 (doi: 10.3103/S0095452712060023).
47. Hu Y.G. *Utilization of dwarfing genes to improve drought tolerance and yield potential in wheat, 2012*. Available http://www.ub.edu/optichinagriculture/data/uploads/workshop2/presentations/hu-yin-gang-nwaandfu.pdf. Accessed 20.04.2018.
48. Miralles D.J., Katz S.D., Colloca A., Slafer G.A. Floret development in near isogenic wheat lines differing in plant height. *Field Crops Research*, 1998, 59(1): 21-30 (doi: 10.1016/S0378-4290(98)00103-8).
49. Miralles D.J., Slafer G.A. Individual grain weight responses to genetic reduction in culm length in wheat as affected by source-sink manipulations. *Field Crops Research*, 1995, 43 (2-3): 55-66 (doi: 10.1016/0378-4290(95)00041-N).