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RESEARCH PAPERS

Mapping QTL for Water Regime in Spring Bread Wheat

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Abstract—For the first time, the authors assessed and mapped the chromosome QTLs (Quantitative Trait Loci) for the manifestation of morpho-physiological and agronomic indices of plant water status and related quantitative traits, such as plant height, weight, and dry matter content in spring bread wheat (*Triticum aestivum* L.). Following the study of ten agronomic traits, 13 QTLs were mapped on linkage groups 1A, 1B, 2B, 2D, 4A, 5A, 5B, 5D, 6A, and 6D. Some of the identified QTLs concurrently determined several traits. The physiological components of water status were shown to correlate with quantitative traits in wheat plants, such as plant height, weight, and dry matter content, and the correlation coefficients were calculated for all traits under study. Water retention capacity after 3 h correlated with water retention capacity after 24 h ($r_{xy} = 0.47$). The correlations were also established between water retention capacity after 3 h and plant height at booting stage ($r_{xy} = 0.29$) and between water retention capacity after 3 h and plant dry weight ($r_{xy} = 0.33$). Statistical calculations supported generally observed negative correlation (up to –1) between leaf water and dry matter contents, as well as between the root indices of variance in the mapping population of wheat lines. The results obtained in the present study will promote future efforts to fine-map the genes residing within the identified QTLs, to eventually clone these genes in order to establish the physiological mechanisms for maintaining water homeostasis in higher plant cells and to accomplish the practical implementation of marker-assisted assessment of water status in wheat plants studied on the basis of morpho-physiological and economical indices.

Keywords: Triticum aestivum, spring bread wheat, water status, morpho-physiological and agronomic traits, QTL mapping

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INTRODUCTION

Water is essential for vital activities of plants and prokaryotes, because in the cell it is the basic medium containing metabolic processes and major components, initial, intermediate, or final, of numerous physiological and biochemical reactions [1, 2]. The special role of water in the life of higher plants is the necessity to continually replenish moisture losses due to water evaporation when plants are affected by various ecological and geographical stress factors. The physiological adaptations to such environmental factors include superior capacity for water retention by cells and tissues due to high cytoplasm viscosity and elasticity, high proportion of tightly bound water in the total moisture content, and the maintenance of water homeostasis in living organisms [1, 3].

Most physiological characteristics important for practical breeding are quantitative and mostly depend on allelic patterns of several genetic loci. The currently accumulated evidence holds that the gene ensembles affecting the means and the genetic variance of a quantitative trait are usually determined by the limiting environmental factor [4]. The changes in limiting factors entail a shift of the spectrum of genetic loci that establish trait variance [5, 6]. Nevertheless, in addition to the above concept, there exist certain key genes [7] that under all conditions contribute to the formation of the particular quantitative traits, even although the effect of this contribution depends on the environment. Such genetic loci dubbed quantitative trait loci (QTLs) are of major interest for the current molecular approach to breeding for polygenic traits, including Marker Assisted Selection (MAS) [7].

QTL analysis in many plant species has already revealed characteristic facets of realization of genetic programs under water stress. For example, corn yield is known to significantly decline when water stress occurs at the flowering stage. Accordingly, one of the main objectives of corn growers is to increase crop production under limited water supply and drought conditions. However, one should keep in mind that the physiological trait of drought resistance is usually polygenic and partially correlates with other charac-

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Abbreviations: LOD—logarithm of odds; MAS—Marker Assisted Selection; QTL—quantitative trait locus.

teristics. To resolve this complex problem, the methodology of QTL identification was worked out in the mid-1990s with the ultimate goal of developing the MAS strategies for particular traits in corn and wheat [8, 9]. This approach served as the basis of further research of physiological and genetic constituents of plant water status.

Most studies on the drought effects in plants are usually carried out using the vegetative organs, especially leaves. The loss of water usually activates two types of responses depending on the age of plant tissues: (1) rapid arrest of cell growth in young growing organs and (2) decline in photosynthesis and sucrose metabolism in leaves. Abscisic acid (ABA) produced in the root apices and circulating in the xylem is an important trigger of such responses to stress. When faced with numerous co-dependent interactions, it is very difficult to attribute the observed responses of growing plants to several putatively key factors. Clarification of this issue is especially important in the case of crop plants, because the identification of key factors or genes would open the possibility to work for sustained plant adaptation and enhanced plant resistance to stress factors. From this prospective, the use of the QTL methodology seems the most assessable approach because it allows associating various traits. Moreover, co-localization of QTLs would provide new information about trait linkage at different levels of integration, from enzyme activities to gas exchange or leaf growth.

The first attempt to identify QTLs that determine the quantitative ABA levels as related to the severity of water stress employed DNA markers and segregating F_2 populations of wheat and corn [8]. Despite the low marker density (32 in corn), the authors managed to demonstrate the principal possibility of using this method. A more thorough analysis was carried out using 81 F_2 corn populations and 84 markers. In addition to water stress, ABA effects were related to other plant indices, such as stomatal conductance, water potential, turgor, the number of roots, root tension, chlorophyll fluorescence, and several others characteristics [10].

Recently [11] QTLs for ABA response were mapped in wheat seedlings. The authors employed the F_2 mapping population developed by crossing var. Chinese Spring (CS) to a CS line with 5A chromosome substituted with that from var. Hope (Hope5A). This experiment identified a QTL on chromosome 5A, which determines the degree of drought tolerance and seed dormancy in wheat. The physiological characteristics defined by this QTL were minor and were limited to physiological indices of drought resistance and similar indices of seed dormancy. These authors suggest that the observed changes in wheat response to ABA, at least in part, are determined by the identified QTL on chromosome 5A and that QTL in question controls both dehydration mechanism and seedling resistance to moisture deficit.

Similar results were obtained in another study using two mapping populations constructed from the $F_{8:9}$ recombinant inbred lines; the experiments were performed under laboratory conditions when wheat plants were exposed to osmotic stress and conventional water regime. Eighty eight QTLs mapped in this experiment explained 3.33–77.01% of the phenotypic variance for physiological drought resistance, and many agronomically important traits were assessed in parallel [12]. The authors found that of 88 identified QTLs, only 22 were related to drought resistance, and besides, not all of these 22 QTL for drought resistance could be identified by direct analysis in the laboratory, demonstrating the importance of field experiments.

The Malaysian scientists identified and mapped several QTLs for drought tolerance in wheat [13]. By comprehensive testing of 120 F_2 genotypes in the mapping population under drought conditions, these authors found that the relative water content under drought resistance exhibited extended variability indicating a minor gene effect on this trait. A single-marker analysis revealed the major QTLs associated with the trait of drought resistance. The results obtained in this study included the development of molecular SSR markers – two on 5D and one on 5A chromosomes; these markers were significantly associated with the trait of drought resistance explaining 30, 22, and 21% of the total variance, respectively.

Plant height is a crucial index when assessing the trait for wheat yield. However, its full manifestation can be repressed in water-limited environments. The Chinese researchers studied the genotype–environment interactions under water stress conditions using the mapping population developed from the doubled haploid lines [14]. They found that none of the identified QTLs was active during all phases of plant ontogenesis and that the additive effects of analyzed QTLs were more important than the epistatic effects or QTL–environment interactions. Some of the identified QTLs signified that the genotypes under study manifested high adaptability to low moisture conditions. As a result, the authors concluded that plant height is a complex trait depending as a whole on the general physiological status of the cells and their water regime in particular.

The architecture and state of the root system are other features essential for maintaining an optimum water regime of plants. In wheat, these traits are especially important when the crop is grown under deep soil moisture conditions where these traits help plants adapt to limited water access. Mapping QTLs for the seminal root angle and the number of embryonic roots was performed using of the mapping population derived of doubled wheat haploids bred from a cross between two varieties SeriM82 and Hartog [15]. Six QTLs with moderate effect were found to determine the seminal root angle, together with other six QTLs, also of moderate effect, which stood for the number of embryonic roots. It should be noted that while QTLs for seminal root angle were located on chromosomes 2A, 3D, 5D, 6A, whereas 6B, QTLs for the number of embryonic roots were found on chromosomes 1B, 3A, 3B, 4A, and 6A. However, the authors failed to establish the relationship between genetic components of plant cells and any physiological index of wheat water regime.

It is quite obvious that the delineating the genomic regions responsible for the water status in higher plants is important both in fundamental and applied aspects. First, such study provides valuable information about the transcription response of higher plant genomes when affected by water stress. Second, it provides new knowledge on the physiological manifestations of genes in water-stressed environments. Third, in future the identification of such regions would probably help identify the individual genes and their promoters that directly respond to water stress and belong to *cis*-elements with a key role in the molecular and physiological mechanisms for the implementation of water homeostasis. Fourth and the final, mapping QTLs that stand for physiological manifestations of economic traits, including those determining plant water status and critical for improving crop agronomic properties by MAS, would promote the breeding process and in this way provide new highly productive varieties and lines, including drought-resistant genotypes [16]. However, despite numerous studies, which identified the genetic determinants responsible for the physiological drought resistance and water regime of plants, including the reports listed above, the genetic determinants of water retention capacity of cells and tissues, and agronomic constituents of plant water status have not been as yet researched by QTL analysis in such most valuable crop as wheat.

To this end, we identified chromosomal loci (QTLs) involved in the control of physiological manifestations of plant moisture content, water retention, and water deficit in spring wheat tissues and established correlations between the physiological components of plant water status and several quantitative morphological and biochemical traits of plant growth and development.

MATERIALS AND METHODS

Plant material. The mapping population ITMI was developed by pollinating plants of spring bread wheat (*Triticum aestivum* L.) cv. Opata 85 with pollen of synthetic hexaploid W7984; the latter is an amphidiploid obtained by crossing *Aegilops tauschii* Coss., accession CIGM86.940 (genome DD) (the male parent) with tetraploid wheat *T. turgidum* var. *durum* cv. Altar 84 (genome AABB) (the female parent). Interspecies cross was accomplished by Dr. A. Mujeeb-Kazi (CIMMYT, Mexico) [5, 17]. Ten seeds from each of randomly chosen lines were selected by Dr. P. Leroy (INRA, Clermont-Ferrand) from the total of 150 recombinant inbred lines developed in the Cornell University (Ithaca, United States) by single-seed descent breeding up to F_8 or F_9. Four of these 114 lines were discarded because of low seed viability. The rest 110 lines were used in the present study carried out on the experimental plots the Vavilov Institute of Plant Industry (St. Petersburg–Pushkin).

Trait analysis. Assessing plant water retention, moisture deficit, and dry matter content was made in triplicate using the standard methods [1, 3]. Plant samples were dried in a thermostated oven at 105°C to constant weight. The total amount of water (x) as a percentage of fresh weight was determined with the formula: $x = 100\,(b - c)/(b - a)$, where a is the weight of an empty weighing bottle, b is the weight of the weighing bottle with fresh plant material, and c is the weight of the weighing bottle with dry plant material. Water deficit in the leaves was calculated as percentage of total water content at the saturation state using the formula: $\mathrm{WD} = 100\ \mathrm{W_a/W}$ where $\mathrm{W_a}$ is the amount of water absorbed at complete leaf saturation calculated as the difference between leaf weight after complete saturation of leaves and before saturation. W is the total water content in the leaves at the state of saturation calculated as the difference between leaf weight after complete saturation of leaves and their dry weight. Water retention capacity (as relative water loss, %) was calculated using the formula: $\mathrm{WRC} = 100\ \mathrm{B/A}$, where WRC is the water loss by leaves through the experiment (3 or 24 h) expressed as a percentage of its initial content in leaves, A is the water content at the beginning of the experiment, and B is the water loss over a wilting period. When leaf water regime was assessed after wilting, the leaves exposed to wilting for 3 or 24 h after sampling were also used for parallel evaluation of the same water regime indices: water content, water deficit and water retention capacity.

Determination of height and weight of growing plants was performed using the standard methods as described previously [6].

Statistical processing. The data were processed using the MAPMAKER/QTL computer program. This program performs calculations using the Haldane function [18], and therefore we used the mapping data from the database GrainGenes (http://www.greengenes.cit.cornell.edu) to convert distances on the map using the MAPMAKER/EXP3.0 program. The data from phenotypic analysis were integrated into the existing basic map developed for the ITMI population [19]. When mapping QTLs, we used only those markers that were consistent with the Kosambi mapping functions [20]. Mapping of QTLs and comparison of the resulting genetic map with the existing chromosome chart were accomplished using the computer program QGENE.

To estimate the accuracy of the relationship established between the identified loci and polymorphisms of particular traits, we used the threshold value of the logarithm of odds (LOD score) [21]. For each trait, we conducted separate QTL analysis, and only loci with

Table 1. QTLs for water status of the ITMI population

Nos.	Trait	Marker	Chromosome/distance	Parent	LOD score	R^2
1	water retention capacity after 3 h, WRC-3	*Xgwm301*	2D/53.7	W7984	3.68	30.78
2	water retention capacity after 24 h, WRC-24	*Xgwm637*	4A/142.8	W7984	3.04	19.94
		Xgwm633	1A/86.6	W7984	2.44	15.67
3	leaf moisture content, W	*Xgwm637*	4A/142.8	Opata 85	2.70	17.92
		Xgwm633	1A/86.6	Opata 85	2.54	16.22
4	dry matter content, DM	*Xgwm637*	4A/142.8	W7984	2.64	17.52
		Xgwm633	1A/86.6	W7984	2.47	15.86
5	water deficit, WD	*Xfba085b*	6A/146.4	Opata 85	2.20	16.84
6	root weight, RW	*Xcdo504*	5B/100.9	W7984	2.92	12.46
7	root water content, RWat	*Xgwm843*	5B/211.3	W7984	3.17	21.91
		Xfbb070b	6D/0.0	Opata 85	2.94	23.28
8	root dry matter content, RDM	*Xfbb070b*	6D/0.0	W7984	3.42	26.56
		Xgwm843	5B/211.3	Opata 85	3.08	21.38
9	plant height at the booting stage, PHbs	*Xrz395b*	5A/89.0	W7984	5.08	19.46
		Xcdo1326a	5A/74.4	W7984	3.40	13.50
		Xgwm153	1B/76.1	Opata 85	3.20	23.49
		Xgwm212	5D/129.5	Opata 85	2.84	31.96
10	plant weight, PW	*Xfba078b*	4A/266.6	W7984	2.30	17.25
		Xfba62a	2B/153.8	Opata 85	2.28	17.10

$\text{LOD} \geq 3.0$ ($p < 0.001$) and $3.0 > \text{LOD} \geq 2.0$ ($p < 0.01$) were taken into account.

To determine the nature of the relationship between the observed traits and conditions of water regime, we calculated correlation coefficients r_{xy}. The ratio between r_{xy} and the corresponding *t*-test value served as a criterion for significance assessment [22]. To integrate the average values of indices estimated under various conditions of water regime, the analysis of variance was employed, in particular, we calculated the mean square deviations and variance ratio F, and the significance of the data was evaluated [23]. The value $p < 0.05$ was considered the acceptable threshold of statistical significance, as this level includes the probability of error of 5%. Results significant at the $p < 0.01$, was considered statistically significant, and the results with the level of $p < 0.001$, as highly significant. All calculations employed the computer program package STATISTICA 6.0.

RESULTS

Our study is based on 1800 measurements of ten identified indices. As a result, we identified 19 QTLs, among which seven with LOD score ≥ 3 and 12, with $3 > \text{LOD} \geq 2$ (Table 1). In one case, the identified QTL was established with LOD score > 4. The loci with LOD scores above 3 were regarded as major, and those with LOD scores between 2 and 3, as strong. Trait names and their codes are listed in Table 1. QTL positions and molecular markers corresponding to the maximum LOD score for each particular QTL are also listed in Table 1; in addition this table presents the information on the parent which was the source of the particular QTL. LOD score and the percentage of phenotypic variance (R^2), determined by the identified QTL, are given separately for each trait and each identified QTL.

As a whole, we found 13 QTLs for ten traits; these QTLs were mapped on the linkage groups 1A, 1B, 2B, 2D, 4A, 5A, 5B, 5D, 6A, and 6D. Some of the identi-

Table 2. Correlation coefficients for the ITMI population

Traits (symbols)	Correlation coefficient, r_{xy}	t value	Significance, p
WRC-3	0.17	1.84	0.068
WRC-24	0.52	6.34	0.000
W	−0.48	−5.67	0.000
DM	0.48	5.70	0.000
WD	−0.36	−4.03	0.000
RW	0.39	4.28	0.000
RWat	0.23	2.35	0.020
RDM	−0.23	−2.33	0.022
PHbs	−0.10	−1.07	0.288
PW	0.28	3.01	0.003

fied QTLs stand for the manifestations of several traits. To illustrate, the measurements of water retention capacity in the lines of the ITMI mapping population after 3 and 24 h revealed three QTLs; two of them were major, and one strong. The trait for water deficit was determined by a strong QTL on chromosome 6A transferred from the female parent.

QTLs for water content in the roots were assembled on chromosomes 5B and 6D. It is notable that the same chromosomes comprise QTLs for traits of root dry matter content. The trait of root weight is determined by a single QTL on the same chromosome 5B, although in a slightly different region of this linkage group. Plant height at the stage of booting was determined by four QTLs located on chromosomes 1B, 5A, and 5D. Three of these four QTLs were major ones, and one was strong. Plant weight was determined by QTLs mapped on the linkage groups 4A and 2B. Both QTLs were strong and explained almost identical percentages of phenotypic variance of this trait.

To relate the physiological components of plant water status with quantitative morphological and biochemical characteristics that determine growth and development of wheat plants, we calculated the correlation coefficients for all traits under study. In general, in the ITMI lines, as seen from the data presented in Table 2, root hydration after 24 h was weakly correlated with plant dry weight. The values of indices for water retention, dry matter content and root weight varied in different lines of the mapping population at the average levels of correlation.

Table 3. Coefficients of correlation between traits

Traits	WRC-3	WRC-24	W	DM	WD	RW	RWat	RDM	PHbs
WRC-24	0.47 $p = 0.000$								
W	0.02 $p = 0.861$	−0.55 $p = 0.000$							
DM	−0.01 $p = 0.915$	0.57 $p = 0.000$	−0.99 $p = 0.000$						
WD	0.07 $p = 0.462$	−0.22 $p = 0.029$	0.12 $p = 0.214$	−0.13 $p = 0.192$					
RW	0.06 $p = 0.554$	0.26 $p = 0.009$	−0.19 $p = 0.056$	0.19 $p = 0.055$	−0.18 $p = 0.073$				
RWat	−0.09 $p = 0.354$	0.13 $p = 0.194$	−0.02 $p = 0.808$	0.03 $p = 0.779$	−0.13 $p = 0.208$	−0.09 $p = 0.384$			
RDM	0.09 $p = 0.373$	−0.12 $p = 0.234$	0.01 $p = 0.905$	−0.02 $p = 0.874$	0.12 $p = 0.218$	0.11 $p = 0.288$	−0.99 $p = 0.000$		
PHbs	0.29 $p = 0.003$	0.11 $p = 0.272$	−0.04 $p = 0.710$	0.04 $p = 0.654$	0.11 $p = 0.263$	0.11 $p = 0.280$	−0.31 $p = 0.002$	0.32 $p = 0.001$	
PW	0.33 $p = 0.001$	0.41 $p = 0.000$	−0.07 $p = 0.480$	0.08 $p = 0.440$	−0.19 $p = 0.062$	0.63 $p = 0.000$	0.03 $p = 0.731$	−0.02 $p = 0.856$	0.47 $p = 0.000$

p—level of significance; $p < 0.01$—statistically significant; $p < 0.001$—statistically highly significant.

As a whole, the correlations between the traits were most vivid (Table 3). Most obvious was the average positive correlation between water retention capacity after 3 h and water retention capacity at 24 h ($r_{xy} = 0.47$). One should also note weak correlation between water retention capacity after 3 h and plant height at the booting stage ($r_{xy} = 0.29$) and between water retention capacity after 3 h and plant dry weight ($r_{xy} = 0.33$).

Concerning the trait water retention after 24 h, we find average negative correlation with the average hydration and weak negative correlation with water deficit; it means that the values of WRC-24 index are associated with declining W and WD indices or vice versa. Another noticeable fact is correlation established between WRC-24 and dry matter content ($r_{xy} = 0.57$) and between WRC-24 plant dry weight ($r_{xy} = 0.41$) and root dry weight ($r_{xy} = 0.26$).

DISCUSSION

Currently numerous laboratory and analytical methods are employed to research into the various mechanisms affecting the degree of drought resistance [1]; these methods are used to study growing plants at various stages of ontogeny. This is primarily the methodology of evaluating various indices of water regime manifesting plants ability to withstand drought through physiological adaptations. Among the most significant indices, we find moisture content, water retention capacity and water deficit. However, as shown recently [13], the manifestation of agronomic traits is immediately related to the activity of particular genetic loci on chromosomes responsible for the manifestation of physiologically vital traits, which determine the basic mechanisms of plant physiological and genetic adaptation to adverse environmental factors, including the ability of higher plants to defy such stress, as dehydration.

In this regard, in the present study, we for the first time identified chromosomal loci (QTLs) involved in the regulation of physiological traits of tissue hydration, water retention capacity, and water deficit in spring wheat. It should be noted that while the water retention capacity after 3 h was determined by a locus mapped on chromosome 2D, later, after 24 h, it was already dependent on the loci on chromosomes 1A and 4A. QTLs for moisture content in leaves and for dry matter content of the aboveground plant organs were also located on chromosomes 4A and 1A, and this evidence generally corresponds to the well-established pattern of the physiological manifestations and biochemical status of plant water regime.

Clearly, root morphology is an important factor of plant resistance to water stress, particularly drought [24]. Apparently, the chromosomal loci for three root traits that determine manifestations of such QTLs as moisture content and plant organ weight on chromosomes 5B and 6D aggregate into a single cluster of genes, allowing plants to carry out the program of genetic control over the water regime under the conditions of physiological stress imposed by lack of soil moisture.

A notable fact that the two major QTLs located on chromosome 5A also formed a single cluster is actually pointing to the complexity of the trait plant height under the present study, whereas the QTL mapped on the linkage group 5D was bringing in the highest percentage of phenotypic variance (31.96%) defined by this trait. The locus on chromosome 1B was no exception: it also explained a large percentage of variance (23.49%), emphasizing the importance of this locus in the manifestation of the plant height trait.

Noteworthy is the fact that in addition to plant dry weight, chromosome 4A comprises QTLs for such traits as water retention capacity after 24 h, leaf moisture content and dry matter content, which in our opinion suggests morpho-physiological relationships of these traits.

Our results match the evidence published by foreign researchers. To illustrate, the Chinese scientists [12] showed that the drought tolerance trait in wheat could be related to QTLs in the linkage groups 1B, 2B, 4A, 5D, 6A, and 6D; the evidence corresponding to our data. The same authors reported that in addition to already listed linkage groups probably involved in wheat drought resistance, the QTLs for this trait were found on chromosomes 2A, 3B, 7B, and 7D. Similar, but less numerous QTLs were identified in other studies of QTLs for physiological characteristics of water regime in wheat plants. Thus, QTLs recognized under conditions of reduced moisture content and elevated temperature were mapped on chromosomes 1B, 2A, 2D, 4A, 4B, and 7B [25], as well as on the linkage groups 1B, 2A, 2D, 3A, 3B, 3D, 4A, 5A, 5D, 6A, and 6B [14, 15]. It should be noted that the QTL on chromosome 5A identified in [11], which was associated with resistance to dehydration in wheat seedlings, was mapped not only in the above mentioned studies and the present work, but also by the Malaysian researchers [13], who showed an association of this locus on chromosome 5A with the manifestation of drought resistance trait. Similarly noteworthy is the QTL located on chromosome 4A: it is also identified in this (Table 1) and the foreign studies [12, 14, 25].

The contribution of the linkage group 4A comprising the whole block of agronomically important genes that play considerable role in several physiologically significant traits of plant water status is very significant, since it is known that the genetic determinants of the manifestations revealed at the later stages of development in higher plants are often linked to the genes affecting plant growth and survival at the earlier stages of development, the pattern called the Morphology–Viability linkage. Such systems are found in homologous chromosome segments in related species within the genera *Gossypium, Lycopersicon, Triticum, Phaseolus*, and several other taxa [4]. Besides, as has been shown previously, many genes that control the same trait are sometimes combined in one block—or mapped to different chromosomes, or to different arms of the same chromosome, and their activation is controlled by a coordinating gene. Therefore, the chromosomal loci should not be envisaged as a purely mechanical linkage of genes: rather, they represent a naturally ordered group of functionally related genes, or blocks of co-adapted genes [4]. Apparently, the same can be said of QTLs for the traits of root water regime and plant height at the booting phase, the manifestation of which is controlled by the loci on chromosomes 5A and 5B, as well as of the traits of water retention after 24 h of hydration and plant dry matter content: these QTLs, in addition to chromosome 4A, were mapped on the linkage group 1A.

Our statistical calculations confirmed the experimentally registered inverse relationship between leaf hydration and dry matter content in the whole plant with the correlation coefficient close to -1; these calculations also confirmed the parameters of variance in roots of the mapping population of wheat lines.

Generally in our experiment, we observed apparent, up to its highest value, positive correlation between plant dry weight and root dry weight ($r_{xy} = 0.63$). Statistical calculations indicate (Table 3) that the average correlation of plant height at the booting stage with plant dry weight ($r_{xy} = 0.47$), and root dry weight ($r_{xy} = 0.32$). In contrast to the positive correlation between the whole plant weight and root weight, these data predict negative correlation between the plant height at the booting stage and root hydration.

Thus, we were first to establish the genetic determinants (QTLs) involved in the genetic regulation of physiological traits of plant hydration, water retention capacity and water deficit in spring wheat; in addition, we registered statistically significant correlations between physiological and genetic components of plant water status and some quantitative morphological and biochemical traits of plant growth and development. Current molecular genetic approaches and the results obtained in this study are of fundamental importance for further fine mapping of genes within the identified QTLs, the possible cloning of these QTLs and the marker-assisted evaluation of wheat genotypes using the morpho-physiological and agronomically important traits described above.

REFERENCES

1. Goncharova, E.A., *Vodnyi status kul'turnykh rastenii i ego diagnostika* (Water Status of Crops and Its Diagnostics), St. Petersburg: Vavilov Institute of Plant Industry, 2005.
2. Ermilova, E.V., *Molekulyarnye aspekty adaptatsii prokariot* (Molecular Aspects of Prokaryote Adaptation), St. Petersburg: Khimizdat, 2012.
3. Goncharova, E.A., Evaluation of resistance of fruit crops with juicy fruits to various stresses, *Diagnostika ustoichivosti rastenii k stressovym vozdeistviyam (Metodicheskoe rukovodstvo)* (Diagnostics of Plant Resistance to Stresses: Guidance), Leningrad: Vavilov Institute of Plant Industry, 1988, pp. 46–62.
4. Zhuchenko, A.A., *Adaptivnoe rastenievodstvo (ekologo-geneticheskie osnovy). Teoriya i praktika* (Ecological and Genetic Basics for Adaptive Plant Industry. Theory and Practice), Moscow: Agrorus, 2008.
5. Chesnokov, Yu.V., Pochepnya, N.V., Börner, A., Lohwasser, U., Goncharova, E.A., and Dragavtsev, V.A., Ecological and genetic organization of plant quantitative traits and mapping of loci determining agronomically important wheat traits, *Dokl. Akad. Nauk*, 2008, vol. 418, pp. 693–696.
6. Chesnokov, Yu.V., Pochepnya, N.V., Kozlenko, L.V., Sitnikov, M.N., Mitrofanova, O.P., Syukov, V.V., Kochetkov, D.V., Lohwasser, U., and Börner, A., Mapping of QTL determining the manifestation of agronomically and economically valuable symptoms in *Triticum aestivum* L. from different ecological zones of Russia, *Vavilovskii Zhurn. Genetiki i Selektsii*, 2012, vol. 16, pp. 970–986.
7. Tanksley, S.D., Mapping polygenes, *Annu. Rev. Genet.*, 1993, vol. 27, pp. 205–233.
8. Quarrie, S.A., Steed, A., Lebreton, C., Gulli, M., Calestani, C., and Marmiroli, N., QTL analysis of ABA production in wheat and maize and associated physiological traits, *Russ. J. Plant Physiol.*, 1994, vol. 41, pp. 572–576.
9. Ribaut, J.M., Hoisington, D.A., Deutsch, J.A., Jiang, C., and Gonzalezdelon, D., Identification of quantitative trait loci under drought conditions in tropical maize: 1. Flowering parameters and the anthesis-silking interval, *Theor. Appl. Genet.*, 1996, vol. 94, pp. 887–896.
10. Lebreton, C., Lazicjancic, V., Steed, A., Pekic, S., and Quarrie, S.A., Identification of QTL for drought responses in maize and their use in testing causal relationships between traits, *J. Exp. Bot.*, 1995, vol. 46, pp. 853–865.
11. Iehisa, J.C., Matsuura, T., Mori, I.C., and Takumi, S., Identification of quantitative trait locus for abscisic acid responsiveness on chromosome 5A and association with dehydration tolerance in common wheat seedlings, *J. Plant Physiol.*, 2014, vol. 171, pp. 25–34.
12. Zhang, H., Cui, F., Wang, L., Li, J., Ding, A., Zhao, C., Bao, Y., Yang, Q., and Wang, H., Conditional and unconditional QTL mapping of drought-tolerance-related traits of wheat seedling using two related RIL populations, *J. Genet.*, 2013, vol. 92, pp. 213–231.
13. Naroui, Rad, M.R., Abdul, Kadir, M., Rafii, M.Y., Jaafar, H.Z., and Naghavi, M.R., Bulked segregant analysis for relative water content to detect quantitative trait loci in wheat under drought stress, *Genet. Mol. Res.*, 2012, vol. 11, pp. 882–888.
14. Wu, X., Wang, Z., Chang, X., and Jing, R., Genetic dissection of the developmental behaviours of plant height in wheat under diverse water regimes, *J. Exp. Bot.*, 2010, vol. 61, pp. 2923–2937.
15. Christopher, J., Christopher, M., Jennings, R., Jones, S., Fletcher, S., Borrell, A., Manschadi, A.M., Jordan, D., Mace, E., and Hammer, G., QTL for root angle and number in a population developed from bread wheats (*Triticum aestivum*) with contrasting adaptation to

water-limited environments, *Theor. Appl. Genet.*, 2013, vol. 126, pp. 1563–1574.

16. Chesnokov, Yu.V., *Molekulyarno-geneticheskie markery i ikh ispol'zovanie v predselektsionnykh issledovaniyakh* (Molecular and Genetic Markers and Their Use in Prebreeding Research), St. Petersburg: Agrophysical Inst., 2013.
17. Börner, A., Schumann, E., Fürste, A., Göster, H., Leithold, B., Röder, M.S., and Weber, W.E., Mapping of quantitative trait loci determining agronomic important characters in hexaploid wheat (*Triticum aestivum* L.), *Theor. Appl. Genet.*, 2002, vol. 105, pp. 921–936.
18. Haldane, J.B.S., The recombination of linkage values and the calculation of distance between the loci of linkage factors, *J. Genet.*, 1919, vol. 8, pp. 299–309.
19. Ganal, M.W. and Röder, M.S., Microsattelite and SNP markers in wheat breeding, *Genomics Assisted Crop Improvement: Genomics Applications in Crops*, Varshney, R.K. and Tuberosa, R., Eds., Berlin: Springer-Verlag, 2007, vol. 2, pp. 1–24.
20. Kosambi, D.D., The estimation of map distances from recombination values, *Ann. Eugen.*, 1944, vol. 12, pp. 172–175.
21. Kocherina, N.V., Artem'eva, A.M., and Chesnokov, Yu.V., Use of lod-score in mapping quantitative trait loci in plants, *Dokl. Ross. Akad. S-kh. Nauk*, 2011, no. 3, pp. 14–17.
22. Lakin, G.F., *Biometriya* (Biometrics), Moscow: Vyssh. shkola, 1990.
23. Fisher, R.E., *Statisticheskie metody dlya issledovatelei* (Statistical Methods for Researches), Moscow: Gosstatizdat, 1958.
24. Champoux, M.C., Wang, G., Sarkarung, S., Mackill, D.J., Otoole, J.C., Huang, N., and McCouch, S.R., Locating genes associated with root morphology and drought avoidance in rice via linkage to molecular markers, *Theor. Appl. Genet.*, 1995, vol. 90, pp. 969–981.
25. Li, S., Wang, C., Chang, X., and Jing, R., Genetic dissection of developmental behavior of grain weight in wheat under diverse temperature and water regimes, *Genetics*, 2012, vol. 140, pp. 393–405.

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