



The Influence of Salinity Stress on Plants and Their Molecular Mechanisms[†]

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[†] Presented at the 2nd International Electronic Conference on Plant Sciences—10th Anniversary of Journal Plants,
1–15 December 2021; Available online: <https://iecps2021.sciforum.net/>.

Abstract: Salt stress is one of the major threats to sustainable agriculture, as it is considered as an external environmental constraint that limits the growth and productivity of plants. It is more common in arid regions due to excessive evaporation, which causes the accumulation of inorganic salts that disrupts plant metabolism. It also makes as plants unable to absorb water due to higher Na⁺ ions in the root zone. It disrupts the normal functioning of the plants and triggers secondary stresses resulting in oxidative bursts. Plants exposure to salt stress stimulate signaling pathways that help the plants to establish cellular ionic homeostasis. Additionally, stress-responsive transcription factors play crucial roles in salt-stress responses and tolerance. The main transcription factors include bZIP, AP2/ERF, WRKY, NAC, bHLH, and MYB families, for the mediation of stress response.

Keywords: salt stress; sensing; transcription factors



Citation: Chaudhry, U.K.; Gökçe, Z.N.Ö.; Gökçe, A.F. The Influence of Salinity Stress on Plants and Their Molecular Mechanisms. *Biol. Life Sci. Forum* **2022**, *11*, 31. <https://doi.org/10.3390/IECPS2021-12017>

Academic Editor: Iker
Aranjuelo Michelena

Published: 2 December 2021

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1. Introduction

Plants are immutable beings that suffer from fluctuating climatic conditions in the field [1]. Various abiotic stress factors are involved in curtailing the growth of plants. Major abiotic stresses include drought, heat, cold, salinity, and heavy metal stress. Out of these stresses, salinity is considered as being more lethal to plant growth [2]. It affects the ionic homeostasis leading to ionic toxicity in plants. The higher accumulation of salts in the vicinity of plant roots results in the least absorption of water, causing water-deficit conditions. Moreover, it also disrupts the uptake of essential nutrients, causing nutrient-deficient conditions for the plants [3]. Plant cells communicate to direct cellular changes in plants with the help of numerous signaling cascades. Plants can sense salt stress via the plasma membrane or intracellular families. The available literature shows that important salt sensors are reactive oxygen species (ROS)-based sensors and Na⁺/Ca²⁺ membrane transporters. They sense and stimulate the higher accumulation of abscisic acid (ABA) that plays a vital role in the regulation of stomatal closure and gene expression [4]. Transcriptomic studies revealed that transcription factors (TFs) regulated by salinity stress turn on/off genes to cope with negative influence of stress. They regulate genes by binding in the promoter regions to cis-regulatory elements. The TFs are important to be studied due to their function as a molecular switch of associated genes with the binding to cis regulatory elements [5]. The key characteristic of TFs is their interaction with various proteins in transcriptional complexes for the regulation of gene expression of several genes. The regulation of gene expression plays a pivotal role, ranging from the activation of the sensory salt pathways to physio-biochemical changes in plants. In plants, 10% of the genes potentially encode TFs and are classified based on their distinctive DNA-binding domain structure [6]. From the consideration of the role of salinity sensors and TFs that positively regulate gene expression, it demonstrates that the study of these molecular mechanisms

is beneficial for the development of stress resilient crops. A greater expression of the mentioned TFs can alleviate the negative influence of ROS species and oxidative stress that can protect plant cellular membranes.

2. Salinity Stress and Molecular Mechanisms

Salinity-stress tolerance is a polygenic trait that has constant variations that can be influenced by environmental or genetic factors for the phenotypic responses of plants. Several molecular mechanisms are involved, resulting in various positive physiological and biochemical changes related with stress tolerance/adaptation. The main molecular mechanisms include sensing, signaling, and TFs for the regulation of gene expression [7].

2.1. Sensing and Signaling

Plants respond to salinity stress with the perception/transduction of osmotic and ionic signaling to the interior of the cell that modifies cellular characteristics. To date, no specific salinity sensor/receptor has been reported in plants [8]. However, the Arabidopsis signaling pathway, such as salt overly sensitive (SOS) and calcineurin B-like (CBL)/CBL-interacting kinase, has been characterized. The elevated levels of cytosolic Ca^{2+} stimulates Ca^{2+} -dependent protein kinase complex (SOS2-SOS3) that phosphorylates and initiates the activity of SOS1. Additionally, the complex of CBL10-CIPK24 was observed for the modulation of a novel pathway for the regulation of vacuolar Na^{+} sequestration. Salinity stress also stimulates the elevated accumulation of ABA that initiates signaling, and TFs are also based on ABA-dependent and ABA-independent pathways (Figure 1). It activates sucrose nonfermenting 1-related protein kinase 2 (SnRK2) by phosphorylation. Plants under control conditions exhibits the inhibition of snRK2; contrarily, in response to stress, it binds to the receptor protein known as PYRABACTIN RESISTANCE 1 (PYR1). When PP2C is released from SnRK2, it self-phosphorylates and activates/inhibits a group of downstream TFs, i.e., the abscisic acid (ABA)-responsive element (ABRE)-binding protein (AREB)/ABA-responsive factors (ABF) [9]. There is another potential candidate for salt-stress sensing known as the mitogen-activated protein kinases (MAPKs). It mediates the homeostasis of secondary stresses, such as ionic, osmotic, and oxidative stresses. It is classified into three different classes, based on the phosphorylation and activation of elements, i.e., MAPK, MAPKK, and MAPKKK [10].

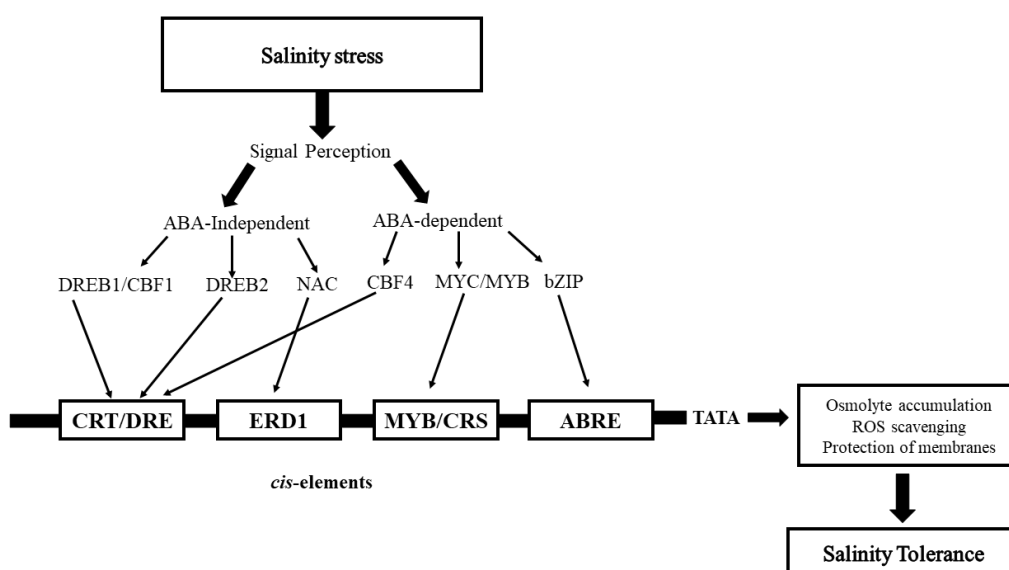


Figure 1. Schematic representation of the salinity-stress-signal perception and gene expression.

2.2. Transcription Factors

TFs are proteins that attach to the regulatory sequences of DNA, which are found in the 5'-upstream region of target genes to control the stimulation rate of transcribed genes. Therefore, TFs play a pivotal role by turning “on” and “off” particular genes that bind with other DNA. It ultimately controls the gene transcription protein synthesis that results in the modification of the cellular function in plant tissues [11]. The TFs are highly conserved in plant genomes that regulates gene expression, and helps plants rescue salinity stress. Transcription factors are crucial for controlling gene expression, which results in developmental changes. Firstly, it is important to understand transcription mechanisms as changes in the gene transcription are regulated by transcription factors. In all eukaryotes, transcription is performed by the RNA polymerase 2 (RNAP II) enzyme. Specifically, RNAP II cannot move alone. This enzyme's activity is controlled by the cis-regulatory region, which is the DNA sequence located within the gene and by proteins (trans-acting factors) called transcription factors. The cis-acting elements are the DNA segments that regulate transcription [12]. The six important TF families linked to stress tolerance are bZIP, DREB, MYB, NAC, and WRKY [13]. The list of TFs that alleviate salinity stress is presented in Table 1.

Table 1. Potential role of the transcription factors in response to salinity stress.

Transcription Factor	Response	Reference
WRKY	Protects the cell membrane by mitigating toxic levels of ROS	[14]
NAC	Triggers the germination/growth rate	[15]
bZIP	Scavenges ROS by modulating specific gene expressions	[16]
MYB	Transcriptional response to cope with osmotic stress/osmolyte formation	[17]

2.2.1. WRKY

The WRKY is reported to be the largest gene family among all the TFs in plants. It plays a critical role in the regulation of signal transduction pathways to synthesize plant hormones in response to salinity stress. It also participates in the synthesis of secondary metabolites, development, and carbohydrate synthesis. It binds to W-box in the promoter region of its target gene that suppress/activate gene expression [18].

2.2.2. NAC

The TFs NAC is also important in mitigating salinity stress, and it has been discovered in several plant species [19]. They are also known as a stress responsive NAC. The DNA-binding ability of NAC is confined to NAC domain, whereas the C terminus regions are transcriptional activation domains [20]. They play a key role in the development, cell division, root elongation, and formation of apical meristem in response to stress. The overexpression of NAC alleviates the negative influence of salt stress. Additionally, the upregulation of NAC5 is positively correlated with resilient behavior [21].

2.2.3. DREB

It is an important TF that stimulates a set of stress-related genes that can impart stress endurance. It comprise of ethylene-responsive element-binding factor (ERF) family of TFs and contains highly conserved DNA-binding domain. It influences gene expression by DRE-cis-acting elements that in turn confers stress tolerance [22]. Several studies reported the positive role of the ERF in response to oxidative stress. Its overexpression accumulates higher levels of osmoprotectants that include proline and soluble sugars. The higher expression levels of the ERF gene resulted in higher transcript levels of superoxide dismutase and the catalase gene to alleviate the ROS [11].

2.2.4. bZIP

It is very large class of TF distributed in eukaryotes. Its distinctive feature is highly conserved bZIP domain, containing conserved region at N-terminus and leucine zipper region at C-terminus [23]. It contributes to the positive regulation of the physiological functioning by maintaining ionic and osmotic balance involving heterodimerization/post-transcriptional modification [24]. Furthermore, it is important for seed germination and plant senescence. Additionally, it confers salt resistance by suppressing oxidative stress with the least accumulation of the ROS. The overexpression of bZIP genes has been reported to overcome dehydration in plant cells due to salinity [16].

2.2.5. MYB

Plants exposed to salinity stress regulate differential gene expression with the activation of TFs. It is evident from several studies that salinity stress requires the activation of multifarious genes, and MYB have the potential to simultaneously regulate different sets of genes. Furthermore, TFs can play a part in salinity-stress signaling. For instance, TF (MYB) plays a key role in the stress signaling system. Almost all eukaryotes have MYB family protein that is a conserved DNA-binding domain. The MYB family protein can exhibit suppressed/induced gene expression with the acclimatization of plants to salinity stress. Additionally, it is also involved in the synthesis of secondary metabolites, e.g., anthocyanin that plays an essential role in the protection of plants against adverse salinity conditions. The MYB proteins bind with anthocyanin-associated genes and induce its synthesis resulting in higher gene expression [17].

Author Contributions: All the authors contributed equally. All authors have read and agreed to the published version of the manuscript.

Funding: This study received no external funding.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Conflicts of Interest: The authors declare no conflict of interest.

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