

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

Usman Khalid Chaudhry *, Zahide Neslihan Öztürk Gökçe and Ali Fuat Gökçe

Department of Agricultural Genetic Engineering, Faculty of Agricultural Sciences and Technologies, Nigde Omer Halisdemir University, Nigde, Turkey

* Correspondence: ukojla0455@gmail.com; Tel.: +905515881455

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Abstract: Salt stress is one of the major threats to sustainable agriculture as it is considered as an external environmental constraint that limits growth and productivity of plants. It is more common in arid regions due to excessive evaporation which causes accumulation of inorganic salts that disrupts the plant metabolism. It also increases the negative influence of drought stress as plants being unable to absorb water due to osmotic effects. It disrupts the normal functioning of the plants and triggers secondary stresses resulting in oxidative burst. Thereby, plants adaptation to salt stress, a rely on signals and pathways that helps plant in establishing cellular ionic and osmotic 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

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1. Introduction

Plants as being immutable suffer from fluctuating climatic conditions in field [1]. Various abiotic stress factors are involved for curtailing growth of plants. Major abiotic stresses include drought, heat, cold, salinity and heavy metal stress. Out of these stresses, salinity is considered more lethal to plant growth [2]. It affects the ionic homeostasis leading to ionic toxicity in plants. Higher accumulation of salts in the vicinity of plant roots results in least absorption of water causing water deficit conditions. Moreover, it also disrupts the uptake of essential nutrients causing nutrient deficient conditions to plants [3]. Plant cells communicate for the coordination of salinity stress responsive activities with the help of numerous signaling cascades. Plants can sense salt stress via 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 stimulates the higher accumulation of abscisic acid (ABA) that plays vital role with the regulation of stomatal closure and gene expression [4]. Transcriptomic studies revealed that transcription factors (TFs) regulated by salinity stress have potential of activating specified genetic programs. They regulate salt stress responsive genes with binding in the promoter regions to cis-regulatory elements. The TFs have attained consideration 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 interaction with various proteins in transcriptional complexes for the regulation gene expression of several genes. The regulated gene expression can play pivotal role from activation of sensory salt pathways to the various physio-biochemical changes in plants. In plants approximately 10% of the genes code for TFs that are classified based on their distinctive DNA-binding do-

main structure [6]. By considering the role of salinity sensors and TFs that positively regulate gene expression. It was demonstrated that study of these molecular mechanisms will be beneficial for the development of stress resilient crops. Higher expression of 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 phenotypic responses of plants. Several molecular mechanisms are involved resulting various positive physiological and biochemical changes for stress tolerance/adaptation. The main molecular mechanisms include sensing, signaling and TFs for 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. Until now, no specific salinity sensor/receptor has been reported in plants [8]. However, in 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 Ca²⁺ stimulates protein kinases complex (SOS2-SOS3) that phosphorylates and initiates the activity of SOS1. Additionally, the complex of CBL10-CIPK24 has been observed for the modulation of novel pathway for the regulation of vacuolar Na⁺ sequestration. Salinity stress also stimulates elevated accumulation of ABA that initiates signaling, and TFs are also based on ABA-dependent and ABA-independent pathways (Figure1). It activates sucrose nonfermenting 1-related protein kinase 2 (SnRK2) by phosphorylation. Plants under control conditions exhibited the inhibition of snRK2, contrarily in response to stress it binds to the receptor protein known as PYRABACTIN RESISTANCE 1 (PYR1). When PP2C released from SnRK2, it self-phosphorylates and activates/inhibits a group of downstream TFs i.e., Abscisic acid-responsive element binding protein (AREB)/ABA-responsive element binding factors (ABF) [9]. There is another potential candidate of salt stress sensing known as mitogen activated protein kinases (MAPK). It mediates homeostasis of secondary stresses such as ionic, osmotic, and oxidative stress. It is classified into three different classes based on phosphorylation and activation of elements i.e., MAPK, MAPKK, and MAPKKK. Approximately, 20 MAPKs, 10 MAPKKs, and 60 MAPKKKs have been encoded in *A. thaliana* genome based on similarity in sequences [10].

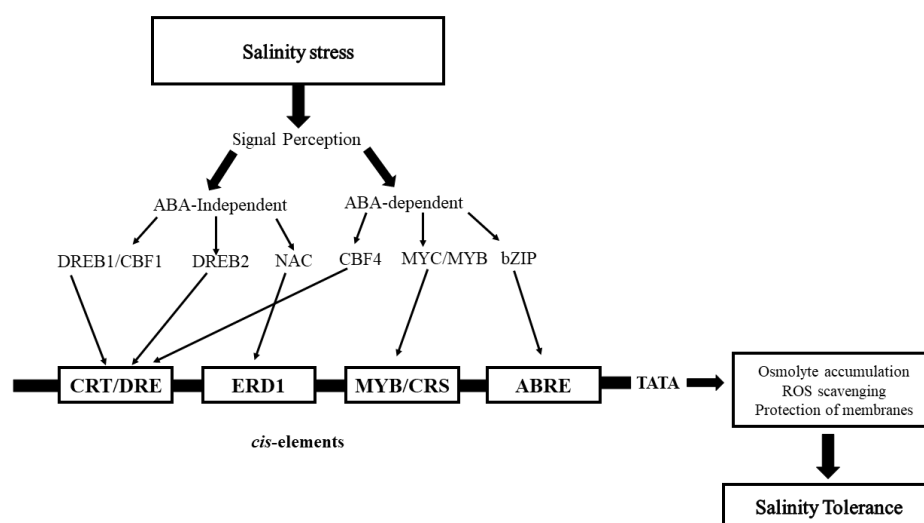


Figure 1. Schematic representation of salinity stress signal perception and gene expression.

2.2. Transcription Factors

The TFs are proteins that attaches with the regulatory sequences of DNA, that are found in the 5'-upstream region of target genes to control the stimulation rate of transcribed genes. Therefore, TFs play pivotal role by turning "on" and "off" particular genes that binds with other DNA. It ultimately controls the gene transcription, protein synthesis that results in modification of cellular function in plant tissues [11]. The TFs are highly conserved in plant genome that alters gene expression and makes plant resilient to salinity. Some of them are general which are found in all cells of a plants. Others are specific for some types of cells and development stages. Specific transcription factors are mostly important for the gene expression which can result in developmental changes. Firstly, it's important to understand transcription mechanism because changes of gene transcription are regulated by transcription factors. In all eukaryotes, transcription is performed by the RNA Polymerase 2 (RNAP II) enzyme. Specifically, RNAP II can't move alone. This enzyme's activity is controlled by cis-regulatory region which is the DNA sequences located within the gene and by proteins (trans- acting factors) called transcription factors. In that case, to transcribe DNA, TFs are required for the enzyme RNAP II. The cis-acting elements are the DNA segments which regulates transcription [12]. The six important TFs families linked with stress tolerance are bZIP, DREB, MYB, NAC, and WRKY [13]. The role of TFs to alleviate salinity stress is briefly given in Table 1.

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

Transcription Factor	Response	Reference
WRKY	Protects cell membrane by mitigating toxic levels of ROS	[18]
NAC	Triggers germination/growth rate	[19]
bZIP	Scavenges ROS by modulating specific gene expression	[16]
MYB	Transcriptional response to cope osmotic stress/osmolyte formation	[17]

2.1.1. WRKY

The WRKY is reported to be the largest gene family among all the TFs in plants. It plays critical role with 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 the gene expression. Additionally, overexpression WRKY also conferred salinity stress tolerance in plants [14].

2.1.2. NAC

The TFs NAC also holds significant position to mitigate salinity stress. It has been found in several plant species. They are also known as super-family compared to other TFs. Their conserved DNA-binding domain at the N-terminus is NAC-domain whereas at C-terminus is transcription regulatory region. They play key role for the development, cell division, root elongation, and formation of apical meristem in response to stress. Overexpression of NAC alleviated the negative influence salt stress. Additionally, upregulation of NAC5 was positively correlated for resilient behavior [15].

2.1.3. DREB

It is an important TF that stimulates a set of salt stress related genes that can impart stress endurance. It particularly belongs to ethylene responsive element binding factor (ERF) family of TF. interacts with the dehydration responsive element. Several studies have reported the positive role of ERF in response to oxidative stress. Its overexpression accumulates higher levels of osmoprotectants that includes proline and soluble sugars. The higher expressional levels of ERF gene resulted in higher transcript levels of superoxide dismutase and catalase gene to alleviate ROS species [11].

2.1.4. bZIP

It is also abundantly found in plants and highly conserved for specific sequence of DNA binding adjacent to heptad leucine repeat domain. It contributes to positively regulate physiological functioning of the plants. It is important for seed germination, plant senescence. The overexpression of bZIP genes reported to overcome dehydration in plant cells due to salinity. Besides this, it can confer salt resistance by suppressing the oxidative stress with least accumulation of ROS species. The higher bZIP gene expression was reported to confer salinity stress tolerance [16].

2.1.5. MYB

Plants exposed to salinity stress regulates differential gene expression with the activation of TFs. It is evident from several studies that salinity stress requires the activation of multifarious genes and TFs have the potential to regulate different set of genes simultaneously. Furthermore, TFs can play part in salinity stress signaling. For instance, TF (MYB) plays key role in stress signaling system. Almost all eukaryotes have MYB family protein that is conserved DNA binding domain and most of them function as a TF due to its binding ability with DNA. It is also important to know that MYB family protein can exhibit suppressed/induced gene expression with the acclimatization of plants to salinity stress. Additionally, it is also involved for the synthesis of secondary metabolites e.g., anthocyanin. It is a flavonoid pigment and plays essential role to protect plant from adverse salinity conditions. Its upregulated gene expression might be attributed to MYB protein. As these proteins binds with anthocyanin associated genes and induces its synthesis [17].

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