

## QTL MAPPING IN HEXAPLOID SOFT WHEAT (*Triticum aestivum* L.) IN WEST SIBERIAN PLAIN

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### Abstract

Mapping of quantitative traits loci (QTL) is a modern approach to studying their genetic variability. In this, mapping QTL which determine the economically valuable traits and their effective use in the marker assisted selection are of practical interest. Here, we report evaluation of a set of 114 recombinant inbred lines of spring wheat (*Triticum aestivum* L.) mapping population ITMI (International Triticeae Mapping Initiative) in the conditions of West-Siberian plain, Russia. The ITMI mapping population was obtained by crossing spring wheat *Triticum aestivum* L. cultivar Opata 85 with a synthetic hexaploid W7984, the amphidiploid which was produced by crossing *Aegilops tauschii* Coss. (DD) sample CIGM86.940 and tetraploid wheat *T. turgidum* var. *durum* cultivar Altar 84 (AABB). In total, 42 different economically valuable traits were evaluation during the vegetation period, and 55 quantitative trait loci were identified. The dependence fidelity between the identified loci and trait polymorphism was estimated based on the threshold of the likelihood ratio of LOD-score (logarithm of odds). For 35 identified QTL,  $\text{LOD} \geq 3.0$  was found. Identified QTL were dispersed on 19 linkage groups different chromosomes and expressed in environment conditions of southern forest-steppe zone of West-Siberian plain with varying certainty. It was shown that the manifestation of the identified QTL may be environmentally dependent or independent, and the investigated quantitative traits correlated and were interrelated. To determine the nature of the relationship between the evaluated traits, the correlation coefficients  $r_{xy}$  were calculated. We revealed different correlations between expression of the evaluated economically valuable traits studied which stresses on the complex nature of their manifestation. It is established that the genetic variability of most of the traits evaluated is usually controlled by several QTL with broad effects which correlate with one another or by a large number of QTL with small effects. The detected QTL and linked molecular markers may be of interest for further study of the genetic control of economically valuable traits determined by identified QTL and for implementing marker-assisted selection in bread wheat.

Keywords: *Triticum aestivum*, quantitative economically valuable traits, ecology and genetic mapping, southern forest-steppe zone of West-Siberian plain of Russia

Mapping of quantitative traits loci (QTL) is a modern molecular approach to selection based on polygenic traits, including marker-assisted selection (MAS) [1-3]. The purpose of these researches is to identify, to study, to map and to introduce QTLs, effectively influencing variation of phenotypic traits, into varieties and lines which are of breeders' interest. The modern QTL mapping methodology is described in detail [4-6], including publications in Russian [7-9]. Summing up the available information, it can be concluded that in the

absence of expressed molecular genetic differences between the genes types, regulating quantitative and qualitative characteristics, gene mapping techniques using for qualitative (Mendelian) factors is not directly applicable to quantitative traits, in which case offspring individuals cannot be classified or separated into discrete phenotypic classes.

Currently, there are practical results of QTL analysis used both for mapping of identified QTLs and for their cloning and transfer to lines and varieties [8]. Estimation of environmental impact on the manifestation of studied traits is one of the most important steps in QTL mapping. Breeders can use only reproducible data of QTL analysis [10]. As QTL manifestation can depend on the environmental impact, the breeder can adjust the plant growing conditions (for example, under the Precision Farming Program) [11] to provide manifestation of the needed traits. Consequently, the QTL mapping at different ecological and geographical areas have both fundamental and practical breeding importance. The ecological genetic QTL mapping started from the papers in which it was shown that the QTL localization can vary in different experiments and relatively to other QTL, indicating a significant effect of external conditions on trait manifestation [12, 13].

To establish the genotype  $\times$  environment interactions, the stability of QTL location in the identified linkage groups was tested depending on external conditions. In tomato, 350 F<sub>2</sub> descendants were grown in three different eco-geographic locations (two in the USA, one in Israel). As a result, the authors identified 29 QTLs; 15 were specific for only one area and only 5 were common to all three [12]. At the same time, corn cultivated in the United States at the six areas (two in the states of North Carolina, Iowa and Illinois), were weaker influenced by the environment [13]. In this experiment, the total number of the identified QTLs was higher. One hundred twenty six doubled-haploid rice lines were studied in nine geographical locations of Philippines [14]. Assessing the height of plants and the time of ear formation, the authors identified 37 main QTLs determining these traits, and 29 QTL with an epistatic effect. In Italy, QTL controlling grain protein content [15] was studied. Because this trait also depends on growing conditions, 65 recombinant inbred lines (RIL) of tetraploid wheats were used for QTL identification. As a result, authors localized seven QTLs for grain protein content (GPC) located on the chromosome arms 4BS, 5AL, 6AS (two loci), 6BS, 7AS and 7BS, and their manifestation directly depended on the growing conditions. These data are similar to obtained on hexaploid wheat by Russian scientists together with German colleagues [16, 17], when the mapping population was grown in Germany. The authors evaluated 51 RILs of soft wheat. As a result, 32 loci on 12 chromosomes of different homeological groups were mapped by 14 traits associated with the indicators of soft wheat quality. Earlier, the same German colleagues mapped QTLs determining agronomically important traits of the same RIL [18]. In contrast to the previous research, the authors used 114 RILs and made observations at three geographical locations in Germany for four vegetation periods. As a result, they mapped 210 QTLs with a minor effect and about 64 basic QTLs that determine the morphological and economically valuable traits of soft wheat [18]. However, it should be pointed out that, at the seeming wide scale of this work, the plot size in the experiment was 3, 4, 5 and 9 m<sup>2</sup> for each vegetation period, and the assessment for only 5 genotypes (individuals) for each RIL mapping population was performed. In addition, the eco-geographic conditions of Germany, of course, differ from Russian (at least because of the difference in geographical location of the countries).

In Russia, QTL mapping of higher plants in different eco-geographic areas has been carried out since 2005 [10]. So, a group of Russian and German scientists performed a series of studies on the mapping RIL population in various eco-

geographic zones, as well as under controlled conditions of an agroecobiological testing ground (agroecobiopolygon) [10, 19-21]. It is found that QTLs can either depend on environmental conditions, or not manifest such dependence. The reliability of the interrelation between the identified QTL and the polymorphism for one or another parameter was evaluated based on the threshold value of the likelihood ratio of the logarithm of odds (LOD-score). In some cases, the localization of the identified QTL position in the linkage groups persisted for a number of years and in different areas, although the LOD value could vary. In addition, the QTL analysis revealed the block structure of the *T. aestivum* genome and the percentage of phenotypic variability determined by each of the identified QTLs, and also which of the parents introduced the QTL allele.

Important results are obtained by estimation of the number and exact chromosomal localization of the QTLs involved in the physiological and genetic control of complex agronomically important traits of spring wheat (*T. aestivum*) under the conditions of agroecobiopolygon [21] where it is possible to selectively modify an analyzed environmental parameter, keeping all the others without changes. These results unambiguously confirmed that in fixed conditions the QTL localization is stable, and the manifestation of some QTLs is associated with the impact of certain external factors. One-factor analysis of variance showed that the change in the temperature and light regime did not affect only 21 of 30 estimated traits (70 %). Four of the remaining traits that are susceptible for temperature and light impact, are directly associated with grain efficiency, which determines not only their economic value, but also the importance for the survival, preservation and species distribution. Four more traits perform a protective adaptive function in vegetation, and one is realized during initial growth and development, participating in the initiation of a cascade of physiological and genetic mechanisms that ensure the maximum possible performance of plants in specific environmental conditions.

In spite of considerable number of papers on genetic and environmental QTL mapping in Russia, information about the genome functioning and mechanisms of manifestation of commercially important traits of spring wheat is still not complete. In the present research, we for the first performed a large scale test of 114 recombinant inbred lines of the ITMI (International Triticeae Mapping Initiative) of hexaploid spring wheat in the conditions of Omsk city. As a result, QTLs for 42 agronomically important traits are identified and localized. The QTL locations depend on the eco-geographical conditions of plant growing. It is shown that the studied quantitative traits are interrelated. Molecular markers linked to detected and identified QTL are established.

The aim of the research was to identify and to map loci that determine economically valuable traits of soft wheat in the conditions of southern forest-steppe areas of the West Siberian Plain.

*Techniques.* The recombinant inbred lines (RIL) of hexaploid spring wheat (*Triticum aestivum* L.) of mapping population ITMI (International Triticeae Mapping Initiative) were used. The ITMI population was created by pollination of spring Opata 85 soft wheat (*Triticum aestivum*) variety with the pollen of the synthetic hexaploid W7984. Amphidiploid W7984 was obtained by crossing *Aegilops tauschii* Coss. (CIGM86.940, DD) as a male parent and tetraploid wheat *T. turgidum* var. *durum* Altar 84 (AABB) variety as a female parent [19, 20]. In these papers [19, 20] we also described selection of genotypes for the RILs of ITMI mapping population and their properties.

RILs of ITMI were grown and evaluated on an experimental field in 2016 in the conditions of the southern forest-steppe of the West Siberian Plain, in the center of the southern part of the Omsk area. The Omsk area is a zone of insuffi-

cient moisture. The limiting factors in the region are periodically recurring droughts of different intensity and epiphytotics of brown and stem rust [22]. In general, the weather conditions of the vegetation period of 2016 were quite favorable and typical for the region: in the first half of June, there were high temperatures and no precipitation, in July the warm, rainy weather favorable for plant development was prevalent, and in August the weather was warm and dry. On some days the maximum air temperature in June, July and August reached 32-35 °C. Brown and stem rust infections were noted in the third decade of August.

Manual sowing of recombinant inbred lines of the ITMI mapping population (40 grains per a row at 5 cm depth, 1 m wide strips with 15 cm row spacing) was performed on May 17, 2016. Manual harvesting (each row separately) was carried out on September 5.

The analysis of trait was performed according to the VIR methodology [23]. The traits with expressiveness sufficient for estimation were scored. A total of 42 traits were analyzed during the growing season.

QTL analysis was performed with MAPMAKER/QTL program [18, 24]. As this program is based on the J.B.S. Haldane's formula [25], MAPMAKER/EXP 3.0 software [24] and the data of the GrainGenes database (gopher: <http://www.green-genes.cit.cornell.edu>) were used for re-calculation of distances. The results of phenotype analysis were integrated into the existing basic map of ITMI population [26]. QTL localization in the linkage groups was identified with QGENE [27] as described [18-20], using only the markers which correspond to the D.D. Kosambi's mapping function considering interference [28].

The reliability of interrelation between the identified loci and polymorphism on a trait was evaluated based on the threshold value of the likelihood logarithm of odds (LOD-score ratio) [29, 30]. For each trait in each experiment, individual QTL analysis was performed and the degree of variations ( $R^2$ ) was determined for phenotypic traits associated with the corresponding QTL. Significance of each LOD was determined by permutation test (1000 replications). Only loci with  $\text{LOD} \geq 3.0$  ( $p < 0.001$ ),  $2 < \text{LOD} < 3$  ( $p < 0.01$ ) and  $1.5 < \text{LOD} < 2$  ( $p < 0.1$ ) [18-20] were considered.

Correlation coefficients  $r_{xy}$  were calculated to determine the nature of the interaction contingency between the traits. Under the assumption that  $(x_1, y_1), (x_2, y_2), \dots, (x_n, y_n)$  is a sample of  $n$  observations for a pair of variables  $(x, y)$ , the correlation coefficient  $r_{xy}$  is calculated as follows [31]:

$$r_{xy} = \frac{\sum_{i=1}^n (x_i - \bar{x})(y_i - \bar{y})}{\sqrt{\sum_{i=1}^n (x_i - \bar{x})^2 \sum_{j=1}^n (y_j - \bar{y})^2}}$$

where  $\bar{x}$ ,  $\bar{y}$  are selective averages calculated as

$$\bar{x} = \frac{1}{n} \sum_{i=1}^n x_i, \quad \bar{y} = \frac{1}{n} \sum_{i=1}^n y_i.$$

Negative correlations indicate the relationship between the traits, at which the mean values of one trait decrease with increasing values of the other trait.

Correlation coefficients were reliable at  $p < 0.05$ . Such a value is an acceptable boundary of statistical significance, because it includes an error rate of 5% [32]. All indicators were calculated using the STATISTICA 10.0 software (StatSoft, Inc., USA).

*Results.* Molecular mapping (Table 1 at the <http://www.agrobiolgy.ru>) showed that sprouting-tillering period is determined by a QTL located on chromosome 6B. The phenotypic variation associated with the allele obtained from the male W7984 parent was rather high and reached 18.70%. The sprouting-booting period was also determined by one QTL which was located on chromosome 5A (phenotypic variability was 5.60%), but in this case the allele was in-

troduced by the female Opatá 85 form.

QTLs for sprouting-earing and sprouting-maturation periods, as well as for plant shape were located on chromosome 5D. All of the identified QTLs were located close to each other, but the percentage of phenotypic variation for each QTL for these three traits varied (from 10.05 to 18.97 %). One of the two QTLs associated with plant height was also mapped on chromosome 5D. The second QTL of the same trait was on chromosome 4A. Note, all the QTLs identified in the 5D linkage group are introduced by the male parent, and the allele on chromosome 4A is inherited from the female one.

Three QTLs (linkage groups 1A, 3A and 7A) determine the length of the upper internode, alleles on 1A and 3A are obtained from the female parent, on 7A from the male parent. The observed phenotypic variation was quite high and varied from 23.48 % (7A) to 28.69 % (1A, 3A). A single QTL on 3D determines the flag position at the beginning of earing, with lower percentage of phenotypic variation (only 14.03 %), although the LOD score is 3.25.

The location of QTLs identified on chromosomes 2D and 7D and determining the wax appearance on stem and front side of leaf coincides completely, although phenotypic variation ranges from 28.52 % (7D) to 52.42 % (2D). The wax coating on the ear is also determined by two QTLs, on 2D and 1D (27.32 and 12.77 % phenotypic variations, respectively).

QTLs for traits determining yield (ear length, spikelet number per ear, grain number per spikelet, grain number per ear, grain weigh per ear, 1000 grain weigh and ear number) are identified in seven different linkage groups. In this case, QTLs for grain number per spikelet, grain number per ear, grain weight per ear are located in one site on chromosome 1B, for 1000 grain weigh and ear number — on chromosomes 6A and 1A, respectively, and for ear length and spikelet number per ear — in the linkage groups 4A, 5D and 5A, 3A. The phenotypic variations range from 10.41 % for 1000 grain weight up to 25.07 % for ear length. Both QTL alleles associated with spikelet number per ear and also QTL allele for ear length identified on 4A chromosome are introduced from the Opatá 85 variety, the rest are from W7984.

QTLs mapped on chromosomes 7B, 3B and 2B are associated with resistance to powdery mildew, brown rust, septoria and root rot, QTLs for resistance to stem rust are located on chromosomes 7A and 4B. Phenotypic variations are from 10.68 % (resistance to root rot) up to 26.75 % (resistance to stem rust). The QTL alleles for resistance identified on 7B, 4B and 2B are inherited from the female parent, on 7A and 3B — from the male parent.

QTLs for flag appearance, main stem leaf number and stem node pubescence are identified on chromosomes 4D, 1B and 7B, respectively. Alleles on 4D and 1B from the male parent determine 11.63 and 12.29 % of the phenotypic variations, respectively, on 7B from the female parent — 19.17 % of stem node pubescence.

Sheaf weigh with roots, plant number per sheaf, quality retained till harvesting, and grain weight per sheaf are determined by QTLs introduced only by the female Opatá 85 form. QTLs for weigh with roots, plant number per sheaf are identified on chromosome 4A at 87.5 cM. QTLs for plant number per sheaf and quality at harvesting are on chromosome 5B at 128.8 cM. Identification of such QTLs and their location indicate that sheaf weigh with roots and grain weight per sheaf are determined by one locus of chromosome 4A, and plant number per sheaf and quality at harvesting are determined by one locus of chromosome 5B.

It is of interest that plant weight is determined by a locus introduced by the female form, but this QTL is mapped on chromosome 3A at 120.9 cM. Total

stem number and productive stem number are determined by QTLs identified by on 3B and 2A, respectively, and three QTLs located on chromosomes 1A, 3A and 4A at 205.7 cM, 56.3 cM and 63.2 cM, respectively, are for stem length (all these QTLs are also obtained from the female Opata 85 form).

QTL identified on chromosome 1B at 23.8 cm mainly influences the traits determining the grain yield (main ear weight, ear density, grain number per plant, grain weight per plant, 1000 grain weight per the main ear and the main ear weight). The exception is ear density and 1000 grain weight per the main ear: QTLs for these traits are identified in the linkage groups 5A and 6A, respectively. All QTLs are introduced by the male form; exception is an allele from the female form which determines ear density. The observed phenotypic variability is relatively low and alter from 10.24 % (1000 grain weight per the main ear) up to 16.84 % (grain weight per the main ear).

The coefficients of plant economic value ( $K_{\text{econ.plant}}$ ) and the economic value of the ear ( $K_{\text{econ.ear}}$ ) are the indices of plant and ear productivity. In Western Siberia, these values usually vary from 25 to 45 %.  $K_{\text{econ.plant}}$  is calculated as the percentage ratio of the grain weight per plant to total plant weight (without roots, but with ears and grain).  $K_{\text{econ.ear}}$  is the grain weight per ear percentage to total grain weight per ear. QTLs for these two traits are detected on chromosomes 1B (for both coefficients) and 5D (for  $K_{\text{econ.plant}}$ ). All these QTLs are introduced by the male form; the phenotypic variability ranges from 11.30 % ( $K_{\text{econ.ear}}$ ) up to 15.03 % ( $K_{\text{econ.plant}}$ ). Their phenotypic variation is determined by the same QTL allele located on chromosome 1B at 23.8 cM.

Note, a locus identified on chromosome 1B at 23.8 cM includes genes which are responsible for plant productivity and grain yield traits (grains number per spikelet, grain number per ear, grain weight per ear, the main ear weight, grain number per plant, grain weight per plant, grain weight per the main ear,  $K_{\text{econ.plant}}$  and  $K_{\text{econ.ear}}$ ). QTL determining leaf number per the main stem is also located on chromosome 1B, but at 176.0 cM, so it is another locus different from the 23.8 cM locus. The 1000 grain weight and 1000 grain weight per the main ear are also determined by one locus mapped on 6A at 101.9 cM. Two blocks of genes are identified on chromosome 4A, which are formed by loci at 87.5 cM (for sheaf weight with roots and grain weight per sheaf) with a nearby loci at 63.2 cM (for stem length) and 206.5 cM (for ear length and plant height). The presence of such gene blocks assembled in one or more linkage groups indicate an evolutionary co-inheritance of the traits which are responsible for certain stages of plant ontogenesis and its individual features under specific growth conditions. Of course, canalization of variability and conservatism of genetic systems of ontogenetic and phylogenetic adaptation (F and R systems), as well as their subcomponents are rather relative in natural evolution, but are significant for human practical activities, especially in breeding [33]. Thence induced recombinationogenesis plays the special role in increasing efficiency of breeding programs [34]. Genomic maps facilitate dividing quantitative trait into simpler genetic components (QTLs) and simplify their identification, especially under genotype  $\times$  environment interaction. Obviously, the character of this interaction depends on plant adaptive potential [34-38]. Effects of environmental factors apparently much determine the evolutionally formed blocks of co-adapted genes in each species, including wheat, and also the co-adaptation specificity of its genetic system as a whole. This is the base for evolutionary and ontogenetic "memory" of the genetic F and R systems which are specific to each plant species [33, 34, 38-40]. Theoretically, QTL can be detected only if the parents carry different alleles [4, 9]. The desired allele may be very specific for one parent and absent in other genotypes, for example, in those making up the mapping popula-

tion. Nevertheless, the identified QTLs indicate the possibility to improve breeding material by grouping chromosome regions with the desired positive effects. Our research revealed that the quantitative traits correlate with each other. This follows from the presence of more than one QTL for two or more traits in the same locus on the chromosome and the nature of their manifestation. However, the obtained results do not allow us to separate the effects of close loci linkage and pleiotropy. To establish statistically reliable interactions of the studied traits, we performed correlation analysis (Table 2, <http://www.agrobiology.ru>).

The correlation analysis identified completely linear relationship (with  $r$  almost equal to 1) between plant height and ear length, and plant number per sheaf and quality at harvesting (here and farther, only the results that are statistically significant at  $p < 0.05$  are considered). Thence the correlations of these pairs with the rest traits coincide.

The correlations of sprouting—tillering period with sprouting—booting ( $r = 0.73$ ) and sprouting—maturation ( $r = 0.79$ ) periods are rather high. Waxy coating of the outer side of leaves tightly correlates with the wax appearance on stem ( $r = 0.98$ ) and ear ( $r = 0.77$ ). A strong correlation ( $r = 0.75$ ) is also found between waxy coating on stem and on ear.

Grain numbers per ear and per spikelet correlate at  $r = 0.91$ . These traits also have high correlation coefficients with grain weight per ear (0.89 and 0.84, respectively), with the main ear weight (0.94 and 0.86), with grain weight per plant (0.85 and 0.78), with grain number per plant (0.93 and 0.83), with  $K_{\text{econ.plant}}$  (0.71 and 0.83), and with  $K_{\text{econ.ear}}$  (0.78 and 0.87). Additionally, grain numbers per ear is highly associated with grain weight per sheaf ( $r = 0.75$ ) and the main ear weight ( $r = 0.73$ ). Spikelet number per ear also has strong correlations with plant height and ear length ( $r = 0.70$ ). Ear number strongly correlates with sheaf weight with roots ( $r = 0.79$ ), plant number per sheaf and quality at harvesting ( $r = 0.92$ ).

Grain weight per ear closely correlates with grain weight per the main ear ( $r = 0.97$ ). Estimates for the relationship between these and other tested traits are similar:  $r = 0.80$  and  $r = 0.82$ , respectively, for grain weight per sheaf,  $r = 0.86$  and  $r = 0.90$  for the main ear weight,  $r = 0.89$  and  $r = 0.92$  for grain number per plant,  $r = 0.92$  and  $r = 0.94$  for grain weight per plant,  $r = 0.73$  and  $r = 0.74$  for  $K_{\text{econ.plant}}$  and, finally,  $r = 0.77$  and  $r = 0.79$  for  $K_{\text{econ.ear}}$ . Also note the correlation coefficient between grain weight per the main ear and plant weight ( $r = 0.70$ ).

Grain weigh per plant also shows strong correlations with grain weight per sheaf ( $r = 0.87$ ), grain number per plant ( $r = 0.96$ ),  $K_{\text{econ.ear}}$  ( $r = 0.76$ ), plant weight ( $r = 0.78$ ), and the main ear weight ( $r = 0.84$ ). In turn, the main ear weight quite strongly correlates with grain weight per sheaf ( $r = 0.71$ ), plant weight ( $r = 0.80$ ), grain number per plant ( $r = 0.81$ ), and the stem length, plant height and ear length ( $r = 0.72$ ). Correlation between stem length and upper internode length is characterized by  $r = 0.86$ .

It is a peculiar that grain number per plant also strongly correlates with plant weight ( $r = 0.73$ ), grain weigh per sheaf ( $r = 0.86$ ), and  $K_{\text{econ.ear}}$  ( $r = 0.77$ ). Note, sheaf weigh (with roots) strongly correlates with grain weight per sheaf ( $r = 0.80$ ), plant number per sheaf and quality at harvesting ( $r = 0.74$ ).  $K_{\text{econ.plant}}$  correlates with  $K_{\text{econ.ear}}$  at  $r = 0.91$ , total stem number and productive stem number correlate at  $r = 0.89$ , and correlation between 1000 grain weigh and 1000 grain weight per the main ear is at  $r = 0.90$  level.

Also, we revealed medium ( $0.3 \leq r < 0.7$ ) and weak ( $r < 0.3$ ) reliable correlations. Notably, negative correlations were also found. Sprouting—tillering period negatively correlates with sheaf weight (with roots) ( $r = -0.37$ ), and with

ear number, plants number per sheaf and quality at harvesting ( $r = -0.32$ ).

In general, the correlation analysis performed in this work shows that the manifestations of the studied economically valuable traits correlate, but with different strengths, which indicates their complex nature. Elucidation of genetic and physiological mechanisms underlying these traits may be the next step in practical application of identified QTLs for spring soft wheat breeding. It should be noted that this requires a complex study with a detailed planning of experiments. Nevertheless, the obtained results already make it possible to use the identified molecular markers associated with mapped QTLs in MAS.

Gene effects in different loci are commonly described by a negative exponential distribution [41]. Segregation analysis is applicable for most genes, but many genes and QTLs with small effects cannot be studied by the same method. Therefore, the hypothesis of negative exponential distribution of gene effects is not yet possible to prove or disprove, and its verification requires further research.

So, we for the first time identified and mapped QTLs for 42 economically and agronomically valuable traits of soft wheat in the conditions of southern forest-steppe of the West Siberian Plain. It is established that the genetic variability of most studied traits is usually controlled either by few correlating QTLs with wide range of effects, or by a large number of loci having small effects. The data obtained in this study allow evaluation of polygenic QTL effects and genotype  $\times$  environment interaction for use in spring wheat breeding.

## REFERENCES

1. Tanksley S.D. Mendelian factors underlying quantitative traits in tomato: comparison across species, generations and environments. *Genetics*, 1991, 127: 181-187.
2. Kearsey M.J., Farquhar A.G. QTL analysis in plants: where are we now? *Heredity*, 1998, 80: 137-142 (doi: 10.1046/j.1365-2540.1998.00500.x).
3. Morgante M., Salamini F. From plant genomics to breeding practice. *Curr. Opin. Biotech.*, 2003, 14: 214-219 (doi: 10.1016/S0958-1669(03)00028-4).
4. Tanksley S.D. Mapping polygenes. *Annu. Rev. Genet.*, 1993, 27: 205-233 (doi: 10.1146/annurev.ge.27.120193.001225).
5. Liu B.H. *Statistical genomics: linkage, mapping, and QTL analysis*. London, NY, Washington, 1998.
6. Collard B.C., Mackill D.J. Marker-assisted selection: an approach for precision plant breeding in the twenty-first century. *Phil. Trans. R. Soc. B*, 2008, 363: 557-572 (doi: 10.1098/rstb.2007.2170).
7. Khavkin E.E. Molekulyarnye markery v rasteniyevodstve [Molecular markers in plant breeding]. *Sel'skokhozyaystvennaya Biologiya [Agricultural Biology]*, 1997, 5: 3-21 (in Russ.).
8. Potokina E.K., Chesnokov Yu.V. Sovremennyye metody genomnogo analiza v issledovaniyakh genetik kolichestvennykh priznakov u rastenii [Modern methods of genome analysis in studies of quantitative traits in plants]. *Sel'skokhozyaystvennaya Biologiya [Agricultural Biology]*, 2005, 3: 3-18 (in Russ.).
9. Chesnokov Yu.V. *Kartirovanie lokusov kolichestvennykh priznakov u rastenii* [QTL mapping in plants]. St. Petersburg, 2009 (in Russ.).
10. Chesnokov Yu.V. *Molekulyarno-geneticheskie markery i ikh ispol'zovanie v predselektionnykh issledovaniyakh* [Molecular markers and their use in pre-breeding]. St. Petersburg, 2013 (in Russ.).
11. Yakushev V.P. *Na puti k tochnomu zemledeliyu* [Towards precision agriculture]. St. Petersburg, 2002 (in Russ.).
12. Paterson A.H., Damon S., Hewitt J.D., Zamir D., Rabinowitch H.D., Lincoln S.E., Lander E.S., Tanksley S.D. Mendelian factors underlying quantitative traits in tomato: comparison across species, generations and environments. *Genetics*, 1991, 127(1): 181-187.
13. Stuber C.W., Lincoln S.E., Wolf D.W., Helentjaris T., Lander E.S. Identification of genetic factors contributing to heterosis in a hybrid from two elite maize inbred lines using molecular markers. *Genetics*, 1992, 132: 823-839.
14. Li Z.K., Yu S.B., Lafitte H.R., Huang N., Courtois B., Hittalmani S., Vijayakumar C.H.M., Liu G.F., Wang G.C., Shashidhar H.E., Zhuang J.Y., Zheng K.L., Singh V.P., Sidhu J.S., Srivantaneeyakul S., Khush G.S. QTL  $\times$  environment interactions in rice. I. Heading date and plant height. *Theor. Appl. Genet.*, 2003, 108: 141-153 (doi: 10.1007/s00122-003-1401-2).
15. Blanco A., Pasqualone A., Troccoli A., Di Fonzo N., Simeone R. Detection of grain protein content QTLs across environment in tetraploid wheats. *Plant Mol. Biol.*, 2002, 48: 615-623 (doi: 10.1023/A:1014864230933).
16. Pshenichnikova T.A., Ermakova M.F., Chistyakova A.K., Shchukina L.V., Berner A., Reder M.



- Molekulyarnoe kartirovanie lokusov, svyazannykh s pokazatelyami kachestva zerna myagkoi pshenitsy [Molecular mapping of loci associated with grain quality in soft wheat]. *Sel'skokhozyaystvennaya Biologiya* [Agricultural Biology], 2006, 5: 41-47 (in Russ.).
17. Pshenichnikova T.A., Ermakova M.F., Chistyakova A.K., Shchukina L.V., Berezovskaya E.V., Lohwasser U., Reder M., Berner A. *Genetika*, 2008, 44: 90-101 (in Russ.).
  18. Börner A., Schumann E., Fürste A., Cöster H., Leithold B., Ruder M., Weber W. Mapping of quantitative trait loci determining agronomic important characters in hexaploid wheat (*Triticum aestivum* L.). *Theor. Appl. Genet.*, 2002, 105: 921-936 (doi: 10.1007/s00122-002-0994-1).
  19. Batalova G.A., Rusakova I.I., Kocherina N.V., Lovasser U., Berner A., Chesnokov Yu.V. *Otsenka linii ITMI i kartirovanie QTL u yarovoi myagkoi pshenitsy (Triticum aestivum L.) v usloviyakh Severo-Vostoka Rossiiskoi Federatsii* [Evaluation of ITMI lines and QTL mapping in spring soft wheat (*Triticum aestivum* L.) in the North-East of the Russian Federation]. Kirov, 2016 (in Russ.).
  20. Chesnokov Yu.V., Sitnikov M.N., Schumlyanskaya N.V., Kocherina N.V., Goncharova E.A., Kozlenko L.V., Syukov V.V., Kochetkov D.V., Lohwasser U., Börner A. *Catalogue of recombinant inbred lines of mapping population ITMI of soft spring wheat Triticum aestivum L. (ecological and geographical trials and QTL mapping)*. St. Petersburg—Gatersleben, 2014.
  21. Chesnokov Yu.V., Mirskaya G.V., Kanash E.V., Kocherina N.V., Lohwasser U., Börner A. QTL mapping in spring soft wheat (*Triticum aestivum* L.) in controlled conditions of agroecobiopolygon. *Russian Journal of Plant Physiology*, 2017, 64(1): 55-68 (doi: 10.1134/S1021443716060029).
  22. Shamanin V., Salina E., Wanyera R., Zelenskiy Y., Olivera P., Morgounov A. Genetic diversity of spring wheat from Kazakhstan and Russia for resistance to stem rust Ug99. *Euphytica*, 2016, 212(2): 287-296 (doi: 10.1007/s10681-016-1769-0).
  23. Filatova A.A., Shitova I.P. *Shirokii unifikirovannyy klassifikator SEV roda Triticum L.* [A broad unified Comecon classifier of genus *Triticum* L.]. Leningrad, 1989 (in Russ.).
  24. Lander E.S., Green P., Abrahamson J., Barlow A., Daly M.J., Lincoln S.E., Newburg L. MAP-MAKER: an interactive computer package for constructing primary genetic linkage maps of experimental and natural populations. *Genomics*, 1987, 1: 174-181 (doi: 10.1016/0888-7543(87)90010-3).
  25. Haldane J.B.S. The recombination of linkage values and the calculation of distance between the loci of linkage factors. *J. Genet.*, 1919, 8: 299-309.
  26. Ganai M.W., Röder M.S. Microsatellite and SNP markers in wheat breeding. In: *Genomics-assisted crop improvement*. R.K. Varshney, R. Tuberosa (eds.). Springer, Dordrecht, 2007: 1-24 (doi: 10.1007/978-1-4020-6297-1\_1).
  27. Nelson J.C. QGENE: software for mapping-based genomic analysis and breeding. *Mol. Breeding*, 1997, 3(3): 239-245 (doi: 10.1023/A:1009604312050).
  28. Kosambi D.D. The estimation of map distances from recombination values. *Annals of Human Genetics*, 1944, 12(1): 172-175 (doi: 10.1111/j.1469-1809.1943.tb02321.x).
  29. Morton N.E. Sequential test for the detection of linkage. *Am. J. Hum. Genet.*, 1955, 7: 277-318.
  30. Kocherina N.V., Artemyeva A.M., Chesnokov Yu.V. Use of LOD-score technology in mapping quantitative trait loci in plants. *Russian Agricultural Sciences*, 2011, 37: 201-204 (doi: 10.3103/S1068367411030098).
  31. Kendall M., St'yuart A. *Statisticheskie vyvody i svyazi* [Statistical inferences and correlations]. Moscow, 1973 (in Russ.).
  32. Fisher R.E. *Statisticheskie metody dlya issledovatelei* [Statistical methods for researchers]. Moscow, 1958 (in Russ.).
  33. Zhuchenko A.A., Korol' A.B. *Rekombinatsiya v evolyutsii i selektsii* [Recombination in evolution and breeding]. Moscow, 1985 (in Russ.).
  34. Zhuchenko A.A. *Adaptivnoe rastenievodstvo (ekologo-geneticheskie osnovy). Teoriya i praktika* Adaptive plant growing (ecological and genetic basis) — theory and practice]. Moscow, 2008 (in Russ.).
  35. Worland A.J. The influence of flowering time genes on environmental adaptability in European wheats. *Euphytica*, 1996, 89: 49-57 (doi: 10.1007/BF00015718).
  36. Worland A.J., Börner A., Korzun V., Li W.M., Petrovic S., Sayers E.J. The influence of photoperiod genes on the adaptability of European winter wheats. *Euphytica*, 1998, 100: 385-394 (doi: 10.1023/A:1018327700985).
  37. Iwaki K., Haruna S., Niwa T., Kato K. Adaptation and ecological differentiation in wheat with special reference to geographical variation of growth habit and *Vrn* genotype. *Plant Breeding*, 2001, 120: 107-114 (doi: 10.1046/j.1439-0523.2001.00574.x).
  38. Zhuchenko A.A. *Adaptivnyi potentsial kul'turnykh rastenii: ekologo-geneticheskie osnovy* [Adaptive potential of cultivated plants: ecological and genetic basis]. Kishinev, 1988 (in Russ.).
  39. Zhuchenko A.A. *Ekologicheskaya genetika kul'turnykh rastenii (adaptatsiya, rekombinogenez, agrobiotsenoz)* [Ecological genetics of cultivated plants (adaptation, recombination, agrobiocenosis)]. Kishinev, 1980 (in Russ.).
  40. Zhuchenko A.A. *Adaptivnoe rastenievodstvo (ekologo-geneticheskie osnovy)* [Adaptive plant growing (ecological and genetic basis)]. Kishinev, 1990 (in Russ.).
  41. Otto S.P., Jones C.D. Detecting the undetected: estimating the total number of loci underlying a quantitative trait. *Genetics*, 2000, 156(4): 2093-2107.