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Salt Tolerance of Wheat (*Triticum aestivum*) Varieties Grown Under Laboratory and Field Conditions

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Abstract: High salt concentration limits plant growth. Wheat (*Triticum aestivum*) is sensitive to toxic levels of mineral salts. Therefore, studies of the level of salt tolerance of various wheat varieties are of crucial importance. Plant resistance to stress factors is often controlled not by one, but by several factors. In this study, we carried out a thorough characterization of two wheat varieties, Uchitel and Orenburgskaya 22, which exhibit different levels of salt tolerance in laboratory and field conditions. The biomass of wheat cultivar Orenburgskaya 22 when grown in field conditions under salinity is higher than that of cultivar Uchitel, although the length of the root system decreases compared to cultivar Uchitel. The use of the methods of fluorescence and light-optical microscopy made it possible to obtain more complete information on the salt sensitivity of wheat. Variety Orenburgskaya 22 is more resistant to the negative effect of sodium chloride in comparison with variety Uchitel. The plant response to abiotic stress is a complex process in which many genes are involved. We analyzed the expression of genes for transporters (HKT), superoxide dismutase (SOD), and MYB genes. Under the influence of sodium chloride, the level of expression of genes of the MYB family increased, while the level of expression of genes of the HKT family decreased in both Uchitel and Orenburgskaya 22 both in the laboratory and in the field. Our results indicate that in-depth analysis under various growing conditions is important for studying wheat tolerance to salt stress.

Keywords: *Triticum aestivum* Host, Salt Tolerance, Roll Culture, Field, Morphology, Gene Expression

1. Introduction

Excessive soil salinity affect the physiology, biochemistry and molecular functions of plants, thus decreasing plant productivity and quality [1].

Understanding the abiotic stress responses of plants is vital for improving their yield. Transcription factors (TFs) in plants regulate expressions of genes to respond to abiotic and biotic stresses and modulate development processes [2]. MYB TFs are involved in almost all aspects of plant development and metabolism [3, 4]. A distinctive feature of MYB TFs is the presence of conserved DNA-binding domain [5], which consists of 1–4 repeats motives located at the N-terminus. In plant genomes, R2R3-MYB subfamily, which includes the largest number of MYB TFs, is of great interest to researchers because of its diverse roles in primary and secondary metabolism, development processes and biotic and abiotic stress response [6].

A high concentration of salts has a negative effect on plant growth mainly because of the disruption of the ionic and osmotic balance of the cell. In saline soils, high levels of sodium ions (Na^+) inhibit plant growth and can cause plant death. Salt tolerance mechanisms include the removal of Na^+ and chloride ions (Cl^-) from vacuoles, blocking Na^+ transport into cells and exclusion of Na^+ from the transpiration flow, among others [6].

The susceptibility to high levels of NaCl is the result of a coordinated action of many stress-responsive genes [7, 8]. Cellular toxicity inhibits enzyme activity and disrupts various physiological processes, such as potassium ion (K^+) uptake [9, 10] and photosynthesis [11]. Several important Na^+

transporters have been identified in plants that reduce high Na^+ concentrations [12–14].

Plant *high-affinity potassium transporter* (*HKT*) genes, which transport K^+ and Na^+, are divided into two subfamilies. The *HKT1* subfamily genes are found in all higher plants and encode selective ionic transporters, whereas subfamily 2 genes encode transporters that are permeable to both K^+ and Na^+ [15, 16]. Disruption of the expression of *HKT1* family genes leads to Na^+ hypersensitivity and excessive accumulation of Na^+ in shoots.

Salt resistance in plants is caused by specific and/or nonspecific mechanisms associated with sensitivity to one or several types of stress factors, namely osmotic and toxic, including oxidative stress [12]. Salt-induced oxidative stress increases the production of superoxide in plant cells, which is one of the main prooxidants [17].

Superoxide dismutase (SOD) is an antioxidant enzyme that protects cells from ROS and converts superoxide into free oxygen and hydrogen peroxide. Thus, SOD plays a key role in protecting the plant from oxidative stress [18].

Numerous studies have been carried out under laboratory conditions. However, the results of laboratory studies do not always correspond to the results obtained in field conditions. In this study, we thoroughly characterized two wheat varieties, Uchitel and Orenburgskaya 22, which exhibit different levels of salt stress resistance, under both laboratory and field conditions.

2. Material and Methods

2.1. Plant Material

Two varieties of spring bread Uchitel and Orenburgskaya 22, developed by the Orenburg steppe ecological group (FGBNU), were used in this study.

The sensitivity of wheat seedlings to salinity was assessed using the roll culture method [19]. After 10 days of growth, the fresh plant biomass, root length, shoot length, and plant height were measured.

Field experiments were carried out in the central zone of the Orenburg region, which has alkaline black soil with the following characteristics: humus layer thickness=45–55 cm; pH=6.8–7.0; humus content in the arable layer 3=5–4.2%; total nitrogen content=0.2–0.6%; available phosphorus (P)=1.5–2.5 mg; exchangeable K=30–40 mg per 100 g of soil. Wheat seedlings were harvested at 14 days after seed germination, and biometric parameters were determined.

Statistical analysis of data was carried out using Statistica 10.0 and STATAN programs.

2.2. Trypan Blue Staining

Coleoptiles of 10-day-old seedlings were stained with 0.5% trypan blue. Samples were visualized light microscopy (Olympus BX51 microscope; 10X lens) and photographed using a Color View digital camera (Germany).

2.3. Microscopy

Tips seedlings excised (five root tips per glass slide). To determine ROS levels in cells, the root tips were incubated in 25–50 nM carboxy-H2DFFDA (Thermo Fisher Scientific, USA) for 30 min.

2.4. Total RNA Isolation and Gene Expression Analysis

Total RNA was isolated from individual shoots and roots using reagent kits for the isolation of RNA-Extran RNA Syntol (Russia), according to [20].

To analyze gene expression, the cDNA was amplified by real-time polymerase chain reaction (RT-PCR) using SYBR Green I (Syntol) on CFX 96 Real-Time System thermal cycler (BioRad, USA). Information on the structure of *Triticum aestivum* genes was obtained from the National Center for Biotechnology Information (NCBI). Gene-specific primers were designed using NCBI Primer-BLAST and synthesized by Syntol (Table 1). The RT-PCR was carried according [20]. Each RT-PCR reaction was performed in three replicates.

Table 1. *List of primers used for RT-PCR.*

gene	Primer sequence (5'→3')	Encoded protein	Protein function
TaHKT1;4	ATT CAG GCA ACA CCT AAT CAT GC GCA TCA CAA GAA TGA GGA TGA GC	K^+/Na^+ transporter	Reduces the accumulation of Na^+ in leaves
TaHKT2;1	TAT GTG ATG AGT CGC AGC TTG AA GCA ACA AGA GGC CTG AAT TCT TT	K^+/Na^+ transporter	Reduces the accumulation of Na^+ in leaves
TaMYB1	GCG TCA TGA CCC GCC AGT AA CAG CTC AGC GCT ACA CTT CA	MYB1 TF	Gene expression regulation
TaMYB29	CTG GAA CAC GCA CAT CAG GA GAT CCC CGC TGA CGC TAC	MYB29 TF	Gene expression regulation
MnSOD	TGC TTG CGT GAT TTG TCT GAT AGA AGG TCC CGA CAG TGG AA	Mn superoxide dismutase	ROS scavenger

Relative gene expression was calculated using the *GAPDH* gene as a reference.

2.5. Data Analysis

The main statistical parameters were calculated using standard methods and analyzed using Statistica 10.0 and STATAN programs. Data were expressed as mean ± SD), and significant differences were determined using Student's *t*-test ($p < 0.05$).

3. Results and Discussion

3.1. Biometric Data

High salinity negatively impacts seed germination by inhibiting seed imbibition and disturbing seed peaking. Cells in the root cortex act as a barrier to the radial transport of ions into the central cylinder, where ions bind to pectins and lignins in cell walls, thus reducing cell wall elasticity [20].

The response of each cultivar to salinity has unique characteristics. Here, we examined the salt stress responses of two wheat varieties, Uchitel and Orenburgskaya 22, in the laboratory (roll culture method) and field. The biomass of salt treated seedlings of both varieties was lower than that of control seedlings at the early stages of development (Figure 1). Consistent with this result, lengths of the main root and shoot were decreased under salt stress. Thus, high salt concentration decreased the accumulation of seedling biomass (Figure 1), suggesting that salt stress suppresses the general metabolism of shoot tissues. The negative impact of salt stress on plant biomass was less pronounced in Orenburgskaya 22 than in Uchitel. Thus, salt stress decreased the growth of roots and shoots, thus decreasing plant biomass.

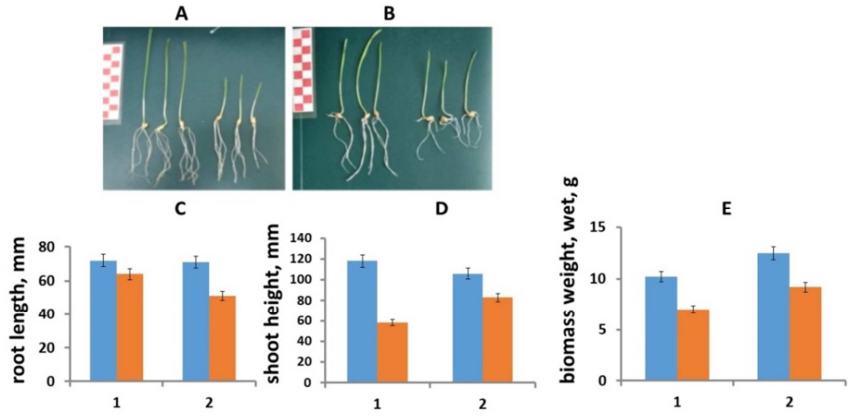

Figure 1. *10 days seedlings of wheat after germination under normal conditions (left) and chloride salinization (right) in roll culture. A – variety Uchitel; B – variety Orenburgskaya 22; Scale ruler with 1 cm divisions. C, D, E – biometric parameters; 1 - variety Uchitel'; 2 – variety Orenburgskaya 22. Blue – control, orange – 150 mM NaCl. The mean values (n=30) and their standard deviations are shown according to Student's criterion, p<0.05.*

The effect of NaCl reduced the growth of aboveground parts by more than 2 times in the "Teacher" and only by 20% in the "Orenburg" compared to the control (Figure 1).

Thus, morphometric changes showed the same trends in both wheat varieties, suggesting that, in terms of morphometric parameters, soft wheat varieties have a high tolerance to salinity.

Violation of water metabolism and respiration affects the growth rate [21].

Respiration and the production of superoxide radicals are also dramatically increased under stress [22]. In wheat, the respiration rate gradually increases during seed germination, which provides the main energy processes due to the use of resources of reserve polysaccharides, mainly endosperm starch.

Based on the comparison of morphometric parameters, we concluded that Orenburgskaya 22 is more salt tolerant than Uchitel. The root and shoot growth of Orenburgskaya 22 were inhibited by ~30% and ~20%, respectively; Uchitel showed higher parameters.

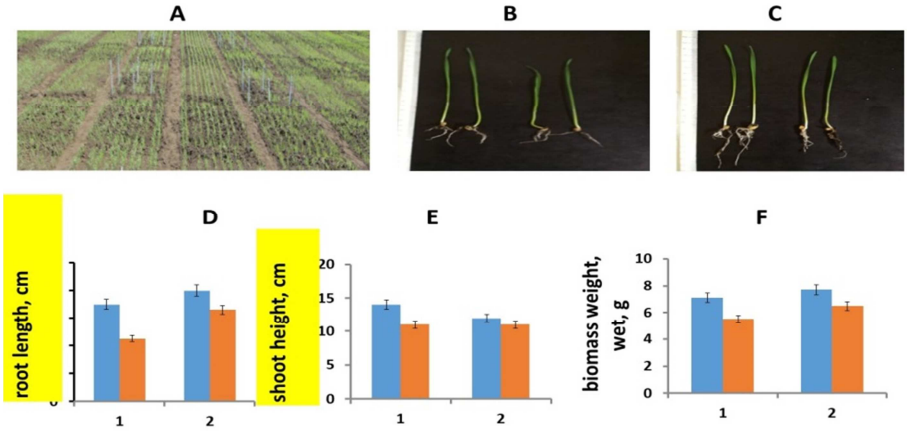

Figure 2. *10 days seedlings of wheat after under normal conditions (left) and chloride salinization (right) in field culture. A- wheat in the field; B – variety Uchitel; C – variety Orenburgskaya 22; Scale ruler with 1 cm divisions. D, E, F – biometric parameters; 1 - variety Uchitel; 2 – variety Orenburgskaya 22. Blue – control, orange – 150 mM NaCl.*

However, when plants were grown in soil, a different picture was observed compared with the roll culture method. Under salt stress, the root length, shoot length and biomass of Uchitel seedlings decreased by ~35%, ~20% and ~25%, respectively, compared with the control, whereas those of Orenburgskaya 22 seedlings decreased by ~20%, ~10% and 15%, respectively (Figure 2).

These data indicate that Uchitel and Orenburgskaya 22 exhibit different levels of salt tolerance. Moreover, both wheat varieties exhibit greater resistance to high NaCl concentration when grown in soil than when grown in roll culture.

3.2. Determination of Cell Viability

The toxic effects of high salt concentration can cause significant damage to plant tissues, ultimately causing plant death. Grain seedlings proved to be a good model for PCD due to two main reasons: the possibility of synchronization of metabolic processes [22] and the presence of organoptosis in organs [23]. The problem is to quantify the status of cells over a certain period of time [24, 25]. To determine the degree of tissue damage caused by high salinity, we stained wheat seedling coleoptiles, thus enabling the visualization of the degree of damage to plant tissues. Cell death was minimal in control coleoptiles but higher in salt treated coleoptiles; this was evident from the photographs, as dead cells stained darker than living cells. Additionally, the photographs showed that Orenburgskaya 22 samples contained more than 20-30% dead cells, whereas Uchitel contained more than 50-60% dead cells, indicating that Orenburgskaya 22 is more resistant to salt stress than Uchitel (Figure 3).

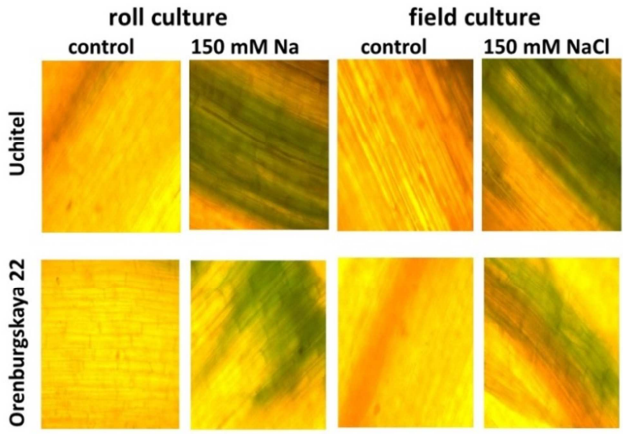

Figure 3. *Trypan blue staining of wheat coleoptile samples.*

3.3. Expression Analysis of MYB TF Genes

In this study, we focused on the effect of salt stress on morphological, cytological and genetic processes in roots. The size, properties and distribution of the root system ultimately determine the access of plants to water.

Studies in various plant species have improved our understanding of the *MYB* gene family; however, little is known about this gene family in bread wheat. The analysis of genes involved in stress response and tolerance will help elucidate the molecular mechanisms of stress response and plant tolerance, ultimately leading to enhanced stress tolerance in wheat.

MYB proteins perform multiple functions in plants, including abiotic stress response, and several aspects of the *MYB* gene family have been investigated in wheat. In a previous study, 60 cDNA sequences encoding wheat MYB proteins were analyzed [26]. The results showed that most MYB proteins are homologous and differ in the C-terminal sequence. Additionally, MYB proteins perform overlapping functions, i.e., they can respond to both salt stress and temperature or other abiotic stress. In the current study, we examined only salt-responsive *MYB* genes, including *MYB1*, *MYB29, MYB43*, *MYB45*, *MYB48* and *MYB68*. The nature of change in the expression level of these genes in Uchitel and Orenburgskaya 22 seedlings grown in the laboratory and field was similar. Therefore, for comparison, we presented data only for *MYB1* and *MYB29* genes (Figure 4).

The relative level of expression of *MYB* genes in both wheat varieties grown in the laboratory was 2–2.5-fold higher than that in field-grown seedlings. We speculate that the cultivation of wheat in a roll is stressful.

In the absence of NaCl, Orenburgskaya 22 seedlings grown both in roll culture and in the field were more resistant than Uchitel seedlings. The addition of 150 mM NaCl increased the expression level of *MYB1* in all variant. Moreover, in the presence of NaCl, the expression level of *MYB* genes in Orenburgskaya 22 seedlings was essentially the same as that in Uchitel seedlings under both laboratory and field conditions. Thus, it can be concluded that Orenburgskaya 22 exhibit more higher level of resistance to salt stress than. Variety Uchitel. It can be noted that the relative level of *Myb 29* gene expression in both wheat cultivars grown in the presence of sodium chloride in the field decreases by almost two compared to the control variants.

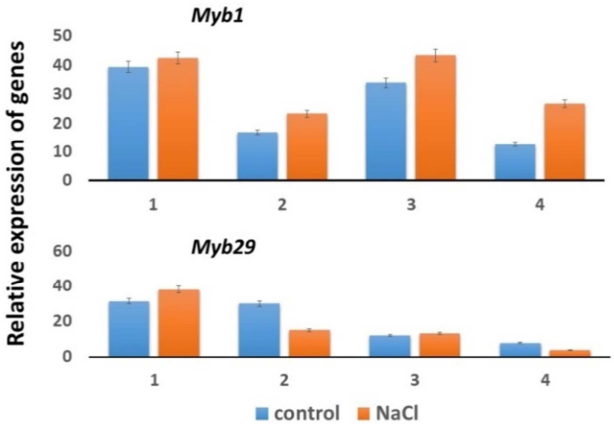

Figure 4. *Expression of genes Myb in root of wheat Uchitel (1,2) and Orenburgskaya 22 (3,4) grown in roll culture (1,3) and in the field (2,4). Blue lane –control, orange lane – 150 mM NaCl. The results are presented as means of three independent replicates. Bar represent standard deviation.*

3.4. Expression Analysis of HKT Genes

The relative expression of *HKT1;4* was higher in Uchitel seedlings than in Orenburgskaya 22 seedlings, and higher under laboratory conditions in both wheat varieties than under field conditions. Additionally, salt stress reduced the expression of *HKT1;4* in both wheat varieties (Figure 5).

Under conditions of salt stress, class I ion transporters remove Na^+ from the xylem in roots in order to reduce Na^+ content in shoots [7,8]. Under constant high salt stress, the higher the expression level of *HKT1;4*, the greater the morphological changes in wheat plants.

HKT2 transporters carry both Na^+ and K^+. Ionic channels possess loops containing four glycine residues, and the replacement anyone of these glycine residues with serine can alter channel selectivity. In this study, the expression level of *HKT2* in Uchitel seedlings was approximately 2.5-fold lower than that of *HKT1* under both laboratory and field conditions. By contrast, the expression level of *HKT2* in Orenburgskaya 22 seedlings was equal to that of *HKT1*. Additionally, in field-grown Orenburgskaya 22 seedlings, the fold increase in *HKT2* expression compared with *HKT1* expression was higher than that observed in the laboratory. However, high salt concentration significantly decreased the expression of *HKT2;1* in Orenburgskaya 22 roots. Under high NaCl concentration, the expression level of *HKT2;1* was the same in both varieties and under both growth conditions.

We speculate that HKT1 proteins play a more important role in the resistance of wheat cultivar Uchitel to salt stress than HKT2 proteins, which most likely perform an additional function in removing toxic ions. However, in Orenburgskaya 22, class I and II transporters play an equally important in the elimination of toxic ions. This fact turned out to be important for the resistance of Orenburgskaya 22 to chloride salinity.

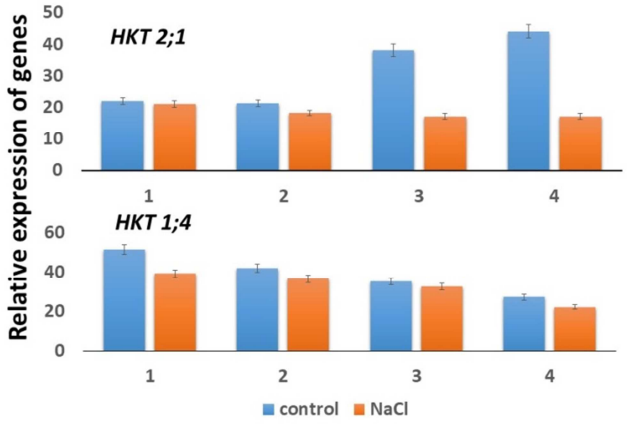

Figure 5. *Expression of genes HKT in root of wheat Uchitel' (1,2) and Orenburgskaya 22 (3,4) grown in roll culture (1,3) and in the field (2,4). Blue lane –control, orange lane – 150 mM NaCl. independent replicates. Bar represent standard deviation.*

3.5. Assessment of ROS Accumulation

Excess NaCl leads to the hyperproduction of ROS, which decreases photosynthesis and respiration and consequently plant productivity [21]. It is believed that plants are most sensitive to stressors at the seedling stage, which makes them convenient subject for the early diagnosis of stress resistance. In addition, ROS act as signaling intermediates [18]. Peroxidation and destruction of macromolecules by ROS causes damage to cell membranes, which ultimately leads to cell death [28].

Ion imbalance causes growth inhibition during ROS production [29]. ROS marker carboxy-H2DFFDA was detected in roots after exposure to NaCl, more often with more intense fluorescence compared to the control. An increased content of the fluorescent ROS marker, carboxy-H2DFFDA, in root cells under salt stress can initiate PCD because of the disruption of ROS homeostasis.

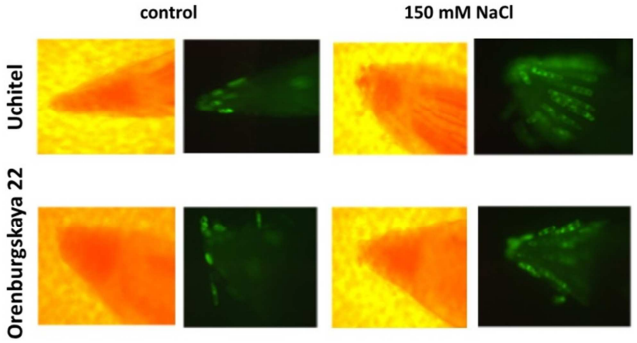

Figure 6. *H2D2FFDA staining of wheat roots samples.*

The staining of Uchitel and Orenburgskaya 22 roots with carboxy-H2DFFDA revealed the presence of ROS in all root tissues under salt stress, staining varied between cells from different zones. (Figure 6). Under salt stress, the most intense staining was observed in the cap zone and division zone.

In plants, there are various mechanisms to reduce the negative effects of ROS. One such mechanism is the enzymatic reduction of ROS toxicity. In this study, we examined the expression of the *MnSOD* gene in the two wheat varieties under salt stress (Figure 7). The expression level of *MnSOD* was not affected by the wheat genotype or the growing conditions.

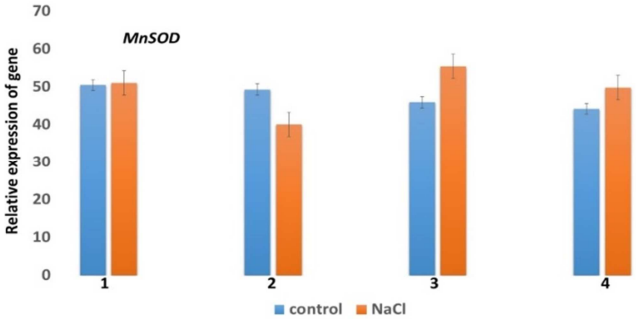

Figure 7. *Expression of genes MnSOD in root of wheat Uchitel (1,2) and Orenburgskaya 22 (3,4) grown in roll culture (1,3) and in the field (2,4). Blue lane –control, orange lane – 150 mM NaCl. Bar represent standard deviation.*

Notably, high salt stress (150 M NaCl) caused only a slight increase in *MnSOD* expression in Orenburgskaya 22. An

increase in *SOD* expression in Orenburgskaya 22 likely indicates that this wheat variety is better adapted to salt stress than Uchitel.

4. Conclusions

High salt concentration limits plant growth. The higher the ability of a plant to withstand abiotic stress, the more efficient it is in triggering various physiological and biochemical reactions, thus reducing plant damage. Plant abiotic stress response is a complex process involving many genes, proteins and signaling pathways. Plant resistance to stressors often depends on, not one, but many factors.

The use of morphometric and cytological criteria, which determine the functional state of cells in plant roots of a whole plant at early stages of development, makes it possible to assess the manifestations and parameters of stress: stability, destruction of the structural organization of cells and destruction in cells. Comparison of the functional state of cells using *in vivo* markers in wheat varieties with different levels of salt stress resistance can be effectively used to assess the oxidative status of plant root cells.

Studying expression HKT, SOD and MYB genes is important for characterizing wheat salt tolerance. It should be noted that in both wheat varieties, regardless of the growth conditions, the expression level of *MYB* family genes increased, while that of *HKT* family genes decreased in the presence of NaCl. presence of NaCl. A decrease in the size of the root system in wheat is accompanied by a decrease in the absorption of toxic ions, which leads to a decrease in the expression level of ionic transporters. However, this is stressful for the plant, which is accompanied by an increase in the expression of MYB family genes.

Thus, in plants, everything is interconnected and interdependent; a change in some parameters leads to a change in others. A decrease in the expression of genes of *HKT* genes is compensated by an increase in the expression of *MYB* TF genes and morphometric changes.

Our data suggest that wheat varieties Uchitel and Orenburgskaya 22 exhibit different levels of resistance to prolonged NaCl exposure. Understanding the mechanisms of ion transport is important for elucidating the function of HKT genes in plants. Elucidation of the tissue-specific expression patterns of HKT, SOD and MYB genes and their control mechanisms is of great interest to researchers for increasing plant tolerance to salt stress.

Based on the comparison morphometric and molecular data of two wheat varieties, Uchitel and Orenburgskaya 22, grown under laboratory and field conditions, it can be concluded that although growing wheat in roll culture is more stressful than growing wheat under natural conditions, there are some general patterns in the response to salinity. Therefore, some mechanisms of plant adaptation to abiotic stress can be investigated in the laboratory. Moreover, under laboratory conditions, it is possible to study plant response to only one stress factor at a time, whereas in real (field) conditions, several adverse factors affect the plant simultaneously.

Conflict of Interest

The authors declare no conflicts of interest.

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