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CREATION OF A SPRING SOFT WHEAT VARIETY GRENADA WITH THE USE OF INNOVATIVE BREEDING TECHNOLOGIES BASED ON THE ORIGINAL THEORY OF ECO-GENETIC ARRANGEMENT OF QUANTITATIVE TRAITS

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Abstract

Today, there is an excessive belief in the promise of molecular approaches to the problem of increasing yields, although so far there is not a single variety created by purely molecular methods. In addition, representatives of the new science, the epigenetics, rightly argue that in nature there are no specific genes for productivity and yield that could be molecularly marked or subjected to genomic editing. This article is the first to describe creation of a wheat variety Grenada using innovative breeding technologies emerged from the priority Russian Theory of Eco-Genetic Organization of Quantitative Traits (TEGOQT) which derived from the results of the Interdisciplinary DIAS Program (genetics of spring wheat productivity in Western Siberia) (1973-1984). The essence of these technologies are 1) a special selection of parental pairs on the basis of a deep analysis of the longest pedigrees of the old breeds of parents taken in crosses, 2) priority phenotyping of the group of the most productive varieties of the collection nursery for seven genetic-physiological systems (GPS) which positively or negatively contribute to the harvest, 3) selection of genotypes that have at least one GPS with the maximum plus contribution to the crop, 4) crossing of these genotypes to combine the plus contributions of all seven GPS in the future variety (with several saturations with the genome of one of the parents with the most valuable properties), 6) selection of elite plants after a number of stabilizing reproduction of the hybrid population under the conditions of typical dynamics of the environment lim-factors (in typical years for the breeding zone). Applying these technologies, we obtained a hybrid combination [F_1 (Kazakhstanskaya rannespelaya × Tulunskaya 12) with five subsequent saturations with Tulunskaya 12 genome], from which the variety Grenada derived. Both parents of the maternal form Kazakhstanskaya rannespelaya, the Novosibirskaya 67 × Omskaya 9, having wide general adaptability, showed a much lower changes in GPS contribution to productivity as a response to changing environment and good combining ability. The Kazakhstanskaya rannespelaya variety created on their basis combines the best traits of the parents. As to the paternal and saturating form Tulunskaya 12, the improvement in quantitative traits is discrete-accumulative due to the genetic diversity of the East Siberian genotypes. The selection of elite plants under typical agroclimatic conditions resulted in higher yielding genotypes with a pronounced plasticity. A comprehensive assessment of the biotypes from this population in F_5 according to seven GPS, positively contributing to productivity, showed their synergetic effect. This was well manifested in the early ripening line Lutescens 506-11 from which the Grenada variety derived. This variety successfully combines high productivity (26-39 % higher compared to the standard) with the resistance to lodging, drought, pre-harvest germination and the grain quality of valuable and strong varieties. A distinctive feature of the variety is the horizontal resistance to Septoria diseases, a dusty smut, powdery mildew, a red-breasted leech, and intra-stem pests. Grenada variety is much lower affected by rust fungi compared to the standard. From one hectare of arable land the Grenada variety gives 628 kg of protein (+119 kg to the standard variety). In 2019, the variety Grenada is zoned by State Commission on Variety Testing of the Ministry of Agriculture of the Russian Federation for the 9th (Ural) crop region including Bashkiria (about 1 million hectares), Chelyabinsk (1 million hectares), Orenburg (4 million hectares), Kurgan (1 million hectares), and Tyumen (500 thousand hectares) regions. When Grenada occupies these areas (about 7 million hectares), an increase in grain yield will provide an annual economic effect of about 30 million rubles.

Keywords: *Triticum aestivum* L., soft wheat, breeding, variety, population, selection, biotype, geno-physiological system, grain, immunity

Increasing yields of various crops is currently not quite adequately associated with technologies based mainly on cell and tissue cultures [1, 2] and molecular genetics [3-6], i.e. different molecular markers [7, 8], marker-assisted selection (MAS), marker-assisted back-crossing (MABC), marker-assisted recurrent selection (MARS), genome-wide selection (GWS) or genomic selection (GS) [9, 10], and genomic editing [11].

It is commonly believed that key traits (corn yield, protein content, horizontal immunity) are controlled by a multiplicity of genes. Such traits were called quantitative (QT) or complex polygenic traits [12-15]. QT depends on combined activity of a set of genes and environment. Quantitative traits loci (QTL) may include a single gene or a group of genes contributing to trait value, and the effects normally change depending on conditions in which the trait is manifested [16]. Use of molecular markers enables examination of quantitative traits and identification of contributions to trait of the QTL, i.e. genes controlling complex traits of interest in breeding [17-19]).

In our opinion, however, the expectations that a key to a rapid breeding varieties required to meet the growing needs of the Earth population will be solely genetic-engineering together with molecular methods are excessive. There is still no literature mentioning the creation of a variety solely via molecular approach. In addition, epigenetics [20-22] rightly argue that in nature there are no specific genes for productivity and yield that could be molecularly marked or subjected to genomic editing. Even now in genetics and breeding, diallel analysis, despite it does not include any molecular characteristics of plant productivity traits, remains vastly effective in creating varieties of high yield and quality [23-25].

In 1973-1984 the USSR's Interdisciplinary DIAS (diallel crossing) Program was aimed at studying genetics of spring wheat productivity in Western Siberia and Kazakhstan [26]. The experts of eight Siberian plant breeding centers and two research centers (Institute of Cytology and Genetics of the Siberian Branch of the USSR Academy of Sciences and Computing Center of the Siberian Branch of the USSR Academy of Sciences) participated in the study. The territory where the experiments took place spanned the area from Krasnoufimsk (Ural) to Ivolginsk (Transbaikalia) in latitude and from Tyumen to Ust-Kamenogorsk in longitude. Fifteen parental varieties from Russia, USA, Japan, Sweden, Canada and India were diallel-crossed (each one with each other one). In winter, F_1 breed seeds were sowed in Krasnoyarsk phytotron to obtain F_2 seeds, and in summer parent varieties, hybrid breed F_1 and hybrid breed F_2 were sowed in a complete randomized block pattern with 4 replications in 8 geographical points. The experiments ran for 2 years. For each plant, 15 productivity traits were assessed, the estimates (about 5 million measurements) were entered in a DIAS databank and processed with the original programs developed in the Computing Center. For F_2 and further generations, the breeders applied individual selection in all 8 points, propagated the families and conducted the complete cycle of a standard breeding process with the assessment of the breeding material in a number of breeding nurseries. These experiments, in addition to new varieties, resulted in a discovered new system of productivity and yield regulation via a shift in a set of products of genes determining the productivity trait when the limiting environmental factor changes. Based on this discovery, a priority Russian Theory of Eco-Genetic Organization of Quantitative Traits (TEGOQT, V.A. Dragavtsev Science School) gained momentum in 1984-2014 [27-29]. This theory generated 24 entirely new deductions that enabled 24 forecasts for any temporal dynamics of the environment lim-factors, and 10 know-hows to improve crop breeding for yield and quality.

Concurrently with development of TEGOQT, seven genetic-physiological systems (GPS) were discovered and described, which the breeders de facto use (often without realizing it) to enhance the productivity and yields of new varieties. An original method of phenotyping each of seven GPS was developed based on priority methods of quantitative identification of "plus" contributions of such systems to the productivity and yield of standard and new varieties. This distinguishes from conventional foreign phenotyping, where the resulting trait (yield) is consequentially broken down to smaller components, as it is not the traits that are handled, but GPS. The traits there serve as the axes of two-dimensional coordinate system where each GPS manifests its positive or negative input into productivity in free of all noises and genetically "stripped" quantitative value [31]. These GPS are as follows: attraction GPS that ensures during the ripening period an outflow of macronutrients from straw and leaves to the ear (in cereals), or from the stem and leaves to the calathidium (in sunflowers) (ATTR); GPS of microdistributions of attracted macronutrients between the grain and chaff in cereals, or between the kernel and husk in sunflowers (MIC); GPS of adaptability (frost-, cold-, drought-, heat-, salt-resistance, soil pH resistance, etc.) (AD); GPS of polygenic immunity (horizontal resistance) (IMM); GPS of phytocenosis densification tolerance (TOL); GPS of compensation with dry matter of effects of low dosages of soil nutrition (lim-factors of soil nutrition, i.e. N, P, and K) (EFF); GPS of genetic variability of ontogenesis phase length (ONT) [31].

This article, through the example of creation of a spring wheat variety Grenada, is the first to describe innovative technologies of breeding varieties surpassing the existing ones in yields and quality. These technologies became the practical implication of priority Theory of Eco-Genetic Organization of Quantitative Traits (TEGOQT) that has outstripped the global development of environmental plant genetics for 10-15 years. They are unrivaled throughout the world and an alternative to production of genetically modified plants, search for QTLs and attempts to mark productivity traits.

Our goal was to create a wheat variety using new breeding technologies we developed for enhancing the yields based on the theory of quantitative traits' eco-genetic organization and on discovery of seven genetic-physiological systems determining enhancement of the main economically significant properties of plants.

Techniques. Experiments were run in 2001-2016 (an experimental field of the Agricultural Research Institute of Northern Transurals — Branch of Tyumen Scientific Centre of the Siberian Branch RAS) on bare fertilized dark gray soil fallow ($N_{30}P_{45}K_{30}$ per hectare), and in 2013-2014 at Ishim Agricultural Experimental Station (Tyumen province) on bare fertilized black soil fallow ($N_{30}P_{30}$ per hectare). In collection and breeding nurseries, 650 viable seeds per sq.m were sown (SKS-6-10 fractional seeder, Russia). Hybridization was carried out by twirl method (Borlaug method, a pollination method where the blooming father ear is rotated inside an individual insulator in the presence of neutered mother ear). The parents and F_1 and F_2 hybrids were sowed manually on 1 m^2 plots, 20 seeds per 1 running meter. Hybrids F_3-F_5 (stabilizing crops) without selection was sowed on 5 m^2 plots. The first selection was made from F_5 population, the selected elite plants in the first-year breeding nursery (SP-1) were sowed manually in holes (d = 25 cm). Care and observation of hybrid and breeding nurseries were as generally accepted. All crops were subjected to one treatment with herbicides Puma Super® 7.5 oil-water emulsion (Bayer CropScience AG, Germany; 0.8 l/ha) + Granstar® Pro water-dispersible beads (DuPont, USA; 0.015 kg/ha). In hybrid nursery (parents, F_1, F_2), the plants were harvested manually. Hybridologic analysis covered all productivity traits and morphological parameters. In competitive variety testing, bundle and structure analysis was held for sample bundles (for 25 plants with 4 replications).

For quantitative analysis of contributions of each of seven GPS in productivity, phenotyping was carried out in two-dimensional coordinate system of various productivity traits according to proprietary technology developed on the basis of TEGOQT [26, 30].

Results. In DIAS program [26], the following varieties were bred and zoned. DIAS 2 (developed by R.A. Tsilke) was recommended for Omsk and Novosibirsk provinces. Lutescens 70 (developed by V.V. Novokhatin) until lately was the main Transuarls variety that occupied over 60% of wheat plantings. Altaiskaya 88 (developed by N.I. Korobeinikov) until now is grown in Altai, produces high-quality grain. Altaiskaya 92 (developed by N.I. Korobeinikov) is medium-early variety, spread in Western Siberia. Altaiskiy Prostor is a variety of hard wheat widely spread in Altai (developed by N.I. Korobeinikov). Kazakhstanskaya rannespelaya (developed by V.V. Novokhatin) is one of the main varieties in Northern Kazakhstan, produces high-quality hard grain. Kazakhstanskaya 17 (developed: V.V. Novokhatin) is hard wheat variety cultivated in Southern Kazakhstan. Rix (developed V.V. Novokhatin) is a grandchild variety of Kazakhstanskaya 17 × Karabalykskaya 92 producing yield in Northern Transurals (on fertilized fallow) up to 64 centners per hectare. Bagamskaya 93 (developed by V.P. Maksimenko) spread in Baraba Steppes of Western Siberia is distinguished by drought and cold resistance. Kantegeriyskaya 89 (developed by I.F. Demorenko and R.A. Tsilke) is zoned in Khakassia, Tyva and Mongolia. Gornouralskaya (developed by V.A. Vorobyov), a grandchild variety, was zoned in 2009 in the Middle Urals. Tyumenskaya 29 (developed by V.V. Novokhatin), a grandchild variety, was zoned in 10^{th} region of Russia in 2014; Grenada (developed by V.V. Novokhatin and V.A. Dragavtsev), is a grandchild variety, zoned throughout 9^{th} (Ural) region in 2019; the expected annual economic effect of Grenada variety, if growing on areas over 7 million hectares in this region, will make up to 30 billion rubles. Atlanta 1 (developed by V.V. Novokhatin and V.A. Dragavtsev) is a grandchild variety, pending state variety testing since 2018.

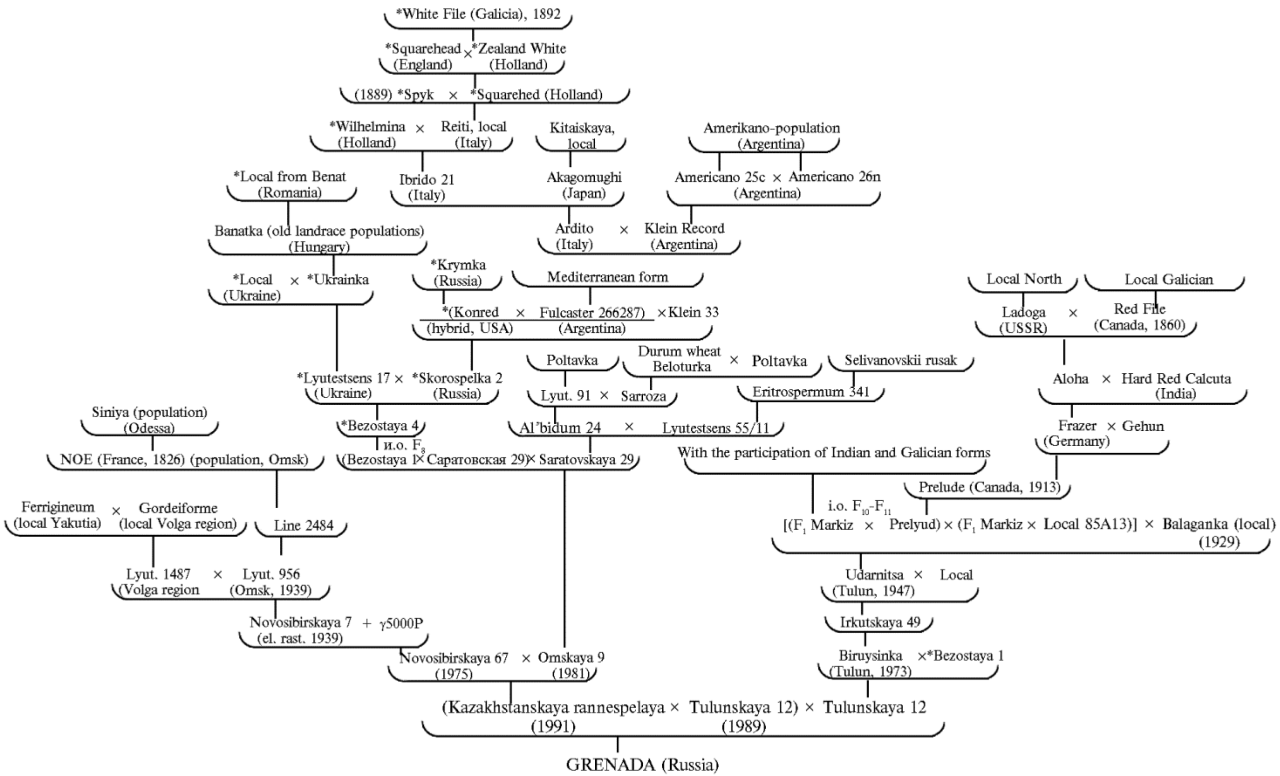
Conventional genetics since rediscovery of Mendel's laws (1900) calls upon studying the genetics of quantitative trait. TEGOQT, however, has demonstrated that for a trait subjected to the phenomenon of genotype-environment interaction it is impossible to give the same genetic characteristic for all environments [27-29, 32]. It means that quantitative traits are determined by "vagrant spectra" (sets) of gene products changing for the same trait upon modification of environmental lim-factors and resulting in sudden vast changes in genotype dispersion (during day, weeks, months, years). For example, we have demonstrated that gene expression product sets determining transpiration intensity change twice a day [33].

In exploring theoretical bases for Grenada variety creation, we proceeded from the fact that analysis of the longest pedigree of varieties makes it possible to qualitatively substantiate how to select pairs for crossbreeding [34, 35] and to directionally configure genotypes via due selections [36]. Pedigree of Grenada variety includes 69 varieties of various genetic and environmental geographical origins (Fig.). Our pedigree analysis was not conventional though. We were interested not only in parents of each ancestor, but dynamics of limiting environmental factors in a geographical point where the respective parent was created. Such approach enabled us to approximately identify which GPSs of adaptability for each of 12 stages of ontogenesis the parent possesses. In addition, it was found that the effectiveness of crossbreeding increases when the parent varieties and forms are close in their morphology but genetically heterogeneous.

This was particularly clear for winter branch that produced a renowned high-yield high-quality variety Bezostaya 1 (developed by P.P. Lukianenko), a mother form of spring intensive high-quality middle-late wheat Omskaya 9. Crossbreeding the latter with hard wheat variety Novosibirskaya 67 showing higher plasticity, in which the enhancement of quantitative productivity traits is caused by mutations due to discrete γ-irradiation (5000 R), created a plastic early-ripe hard variety Kazakhstanskaya rannespelaya. Genetics of quantitative traits of its parents, Novosibirskaya 67 (♀) and Omskaya 9 (♂), was studied under DIAS program [26]. Their combining ability was turned out to be well-defined [26]. Therefore, a hybrid combination Novosibirskaya 67 × Omskaya 9 was paid special attention. After multiple stabilizing cropping, an elite plant (Lutescens 1227-8-79 sample) was selected from F_5 and propagated. It became a parent of hard wheat variety Kazakhstanskaya rannespelaya which has been widely cultivated in Northern Kazakhstan on 450 thousand to 1.2 million hectares for over 20 years. Early ripeness of this variety is caused by amalgamation of *Vrn-1* and *Vrn-3* gene products controlling accelerated organogenesis during the second half of vegetation [37, 38]. Kazakhstanskaya rannespelaya, just as its parents, belongs to West-Siberian ecotype. It is this variety that became a mother form of the new Grenada variety. As a father and saturation (B_1) parent, early-ripe hard variety Tulunskaya 12 (East-Siberian ecotype) was used. The enhancement of its quantitative traits is of a discrete accumulative nature due to use of Canadian varieties (they accommodate old Russian Galician forms and Indian forms) and local East-Siberian genotypes originated in 16th century from Inner Mongolia and Mountainous China [39, 40]. Distinctive features of East-Siberian ecotype varieties are accelerated development, overall drought-resistance and high-quality grain production under chilly conditions. Seeds of these varieties are oblong with 1000-grain weight from 32 g [40], which is also typical for Tulunskaya 12 variety. Both parents of Grenada variety are distinguished by strong pubescence of leaves that have dark color and pronounced waxy coat.

Selection from early hybrid generations is ineffectual as the phenotypes of F_2 plants do not correlate with yield in descendants. Phenotypic manifestation of individual productivity in F_2-F_3 may be due to heterozygous epistasis, dominance effects [41] and complicated by expression of heterozygous loci, i.e. superdominance (for a considerable number of traits) that disappears in three or four reproductions. Consistent decline of non-additive variance towards later generations facilitates selection of productive genotypes [42, 43], as during reproduction (starting from F_2 and on) the population is subjected to natural (evolutionary) selection that eliminates poorly adapting forms thus preserving genotypes that are more productive and better fit to local conditions. Such genotypes usually manifest a well-defined synergistic dynamics with typical environmental lim-factors in the breeding zone [36].

A hybrid population [F_1 (Kazakhstanskaya rannespelaya × Tulunskaya 12)] once saturated with Tulunskaya 12 genome underwent stabilizing propagation up to F_5 on fertilized ($N_{30}P_{45}K_{30}$) dark gray soil fallow in conditions typical



Pedigree of Grenada variety created by innovative breeding technology based on Theory of Eco-Genetic Organization of Quantitative Traits. Winter varieties are marked with asterisks.

for northern forest-steppe zone of North Transurals to select productive forms with genetically moderate development of ear, good ripening and filled grains. As per Kumakov [44], this is due to assimilates distribution (ATTR and MIC systems) and growth functions which differ from those in arid conditions. Potential productivity and resistance to drought are controlled by various GPS, wherefore they may be improved through selection independently from each other [45]. Thus, a single genotype may well combine these complex and, at first glance, contradicting properties [46].

In quantitative analysis of each GPS contributions to productivity, phenotyping was carried out in two-dimensional coordinate systems. For instance, in a system with "main ear culm weight" abscissa and "ear weigh" ordinate, the dots of genotypes with plus- and minus-modifications (particularly, genotype that falls into dry soil on hubble will shift to the left and down, into a hollow with water and nitrogen — to the right and up) and with different adaptability (dots of more adaptive genotypes will go right and up, and those of less adaptive — left and down) will be distributed along the positive regression line. Genotypes with good GPS of attraction will shift along the negative regression line (the higher the attraction, the lighter the culm and the heavier the ear), so that the genotypes with better attraction GPS will congregate in the upper left area of the chart. The attraction deviations will not be masked by the noises of environmental variability of micro-niches under each genotype and variability of genotype adaptability (the effects of such noises will appear along the positive regression line). Thence, plus and minus genetic attraction shifts will be free of any noises and their values will be genetically clear ("stripped", as per Serebrovsky). Use in breeding (phenotyping) of measurable quantitative values for seven GPS [30] each of which makes its plus contribution to the resulting trait (productivity) enabled estimation of plus contributions of different GPS to enhancement of yield resulting in identification in F_5 population of 506-11 Line that later became the Grenada common spring wheat variety. Seven GPS was also used in characterization of this variety.

Morphological features of Grenada variety are as follows: semi-erect bunch of upright tillers, slightly inclined cylindrical white ear of medium density (20.8 spikelets per 10 cm rachis) with waxy coating and asymmetrical awnlike appendices in the upper part. The stem is of average length (78-88 cm), lodge-resistant, with heavy waxy coating, short lower internodes (4.1-4.9 cm the fist, 8-9 cm the second), with of a 2.2-2.5 mm and 2.7-2.9 mm in diameter, respectively; leaves are short, wide, coarse, dark-green, with pubescence and waxy coating, non-inclined; kernels are large, egg-shaped, dark-red, with shallow groove and short pappus.

Grenada is an early-ripe variety (it ripens 3 days earlier than standard Novosibirskaya 31). During grain maturation, green biomass gradually desiccated thus ensuring better matter recycling (ATTR GPS function, attraction of macronutrients from straw and leaves to the ear). Therefore, the seeds of well-grained ear are weighty and well-filled both in the upper and lower parts. The grains are large with net weight of 39.7 g (+7.7 g to the standard) and high test weight of 798 g/l (+35 g/l to the standard). Technological indicators of grain and bread are at the level of hard and premium varieties. Protein yield per 1 ha is 628 kg, which is 119 kg more than the standard (Novosibirskaya 31). Even in provocative conditions this variety is resistant to grain pre-harvest sprouting.

New variety demonstrates well-defined GPS of microdistributions of attracted macronutrients between the grain and chaff in the ear, as ear chaff to total weight ratio indicates. It makes 23% and 19%, respectively, in parent varieties Kazakhstanskaya rannespelaya and Tulunskaya 12, 27% in Novosibirskaya

31, 30% in Iren, and 20% in new Grenada variety which convincingly proves the effectiveness of MIC GPS in this variety. Adaptability GPS (AD) ensures overall adaptability to particular combination of various lim-factors in the breeding zone. Their set changes depending on shifts in lim-factors. Such change results in the phenomenon of productivity rank shifts within the set of varieties from year to year, i.e. to the "genotype-environment interaction" (GEI) phenomenon [25, 47]. In North Transurals conditions, 25% phenotypic dispersion of yields is genotype-specific, while 80% genotypic dispersion is caused by GEI and only 20% by additive gene effects.

It is known [48] that while in the component productivity traits additive effects of gene often prevail, in the resulting productivity trait (weight of grains per plant) non-additive effects typically prevail. Therefore GEI control is the main reserve for increasing the yield [33, 49]. Recently, the nature of GEI phenomenon was completely decrypted [47]. AD GPS functioning in Grenada is manifested by tolerance to early summer drought due to well-developed root system, good overall drought-resistance due to dense cuticular waxy coating [50], good development on subacid soils and production of grain with high test weight in chilly months. These data result from by both 4-year competitive testing and state testing of Grenada variety in contrasting agroclimatic conditions on an extensive territory of 9^{th} (Ural) plant-growing region.

GPS of polygenic immunity (horizontal resistance) in the new variety is due to dense cuticular waxy coating on the leaves and stems, which prevents germination of spores of pathogenic fungi. In provocative conditions (artificial contagion background) Grenada variety demonstrates high horizontal tolerance to Septoria disease, dust brand, mildew; as compared to standard, Grenada plants are much less affected by rust fungi, and is tolerant to cereal leaf beetle. Presence of dense pubescence of the leaves and stem also protects Grenada plants from intra-stem pests (Table).

Intensive breeding is accompanied by microevolutionary processes [51-54] due to recombinogenesis [55], effects of abiotic factors [56, 57], infections [58, 59], natural and artificial selection [46, 60], which enables the creation of productive, locally-adapted genotypes with well-defined synergism of their biotypes with the environment [61, 62]. This fosters the selection of forms containing densification tolerance GPS (TOL), which is well-demonstrated in Grenada variety. In North Transurals, due to limited vegetation period, wheat plants form yield mainly due to main stems [62]. At the standard seeding rate of 6.5 million seeds per 1 ha, a field germination rate within 70%, plant survivability of 93% and productive tilling capacity of 1.22, Grenada plants, according to long-term annual average data, form about 517 productive stems per 1 m^2. At the ear productivity of 1.1-1.2 g (28-30 grains of 0.04 g each), biological yield of the new variety is 5.7-6.2 t/ha.

GPS of dry matter production depending on soil nutrition (N, P, K lim-factors of soil; EFF) to a large extent determines the effectiveness of the variety at low doses of nitrogen, phosphorus, potassium. Fairly objective indicator of ATTR GPS and EFF GPS is the harvest index (plot grain weight to total dry biomass ratio). It makes 0.30-0.34 in the standard and compared varieties, and 0.42 in Grenada (i.e. grain percentage in total dry biomass of plants is 42%). This index enables the variety to form on dark gray soils (at low doses of mineral fertilizers $N_{30}P_{45}K_{30}$) the plants of average height (up to 88 cm) with limited tilling capacity (tilling factor of 1.22) and productively operating assimilation apparatus (due to short wide thick coarse non-drooping leaves that are not affected by pathogens, which is true for the stem as well). The plants vegetate long, effectively use photosynthetically active radiation (PAR) and also have well-developed and active roots.

In the aggregate, the changes in GPS that were achieved as a result of hybridization and breeding ensured significant increase in grain yield. In competitive variety testing (Agricultural Research Institute of North Transurals), at high natural pathogenic impact on dark gray soil ($N_{30}P_{45}K_{30}$ fertilized fallow), the average yield of Grenada variety over 4 years (2013-2016) was 4.24 t/ha, i.e. 0.87 t/ha significantly higher (+26%) than in the standard Novosibirskaya 31 variety (LSD_{05} = 0.24 t/ha) (see Table). An increase was similar, although with lower yield (3.31 t/ha, +39% to the standard), on unfertilized fall-plowed fields. The increase of yield against the standard (+0.47 t/ha, or +17%) also occurred at Ishim Agricultural Experimental Station in south of Tyumen province during environmental tests in 2013-2014.

Economic and biological characterization of Grenada common spring wheat variety as compared to the standard

Indicator	Units	Grenada	Novosibirskaya 31 (standard)	Deviation from standard +/–	Deviation from standard +/–
Yield					
Agricultural Research Institute of North Transurals (Tyumen Province, 2013-2016):					
fallow	t/ha	4.24	3.37	+0.87	+26
LSD_{05}	t/ha	0.24			
fall-plowed field	t/ha	3.31	2.38	+0.93	+39
LSD_{05}	t/ha	0.26			
Ishim Agricultural Experimental Station, ((Tyumen Province, 2013-2014)	t/ha	4.53	4.06	+0.47	+17
LSD_{05}	t/ha	0.18			
Biological and technological parameters (Agricultural Research Institute of North Transurals, Tyumen Province, 2013-2016)					
Vegetation period	day	82	85	–3	
Plant height	cm	76	82	–6	
Resistance:					
to lodging	points	5	4	+1	
to drought	points	5	5	0	
to drooping	points	1	1	0	
Grain sprouting in ear (provocative conditions)	%	1.03	13.40	–12.37	
Weight of 1000 grains	g	39.7	32.0	+7.7	
Grain unit	g/l	798	763	+35	
Vitreousness	%	59	62	–3	
Content:					
of protein		14.8	15.1	–0.3	
of gluten	%	33.1	33.8	–0.7	
Flour strength	a.u.	386	311	+75	
P/L alveograph ratio		1.3	0.9	+0.4	
Valorimetric value	a.u.	52	70	–18	
Attenuation	f.u.	64	69	–5	
Gluten deformation index	gluten deformation units	80	78	+2	
Bread volume (no additives)	ml	720	697	+23	
Bread rating	points	4.5	4.0	+0.5	
Resistance to pathogens (Agricultural Research Institute of North Transurals, Tyumen Province, 2014-2016)					
Puccinia recondita Dietel & Holw., 1857 (artificial infection load)	type/%	1/10-2/20	2/20-3/60		
Ustilago tritici (Pers.) C.N. Jensen, Kellerm. & Swingle (artificial infection load)	%	0.1-0.2	2.3-4.2		
Septoria tritici (high natural load)	type/%	Traces-1/5	2/20-3/60		

Note. P/L — dough tenacity to extensibility ratio, units. Gluten deformation index indicates quality of gluten (in gluten deformation units); a.u. — alveograph units, f.u. — farinograph unit.

Stages of ontogenesis in Grenada plants in majority of years complied with the typical dynamics of lim-factors for Tyumen province. Therefore, no breeding-born shift in ONT GPS occurred. However, there are genetic bases for changing this trait as varieties with respective genotype are known [63].

The created variety is recommended for subtaiga, northern and southern forest-steppe areas of Siberia, Transurals and the western piedmont of the Ural Mountains.

Thus, the scientific outcome of DIAS is the development of TEGOQT with its 24 deductions and 10 know-hows [7]. For the first time ever we have implemented a priority complex of innovative breeding technologies based on TEGOQT and discovered seven plant genetic-physiological systems (GPS) which in the end determine the yield of any varieties. Creation of the initial breeding material by these new technologies, including selection of parent pairs on the basis of GPS, crossbreeding, stabilizing reproduction, and final selection, was performed by a six-stage algorithm suggested and tested for the first time. The stage order is as follows: i) special selection of parental pairs based on deep analysis of the longest pedigrees of the old breeds with regard to typical dynamics of lim-factors in the areas of creation of such parent varieties; ii) phenotyping for seven GPS contributing to yield within the group of the most productive varieties of the breeding nursery (carried out according to the priority proprietary methodology); iii) selection of genotypes that have at least one GPS with the maximum plus contribution to the crop; iv) crossing of these genotypes to combine the plus contributions of all seven GPS in the expected variety; v) stabilizing reproduction of segregating generations to eliminate the effects of dominance, superdominance and heterozygous epistasis (with several saturations with the genome of one of the parents possessing the most valuable properties); vi) selection of elite plants after a number of stabilizing reproductions of the hybrid population under the typical dynamics of the environment lim-factors (in typical years).

So, a six-stage innovative technology that we suggest enables breeding varieties with the yield exceeding standard by up to 40% and more that guarantees considerable increase in grain harvesting in a particular territory. Of particular importance is the evaluation of selected genotypes by functional activity of seven genetic-physiological systems (GPS), i.e. by their plus contributions to yield, throughout breeding (from collection nursery, through nurseries for hybridization, selections, testing of families, to preliminary, environmental and competitive trials and trials in state variety testing network). Combining contributions of all seven GPS within the single designed variety allows breeders to create high-yield lodging- and pathogen-resistant adaptive and plastic varieties of common spring wheat with high-quality grain. The suggested innovative technology based on forecast of plus contributions of GPS to yield provided correct evaluation of breeding material and selection of early-ripe, high-yield, intensive plastic line Lutescens 506-11 from which the Grenada variety derived. Use of these technologies considerably reduces the number of breeding nurseries and, as a result, breeding costs.

REFERENCES

1. Loyola-Vargas V.M., Ochoa-Alejo N. An introduction to plant tissue culture: advances and perspectives. In: *Plant cell culture protocols. Methods in molecular biology, Vol. 1815.* V. Loyola-Vargas, N. Ochoa-Alejo (eds.). Humana Press, New York, NY, 2018: 3-13 (doi: 10.1007/978-1-4939-8594-4_1).
2. Bridgen M.P., Van Houtven W., Eeckhaut T. Plant tissue culture techniques for breeding. In: *Ornamental crops. Handbook of plant breeding, Vol. 11.* J. Van Huylenbroeck (ed). Springer, Cham, 2018: 127-144 (doi: 10.1007/978-3-319-90698-0_6).
3. Varshney R.K., Pandey M.K., Chitikineni A. Plant genetics and molecular biology: an introduction. In: *Plant genetics and molecular biology. Advances in biochemical engineering/biotechnology, Vol. 164.* R. Varshney, M. Pandey, A. Chitikineni (eds.). Springer, Cham, 2018: 1-9 (doi: 10.1007/10_2017_45).
4. Pérez-de-Castro A.M., Vilanova S., Cacizares J., Pascual L., Blanca J.M., Díez M.J., Pro-

hens J., Picy B. Application of genomic tools in plant breeding. *Curr. Genomics*, 2012, 13(3): 179-195 (doi: 10.2174/138920212800543084).

5. Ashkani S., Rafii M.Y., Shabanimofrad M., Miah G., Sahebi M., Azizi P., Tanweer F.A., Akhtar M.S., Nasehi A. Molecular breeding strategy and challenges towards improvement of blast disease resistance in rice crop. *Front. Plant Sci.*, 2015, 6: Article 886 (doi: 10.3389/fpls.2015.00886).
6. Prohens J. Plant breeding: a success story to be continued thanks to the advances in genomics. *Front. Plant Sci.*, 2011, 2: Article 51 (doi: 10.3389/fpls.2011.00051).
7. Mammadov J., Aggarwal R., Buyyarapu R., Kumpatla S. SNP markers and their impact on plant breeding. *Int. J. Plant Genomics*, 2012, 2012: 728398 (doi: 10.1155/2012/728398).
8. Kim S.K., Nair R.M., Lee J., Lee S.-H. Genomic resources in mungbean for future breeding programs. *Front. Plant Sci.*, 2015, 6: Article 626 (doi: 10.3389/fpls.2015.00626).
9. Jiang G.-L. Molecular markers and marker-assisted breeding in plants. In: *Plant breeding from laboratories to fields*. S.B. Andersen (ed.). IntechOpen, 2013: 45-83 (doi: 10.5772/52583).
10. Bhat J.A., Ali S., Salgotra R.K., Mir Z.A., Dutta S., Jadon V., Tyagi A., Mushtaq M., Jain N., Singh P.K., Singh G.P., Prabhu K.V. Genomic selection in the *era* of next generation sequencing for complex traits in plant breeding. *Front. Genet.*, 2016, 7: 221 (doi: 10.3389/fgene.2016.00221).
11. Nadeem M.A., Nawaz M.A., Shahid M.Q., Doğan Y., Comertpay G., Yıldız M., Hatipoğlu R., Ahmad F., Alsaleh A., Labhane N., Özkan H., Chung G., Baloch F.S. DNA molecular markers in plant breeding: current status and recent advancements in genomic selection and genome editing. *Biotechnology & Biotechnological Equipment*, 2018, 32(2): 261-285 (doi: 10.1080/13102818.2017.1400401).
12. Kumari S., Jaiswal V., Mishra V.K., Paliwal R., Balyan H.S., Gupta P.K. QTL mapping for some grain traits in bread wheat (*Triticum aestivum* L.). *Physiol. Mol. Biol. Plants*, 2018, 24(5): 909-920 (doi: 10.1007/s12298-018-0552-1).
13. Lozada D.N., Mason R.E., Sukumaran S., Dreisigacker S. Validation of grain yield QTLs from soft winter wheat using a CIMMYT spring wheat panel. *Crop Sci.*, 2018, 58: 1964-1971 (doi: 10.2135/cropsci2018.04.0232).
14. Nedelkou I.-P., Maurer A., Schubert A., Léon J., Pillen K. Exotic QTL improve grain quality in the tri-parental wheat population SW84. *PLoS ONE*, 2017, 12(7): e0179851 (doi: 10.1371/journal.pone.0179851).
15. Guo Y., Du Z., Chen J., Zhang Z. QTL mapping of wheat plant architectural characteristics and their genetic relationship with seven QTLs conferring resistance to sheath blight. *PLoS ONE*, 2017, 12(4): e0174939 (doi: 10.1371/journal.pone.0174939).
16. Gahlaut V., Jaiswal V., Tyagi B.S., Singh G., Sareen S., Balyan H.S., Gupta P.K. QTL mapping for nine drought-responsive agronomic traits in bread wheat under irrigated and rain-fed environments. *PLoS ONE*, 2017, 12(8): e0182857 (doi: 10.1371/journal.pone.0182857).
17. Imai A., Yoshioka T., Hayashi T. Quantitative trait locus (QTL) analysis of fruit-quality traits for mandarin breeding in Japan. *Tree Genetics & Genomes*, 2017, 13: 79 (doi: 10.1007/s11295-017-1162-8).
18. Hernández Mora J.R., Micheletti D., Bink M., Van de Weg E., Cantín C., Nazzicari N., Caprera A., Dettori M.T., Micali S., Banchi E., Campoy J.A., Dirlewanger E., Lambert P., Pascal T., Troggio M., Bassi D., Rossini L., Verde I., Quilot-Turion B., Laurens F., Arús P., Aranzana M.J. Integrated QTL detection for key breeding traits in multiple peach progenies. *BMC Genomics*, 2017, 18: 404 (doi: 10.1186/s12864-017-3783-6).
19. Tan Z., Zhang Z., Sun X., Li Q., Sun Y., Yang P., Wang W., Liu X., Chen C., Liu D., Teng Z., Guo K., Zhang J., Liu D., Zhang Z. Genetic map construction and fiber quality QTL mapping using the CottonSNP80K array in upland cotton. *Front. Plant Sci.*, 2018, 9: Article 225 (doi: 10.3389/fpls.2018.00225).
20. Weinhold B. Epigenetics: the science of change. *Environ. Health Perspect.*, 2006, 114(3): A160-A167 (doi: 10.1289/ehp.114-a160).
21. Chen M., Lv S., Meng Y. Epigenetic performers in plants. *Develop. Growth Differ.*, 2010, 52: 555-566 (doi: 10.1111/j.1440-169X.2010.01192.x).
22. Gallusci P., Dai Z., Génard M., Gauffretau A., Leblanc-Fournier N., Richard-Molard C., Vile D., Brunel-Muguet S. Epigenetics for plant improvement: current knowledge and modeling avenues. *Trends in Plant Science*, 2017, 22(7): P610-623 (doi: 10.1016/j.tplants.2017.04.009).
23. Milomrica R.M., Dragan S.D., Desimir S.K., Fleksandar S.P., Snezana T.T. Combining abilities for spike traits in diallel cross of barley. *J. Central Eur. Agric.*, 2014, 15(1): 198-116 (doi: 10.5513/JCEA01/15.1.1419).
24. Sing B., Sharma A., Joshi N., Mittal P., Singh S. Combining ability analysis for grain yield and its components in malt barley (*Hordeum vulgare* L.). *Indian Journal of Agricultural Sciences*, 2013, 83(1): 96-98.
25. Kompanets E.V., Kozachenko M.R., Vas'ko A.G., Naumov A.G., Solonechnyi P.N., Svyatchenko S.I. *Vavilovskii zhurnal genetiki i selektsii*, 2017, 21(5): 537-544 (doi: 10.18699/VJ17.27) (in Russ.).

26. Dragavtsev V.A., Tsil'ke R.A., Reiter B.G., Vorob'ev V.A., Dubrovskaya A.G., Korobeinikov N.I., Novokhatin V.V., Maksimenko V.P., Babakishiev A.G., Ilyushchenko V.G., Kalashnik N.A., Zuikov Yu.P., Fedotov A.M. *Genetika priznakov produktivnosti yarovykh pshenits v Zapadnoi Sibiri*. Pod redaktsiei D.K. Belyaeva [Genetics of spring wheat productivity traits in Western Siberia. D.K. Belyaev (ed.)]. Novosibirsk, 1984 (in Russ.).
27. Glazko V.I., Glazko G.V. *Tolkovyi slovar' terminov po obshchei i molekulyarnoi biologii, obshchei i prikladnoi genetike, selektsii, DNK-tekhnologii i bioinformatike. Tom 2* [Glossary of general and molecular biology, general and applied genetics, selection, DNA technology and bioinformatics. Vol. 2]. Moscow, 2008: 308 (in Russ.).
28. Dragavtsev V.A., Litun P.P., Shkel' N.M., Nechiporenko N.N. *Doklady AN SSSR*, 1984, 274(3): 720-723 (in Russ.).
29. Dragavtsev V.A. *Biosfera,* 2012, 4(3): 251-262 (in Russ.).
30. D'yakov A.B., Dragavtsev V.A. V knige: *Ekologo-geneticheskii skrining genofonda i metody konstruirovaniya sortov sel'skokhozyaistvennykh rastenii po urozhainosti, ustoichivosti i kachestvu* [In: Ecogenetic screening of the gene pool and constructing cultivars for yield, sustainability and quality]. St. Petersburg, 1998: 23-47 (in Russ.).
31. Kocherina N.V., Dragavtsev V.A. *Vvedenie v teoriyu ekologo-geneticheskoi organizatsii poligennykh priznakov rastenii i teoriyu selektsionnykh indeksov* [Introduction to the theory of ecological and genetic organization of plants polygenic traits and the theory of breeding indices]. St. Petersburg, 2008 (in Russ.).
32. Börner A., Schumann E., Fürste A., Cöster H., Leithold B., Röder M., Weber W. Mapping of quantitative trait loci determining agronomic important characters in hexaploid wheat (*Triticum aestivum* L.). *Theor. Appl. Genet.*, 2002, 105(6-7): 921-936 (doi: 10.1007/s00122-002-0994-1).
33. Dragavtsev V.A., Dragavtseva I.A., Efimova I.L., Morenets A.S., Savin I.Yu. *Trudy Kubanskogo GAU,* 2016, 2(59): 105-121 (in Russ.).
34. Ushiyama T., Nakamura K., Anas A., Yoshida T. Pedigree analysis of early maturing wheat cultivars in Japan for breeding cultivars with higher performance. *Plant Production Science*, 2009, 12(1): 80-87 (doi: 10.1626/pps.12.80).
35. Witcombe J.R., Virk D.S. Methodologies for generating variability. Part 2: selection of parents and crossing strategies. In: *Plant breeding and farmer participation.* S. Ceccarelli, E.P. Guinarres, E. Weltizienm (eds.). Rome, 2009: 129-138.
36. Novokhatin V.V. *Dostizheniya nauki i tekhniki APK*, 2016, 3: 42-45 (in Russ.).
37. Voronin A.N., Stel'makh A.F. *Nauchno-tekhnicheskii byulleten' VSGI,* 1985, 3: 25-30 (in Russ.).
38. Stel'makh A.F. *Vestnik sel'skokhozyaistvennoi nauki*, 1987, 6: 47-53 (in Russ.).
39. Pisarev V.E. *Selektsiya zernovykh kul'tur* [Breeding of cereal crops]. Moscow, 1964 (in Russ.).
40. Vedrov N.G. *Yarovaya pshenitsa v Vostochnoi Sibiri* [Spring wheat in Eastern Siberia]. Krasnoyarsk, 1998 (in Russ.).
41. Jiang Z., Zhang B., Teng W., Han Y., Zhao X., Sun D., Zhang Z., Li W. Impact of epistasis and QTL × environmental interaction on the oil filling rate of soybean seed at different stages. *Euphytica*, 2011, 177(3): 431-442 (doi: 10.1007/s10681-010-0290-0).
42. Zhuchenko A.A. *Ekologicheskaya genetika kul'turnykh rastenii: adaptatsiya, rekombinogenez, agrobiotsenoz* [Ecological genetics of cultivated plants: adaptation, recombinogenesis, agrobiocenosis]. Kishinev, 1980 (in Russ.).
43. Gill K.S. *Karlikovye pshenitsy* [Dwarf wheats]. Moscow, 1984 (in Russ.).
44. Kumakov V.A. *Tezisy dokladov IV S"ezda obshchestva fiziologov rastenii Rossii. Mezhdunarodnaya konferentsiya «Fiziologiya rastenii — nauka 3-go tysyacheletiya» (Moskva, 4-9 oktyabrya 1999 goda)* [Proc. VI Congr. of Russian Society of Plant Physiologists, Int. Conf. «Plant physiology — science of the 3rd millennium» (Moscow, October 4-9, 1999)]. Moscow, 1999, V. 1: 400 (in Russ.).
45. Zhuchenko A.A. *Adaptivnyi potentsial kul'turnykh rastenii (ekologicheskie osnovy)* [Adaptive potential of cultivated plants (ecological basis)]. Kishinev, 1988 (in Russ.).
46. Guo R., Wu Q., Liu Y. Single-plant similarity-difference selection in wheat breeding. *Advance Journal of Food Science and Technology*, 2013, 5(11): 1413-1417 (doi: 10.19026/ajfst.5.3358).
47. Dragavtsev V.A., Dragavtseva I.A., Efimova I.L., Kuznetsova A.P., Morenets A.S. To the experimental confirmation of the hypothesis about an eco-genetic nature of the phenomenon genotype × environment interaction for woody plants. *Agricultural Biology* [*Sel'skokhozyaistvennaya biologiya*], 2018, 53(1): 151-156 (doi: 10.15389/agrobiology.2018.1.151eng).
48. Singh S., Dhindsa G.S., Sharma A., Singh P. Combining ability for grain yield and its components in barley (*Hordeum vulgare* L.). *Crop Improvement,* 2007, 34: 128-132.
49. Novokhatin V.V., Shelomentseva T.V. *Vestnik Rossiiskoi akademii sel'skokhozyaistvennykh nauk*, 2014, 4: 14-17 (in Russ.).
50. Li W.-Q., Zhang Z.-B., Li J.-J. Plant epicuticular wax and drought resistance as well as its molecular biology. *Zhi wu sheng li yu fen zi sheng wu xue xue bao = Journal of plant physiology and molecular biology*, 2006, 32(5): 505-512 (Article in Chinese).
51. Syukov V.V., Zakharov V.G., Menibaev A.I. *Vavilovskii zhurnal genetiki i selektsii*, 2017, 21(5):

534-536 (doi: 10.18699/VJ17.290) (in Russ.).
52. Borlaug N.E. Wheat breeding and its impact on world food supply. *Proc. 3rd Int. Wheat Symp. Canberra-Australia*. Canberra, 1968: 1-36.
53. Rajaram S., Borlaug N.E., van Ginkel M. CIMMIT international wheat breeding. In: *FAO Plant Production and Protection Series. No. 30. Bread wheat — improvement and production*. B.C. Curtis, S. Rajaram, H. Gymez Macpherson (eds.). FAO, Rome, 2002: 103-117.
54. Srinivasan C.S., Thirtle C., Palladino P. Winter wheat in England and Walles, 1923-1995: what do indicates of genetic diversity reveal? *Plant Genetic Resources: Characterization and Utilization*, 2003; 1(1): 43-57 (doi: 10.1079/PGR20031).
55. Zhuchenko A.A., Korol' A.B. *Rekombinatsiya v evolyutsii i selektsii* [Recombination in evolution and breeding]. Moscow, 1985 (in Russ.).
56. Fujimura S., Shi P., Iwama K., Zhang X., Gopal J., Jitsuyama Y. Comparison of growth and grain yield of spring wheat in Lhasa, the Tibetan Plateau, with those in Sapporo, Japan. *Plant Prod. Sci.,* 2009, 12(1): 116-123 (doi: 10.1626/pps.12.116).
57. Malik A.H., Prieto-Linde M.L., Kuktaite R., Andersson A., Johansson E. Individual and interactive effects of genetic background and environmental conditions on amount and size distribution of polymeric proteins in wheat grain. *Czech J. Genet. Plant Breeding,* 2011, 47(spec. Iss.): S186-S189 (doi: 10.17221/3278-CJGPB).
58. Haberle J., Holzapfel J., Hartl L. Die Genetik der Fusariumresistens in ropaischem Winterweizen. In: *Abwehrstrategien gegen biotische Schaderreger, Zuchtung Hackfruchten und Sonderkulturen*. Irdning, 2009: 5-8.
59. Kosova K., Chrpova J., Sip V. Cereal resistance to Fusarium head blight and possibilities of its improvement through breeding. *Czech J. Genet. Plant Breeding,* 2009, 45(3): 87-105 (doi: 10.17221/63/2009-CJGPB).
60. El-Hendawy S.E., Ruan Y., Hu Y., Schmidhalter U. A comparison of screen criteria for salt tolerance in wheat under field and controlled environmental conditions. *Journal of Agronomy & Crop Science*, 2009, 195(5): 356-367 (doi: 10.1111/j.1439-037X.2009.00372).
61. Novokhatin V.V. The theoretical justification of intensive genetic potential of the varieties of soft wheat (*Triticum aestivum* L.). *Agricultural Biology* [*Sel'skokhozyaistvennaya biologiya*], 2016, 51(5): 627-635 (doi: 10.15389/agrobiology.2016.5.627eng).
62. Novokhatin V.V. *Materialy nauchno-prakticheskoi konferentsii «Sel'skokhozyaistvennaya nauka — razvitiyu APK Tyumenskoi oblasti» (15-17 fevralya 2000 goda, Tyumen')* [Proc. Int. Conf. «Agricultural science as a tool to develop agrobusiness in the Tyumen region» (Tyumen', February 15-17, 2000)]. Tyumen', 2000: 50-56 (in Russ.).
63. Mal'chikov P.N., Myasnikova M.G. *Vavilovskii zhurnal genetiki i selektsii*, 2015, 19(2): 176-184 (in Russ.).