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Differential Expression of The Tasos4 Gene in Salt-Tolerant and Salt-Sensitive Wheat (*Triticum aestivum L.*) Varieties

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Abstract

Salinity is a major abiotic stress that significantly impacts crop growth, yield, and quality, particularly in arid and semi-arid regions. The Salt Overly Sensitive (SOS) gene family plays a critical role in plant responses to salt stress by maintaining ion homeostasis. Among these, the TaSOS4 gene, associated with pyridoxal kinase activity, is believed to contribute to salt tolerance by regulating cellular metabolism and ion transport. In this study, we analyzed the differential expression of the TaSOS4 gene in two bread wheat (Triticum aestivum L.) varieties: the salt-tolerant 'E'zoz' and the salt-sensitive 'Faw-43'. Ten-day-old seedlings were subjected to 100 mM and 200 mM NaCl treatments for 48 hours, and quantitative real-time PCR (qRT-PCR) was used to evaluate gene expression levels. Our results revealed that the TaSOS4 gene is highly expressed in the salt-tolerant 'E'zoz' variety under increasing salt concentrations, indicating its potential role in enhancing salt tolerance. In contrast, the salt-sensitive 'Faw-43' exhibited minimal expression of TaSOS4 under both control and stress conditions. These findings suggest that the activation of TaSOS4 contributes to maintaining ion balance and protecting cellular integrity under saline environments. The consistent expression of the reference Actin gene confirmed the reliability of our qRT-PCR data. This study highlights the importance of TaSOS4 as a genetic resource for improving salt tolerance in wheat. The differential expression patterns observed between tolerant and sensitive varieties underscore its potential for breeding programs aimed at developing resilient wheat cultivars. Further research into the regulatory mechanisms of TaSOS4 could provide deeper insights into its role in plant stress responses and its application in sustainable agriculture.

Keywords: Actin, Salinity stress, Bread wheat, TaSOS4 gene, Quantitative real-time polymerase chain reaction (qRT-PCR), Triticum aestivum L.

1. Introduction

Salinity stress is a major threat to agricultural crops, as soil and water salinity adversely affects plant growth, development, and yield. This is particularly relevant in arid and semi-arid regions. Although plant responses to saline environments have been well-studied, this complex system is not yet fully understood (Turaev et al 2023; Baboeva et al 2023). Studying the genetic mechanisms of plant salt tolerance is crucial for improving their resilience. Salt-tolerant genes, such as *TaNHX1*, *TaHKT1*, *TaP5CS*, *TaDREB1*, *TaSOS1*, *TaSOS2*, *TaSOS3*, and *TaSOS4*, play essential roles in maintaining ion homeostasis, producing osmoprotectants, and synthesizing stress-responsive proteins in plant cells. For example, *TaNHX1* encodes a vacuolar Na+/H+ antiporter. *NHX1* reduces the sodium level in the cell cytoplasm by transporting sodium ions into the vacuole, thus protecting cells from salt stress. TaHKT1 encodes a high-affinity sodium/high-affinity potassium transporter. *HKT1* prevents the transport

of sodium ions from roots to leaves, thereby increasing salt tolerance. *TaP5CS* is responsible for proline biosynthesis, which serves as an osmoprotectant for plants. Proline levels increase under salt stress conditions, protecting cells. *TaDREB1* encodes a transcription factor involved in maintaining water balance in plant cells under salt stress conditions. *DREB1* regulates the expression of other salt stress-related genes (Zhu et al 2016).

The *SOS* gene family primarily plays a crucial role in maintaining Na^+ and K^+ homeostasis. These genes contribute significantly to salt tolerance by ensuring proper ion distribution across membranes and cells (Zhu et al 2016; Gamarin et al 2009). The family includes *SOS1*, *SOS2*, *SOS3*, and *SOS4*, each involved in a coordinated response to salinity stress. This regulatory network operates at both the transcriptional and post-transcriptional levels to mitigate ion toxicity, maintain osmotic balance, and support plant survival under saline conditions (Maughan et al 2009; Sathee et al 2015).

TaSOS1 encodes a plasma membrane-localized Na^+/H^+ antiporter that mediates Na^+ efflux from cells, a key defense against cytoplasmic sodium accumulation. *TaSOS2* and *TaSOS3* form a calcium-activated protein kinase complex that regulates *SOS1* activity in response to elevated intracellular Na^+ levels (Amit et al 2018). While these genes have been extensively studied, the *TaSOS4* gene remains relatively less characterized, despite emerging evidence suggesting its unique and critical role in salt stress responses.

TaSOS4 encodes a pyridoxal kinase enzyme involved in the biosynthesis of pyridoxal-5′-phosphate (PLP), the active form of vitamin B6. PLP is an essential cofactor in numerous metabolic processes, including amino acid metabolism, antioxidant defense, and hormone regulation. Importantly, vitamin B6 has been linked to enhanced tolerance to abiotic stresses such as salinity, drought, and oxidative stress due to its role in reactive oxygen species (ROS) detoxification and osmotic adjustment (Bakhadirov et al 2024).

The relative lack of information on *TaSOS4*, compared to other members of the *SOS* pathway, presents a valuable opportunity for exploration. Its dual role—as both a metabolic enzyme and a participant in stress signaling—positions *TaSOS4* as a potential integrative node between metabolic homeostasis and abiotic stress tolerance. Recent transcriptomic studies have hinted at its upregulation in salt-tolerant wheat genotypes, but quantitative expression data under defined salt stress conditions remain scarce (Meliev et al 2023; Ma Y et al 2019).

Therefore, this study aims to investigate the quantitative expression of the *TaSOS4* gene using qRT-PCR in two wheat cultivars with contrasting salt tolerance profiles under controlled salt stress conditions (100 mM and 200 mM NaCl). Understanding the specific behavior of TaSOS4 under salinity stress could reveal new molecular targets for developing salt-tolerant wheat varieties.

2. Material and Methods

2.1. Plant Material

For the quantitative expression analysis of the *TaSOS4* gene under salt stress, the salt-tolerant 'E'zoz' wheat variety from the Institute of Genetics and Plant Experimental Biology of the Academy of Sciences of Uzbekistan and the salt-sensitive 'FAWWON-IR-43' (Faw-43) wheat variety from the ICARDA germplasm collection were selected (Figure 1). These two wheat varieties were chosen based on previous evaluations of salt tolerance. A total of 108 wheat varieties and lines were tested for their salt tolerance by exposing them to different concentrations of NaCl solutions, followed by statistical analysis. The results revealed that the 'E'zoz' variety exhibited high salt tolerance, while the 'Faw-43' variety showed low tolerance under similar conditions. Therefore, the 'E'zoz' and 'Faw-43' cultivars were selected for the study of *TaSOS4* gene expression, as they represent contrasting salt tolerance traits.

This choice was made to investigate the differential expression of the *TaSOS4* gene in relation to the salt tolerance mechanisms of these two varieties. The genetic background of these varieties, particularly their mechanisms of resistance to salt stress, provides valuable insights into the role of the TaSOS4 gene in salt tolerance. The 'E'zoz' variety, known for its salt tolerance, serves as a valuable model for understanding the genetic basis of salt resistance, while the 'Faw-43' variety provides a contrast by highlighting the response of a salt-sensitive cultivar.

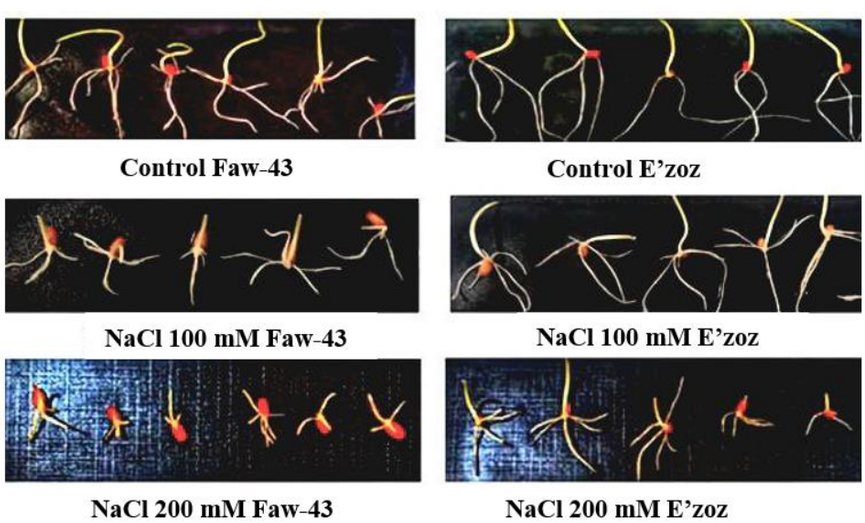

Figure 1. Response of the samples to the control 100 and 200 mM NaCl solution.

3. Research Methods

Wheat seeds were sterilized in 70% ethanol for 3 minutes and then rinsed with sterile water. Sterilized wheat seeds were germinated in a growth chamber (Cooling Incubator SPX-250BIII) at 25°C. 10-day-old seedlings were transferred to Petri dishes containing 100 and 200 mM NaCl solution and grown under light for 48 hours (Fu L et el 2018). Untreated wheat seedlings were used as a control. The experiments were performed in 3 biological and 3 technical replicates. Leaf samples were frozen in liquid nitrogen and then stored at -80°C until RNA extraction.

3.1. RNA Isolation and Quantitative Real-Time PCR

Total RNA from the research samples was isolated using a modified method described by (Abdurakhmonov et al.). Initially, 100 mg of fresh leaf tissue was ground into a powder using liquid nitrogen and a mortar and pestle. Subsequently, 2 ml of preheated Wu buffer at 80°C was added. Then, 60 µl of 25 mg/ml-1 proteinase K was added to the homogenate and mixed. In the next step, the homogenate was transferred to 2 ml plastic tubes and incubated at room temperature for 15 minutes. After incubation, the mixture was centrifuged at high speed for 20 minutes at 4°C in a centrifuge (Eppendorf 5415R, Germany). The upper liquid portion, or supernatant, was transferred to new 2 ml plastic tubes, and phenol (Sigma Aldrich, USA) was added. Then, chloroform:isoamyl alcohol (24:1) was added and vortexed. Subsequently, it was centrifuged as before. 1.2 M NaCl + 150 µl of 0.8 M Na citrate solution and 1 volume of 96% ethanol was added to the resulting supernatant and centrifuged. The precipitate in the tube was washed with 70% ethanol, and the pellet was dried under a laminar flow hood. The pellet was dissolved in 0.1% DEPC-treated water and stored at -80°C until further reactions. The concentration and quality of the total RNA samples were determined using a Qubit3 (ThermoFisher, USA) device.

To remove residual DNA products from total RNA and synthesize cDNA, the SuperScript IV VILO Master Mix with ezDNase Enzyme (Thermo Fisher, USA) kit was used. The resulting cDNA was diluted 1:15 and used for gene expression reactions.

In the qRT-PCR reaction, the wheat SOS4 gene was quantified using the (ACTIN) gene as an endogenous control (Table 1).

Table 1. Gene-specific primers used for RT-PCR analysis.

Gen	Forward sequence	Reverse sequence
SOS4	TGAGATACCCAAGATACCTGCATA	TGATCTCATCCTGGCTTTGTATTA
Actin	CTTGTATGCCAGCGGTCGAACA	CTCATAATCAAGGGCCACGTA

Quantitative real-time PCR (qRT-PCR) analysis was performed using a CFX96 Touch Real-Time PCR Detection System (Bio-Rad, Hercules, CA, USA) to evaluate the actual relative expression of genes. PCR reactions were set up in a 25 µl volume as follows: 95°C for 10 minutes, followed by 40 cycles of 95°C for 15 seconds and 65°C for 45 seconds. Each 25 µl reaction mixture consisted of 12.5 µl SYBR Green Master Mix (2×), 0.35 µl (140 nM) of each primer (10 µM), 6 µl of 1:15 diluted cDNA, and 5.8 µl of sterile water. The 2× SYBR Green PCR Master Mix contained No AmpErase UNG, AmpliTaq Gold DNA polymerase, deoxynucleoside triphosphates with dUTP, and SYBR Green I magnesium chloride reaction buffers (Applied Biosystems, Waltham, MA, USA). To avoid errors in the reactions, all reactions were performed in three biological and three technical replicates. All primers were designed using Integrated DNA Technologies Inc. (Coralville, IA, USA) Primer3 and IDT OligoAnalyzer Tool.

The actual relative expression of genes was evaluated using the software provided with the CFX96 Touch Real-Time PCR Detection System (Bio-Rad, Hercules, CA, USA). Graphs were generated using GraphPad Prism 8.0.1 (www.graphpad.com; GraphPad Software, San Diego, California, USA).

3.2. Statistical Analysis

The data were analyzed using GraphPad Prism 8.0.1 (GraphPad Software, San Diego, CA, USA). Mean ± standard error (SE) values were calculated for each treatment group. Differences in gene expression between control and salt-treated samples were assessed using one-way analysis of variance (ANOVA).

4. Results

Initially, electrophoresis was performed on a 1.5% Agarose D1 High EEO gel (CS-300V) at 125 V for 50 minutes during the study [12]. Visual representation was obtained using a Gel Doc Imaging System (GelDoc Go USA) (Figure 2).

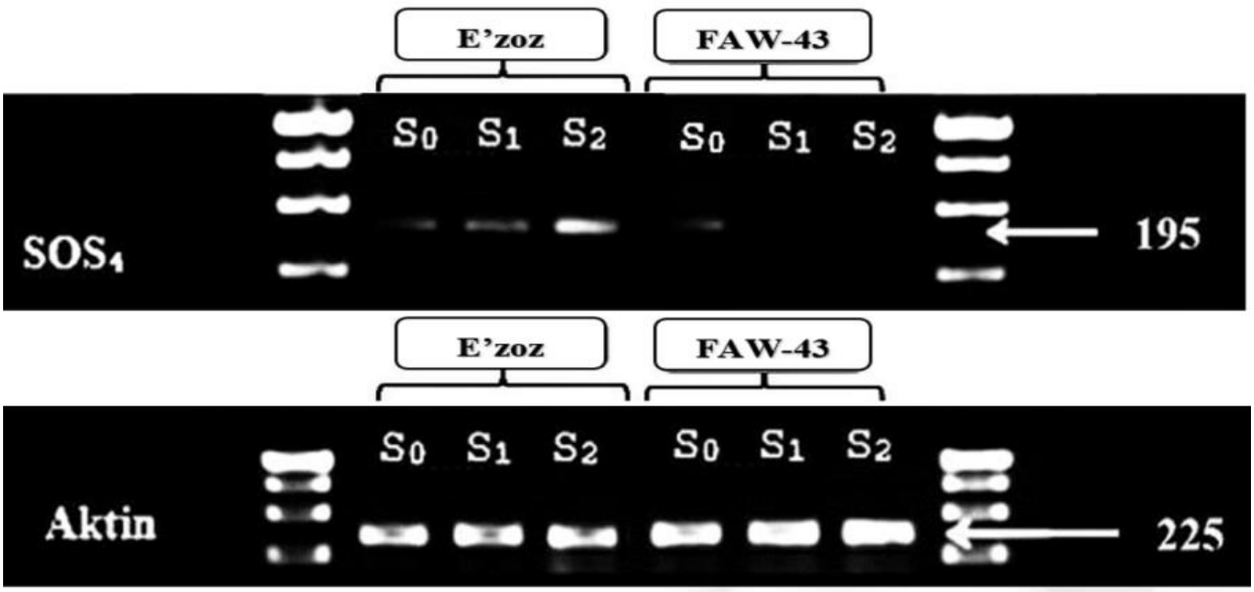

Figure 2. Visualization of SOS4 and Actin genes on a 1.5% agarose gel. (S_0-Control 0 mM NaCl, S_1-100 mM NaCl solution, S_2-200 mM NaCl solution).

In this study, we observed that the expression of the SOS4 gene in the salt-tolerant 'E'zoz' cultivar increased as the salt concentration increased. Specifically, under the 100 mM and 200 mM NaCl conditions, the expression of the SOS4 gene was significantly higher, indicating that this gene plays a crucial role in enhancing salt tolerance. This suggests that in the 'E'zoz' cultivar, the expression of the SOS4 gene is part of the adaptive response to salt stress.

In contrast, the salt-sensitive 'Faw-43' cultivar showed a low level of SOS4 expression under normal conditions (S0 control). Under salt stress conditions with 100 mM and 200 mM NaCl, the expression of the SOS4 gene in this cultivar was significantly reduced, which confirms its susceptibility to salt stress.

The Actin gene was used as a reference to assess the expression of the SOS4 gene. Actin gene expression was unaffected by salt stress, as evidenced by the consistent expression levels of Actin across the different salt concentrations (S1 and S2) in the selected samples. This indicates that the Actin gene serves as a stable reference, while the expression of SOS4 is influenced by salt stress.

The results of the study were graphically represented using GraphPad Prism 8.0.1 (GraphPad Software, San Diego, California, USA) and are presented in (Figure 3).

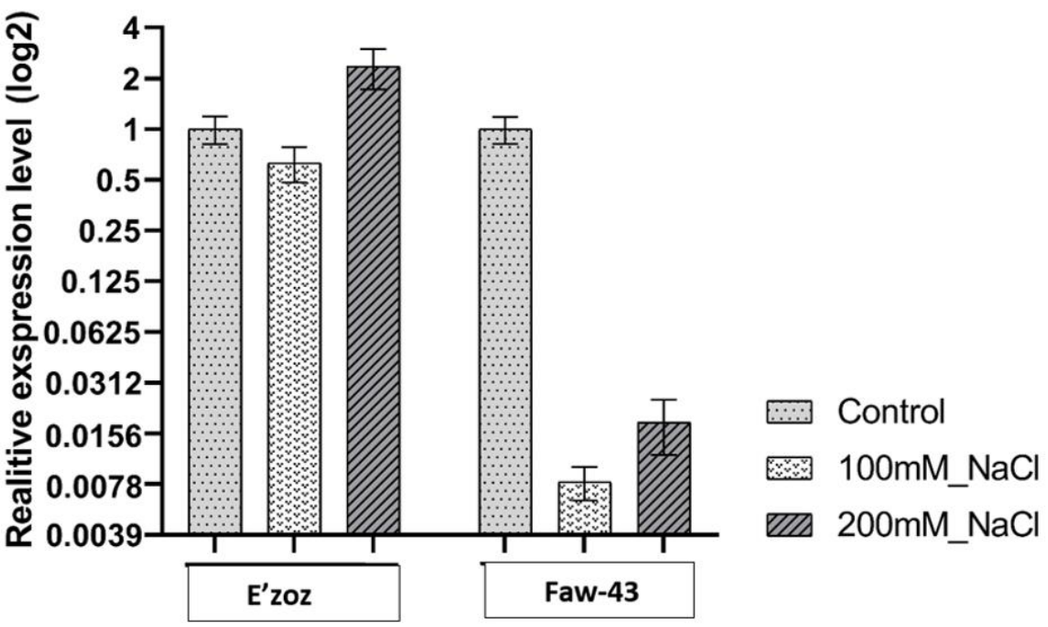

Figure 3. SOS4 gene expression under different NaCl concentrations (control, 100 mM NaCl, and 200 mM NaCl).

To examine the differences in SOS4 gene expression profiles after 48 hours of NaCl treatment in each wheat variety, we utilized GraphPad Prism 8.0.1 (www.graphpad.com; GraphPad Software, San Diego, California, USA) to generate graphical representations. In the 'E'zoz' wheat variety, samples treated with 100 mM NaCl exhibited a 0.25 log2 decrease in SOS4 gene expression compared to the control (1 log2). Conversely, samples treated with 200 mM NaCl showed a 2-fold increase in SOS4 gene expression, reaching 2 log2 relative to the control. In the salt-sensitive 'Faw-43' variety, samples treated with 100 mM NaCl showed a very low level of SOS4 gene expression, at 0.0078 log2 relative to the control. Treatment with 200 mM NaCl resulted in an even lower SOS4 gene expression of 0.0156 log2 compared to the control.

5. Discussion

In this study, we evaluated the expression of the TaSOS4 gene in two wheat (*Triticum aestivum* L.) cultivars with contrasting salt tolerance profiles under varying salinity levels. Our results revealed that the salt-tolerant cultivar 'E'zoz' exhibited a significant upregulation of TaSOS4 expression, particularly at 200 mM NaCl, while the expression remained extremely low in the salt-sensitive cultivar 'FAWWON-IRR-43'. This finding indicates that TaSOS4 may play a crucial role in the salt stress response and may be involved in the regulation of physiological processes necessary for maintaining ion balance under stress conditions.

These results are consistent with previous findings in the field. For instance, Sathee et al. (2015) demonstrated that the expression of SOS pathway genes was significantly higher in salt-tolerant wheat genotypes compared to sensitive ones, particularly under elevated salt stress. Similarly, Rolly et al. (2020) reported that SOS genes—including SOS1, SOS2, and SOS3—exhibited genotype-specific expression patterns, contributing to differential salt tolerance mechanisms among wheat cultivars.

Although the role of TaSOS1-3 has been well studied, the functional characterization of TaSOS4 remains relatively limited. However, studies in Arabidopsis by Ma Y et al. (2019) revealed that SOS4 encodes a pyridoxal kinase involved in vitamin B6 biosynthesis, which is essential for cellular redox homeostasis and stress-related metabolic functions. Given the antioxidant and metabolic roles of vitamin B6, upregulation of TaSOS4 may help reduce oxidative stress and support osmotic adjustment in tolerant wheat genotypes.

The higher expression of TaSOS4 observed in 'E'zoz' under 200 mM NaCl suggests its involvement in both early signaling and long-term metabolic adaptation. This aligns with the findings of Vaseem Raja et al. (2017), who identified strong SOS system activity as a key determinant of salinity tolerance in wheat genotypes from saline-prone regions of the Balkans. The present results also support the theory that enhanced activation of specific SOS genes under stress facilitates ion homeostasis by maintaining favorable Na^+/K^+ ratios, as outlined in the review by El Mahi et al. (2019).

Furthermore, our findings contribute to the existing knowledge by providing the first quantitative comparison of TaSOS4 expression in two wheat cultivars exposed to multiple salt concentrations using a controlled experimental setup. While earlier studies have focused mainly on structural and transcriptional analysis, our results offer practical expression-level data that directly links TaSOS4 activity to phenotypic salt tolerance. This provides a promising foundation for future functional genomics studies, including overexpression or knockout strategies to validate its role in stress adaptation.

In conclusion, this study expands the understanding of the SOS signaling pathway by highlighting the overlooked role of TaSOS4 in salt stress response. Its cultivar-specific expression suggests potential as a molecular marker for screening salt-tolerant genotypes. Continued exploration of its regulatory network and interaction with other SOS and stress-responsive genes will further elucidate its role in salt adaptation and guide the development of stress-resilient wheat varieties.

6. Conclusion

This study, by investigating the expression of the TaSOS4 gene under salt stress conditions, has provided valuable and new insights into the salt tolerance mechanisms of soft wheat varieties. The differences in the expression of the TaSOS4 gene across various wheat varieties play a crucial role in understanding how this gene influences salt tolerance mechanisms. Specifically, the higher expression of the TaSOS4 gene in the 'E'zoz' variety indicates that this gene contributes to enhancing salt tolerance. The increased expression of TaSOS4, in turn, helps the variety to develop and grow better under salt stress conditions. Such findings open up the potential for applying genetic manipulations in developing salt-tolerant wheat varieties.

The role of TaSOS4 gene in enhancing salt tolerance suggests that new genetic strategies can be developed to increase salt tolerance in soft wheat varieties by regulating the expression of this gene. Increasing the expression of TaSOS4 or modifying its expression could be widely applied to improve these varieties and optimize their growth conditions.

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