ABOUT TETRAPLOID LEVEL OF CONTROL OF COMPLEX QUANTITATIVE DETERMINANTS IN HEXAPLOID WHEAT CULTIVARS

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S u m m a r y

In soft species of *Triticum spelta* L., *T. compactum* Host. and *T.sphaerococcum* Persiv. the author studied manifestation of complex quantitative determinants on basis of phenome—genome approach, when the genome-phenome interrelation are considered similarly to gene— phene. It was shown, that at identical genome composition (AABBDD) in *T. aestivum* L.,*T.spelta* L., *T. compactum* Host. and *T. sphaerococcum* Persiv. , in three last-named cultivars the quantitative determinants are controlled on tetraploid twophenome level (diploid genome—phenome), that the author suggests to reflect in genomic formulae and take into account in selection and practical work.

The secondary origin of *Triticum spelta*, *T. compactum* and *T. sphaerococcum* from *T. aestivum L.* has been discussed in the literature (1). Many researchers have reported about complex mutations of speltoid, compactoid and sphaerococcoid type in soft wheat (2-5). There are major sets of genes that are assumed to encode traits (including quantitative): in *T. sphaerococcum - QQccss*, in *T. compactum - QQCCSS*, in *T. aestivum - QQccSS*, and *qqccSS* in all speltoid varieties (*T. spelta*, *T. macha* Dek. et Men., *T. vavilovii* Jakuvz., *T. zhukovskyi* Men. et Er.) (6, 7).

It has been shown the difference in weight of 1000 grains amounted to 29,0-35,0 % (mean 32,7%) during 3 years between the original soft hexaploid wheat cv Belotserkovskaya 198 and its sphaerococcoid mutant descendants (2). The weight of grains per ear in compactoid, sphaerococcoid and speltoid mutants of *T. aestivum* (cv Norran and cv Bezostaya 1) obtained via a mutagenic impact was 32-40% lower than that of the original form (3). As a rule, macromutants manifest the weaker habitus than an original form. Studying the hybrids F_1, F_2 and F_3 obtained by crossing *T. sphaerococcum* × *T. aestivum*, resulting sphaerococcoid mutants were found to develop the 31% lower weight of grains in than the soft wheat (8). Therefore, speltoid, compactoid and sphaerococcoid macromutants are qualitatively distinct from the original form, and their productivity is reduced by one third.

At the same time, the difference in weight of 1000 grains between *T. aestivum* A^uBD cv Cantach (30,0 g) and the tetra-form A^uV Cantach (19,8 g) amounts to10,2 g (9). This difference was 34% determined by the contribution of DD genome – this fact was proved by creation of synthetic hexaploid mutants obtained by crossing the tetraform A^uA^uVV with different samples of *Aegilops squarrosa* (the source of DD genome). Such hexaploids exhibit the weight of 1000 grains amounted to 32,0 g and more (depending on the used sample of *Aegilops*), so this trait had been improved by the effect of diploid DD genome.

The role of diploid genomes in formation of this quantitative trait can be easily described by a phenomic-genomic approach that allows studying the relations between genome and phenome similarly to interactions between gene and phene (10). Such research is quite relevant in wheat represented by many polyploid polygenomic species.

Considering the relationship "diploid genome-phenome", it becomes possible to calculate the contribution (phenome) provided by one of two diploid genomes into the manifested trait of the tetraform A^uA^uVV: 19,8 g : 2 = 9,9 g. Since A^uA^uVV is a componental part of hexaploid soft wheat, the 3-phenome expression level of this trait in cv Cantach can be described as A^uA^u (9,9 g) + BB (9,9 g) + DD (10,2 g) = A^uA^uBBDD (30,0 g). Similar calculations were performed by V.A. Strunnikov, who described genomic contribution in the quantitative trait "silk productivity of cocoons" in diploid and triploid hybrids of silkworm (11). According to the authors' data, grain productivity in hexaploid soft wheat (A^uA^uBBDD) is the complex trait influenced by each genome (A^uA^u + BB + DD) (12, 13). It should be emphasized that contributions of A^uA^u and BB genomes are almost equal and they are slightly lower than that of DD genome.

At the same time, the calculated contribution provided by one of the three diploid genomes in a quantitative trait of hexaploid soft wheat AuAuBBDD (30,0 g) is close to the abovementioned (30,0 g : 3 = 10,0 g). The weighs of 10,0; 9,9 and 10,2 g correspond to contributions of diploid genomes in productivity of hexaploid, tetraploid and diploid forms, and these values are of the same order. Therefore, the formation of this quantitative trait in hexaploid soft wheat can be conventionally represented as 10,0 g (AA) + 10,0 g (BB) + 10,0 g (DD) = 30,0 g (AABBDD); so, the phenome for each of the three diploid genomes can be assumed as 10,0 g. The theoretically calculated value in hexaploid soft wheat corresponds to the observed trait, which fact is confirmed by calculation using χ^2 at the appropriate modification (14). The observed frequencies were taken from observed contributions of diploid genomes in manifestation of the trait (Table 1).

1. Degree of coincidence (χ^2) of calculated and actual weigh of 1000 grains in soft wheat

Parameter	Genome			Sum
	AA	BB	DD	AABBDD
Expected split (H_0)	1	1	1	3
Actual frequencies (f)	9,9	9,9	10,2	30,0
Expected frequencies (F)	10,0	10,0	10,0	30,0
Difference (f − F)	−0,1	−0,1	+0,2	
Squared difference (f − F)²	0,01	0,01	0,04	
Ratio (f − F)²/F	0,001	0,001	0,004	

While $\quad \chi^2 = \dfrac{(f - F)^2}{F} = 0,006; \chi^2_{05} = 5,99.$

Differences between observed and expected frequencies were insignificant (χ^2_{actual} 0,06 < χ^2_{05} 5,99), H$_0$ is not rejected. Therefore, in any case, the degree of quantitative trait in three-genomic hexaploid soft wheat is determined by contributions of the three phenomes provided by each genome (three-phenomic level of character manifestation; in a tetraploid two-genomic wheat – respectively, two-genomic level). In the tetraform AABB (tetraploid), the $^1/_3$ lower expression of the quantitative trait is accompanied by qualitative changes (phenotypical resemblance with a compact wheat). Thus, knowing the three-phenomic level of manifestation of quantitative traits in tree-genomic (hexaploid) wheat *T. aestivum* allows to calculate the contribution of one diploid genome (phenome).

The abovementioned decrease of quantitative traits in macromutants *T. spelta* AABBDD, *T. compactum* AABBDD, *T. sphaerococcum* AABBDD compared with the original *T. aestivum* AABBDD can be the result of the missing contribution from one of the three diploid genomes. However, in contrast to the tetraploid, there occurred a suppression of diploid genome, because quantitative traits of these samples are actually reduced by $^1/_3$ while their genomic composition is equal to that of soft wheat.

In experiments of A.V. Pukhal'skii and I.L. Maximov, the chronic γ-irradiation of *T. spelta* has resulted in soft wheat split out progeny (15). In wheat species *T. kiharae* homologous to *T. spelta*, seed exposure to supermutagen nitrozomethylurea has led to the form completely homologous to *T. aestivum* L. and morphologically identical to soft wheat (16, 17); this derivative demonstrated the grain yield by $^1/_3$ greater than the original speltoid *T. kiharae* (18) (the actually restored wheat).

Essential morphological changes in speltoid, compactoid and sphaerococcoid macromutants have been reported by many researchers who highlighted that a single gene can't cause such significant phenotypic effects (cited from 5). It has been assumed (19) that *S* locus, as well as *Q* and *C* loci providing phenotypic distinctions of *T. aestivum*, *T. sphaerococcum*, *T. spelta* and *T. compactum* are formed by groups of closely linked genes. This fact gives more reasons to any conclusions about the possible control of these changes by a discrete genetic unit of diploid genome. The authors explain macromutant transformations of the studied forms using the guess that they carry the determinants encoded by diploid genomes AA, BB, DD which are the components of polygenome. From this point of view, the reciprocal macromutations *T. sphaerococcum* ⇔ *T. aestivum*, as well as obtaining soft wheat from spelt can be rather provided by dominant or recessive state of certain diploid genomes in the polygenome rather than the influence of individual genes or groups of genes.

According to V.D. Kobylyansky, dwarfism in rye and wheat *T. sphaerococcum* is controlled by homologous genes that similarly cause shortening of plant organs (20). There were numerous attempts of plant breeders to use sphaerococcoid dwarf wheat to create the soft wheat having short culms and big long spikes with a large round grain, though with no success. The same was observed during hybridization of dwarf rye with normal tall and large-grained cultivars as well: none of 900 F$_2$ plants developed short stems along with the ear shape and size typical to tall parental varieties. Characteristics of dwarfism (smaller plant height, size of grains and other organs) are monogenically inherited in rye and sphaerococcoid wheat (20). It's unlikely that a single gene causes simultaneous reduction of many traits peculiar to dwarfism. Probably, dwarfism is inherited as a single trait controlled by many genes, working jointly as "monogene". In certain circumstances, such unit can be represented by a whole diploid genome that controls $^1/_3$ of characters' expression in hexaploid. This type of changes reflects macroevolution of wheat. It is possible that the diploid genome ($2n$ = 2x = 14) represents a single genetic unit in the genome of polyploid polygenomic plants, and significant modifications of species involve most of genes of such units. This also complicated obtaining of desired complex traits by hybridization. However, in such wheat species it is possible to realize the contribution of diploid genome – and this attempt has resulted in obtaining the complete homologue of wheat. Recently, the similar macromutation was induced by colchicine in the sphaerococcoid wheat cultivar Sharada; the resulting form has maintained its morphological features while the $^1/_3$ higher productivity characteristics compared to the original form (21). This fact largely confirms that complex quantitative traits are controlled at the level of diploid genome working as a single genetic unit.

The formation from soft wheat of speltoid, compactoid and sphaerococcoid macromutants manifesting a complex of distinct features can be the result of absence in their phenotype of a contribution resulting from one of three elementary diploid genomes. That's why they develop quantitative traits at about $^1/_3$ lower degree along with qualitative differences from the original wheat. Should this difference be much greater or less than $^1/_3$, this possibly means the "excessively" or "insufficiently" expressed features of speltoidy, compactoidy and sphaerococcoidy in these macromutants. In this case, it should be considered how qualitative transformations are accompanied by corresponding quantitative changes. For example, weight of grain per ear in soft wheat *T. aestivum* A^{u}BD was 1,8 g, while in speltoid forms derived from it – Spelta awnless (A^{u}BD), Speltoid awnless (A^{u}BD), Spelta compactum (A^{u}BD) - respectively 1,2; 1,3 and 1,7 g (22). Spelta awnless demonstrates the greatest similarity with *T. spelta* L., while Spelta compactum has quantitative characteristics similar to the original soft wheat. The first assertion is confirmed by revealing in Spelta awnless of two-phenomic tetraploid nature of trait "weight of grain per ear". Since the three-genomic nature of the original hexaploid soft wheat, the calculated contribution from one of its three diploid genomes is equal to 1,8 g : 3 = 0,6 g. This value is equal to the difference between trait expression in the original wheat and Spelta awnless (1,8 g – 1,2 g = 0,6 g). That is, the degree of trait expression in hexaploid wheat is 0,6 g + 0,6 g + 0,6 g = 1,8 g, whereas in Spelta awnless – 0,6 g + 0,6 g = 1,2 g. It's notably that the closer is morphology of the split out form to speltoid, compactoid or sphaerococcoid type, the more (within $^1/_3$) decrease characteristics peculiar to a corresponding complex quantitative trait relative to that in the original wheat. It can be assumed that wheat forms not meeting this criteria have no evolutionary capabilities and further will be eliminated, while those satisfying these standards can transform in the future into speltoid, sphaerococcoid and compactoid samples. This process can be compared with morphogenesis in hybrids of soft and durum wheat: intermediate forms carrying 35 chromosomes are eliminated over time to be replaced by those having a chromosome number and ear morphology identical or close to original soft or durum wheat.

In *T. spelta*, *T. sphaerococcum* and *T. compactum*, such complex quantitative traits as flag leaf area and weight of grain per ear are also manifested on two-phenomic level. The authors compared the parameters of speltoid *T. kiharae* obtained from the complete homologue cv Rassvet 1 and different samples of *Triticum* species (Table 2). In the first year of testing, characteristics of diploid *T. monococcum* were the phenome-genome markers for assessment of identified phenomes.

2. Two-phenomic and tree-phenomic levels of manifestation of complex quantitative traits in hexaploid wheat samples (Rostov province)

Genotype	Genome	Level of trait manifestation	Flag leaf area, cm²		Weight of grain per ear, g		Protein, %
			2005	2006	2005	2006	2006
T. spelta	$A^{u}BD$	2ph	19,8	20,3	1,33	1,12	
T. kiharae	$A^{b}GD$	2ph	21,4	18,4	1,37	1,08	22,5
T. aestivum TM (complete homologue derived from *T. kiharae*), cv Rassvet 1	$A^{b}BD$	3ph	32,3	28,0	2,23	1,68	14,4
T. aestivum, cv Yubileynaya 100	$A^{u}BD$	3ph	–	29,4	–	1,84	15,0
T. aestivum, cv Krasota	$A^{u}BD$	3ph		29,3		1,67	15,4
T. sphaerococcum, cv Sharada	$A^{u}BD$	2ph	18,9	21,0	1,47	1,21	18,8
T. compactum [1]1	$A^{u}BD$	2ph	–	20,0	–	1,05	22,9
T. compactum [1] 2	$A^{u}BD$	2ph	–	16,2	–	1,01	–
T. monococcum	A^{b}	1ph	11,6	–	0,69	–	–
HCP_{05}			1,7	3,9	0,67	0,19	

Note. HCP_{05} between *T. kiharae* and its complete homologue; ph — phenome (quantitative value of the character equal to the contribution of diploid genome in manifestation of a corresponding trait). Dashes: the samples were not used in this year.

Flag leaf area in the complete homologue was $1/3$ larger than the initial value in *T. kiharae*. Thus, in the first year, the contribution from diploid genome in three-genomic complete homologue equaled 32,3 cm² : 3 = 10,8 cm². Accordingly, the trait manifestation degree in *T. kiharae* can be defined as 21,4 cm² : 10,8 cm² = 1,98 ($\approx$2). Considering the two-phenomic level of trait manifestation in *T. kiharae*, flag leaf area is calculated as 10,8 cm² × 2 = 21,6 cm², which value corresponds to that observed in 2005 (21,4 cm²) (Table 2). The same was detected for weight of grains per ear (Table 2). Characteristics of sphaerococcoid wheat and two compactoid samples were close to those in *T. kiharae* as well, therefore, these species also have two-phenomic tetraploid level of trait expression.

In hexaploid soft wheat cultivars Yubileynaya 100, Krasota and the complete homologue (cv Rassvet 1), the values of quantitative traits coincided, which proved their identical three-phenomic hexaploid status. The diploid sample *T. monococcum* was used as a phenome-genome marker; its manifested quantitative characteristics corresponded to the calculated contribution from one diploid genome in expression of traits in polyploid forms: in *T. monococcum*, flag leaf area was 11,6 cm², while the contribution of a single diploid genome in hexaploid full homologue amounted to 10,8 cm², weight of grain per ear – respectively, 0,69 and 0,74.

Along with it, the three-phenomic wheat cultivars Yubileynaya 100, Krasota and its complete homologue cv Rassvet 1 developed significantly lower protein content in grain than two-phenomic samples.

Reliability of the performed comparative analysis was achieved by using genetically related samples - *T. kiharae* and the complete homologue derived from it. To ensure a correct comparison in other cases, it is desirable to select samples from identical homologous series. This issue has been studied in detail earlier (13).

The further step in studying the nature of complex quantitative traits was comparing the corresponding characteristics of sphaerococcoid wheat cultivar Sharada and cv Obriy involved in its origin, which ensured genetic purity of the analysis. In addition, the experiment included using the three-phenomic hexaploid cv Rassvet 1 showing a complex manifestation of quantitative traits. Experiments were performed on different fields at quite different conditions of cultivation: field 1 – testing cv Rassvet 1 and cv Sharada at optimum sowing terms, field 2 – testing cv Obriy and cv Sharada at later term of sowing (owing to technical reasons). Nevertheless, there were observed the typical values corresponding to two- and three-phenomic formation of complex quantitative traits (difference at $\approx 1/3$). Thus, the flag leaf area of plants grown on the first field (1st experiment) amounted to 29,2 in cv Rassvet 1 and and 20,3 cm² in cv Sharada, while on the second field (2nd experiment) – 8,9 in cv Obriy and 6,0 cm² in cv Sharada. (LSD_{05} for the tests, respectively, 4,4 and 1,2 cm²). Knowing the three-phenomic nature of soft wheat (including cv Obriy), the effect of one diploid genome amounts to 8,90 cm² : 3 = 2,97 cm². Therefore, the level of manifestation of the character in cv Sharada can be calculated as 6,00 cm² : 2,97 cm² = 2,02 ($\approx$2). Similar results were obtained for cv Rassvet 1.

Productivity indices in general reflect the hypothesis of two- and three-phenomic level of trait manifestation in hexaploid wheat cultivars (Table 3).

3. Productivity parameters of hexaploid wheat cultivars (Rostov province, 2007)

Cultivar	Weight of 1000 grains		Ear productivity indices					
			Number, pcs				Weight of grains, g	
			spikelets		grains			
	1st experiment	2nd experiment	1st experiment	2nd experiment	1st experiment	2nd experiment	1st experiment	2nd experiment
Rassvet1	37,6		18,3		49,0		1,90	
Obrii		31,0		16,8		27,0		0,81
Sharada	26,0	23,0	19,5	16,9	45,6	20,0	1,20	0,50
HCP_{05}				4,5		6,5	0,20	0,20

Note. 1st and 2nd experiments were performed on different fields. Absence of data in table cell – a cultivar wasn't included in the compared pair.

It should be emphasized that not all quantitative traits changed similarly. Thus, the number of spikelets per ear in sphaerococcoid wheat cv Sharada was not distinct from that in soft wheat cultivars. Small differences were observed in number of grains per ear. At the same time, the earlier found two- and three-phenomic differences between sphaerococcoid and soft wheat samples were most pronounced in such a complex quantitative trait as weight of grains per ear, - 0,31 g, or 38%, between cv Obriy and Sharada, which slightly exceeds the expected 33%. The difference in weight of 1000 grains was 26% (i.e. less than 33%). Insufficient size of grains in cv Obriy was compensated by a large number (27 vs. 20) and, accordingly, the greater weight of grains per ear (38%) (Table 3). The quantity of phenome by weight of grains per ear in cv Obriy equaled 0,81 g : 3 = 0,27 g, in cv Sharada (considering its two-phenomic status) – 0,50 g : 2 = 0,25 g. These are the values of the same order, which certainly confirms three-phenomic hexaploid level of traits' manifestation in soft wheat and two-phenomic tetraploid level – in sphaerococcoid wheat (Table 3). Almost the same differences were established in cultivars Rassvet 1 and Sharada.

Weight of grains per ear is a complex trait provided by expression of several relatively simple quantitative traits - number of spikelets, number of grains and weigh of individual grains. When adding extra diploid genomes, a simple trait - number of spikelets per ear – doesn't grow correspondingly (for example, 20 spikelets in diploid, then 60 in hexaploid, etc.). However, such restriction is compensated by transformations of other traits, such as increasing the number and weight of grains in a spikelet. Though, resources for these simple quantitative traits are limited too: polyploidy leads to increased weigh of individual caryopses at their lower number, or vice versa. At the same time, the resulting complex quantitative trait (weight of grains per ear) formed by simple traits, has a higher limit of variation, and contributions of extra genomes are more pronounced in complex traits rather than in simple quantitative traits (Table 3).

Flag leaf length and width were the other studied quantitative traits of polyploid wheat. Increase of these parameters can't be linearly associated to "dosage" of genomes as well: theoretically, tetraploid is capable to develop the flag leaf twice longer than that of diploid, but it's hardly possible the further increase of this value by one third in hexaploid relative the tetraploid form. Flag leaf area is determined by its length and width, and this complex quantitative trait allows much easier detection of contributions of individual diploid genomes, as was proved by the authors' findings. However, at higher ploidy, this parameter can be insufficiently complex for assessing the contributions of particular genomes, which requires using more complex traits such as leaf volume composed by three variables (length, width and thickness). Plants of the same cultivar can manifest unequal response to polyploidization (23) - some quantitative traits can be enhanced, other traits remain unchanged and some characters weaken.

Thus, the formation from soft wheat of macromutants manifesting a pronounced speltoid, compactoid and sphaerococcoid complex of traits is a process associated with suppression of contributions from individual diploid genomes. As it has been mentioned earlier, the principle of macromutant transformation can be extrapolated on existing species as well (24). The phenomic level of formation of complex quantitative traits is associated with trait manifestation resulting from presence or absence of contributions from individual diploid genomes. This fact suggests the following representation of genomic formula of wheat species: for *T. aestivum* QQccSS - AABBDD, for *T. spelta* qqccSS - DDABab, for *T. compactum* QQCCSS - AABDbd and T. *sphaerococcum* QQccss - BBADad (respectively, actual and proposed one). The proposed denotations show the recessive state of contribution from one of three diploid genomes in *T. spelta*, *T. compactum* and *T. sphaerococcum*. Besides, recessive or dominant state of individual genomes in the polygenome of a particular species to some extent reflects its morphological features. Indeed, some researchers (25, 26) obtained speltoid tetraploids DDAA by crossing *Ae. tauschii* (D genome) with diploid wheat forms - *T. urartu* (A^u) and *T. boeoticum* (A^b) and the resulting forms demonstrated great resemblance to hexaploid *T. spelta*; upon this fact, they concluded that B genome isn't obligatory for development of speltoid wheat type. Moreover, speltoid forms exhibited the pronounced characteristics of *Ae. tauschii* (it is the dominance of DD genome reflected by the proposed genomic formula of spelt). The predominance of "wheat" nature in *T. compactum* is of no doubt despite the reduce of some quantitative traits. This species has a certain similarity to AABB tetra-forms, which is assumed to be the most important for choosing a combination of genomes providing morphostructural characteristics. The genomic formula proposed for *T. sphaerococcum* can be explained similarly.

The revealed morphostructural features of *T. spelta, T. compactum* and *T. sphaerococcum* allow the estimation of prospects for most efficient use of these species. The fact of sharply suppressed expression of certain productivity traits owing to the missed contribution of one diploid genome can be the explanation for the observed relatively low grain productivity in these samples compared to that in *T. aestivum*, while the increased protein content in grain (from 15 to 25% in *T. spelta* and 15-22% - in *T. compactum* and *T. sphaerococcum*) relative to that of *T. aestivum* (8,8-24,0% at average for most of cultivars 12-17%) (1, 27). Sphaerococcoid macromutants develop high protein content in grain relative that in the original soft wheat, which feature has been maintained over all years of research (2). So, the reduced grain productivity of speltoid, compactoid and sphaerococcoid macromutants is associated with higher protein content in grain than in the original soft wheat.

When growing *T. spelta, T. compactum* and *T. sphaerococcum* on fertile soils at high agronomic impact, they can't exceed soft wheat yields owing to relatively lower potential productivity. It seems that these species were gradually rejected from cultivation during the improvement of agriculture techniques and industrial bred bakery. In addition, the dominance of D genome in *T. spelta* contributes to firm loose ears that are hardly threshed. At the same time, hull-less *T. compactum* and *T. sphaerococcum* show earlier ripening, resistance to lodging and tolerant to different soil and agronomic conditions (the latter feature is peculiar to *T. spelta* as well). That's why compactoid wheat cultivars are particularly widespread in the north (including permafrost in Yakutia, where a summer is very short, but fairly warm). Sphaerococcoid wheat has many advantages: it improves flour properties and provides highest flour yield at milling due to a spherical shape of grain, etc.

In earlier works (28), the authors have identified the three-phenomic level of manifestation of quantitative traits in tetraploid wheat reflecting the non-coincidence of its phenomes and genomes, which has been also established now in hexaploid wheat. It's important to know these features of formation of productivity properties, because polyploidy is proposed for fixing heterosis during the creation of a complex genome (29).

Thus, biological characteristics and productivity traits of *T. spelta, T. compactum* and *T. sphaerococcum* to some extent are determined by absence of the contribution (phenome) from one of the three diploid genomes (AABBDD). In this regard, breeding work or commercial use of these forms must consider the two-phenomic tetraploid level of quantitative productivity traits in these species.

REFERENCES

1. *Kul'turnaya flora SSSR* (Cultural Flora of USSR), Vol. 1 Wheat, Leningrad, 1979.
2. Bobrova A.V., Valeeva T.M., Degtyareva S.S. at al., Peculiarities of Protein and Amino Acid Contents in Sphaerococcoid and Compactoid Mutant Lines of Winter Soft Wheat, *Novye sorta, sozdannye metodom khimicheskogo mutageneza* (New Cultivars Created through Chemical Mutagenesis: Compilation of Sci. Works), Moscow, 1988, pp. 92-97.
3. Luk'yanenko P.P. and Zhogin A.F., About Some Mactomutants of Winter Wheat Variety Bezostaya 1, *Dokl. VASKhNIL,* 1970, no. 4, pp. 5-7.
4. Grinval'd K., Taxonomic Mutations Induced in *T. aestivum* L., *Experimental'nyi mutagenez v selektsii* (Experimental Mutagenesis in Selection: Compilation of Sci. Works), Moscow, 1972, pp. 333-347.
5. Makarova S.I. and Zoz N.N., Induced System Mutations in Wheat, *Genetics,* 1965, no. 2, pp. 113-118.
6. MacKey J., Genetic Basis of Wheat Systematics, *S.-kh. biol.,* 1968, vol. 3, no. 1, pp. 12-25.
7. Dorofeev V.F., Problems of Modern Phylogeny and Systematics of Wheat, *Vestn. s.-kh. nauki,* 1969, no. 3, pp. 25-35.
8. Afanas'ev P.D., Hereditary Forms and Grain Size in Crosses *Triticum sphaerococcum* Persiv. ½ *T. aestivum* L., *Sb. nauch. tr. po prikl. bot., genet. is el.,* 1985, vol. 98, pp. 72-75.

9. Konarev V.F., Gubareva N.K., Gavrilyuk I.P. et al, Identification of Genome D in Wheats with Respect to Gliadin, *Vest. s.-kh. nauki,* 1972, no. 7, pp. 108-114.

10. Romanov B.V., Phenome-Genomics of Quantitative Traits in Polyploid Wheat, *Mat. mezhd. nauch.-prakt. konf. "Sostoyanie i perspektivy razvitiya agronomicheskoi nauki"* (Proc. Int. Sci.-Pract. Conf. "State and Prospects of Agronomy"), Persianovsky Town, 2007, vol. 1, pp. 163-166.

11. Strunnikov V.A., Genetic Engineering on Genomic Level in Silkworm, *Uspekhi Sovremennoi Genetiki,* Moscow, 1988, pp. 3-64.

12. Romanov B.V., Logical Stepwise Changes in Grain Productivity of Wheat at Polyploidization, *Dokl. RASKhN,* 1997, no. 4, pp. 8-9.

13. Romanov B.V. and Zelenskaya G.M, *Poliploidiya i produktivnost' pshenitsy* (Polyploidy and Productivity of Wheat), Persianovsky Town, 2005.

14. Dospekhov B.A., *Metodika polevogo opyta* (Technique of Field Experiment), Moscow, 1985.

15. Pukhalsky A.V. and Maksimov I.L., About Appearance of Green Grain Color in Winter Wheat, *Bul. VIR,* Leningrad, 1980, issue 99, pp. 3-6.

16. Romanov B.V., New Hexaploid Wheat Form or Complete Homologue of *T. aestivum* L., *Genetika,* 1994, vol. 30 (appendix), p. 133.

17. Romanov B.V., New Hexaploid Wheat Form – Homologue of *T. aestivum* L., *Tr. III Mezhd. simp. "Novye i netradicionnye rasteniya i perspektivy ikh ispol'zovaniya"* (Proc. III Int. Symp. "New and Non-Conventional Plants and Prospects of Their Use), Moscow – Puschino, 1999, vol. 2, pp. 409-411.

18. Romanov B.V., Change in Parameters of Root System and Productivity of Wheat and Its Responsiveness to Mineral Nutrition, *Extended Abstract of Cand. Sci. Dissertation,* St.Petersburg, 1995.

19. Zoz N.N., Sphaerococcoid Mutants Induced by Chemical Mutagens in Wheat, *Teoriya khimicheskogo mutageneza,* Moscow, 1971, pp. 122-125.

20. Kobylyansky V.D., *Rozh': geneticheskie osnovy selektsii* (Rye: Genetic Basics of Selection), Moscow, 1982.

21. Romanov B.V., Improving Productive Properties of Sphaerococcoid Wheat, *Vest. RASKhN,* 2010, no. 5, pp. 50-52.

22. Burdenuk-Tarasevich L.A., Characteristics of Mutation Process in Winter Wheat Caused by Ionizing Irradiation in Chernobyl Exclusion Zone, *Mat. XI Mezhd. Simp. "Netraditsionnoe rastenievodstvo. Eniologiya. Ekologiya i zdorov'e"* (Proc. XI Int. Symp. "Non-Conventional Plant Growing. Eniology. Ecology and Health"), Simferopol, 2002, pp. 362-366.

23. Savchenko V.K., Experimental Polyploidy and Genomic Effect, *Tez. dokl. III s'ezda VOGiS im. N.I. Vavilova* (Abstracts of Reports III Congress of N.I. Vavilov Society of Genetics and Selection), Leningrad, 1977, vol. 1, part 2, p. 456.

24. Shtubbe G.O., About Relationship between Natural and Artificially Formed Biodiversity and Some Experimental Researches on Evolution of Cultural Plants, *Genetics,* 1966, no. 11, pp. 9-30.

25. Gandilyan P.A., Shakaryan Zh.O. and Petrosyan Je.A., Synthesis of New Emmers and Tetraploid Speltoids and Issues of Wheat Phylogeny, *Biologicheskii zhurnal Armenii,* 1986, vol. 39, no. 1, pp. 5-15.

26. Gandilyan P.A. and Shakaryan Zh.O., Cytogenetic Study of Amphiploid *Triticum boeoticum Boiss. ½ Aegilops tauschii* Goss. (*T. boeoticotau-schicum* Gandil), *Tsitologiya i genetika,* 1992, vol. 26, no. 2, pp. 3-11.

27. *Pshenitsy mira* (Wheats of the World), Leningrad, 1987.

28. Romanov B.V., Agout Hexa- and Octaploid Levels of Quantitative Traits in Hull-less Tetraploid Wheat Species, *S.-kh. biol.,* 2006, no. 3, pp. 101-108.

29. Shumny V.K., Problems of Plant Genetics, *Vest. VOGiS,* 2004, vol. 8, no. 2, pp. 39.