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Pleiotropic Effects of Gibberellin-Sensitive and Giberrellin-Insensitive Dwarfing Genes in Bread Wheat of the Southern Step Region of the Black Sea

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Abstract—Investigation of the pleiotropic effects of GA-sensitive (*Rht8*) and *GA*-insensitive (*Rht-B1* and *Rht-D1*) winter bread wheat dwarfing genes and the gene that determines the response of plants to photoperiod—*Ppd-D1*—were carried out for 3 years in the southern step region of the Black Sea bank on five different genetic backgrounds. It is shown that, in addition to direct effects on plant height, GA-sensitive and GA-insensitive dwarfing genes have pleiotropic effects on all studied traits except the number of fertile spikelets. Presence of the dwarfing genes in the genotype of tall forms led to the decrease of stem and ear length, and, at the same time, to the increase of ear density. The number of spikelets per spike decreased due to sterile spikelets, whereas the number of fertile spikelets did not change. There was a significant increase in the number of grains per ear as a result of increasing of spikelets in ears. The number and weight of grains did not decrease, even though the plants were characterized by a smaller number of productive tillers. The presence of *Rht8x* allele on genetic background of variety Stepnyak resulted in a significant decrease of plants productivity. However, in combination with *Ppd-D1a* allele, plants with *Rht8x* increased the potential productivity and surpassed the parental form (*Rht8x Ppd-D1a*). The presence of *Rht-Ble* allele resulted in reduction of weight of kernels from the main ear and 1000-kernels weight, increase of *l*/*h*, and left the number of seeds per spikelet stable in comparison with *Rht8x*.

Keywords: winter bread wheat, dwarfing genes, photoperiod sensitivity genes, quantitative traits

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INTRODUCTION

Height and productivity of plants are complex quantitative traits subjected to polygenic control [1–3]. Expression of the reduced height genes (*Rht*), as well as their effects on agronomic traits, depends on both environmental conditions and genetic background. Breeding by the reduced height genes is aimed at the combination of advantageous alleles or their complexes with other agriculturally valuable traits in the same genetic background in specific ecological and climatic conditions in order to increase plant productivity. Use of the reduced height genes has become the element of the breeding strategy aimed at the cultivating of highly productive wheat varieties [4].

GA-insensitive plants carrying the *Rht-B1b*, *Rht-B1e*, and *Rht-D1b* alleles are characterized by reduced height, because of decreased sensitivity of their vegetative tissues to endogenous gibberellin (GA) [5]. This effect manifests as the decrease in cell lengthening in almost all vegetative organs, and followed not only by the reduction in height of adult plants but also by the decrease in length of coleoptile, internodes, and leaf area. Analysis of molecular structure of the alleles showed that mutations in *Rht-B1b* and *Rht-D1b* are represented by single nucleotide polymorphisms (C/T in the 64th position and G/T in the 61st position) that transform CGA and GGA-codons into TGA-nonsense codon [7]. The nucleotide sequence of the *Rht-B1e* allele carries the mutation that leads to the formation of TAG nonsense-codon, because of an A to T nucleotide substitution in the K61A codone (AAG), which is located three codons upstream than the *Rht-B1e*-mutated codon [8].

The allele *Rht8c* is not connected with metabolism of GA. It is related to GA-sensitive reduced height genes, and its presence does not lead to the decrease of coleoptile length and leaf lengthening rate [9]. Presence of the *Rht8c* is advantageous for plants that grow in regions suffering from early spring drought and where lack of humidity prevents successful growth and development of GA-sensitive plants [9–11]. Presently, the gene *Rht8* was not sequenced, though attempts to its positioning cloning were made [12]. At the molecular level, the allelic variations of this gene are detected by microsatellite marker *Xgwm261*, which is located 1.95 cM from the gene [12].

Understanding of pleiotropic effects of the *Rht*-genes on the agriculturally important traits is important for their further effective use in order to increase productivity of this culture. Different dwarfing genes

Table 1. Allelic characteristics of the analogue lines by the reduced height genes and *Ppd-D1*

Line	Origin	*Rht8*	*Rht-B1*	*Rht-B1*	*Ppd-D1*
Kooperatorka	Collected from Krymki	*Rht8a*	*Rht-B1a*	*Rht-D1a*	*Ppd-D1b*
Kooperatorka K-90	[(Kooperatorka/Odesskaya semi-dwarf (OSD)/Kooperatorka^6]F∞	*Rht8c*	*Rht-B1a*	*Rht-D1a*	*Ppd-D1a*
Kooperatorka K-70	[(Kooperatorka/OSD)/Kooperatorka^6]F∞	*Rht8c*	*Rht-B1e*	*Rht-D1a*	*Ppd-D1a*
Odesskaya 3	Kooperatorka/Hostianum 237	*Rht8a*	*Rht-B1a*	*Rht-D1a*	*Ppd-D1b*
Odesskaya 3 K-75	[(Odesskaya 3^6/OSD/Odesskaya 3^6]F∞	*Rht8c*	*Rht-B1b*	*Rht-D1a*	*Ppd-D1a*
Odesskaya 51	Odesskaya 16/Bezostaya 1	*Rht8c*	*Rht-B1a*	*Rht-D1a*	*Ppd-D1a*
Odesskaya 51 K-73	(Krasnodarskiy Karlik 1/Odesskaya 51^7)F∞	*Rht8c*	*Rht-B1e*	*Rht-D1a*	*Ppd-D1a*
Stepnyak 1	Lines of the breed Stepnyak selected by molecular markers	*Rht8a*	*Rht-B1a*	*Rht-D1a*	*Ppd-D1b*
Stepnyak 2		*Rht8x*	*Rht-B1a*	*Rht-D1a*	*Ppd-D1a*
Stepnyak 3		*Rht8c*	*Rht-B1a*	*Rht-D1a*	*Ppd-D1a*
Stepnyak 2K	[(Stepnyak 2/OSD//Stepnyak 2^7]F∞	*Rht8c*	*Rht-B1a*	*Rht-D1b*	*Ppd-D1a*
Odesskaya 16	Collected from the breed Odesskaya 12	*Rht8x*	*Rht-B1a*	*Rht-D1a*	*Ppd-D1b*
Bezostaya 1	Collected from the breed Bezostaya 4	*Rht8c*	*Rht-B1a*	*Rht-D1a*	*Ppd-D1a*
Karlik 1 (UA0102183)	Mutant of the breed Bezostaya 1	*Rht8c*	*Rht-B1b*	*Rht-D1a*	*Ppd-D1a*

provide different effects on seed germination, plant height, and productivity. Besides the *Rht*-genotype, these traits are also affected by the growing conditions and genetic background, on whose basis the presence of certain genes of reduced height or their combinations is manifested [13]. Previous studies, which were carried out in northwest Russia, the Lower Volga Region, and Krasnodar Territory, confirmed the influence of these genes on plant height [14, 15]. However, pleiotropic effects of these genes were not studied. The experiments were carried out mostly on spring varieties, though near-isogenic lines may be more representative genetic material to estimate the effects of these genes.

Near-isogenic lines may precisely mirror the effects of different genes of reduced height due to their similar genetic background. However, the development of such lines is a quite complicated and time-consuming procedure. In 2011–2012, in south Ukraine, plants of almost isogenic lines developed on the basis of the *Mercia* variety were destroyed (81%) by −20°C frost in the Plant Breeding and Genetics Institute–National Center of Seed and Cultivar Investigation (PBGI) under field conditions. At the same time, most of the analogous lines developed by V.V. Khangildin on the basis of genetic background of Ukrainian varieties (approximately 95%) survived adverse environmental conditions (unpublished data).

The goal of the present study was to investigate the pleiotropic effects of alleles of GA-sensitive (*Rht8*) and GA-insensitive (*Rht-B1* and *Rht-D1*) dwarfing genes, as well as the *Ppd-D1* gene, which is inherited in coupling with the *Rht8* and controls sensitivity of plants to the photoperiod, and affects agricultural traits of bread wheat in dependance of the genetic background of recurrent forms.

MATERIALS AND METHODS

The object of the study were the analogous lines with reduced height, parental forms, and reduced height gene donors (Table 1), which differed from each other by height and the dwarfing genes, that were identified by molecular markers (Table 1).

The analogous lines were developed in the PBGI, in the 1990s, by V.V. Khangildin (Odessa, Ukraine) by crossing of the parental forms with the reduced height gene donors (Odesskaya semi-dwarf or Krasnodarskiy Karlik 1) and by six-time back-crossing with recurrent forms [19]. The Krasnodarskiy Karlik 1 breed is known to be obtained by artificial mutagenesis of the variety Bezostaya 1. Therefore, these two varieties were considered to be analogous. The line of the Odesskaya 16 variety were considered to be analogous to the lines developed on the basis of the genetic background of the Stepnyak variety, because it is involved in the pedigree of this variety.

Agricultural parameters were analyzed in comparative experiments (2008/2009, 2009/2010, and 2010/2011), which were carried out in the PBGI under field conditions (30°44′′ eastern longitude, 46°28′′ northern latitude). Plants were sowed in the middle of October, which is considered to be the optimal period for sowing of wheat in the Black Sea littoral zone. Plants were grown under the conditions of wide-space sowing: two-space blocks, in three repeats (5 cm space between plants within the row and 27 cm between the rows). The analogous lines were placed within the