

Exploring the Physiological and Molecular Mechanisms of Halophytes' Adaptation to High Salinity Environments: Implications for Enhancing Plant Salinity Tolerance

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ABSTRACT



Salinity stress poses a significant challenge to plant growth and agricultural productivity worldwide. However, certain plant species, known as halophytes, have evolved remarkable adaptive mechanisms to thrive in high salinity environments. Understanding the physiological and molecular mechanisms underlying the salt tolerance of halophytes holds great potential for enhancing salinity tolerance in non-halophytic crop plants. This review aims to explore the adaptive strategies employed by halophytes to cope with salinity stress and their implications for improving plant salinity tolerance. Physiological adaptations of halophytes include mechanisms to regulate ion homeostasis, maintain osmotic balance, and minimize water loss under high salinity conditions. These adaptations involve the accumulation of compatible solutes, such as proline and glycine betaine, as well as the compartmentalization of toxic ions in vacuoles. Halophytes also exhibit efficient antioxidant systems to counteract oxidative stress induced by salt accumulation. At the molecular level, halophytes employ a range of genetic and epigenetic mechanisms to regulate gene expression and enhance salt tolerance. These mechanisms include the activation of stress-responsive transcription factors, modulation of ion transporters and channels, and epigenetic modifications that alter chromatin structure and gene expression patterns. Recent advancements in molecular techniques, such as transcriptomics and proteomics, have provided valuable insights into the complex regulatory networks involved in halophyte salt tolerance. Harnessing the knowledge gained from halophyte adaptation mechanisms can offer promising prospects for improving the salinity tolerance of economically important crop plants. Genetic engineering and breeding approaches can be employed to introduce or enhance the expression of key salt tolerance genes in non-halophytic species. Additionally, the identification and utilization of halophyte-derived salt tolerance traits through conventional breeding strategies hold great potential for developing salt-tolerant crop varieties. Therefore, the investigation of halophytes' physiological and molecular mechanisms of salt tolerance provides valuable insights into the intricate strategies employed by plants to adapt and thrive in high salinity environments. The knowledge gained from these studies can be harnessed to enhance the salinity tolerance of non-halophytic crop plants, thereby contributing to sustainable agriculture in salinity-affected regions.

Keywords: Antioxidants; Compatible solutes; Halophytes; Molecular mechanisms; Physiological adaptations; Oxidative stress; Salinity stress; Salt tolerance;.

INTRODUCTION

Salinity stress, resulting from high salt concentrations in the soil, is a major abiotic stress that severely affects plant growth, agricultural productivity and ecosystem sustainability worldwide. As global climate change and human activities continue to contribute to soil and water salinization, there is an urgent need to develop strategies to mitigate the negative impacts of salinity on plant growth and survival. It also poses a significant threat to food security and sustainable agriculture, particularly in regions where irrigation water or groundwater is saline. However, certain plant species, known as halophytes, have evolved unique adaptive mechanisms that enable them to thrive in high salinity environments. Halophytes have evolved a diverse array of adaptive mechanisms to cope with high salinity levels, enabling them to maintain cellular homeostasis and sustain growth under saline conditions.

These adaptive mechanisms encompass a range of physiological, biochemical, and molecular processes that collectively contribute to their enhanced salt tolerance. Understanding these physiological and molecular mechanisms underlying the salt tolerance of halophytes can provide valuable insights into enhancing salinity tolerance in economically important crops and contribute to sustainable agriculture in saline environments. This review will provide a comprehensive overview of the current knowledge on halophyte adaptive mechanisms and their potential applications in increasing plant salinity tolerance, ultimately paving the way for more resilient and productive agricultural systems in the face of escalating salinity stress. Therefore, this review focuses on the negative impact of salinity on plants and explores the physiological and molecular mechanisms by which halophytes adapt to high salinity environments. The review reveals key findings that provide insights into

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the potential implications of these mechanisms for enhancing plant salinity tolerance.

Mechanisms of salinity-mediated Negative Impacts on Plants

Increasing salinity of soil can have a variety of negative effects on plant performance. One of the negative consequences is the scarcity of water caused by salinity, which hampers seed germination due to a decrease in the osmotic capacity of soil water, making it difficult for plant seeds to absorb water (Uçarlı, 2020; El-Keblawy *et al.*, 2021). Any interruption to seed imbibition can disrupt enzyme and proteins are metabolism, disrupt hormonal equilibrium, slow down the utilization of seed reserves, and often lead to alternation in the ultrastructure of cells, tissues, and organs (Miransari and Smith, 2014; Alencar *et al.*, 2015). The primary adverse impact of soil salinity is a decrease in plant development and biomass following germination, which is influenced by the level of salinity, duration of salt exposure, and plant species (Uçarlı, 2020).

Upon exposure to salinity, plant cells can rapidly lose water, resulting in cell shrinkage within a few seconds (Munns and Tester, 2008). Although cells return to their initial volume over hours, their elongation rates are significantly decreased (Munns, 2002). The rate of cell division is also significantly slowed down over time, which reduces plant development (Arif *et al.*, 2020). Furthermore, salinity results in noticeable harm to the oldest leaves, leading to death of both mature and young leaves, and ultimately resulting in plant mortality before seed maturation (Munns, 2002; Munns and Tester, 2008). However, since roots are directly exposed to saline soils and play a crucial role in transporting minerals to the plant's aboveground parts, root responses primarily contribute to the deceleration of plant growth in saline environments (Arif *et al.*, 2020).

Salinity has been found to also have a negative impact on various root functions, such as nutrient uptake and water transport, ultimately impairing the overall growth and development of plants in high salinity conditions (Arif *et al.*, 2020; Munns and Tester, 2008). The inhibitory effects of salt stress on root systems significantly compromise the ability of plants to uptake water and minerals, resulting in reduced growth and biomass accumulation (Arif *et al.*, 2020).

Negative effect on:

a. photosynthesis

High levels of Cl^- and Na^+ in the soil solution prevent macronutrients like Ca^{2+} and Mg^{2+} from being absorbed and accumulated, which disrupts chlorophyll synthesis, membrane stability, signaling transmission and stomatal opening (Geilfus, 2019; Arif *et al.*, 2020). Additionally, the negative effects of salinity on photosynthesis are directly associated with the oxidation of photosynthetic pigments; however, the essential details continue to be undefined. Plants exposed to salt stress have a reduction in stomatal conductance, stomatal density, photosynthetic activity,

and carbon uptake, although an increment in mesophyll resistance, which lowers the performance of photosystems (PS)-I and PS- II ability to absorb light (Gururani *et al.*, 2015). Under salinity stress another enzyme crucial for assimilating carbon dioxide (CO_2) throughout photosynthesis dark phase, ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) is inhibited (Gururani *et al.*, 2015).

b. ROS generation

Additionally, salinity stimulates ROS generation, like superoxide (O_2^-), hydroxyl radical (OH^\cdot), singlet oxygen (O^2) and hydrogen peroxide (H_2O_2) and in cellular organelles as mitochondria, chloroplasts, endoplasmic reticulum as well as peroxisomes (Zaid and Wani, 2019; Mostofa *et al.*, 2021). Increased ROS levels can harm a plant's ability to grow and develop because they damage cell membranes, reduce protein synthesis, genomic instability, and harm photosynthetic machinery (Czarnocka and Karpiński, 2018; Mostofa *et al.*, 2021).

c. Plant Performance and Crop Yield

The most common anion in salt soils is Cl^- , although compared to Na^+ , less research has been done on how it affects plant performance and how it is absorbed and moved within plants (Geilfus, 2018). As a necessary micronutrient, Cl^- thought to have a role in activation in the cytoplasmic activation of enzymes, stabilization of membrane potential, oxygen evolution during photosynthesis as well as maintaining the pH and turgor pressure of plant cells (Geilfus, 2018). However, excessive accumulation of Cl^- can have more detrimental effects on cellular functionality than Na^+ (Geilfus, 2018). These salinity-induced deleterious effects ultimately lead to a reduction in crop yield, although the severity and extent of damage vary depending on the plant species.

Strategic Approaches for Enhancing Crop Salinity Tolerance in Saline Soil Conditions

To achieve sustainable crop production in saline soil conditions, it is crucial to adopt a strategic approach. Cultivating salt-tolerant crops emerges as the most effective solution to address this environmental challenge. Extensive efforts have been made in the past three decades to gain a deeper understanding of how plants tolerate salt stress. However, translating this valuable knowledge into practical applications to enhance crops' ability to withstand salt stress in real field conditions requires time and dedicated efforts.

a. Physiological Adaptations of Halophytes

Plants employ various physiological and biochemical mechanisms to survive in soils with high salt concentrations. These mechanisms include, but are not limited to, (1) maintaining ion homeostasis and compartmentalization, (2) facilitating ion transport and uptake, (3) synthesizing osmo-protectants and compatible solutes, and (4) activating antioxidant enzymes and synthesizing antioxidant compounds (Figure 1). These adaptations enable plants to cope with the detrimental effects of salt stress and enhance their tolerance to saline soil conditions. Regulation of ion homeostasis and osmotic balance maintaining ion

homeostasis through ion absorption and compartmentalization is not only critical for normal plant growth but is also an important process for growth under salt stress (Niu Xiaomu *et al.*, 1995; Serrano *et al.*, 1999; Hasegawa, 2013). Regardless of their nature, neither halophytes nor glycophytes can handle having a lot of salt in their cytoplasm. Because of this, the extra salt is either transferred to the vacuole or stored in ageing tissues that eventually die, saving the plant from salinity stress (Zhu, 2003). Through number of channels and transporters, halophytic plants' tissues actively accommodate Na^+ , Cl^- , and K^+ .

Generally, root- Na^+ absorption is typically mediated by nonselective cation channels (NSCCs), such as high-affinity K^+ transporters (as, HAK5 and HKT2), plasma membrane intrinsic protein (PIP) isoforms of aqua-porins, cyclic nucleotide-gated channels (CNGCs) and glutamate receptor-like channels (GLRs). Through the Na^+/H^+ antiporter, the Na^+ ion is then moved from the cytoplasm to the vacuole. The vacuolar membrane contains two different types of H^+ pumps: the vacuolar type H^+ -ATPase (V-ATPase) as well as the vacuolar pyrophosphatase (V-PPase) (Dietz *et al.*, 2001; Wang *et al.*, 2001). V-ATPase is the most prevalent H^+ pump present in the plant cell. The plant's ability to survive under stress is dependent on V-ATPase activity (Dietz *et al.*, 2001).

In root cells, the inflow of Cl^- is regulated by H^+/Cl^- symporters, Cl^-/H^+ co-transporters and nitrate transporters (NRTs). Under salt stress, the passive transfer of Cl^- is controlled by a variety of anion channels, including slow anion channels (SLAC channels) (Wu and Li, 2019). Cl^- infiltration into tissues of xylem and shoot is facilitated by Cation chloride cotransporters (CCCs) (Li *et al.*, 2017). While the chloride channels (CLCs) present on tonoplast is responsible for Cl^- sequestration (Tran *et al.*, 2019). In the presence of Na^+ , HAK5, HKT2, and AKT1 aggressively absorb K^+ (Zaid and Wani, 2019).

There is growing evidence supporting that the Salt Overly Sensitive (SOS) stress signaling pathway plays a functional role in salt tolerance and ion homeostasis (Hasegawa *et al.*, 2000; Sanders, 2000). There are three main proteins in the SOS signaling pathway: SOS₁, SOS₂, and SOS₃. SOS₁, which expresses a plasma membrane Na^+/H^+ antiporter, is crucial for controlling Na^+ outflow at cellular level. Additionally, it helps the long-distance movement of Na^+ from the root to the shoot. Overexpression of this protein result in salt tolerance in plants (Shi *et al.*, 2000; Shi *et al.*, 2002). Ca^{2+} signals induced by salt stress cause the SOS2 gene to become active and then, encodes a serine/threonine kinase. The SOS₃ protein, a Ca^{2+} binding protein, is the third kind of protein engaged in the SOS stress signalling pathway. With the quantity of Na^+ rises, the level of intracellular Ca^{2+} also rises dramatically, which helps the SOS₃ protein. The SOS₃-SOS₂ complex interaction is then transported into the plasma membrane, where it phosphorylates SOS₁. The phosphorylated SOS1 causing an increase in Na^+ efflux, and reduction in Na^+ toxicity (Martinez-Atie-

nza *et al.*, 2007).

a. Accumulation of compatible solutes for osmotic adjustment

Compatible solutes, also referred to compatible osmolytes, are a class of chemically varied organic molecules that are polar, uncharged, and soluble by nature and do not disrupt the cellular metabolism even at high levels. They primarily consist of proline (Ahmad *et al.*, 2010; Hossain *et al.*, 2011; Nounjan *et al.*, 2012; Tahir *et al.*, 2012), glycine betaine (Khan *et al.*, 2000), sugar (Kerepesi and Galiba, 2000), and polyols (Ashraf and Foolad, 2007; Saxena *et al.*, 2013). Organic osmolytes are produced and accumulated in different amounts between different plant species. The concentration of suitable solutes within the cell is kept constant either by irreversible synthesis of the chemicals or by a mix of synthesis and degradation. Due to the fact that their accumulation is proportional to the external osmolarity, the primary roles of these osmolytes are to protect the structure and to maintain osmotic balance within the cell by way of continual water input (Hasegawa *et al.*, 2000).

Under salt stress, amino acids including arginine, cysteine, and methionine, which make up roughly 55% of all free amino acids, decline, whereas proline concentration increases (Shintinawy and El-Shourbagy, 2001). Proline accumulation is a common strategy used to reduce salt stress (Ashraf and Foolad, 2007; Saxena *et al.*, 2013). During salt stress, the intracellular proline accumulation, not only increase salt tolerance but also acts as an organic nitrogen store during stress recovery. Its capacity to quench O_2 reveals that it has antioxidant properties. This was noted in a study that was done by Matysik *et al.* (2002). According to reports, proline increases the activity of enzymes involved in the antioxidant defense system in *Nicotiana tabacum*, improving the plant's ability to tolerate salt (Hoque *et al.*, 2008).

Glycine betaine is a nontoxic cellular osmolyte which plays a crucial role in stress reduction by increasing the osmolarity of the cell during period of stress. Additionally, glycine betaine shields the cell by adjusting the osmotic pressure, stabilizes proteins, guards the photosynthetic system against stress damage (Cha-Um and Kirdmanee, 2010), and lowers ROS (Shintinawy and El-Shourbagy, 2001; Saxena *et al.*, 2013). Within the cell, glycine betaine is synthesized from either choline or glycine. Glycine betaine had a positive impact on the ultrastructure of *Oryza sativa* seedlings when they were subjected to salt stress, according to Rahman *et al.* (2002). Under stressed condition (150mM NaCl), the seedling's ultrastructure is damaged such including disintegration of grana and intergranal lamellae, disruption of the mitochondria and enlargement of thylakoids. Nevertheless, pre-treating seedlings with glycine betaine significantly reduced the severity of these damages. Glycine betaine, when used as a foliar spray on a stressed plant, stabilized pigment and acc-

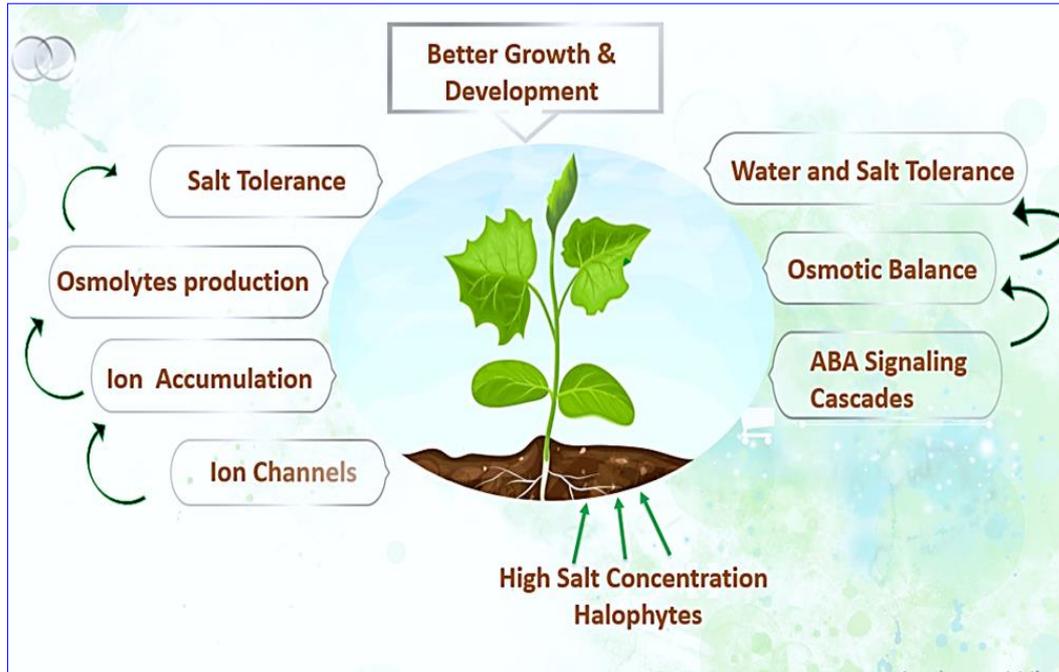


Figure (1): Regulatory mechanisms of physiological and biochemical processes in halophytes for salinity adaptation: Insights on ionic compartmentalization, osmotic adjustment, enzymatic activities, polyamines, and stress signaling regulation.

elerated growth and photosynthetic rate (Cha-Um and Kirdmanee, 2010; Ahmad *et al.*, 2013).

Polyols are compounds having numerous hydroxyl functional groups that can be used in chemical processes. A class of polyols known as sugar alcohols serves as suitable solutes, low-molecular-weight chaperones, and ROS scavengers (Ashraf and Foolad, 2007). They can be divided into two major categories, cyclic (such as pinitol) and acyclic (e.g., mannitol). It was shown that both *Arabidopsis* and tobacco (*Nicotiana tabacum*) plants confer salt tolerance by transforming with the bacterial *mltd* gene, which encodes for mannitol-1-phosphate dehydrogenase, preserving normal growth and development when subjected to high degree of salt stress (Thomas *et al.*, 1995). Based on the distribution of polyols in several species, including microorganisms, plants, and mammals, accumulation of polyols like pinitol and mannitol is related to tolerance to salinity and/or drought (Bohnert *et al.*, 1995).

Under salt stress, accumulating sugars and starches such fructose, fructans, glucose and trehalose take place (Parida *et al.*, 2004). Numerous plants of various species have been shown to respond to salt stress by increasing the amount of reducing sugars (fructans and sucrose) inside the cell. It was shown that tomato (*Solanum lycopersicum*) had higher sucrose content when exposed to salinity due to enhanced activity of sucrose phosphate synthase (Nounjan *et al.*, 2012). There have been reports of both increases and decreases in sugar content in several rice genotypes under salinity stress (Schroeder *et al.*, 2013).

b. Maintenance of water uptake and transpiration rates under saline conditions

The relationship between plants and water can be

used to understand how plants regulate the hydration of their cells, which has significant effects on the physiological and metabolic processes that regulate the quality and quantity of plant growth (Maurel and Nacry, 2020). It is commonly recognized that the buildup of salts in the root zone reduces the amount of water available to the root zone by lowering the osmotic potential and, in turn, the water potential (Karlova *et al.*, 2021).

Plants employ various mechanisms to cope with salinity stress and manage water. Exposure to high concentrations of NaCl reduces the root's hydraulic conductivity by 70% (Boursiac *et al.*, 2005). Suberin deposition decreases root hydraulic conductivity, while aquaporins enhance it (Steudle and Peterson, 1998; Chaumont and Tyerman, 2014). Salt stress and signaling pathways affect the activity and localization of aquaporins (Kaldenhoff *et al.*, 2008; Meng and Fricke, 2017).

In saline soil conditions, ABA-mediated stomatal closure helps reduce water loss through transpiration (Zhu, 2016). Osmotic or salt stresses rapidly upregulate ABA biosynthetic genes, such as ABAs, NCEDs, and ALDEHYDE OXIDASE 3, in vascular tissues (Barrero *et al.*, 2006; Brookbank *et al.*, 2021). ABA is known to be involved in transporting signals from roots to guard cells for stomatal closure, although tomato grafting studies suggest that stomatal closure can occur independently of root-produced ABA (Takahashi *et al.*, 2018).

Transpiration is the process of water loss through leaf stomata in plants. It plays a crucial role in cooling plant tissues and transporting water from roots to leaves. Salt stress can cause stomatal closure by reducing cytokinins and increasing abscisic acid levels,

leading to decreased transpiration rates (Hasegawa *et al.*, 2000). Additionally, salt crusts formed on the soil surface under salt stress can restrict water access and further lower transpiration rates (Munns, 2002). However, halophytes have evolved unique mechanisms to maintain transpiration rates even in high salinity environments (Munns *et al.*, 2006). These unique mechanisms involve: Salt exclusion, halophytes have the ability to selectively uptake essential ions; Salt secretion, some halophytes have salt glands or bladder cells on their leaves that actively secrete excess salt onto the leaf surface; Succulence, certain halophytes have succulent leaves or stems that store water. This adaptation helps to maintain turgor pressure and sustain transpiration even under high salt concentrations; Osmotic adjustment, halophytes can accumulate compatible solutes, such as proline and glycine betaine, in their cells and Anatomical modifications, halophytes may exhibit structural adaptations, such as sunken stomata or thick cuticles, which reduce water loss.

d. Tissue and cellular compartmentalization of toxic ions

It is necessary for a species to survive in salty environment by avoiding the destruction of the metabolism by Na⁺ or Cl⁻. As a result, it is crucial to safeguard the relevant enzymes. For halophytes to exist, plant cells must be able to keep their cytosolic sodium concentrations low (Borsani *et al.*, 2003). Large amounts of sodium are given to leaves by the transpiration stream, so this must be controlled. In response to salt stress, plant cells increase sodium buildup in the vacuole and sodium efflux at the plasma cell membrane. Because of this, the proteins and eventually the genes, engaged in these processes, can be thought of as salt tolerance determinants. In plant salt resistance, the function of intracellular sodium compartmentalization has been explained clearly by the cloning of Na⁺/H⁺ antiporters (Ohta, 2002). Such compartmentalization of sodium and chloride in leaf vacuoles may only be occurred with an active transport into the vacuole and poor tonoplast permeability to these ions.

Ion's transport through the plasma membrane and tonoplast requires energy, that is supplied by plasma membrane and vacuolar ATPase (Koyro and Huchzermeyer, 1997; Leigh, 1997). Via a membrane Na⁺/H⁺ antiporters, sodium ions are exchanged for hydrogen ions using a proton gradient created by these pumps. Glycophytes and halophytes have been demonstrated to have increased Na⁺/H⁺ activity under salt stress (Apse and Blumwald, 2002). Under salinity, the activation of these antiporters probably functions to lessen sodium toxicity in salt-tolerant plants.

c. Activation of antioxidant enzyme and synthesis of antioxidant compounds

Activation of antioxidant enzymes and synthesis of antioxidant compounds contribute to the mitigation of oxidative damage caused by salt stress in plants. Plants possess antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), peroxidase (POX),

and ascorbate peroxidase (APX), along with non-enzymatic antioxidant molecules including glutathione (GSH), ascorbates (ASC), and carotenoids (Azeem *et al.*, 2023). These antioxidant systems effectively quench or scavenge reactive oxygen species (ROS) like hydrogen peroxide (H₂O₂), singlet oxygen (1O₂), hydroxyl radicals (OH[•]), and superoxide (O₂^{•-}) generated under salt stress conditions. The detoxification process involves the sequential action of SOD, POX, and CAT to break down H₂O₂ (Qamer *et al.*, 2021).

Studies have shown that salt-tolerant plant varieties exhibit elevated levels of SOD, ascorbate, and APX, aiding in ROS detoxification (Sarker and Oba, 2020). Reduced membrane lipid peroxidation and lower malondialdehyde (MDA) production are associated with enhanced salt tolerance in wheat genotypes (Hussain *et al.*, 2022). Overexpression of the peroxidase gene GsPRX9 in soybean enhances salt tolerance and antioxidant response (Jin *et al.*, 2019).

Anthocyanins, a group of antioxidants, play a role in salt stress response. The mutant gene anthocyanin-impaired-response-1 (air1) in *Arabidopsis* affects salt tolerance by regulating flavonoid and anthocyanin biosynthesis pathways (Van Oosten *et al.*, 2013). These findings highlight the protective roles of antioxidant enzymes, molecules, and pigments in mitigating oxidative damage and enhancing plant salt tolerance. The sequential detoxification process begins with the production of SOD in plant cells, while Hydrogen peroxides and their derivatives generated under salt-stress conditions are then broken down by POX and CAT (Qamer *et al.*, 2021).

Molecular mechanisms of halophytes' adaptation

Activation of stress-responsive genes in ion transport and osmotic regulation

The cellular balance between sodium (Na⁺) and potassium (K⁺) is crucial for plant survival in saline soils. Despite molecular similarities, sodium cannot fully replace potassium's vital role in cellular processes (Grigore *et al.*, 2014). To maintain this delicate balance, a diverse range of channels, transporters, and antiporters are involved in sodium/potassium homeostasis during salt stress (Cushman, 2001). One notable family of transporters is the Na⁺/H⁺ EXCHANGERS (NHXs). Among the NHX family, NHX7/SOS1, localized in the plasma membrane, plays a predominant role in sodium transport and is vital for excluding sodium from the root (Khan *et al.*, 2016). Additionally, other members of the NHX family, such as NHX8, are also plasma membrane-localized, while the rest are found in intercellular compartments. These transporters have the capability to transport both potassium and sodium, which has demonstrated significant relevance for salt tolerance in crop plants (Cushman, 2001).

Overexpression of NHX1 has been shown to increase salt tolerance and promote sodium accumulation in the shoot under salt stress conditions (Kronzucker and Britto, 2011). This accumulation, along with the tonoplast localization of NHX1 and NHX2, suggests

their involvement in sodium sequestration within the vacuole. However, studies indicate that NHX1 and NHX2 primarily contribute to vacuolar potassium homeostasis due to their equal affinity for potassium (Rozema and Schat, 2013; Sharma *et al.*, 2016).

Experimental evidence supports this hypothesis, as *nhx1 nhx2* double mutants exhibited decreased vacuolar potassium content and increased sodium content in leaf tissue during salt stress (Rigó *et al.*, 2016). This disrupted potassium homeostasis led to reduced growth and delayed stomatal closure. Furthermore, *nhx5 nhx6* mutants displayed heightened salt sensitivity. The endosome-localized NHX5 and NHX6 play a role in modulating the pH of endomembrane compartments, thereby influencing the sorting of transmembrane proteins (Zhu, 2000).

NHX7/SOS1 is crucial for sodium export, while NHXs localized in endomembranes and tonoplast play roles in protein sorting, intercellular potassium transport, and endomembrane pH maintenance during salt stress. Additionally, the HIGH-AFFINITY POTASSIUM TRANSPORTER 5 (HAK5) facilitates potassium transport under low extracellular potassium or high salt conditions. Shaker-type potassium channels, such as GATED OUTWARDLY-RECTIFYING K⁺ CHANNEL (GORK) and ARABIDOPSIS K⁺ TRANSPORTER 1 (AKT1), maintain sodium/potassium balance. K⁺ CHANNEL IN ARABIDOPSIS THALIANA 1 (KAT1) and CATION/H⁺ EXCHANGER 13 (CHX13) are involved in stomatal closure and root growth direction, respectively, on a salt gradient. CHX17 influences K⁺ accumulation in the root, and CHX21 affects Na⁺ accumulation in the shoot (Figure 2).

Expression of transcription factors and protein kinases

Transcription factors are essential proteins involved in chromatin remodeling and protein modification, acting as transcriptional regulators (Udvardi *et al.*, 2007). They connect cis-elements in stress-inducible gene promoter regions, triggering the upregulation of downstream genes crucial for abiotic stress tolerance (Agarwal and Jha, 2010). Riechmann *et al.* (2000) identified 1500 stress-responsive transcription factors in Arabidopsis. The transcriptional control of tolerance or susceptibility to stress has been reported, with plants exhibiting independent responses to different stress conditions (Umezawa *et al.*, 2006).

Several families of transcription factors, including bZIP, WRKY, AP2, NAC, C2H2 zinc finger genes, and DREB, encompass numerous stress-responsive members. These transcription factors regulate the expression of various target genes by binding to specific cis-acting elements in their promoters. Johnson *et al.* (2018) observed upregulation of bZIP genes in a salt-sensitive wheat cultivar under long-term salinity, whereas their expression decreased in a salt-tolerant variety (Figure 2). In halophytes, overexpression of TsNAC1 in *Thellungiella halophila* and Arabidopsis has been shown to enhance abiotic stress resistance, particularly salt stress tolerance (Liu *et al.*, 2018).

Additionally, the SINAC8 gene from *Suaeda liaotungensis* confers improved tolerance to drought and salt stress in Arabidopsis, suggesting its potential to enhance the expression of stress-responsive genes in transgenic plants (Wu *et al.*, 2018).

Another important transcription factor is DREB. It plays an important role in regulating the expression of stress-inducible genes under abiotic stresses. The expression of SsDREBa and SsDREBb genes in *S. salsa* roots and leaves was remarkably induced by high-salt and dehydration treatments, further indicating them as novel stress-responsive transcription factors (Figure 2), through ABA-independent pathways (Sun *et al.* 2014).

Among the important TFs, basic leucine zipper proteins (bZIPs) are one of the large families, where bZIP has been identified as one of the TF having great potential in improving crop tolerance against salinity stress. Like other transcription factors, the bZIPs play important roles in plant growth and developmental processes; apart from this it also responds to numerous other abiotic stresses including drought, salinity (Liu *et al.*, 2014), and cold stresses (Jakoby *et al.* 2002). Increased tolerance to drought and salinity was observed in Arabidopsis due to over-expression of a ThbZIP from the woody halophyte *Tamarix hispida* (Ji *et al.*, 2013).

WRKY transcription factors are one of the largest families of transcriptional regulators in plants with their known functions associated with growth, seed development, leaf senescence, and responses to abiotic and biotic stresses (Rushton *et al.*, 2010). In Arabidopsis, the function of WRKY33 TF is targeting the salt responsive downstream genes that helps in detoxification of ROS and regulation of LOX1 (lipoxygenase), GSTU11 (glutathione-S-transferase), and peroxidases; along with this WRKY25 and WRKY33 are two WRKY factors which have shown to enhance salinity stress tolerance (Jiang and Deyholos, 2009). Salt-specific induced Goup II-b WRKY gene IWRKY2 from *I. lactea* var. *chinensis*. Were cloned indicated that IWRKY2 may play an important role in halophyte *I. lactea* var. *chinensis* adaptation to environmental salt stress (Tang *et al.*, 2018).

Hormones and signaling pathways in salt stress adaptation

Plant hormones, also known as phytohormones, are crucial internal regulatory molecules that play a vital role in controlling plant growth and development. There are nine distinct groups of plant hormones that exhibit diverse functions in mediating stress tolerance and promoting growth in plants. Among these groups, ABA, ethylene, SA, and JA are classified as stress-responsive hormones, while auxin, GA, cytokinins, brassinosteroids (BRs), and strigolactones (SLs) are considered growth-promotion hormones.

In response to salt stress, abscisic acid (ABA) acts as a key stress-responsive hormone, playing a central role in activating adaptive signaling pathways and regulating gene expression. When plants experience salt stress, the levels of endogenous ABA rapidly increase,

triggering a kinase cascade. This cascade involves sucrose nonfermenting 1-related protein kinases (SnRK2s), which are essential components of ABA signaling transduction pathways.

Under salt-stress conditions, the activities of SnRK2.2/2.3/2.6 kinases and ABA-responsive element (ABRE)-binding protein/ABRE-binding factor (AREB/ABF) transcription factors are enhanced. This leads to stomatal closure and improved salt tolerance. However, the abscisic acid insensitive 1 (ABI1) protein inhibits the kinase activity of SnRK2, negatively impacting salt tolerance and primary root growth.

In addition to ABA signaling, salt stress also triggers the upregulation of ABA biosynthesis genes, facilitating ABA production through the methylerythritol 4-phosphate (MEP) pathway. Key enzymes involved in this pathway, such as zeaxanthin oxidase (ZEP), 9-cis-epoxycarotenoid (NCED), and short-chain alcohol dehydrogenase (SCAD), play critical roles in regulating ABA biosynthesis under salt-stress conditions. Moreover, the calcium ion (Ca²⁺) and SOS (salt overly sensitive) pathways collaborate with ABA signaling to prevent excessive activation of SOS2, thereby contributing to the adaptation to salt stress.

Auxin, another plant hormone, regulates root growth plasticity in response to salt stress. Reduced polar auxin transport and lower auxin accumulation in the roots, along with the downregulation of auxin-receptor encoding genes, result in decreased auxin signaling and ultimately downregulate auxin-mediated root growth under salt stress conditions. Moreover, bioactive gibberellin (GA) levels are adjusted at different growth stages of plants to enhance salt tolerance by slowing down growth. The DELLA protein SLR1, an inhibitor of GA signaling, and other GA metabolism-related

genes lead to reduced GA levels or GA signaling after germination, which is necessary for enhancing plant tolerance to salt stress.

Implications for enhancing plant salinity tolerance

Potential of Halophytes as Genetic Resources for the Engineering of Crops with Improved Salt Tolerance

Through harnessing the genetic traits responsible for salt tolerance in halophytes, it is possible to transfer these traits to conventional crops through genetic engineering or breeding approaches. One of the key advantages of using halophytes as genetic resources is their genetic diversity. Halophytes comprise a wide range of species, each with its own set of adaptive traits. This genetic diversity provides a vast pool of potential genes and alleles that can be incorporated into crop plants to confer salt tolerance. By harnessing the genetic variation present in halophytes, it is possible to develop crop varieties with enhanced salt tolerance that can thrive in saline environments.

Furthermore, halophytes offer the advantage of being In addition to ABA signaling, salt stress also triggers the upregulation of ABA biosynthesis genes, facilitating ABA production through the methylerythritol 4-phosphate (MEP) pathway. Key enzymes involved in this pathway, such as zeaxanthin oxidase (ZEP), 9-cis-epoxycarotenoid (NCED), and short-chain alcohol dehydrogenase (SCAD), play critical roles in regulating ABA biosynthesis under salt-stress conditions. Moreover, the calcium ion (Ca²⁺) and SOS (salt overly sensitive) pathways collaborate with ABA signaling to prevent excessive activation of SOS2, thereby contributing to the adaptation to salt stress. the agricultural land available for cultivation. Therefore, the identification and characterization of novel salt tolerance-associated genes from halophytes,

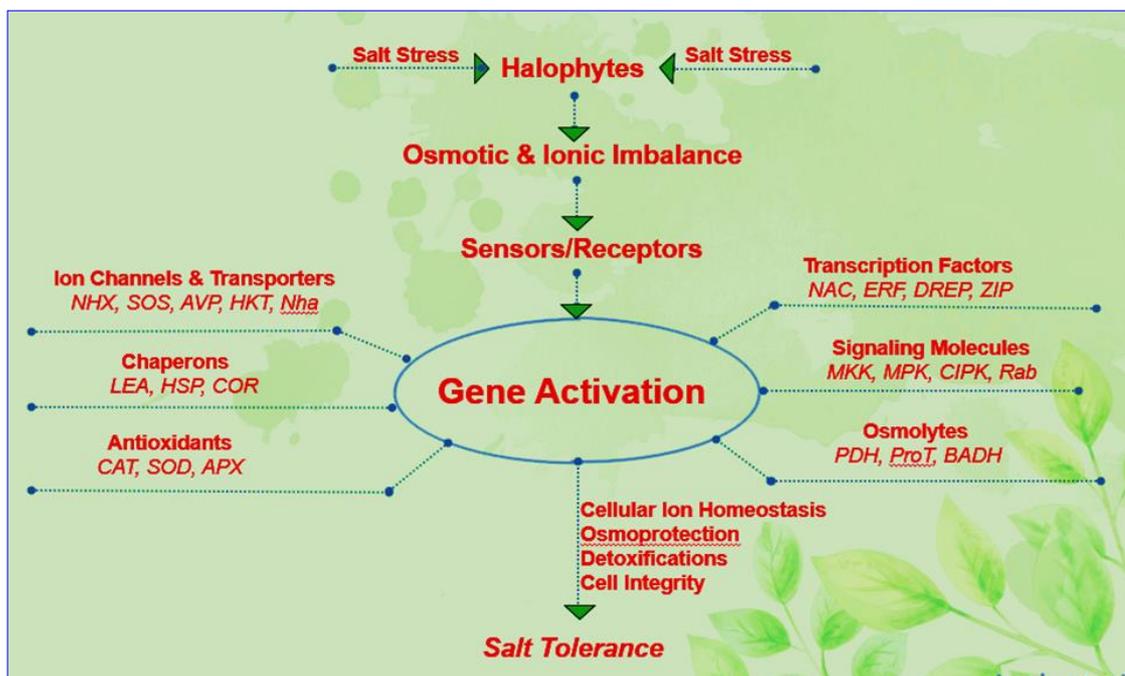


Figure (2): Generalized gene expression schematic representation of salinity stress tolerance mechanism in halophytes: Exploring the molecular mechanisms.

followed by their utilization in genetic engineering, represent crucial areas of plant research. These endeavors deserve increased attention to sustainably enhance crop production and achieve global food security in the face of climate change.

Breeding approaches for developing salt-tolerant crop varieties

Numerous studies have explored the screening and breeding of crop plants to enhance salinity tolerance, and the subject has been periodically reviewed previously (Afzal *et al.*, 2023). Advances in identifying genetic markers, molecular markers, germplasm modification, and mapping have improved salt tolerance. Conventional breeding methods such as hybridization, selection, polyploidy, and introgression are considerably effective in enhancing salt tolerance, and the utilization of wild relatives of crop plants as a source of salt-tolerant genes to increase the range of variation for salt tolerance improvement is still ongoing. However, conventional breeding faces a serious challenge due to the limited genetic variation present in the gene pool of most crop species.

Sustainable agriculture practices in saline-affected regions

Useful techniques for reclaiming salt-affected soils in affected countries along with their major cropping systems are an urgent need. Various organic and inorganic amendments, applications of microorganisms, halophytes, tree species, and innovative irrigation and drainage strategies have been employed to reclaim salt-affected soils worldwide.

a. Amendments

Organic amendments, such as biochar and compost of municipal solid wastes (MSW), as well as inorganic amendments rich in calcium (e.g., fly ash, gypsum, phosphogypsum), and zeolites, have been utilized for the reclamation of sodic soils (Singh *et al.*, 2018; Mishra *et al.*, 2019). The application of these amendment materials has shown positive effects on various soil properties in salt-affected soils. Specifically, improvements in soil bulk density, aggregate stability, hydraulic conductivity, as well as reductions in pH, electrical conductivity (EC), and exchangeable sodium percentage (ESP) have been reported (Mishra *et al.*, 2019; Sundha *et al.*, 2020). Moreover, the application of these amendments has been found to enhance soil biological properties, including soil enzymatic activities, microbial population, and microbial biomass nitrogen (N) and phosphorus (P) contents, thereby indicating their beneficial effects (Mishra *et al.*, 2019; Sundha *et al.*, 2020).

b. Phytoremediation

Phytoremediation is a well-known technique that uses plant species to accumulate salts in order to reduce their soil concentration. Mainly three kinds of approaches of phytoremediation are available to minimize soil salinity: (i) agroforestry and (ii) biodrainage.

i. Agroforestry

Salt-tolerant fruits, fodder, and tree species could

survive under low water requiring saline irrigation in arid and semi-arid regions (Minhas *et al.*, 2020b). alfalfa (*Medicago sativa*) was evaluated for five years, and it reduced salinity considerably and added high C and N in soil to improve the soil quality across the profile (Cao *et al.*, 2012). Biomass mulching, root exclusion and salt removal through alfalfa shoots could be the mechanisms for reduced soil salinity.

ii. Biodrainage

Is a technique of using tree species that reduce the water table by transpiration, mainly in waterlogged areas. Ram *et al.* (2011) evaluated the performance of clonal Eucalyptus (*Eucalyptus tereticornis*) planted on field boundaries in a waterlogged soil and found that groundwater table was lowered down by 2 m after 5 years. Till date, Eucalyptus has been the most efficient species for lowering down of water table in canal command areas (Dagar *et al.*, 2016).

c. Bioremediation

Bioremediation involves the use of various microorganisms or microbial consortium to reclaim salt-affected soil. The soil microbes include plant growth promoting-rhizobacteria (PGPR), bacteria, mycorrhiza, and cyanobacteria able to reclaim salt-affected soil by producing various hormones and beneficial substances that enhance soil quality and plant growth.

i. Plant growth promoting rhizobacteria

Various PGPR showed their impact on salt-affected soil remediation by improving plant growth. They included: *Enterobacter* sp., *Pseudomonas* spp., *Klebsiella* sp., *Azotobacter* sp., *Bacillus amyloliquefaciens*, *Enterobacter cloacae*. The main mechanisms include production of 1-aminocyclo-propane-1-carboxylate (ACC) deaminase, indole acetic acid (IAA), and exopolysaccharides secretion to enhance crop growth (Singh, 2015).

ii. Salt tolerant bacteria

Salt-tolerant bacteria generally show high requirement of salts and exist in highly saline environment to regulate high osmotic pressure. The genera include *Ammoniphilus*, *Arthrobacter*, *Azospirillum*, *Bacillus*, *Brevibacillus*, and *Brevibacterium* which produce IAA, gibberellic acid, and other organic acids that can solubilize and transform nutrients present in soils. Some salt-tolerant endophytes have been reported to show similar mechanisms to PGPR for salt tolerance (Thijs *et al.*, 2014). Research revealed that *Bacillus foraminis* and *Bacillus gibsonii* tolerated up to 7.5% NaCl (Arora *et al.*, 2014). However, future researches should focus on salt-tolerant bacteria and their application to agricultural fields to avail success in this potential area.

iii. Mycorrhiza

Mycorrhiza is the symbiotic association between roots of higher plants and fungi. Mycorrhiza is known for mobilization and solubilisation of nutrients even under saline environment. Reports are available on the beneficial impact of mycorrhiza such as improved mobility and availability of nutrients (Zn^{2+} , Cu^{2+} , P^{3-})

in soils (Chang *et al.*, 2018). Vesicular arbuscular mycorrhizae (VAM) generally helps in solubilization of phosphate and P supply to plant roots in salt-affected soils because phosphate remains in precipitated forms due to presence of Ca^{2+} - and Mg^{2+} -based carbonate salts (Zhu *et al.*, 2016). Other mechanism related to mycorrhizal action to salt-tolerance is the control of abscisic acid accumulation under osmotic stress (Auge *et al.*, 2015).

iii. Cyanobacteria

Cyanobacteria are gram negative, prokaryote, autotrophic, and blue-green bacteria. They can survive in extreme environments including under highly saline condition, and improve soil quality (Rossi *et al.*, 2017). Mostly cyanobacteria were utilized as biofertilizer. It is a challenge to remove salts from soil using cyanobacteria in terms of quantity, but the use of cyanobacteria in association with salt-tolerant plants helps to increase the quantity of removed salts (Jesus *et al.*, 2015). The main mechanisms employed by cyanobacteria are N-fixation, high biomass production, and extra-cellular polymeric substances (EPS) production that help the microorganisms to survive under salt stress conditions.

The cyanobacterial genera which were used in different pot and field studies include *Anabaena*, *Nostoc*, *Calothrix*, and *Spirulina* (Li *et al.*, 2019). Soil pH and EC were decreased (Singh and Singh, 2015), while soil fertility and soil enzyme activities were improved using *Nostoc ellipsosporum* HH- 205 and *Nostoc punctiforme* HH-under saline soil of India (Nisha *et al.*, 2018). Additionally, *Anabaena laxa* RPAN8 showed 21-times higher acetylene reducing activity under salt stress condition, which was an indication of N-fixation (Babu *et al.*, 2015). Similarly, the intracellular trehalose content of *Anabaena fertilissima* increased significantly under mmol NaCl concentration (Swapnil and Rai, 2018).

CONCLUSION

The exploration of the physiological and molecular mechanisms underlying halophytes' adaptation to high salinity environments has provided valuable insights into the strategies employed by these plants to thrive under extreme conditions. This knowledge holds significant potential for enhancing the salinity tolerance of non-halophytic crop plants, thereby contributing to sustainable agriculture in salt-affected areas. By unraveling the involved mechanisms through which halophytes maintain ion homeostasis, osmotic adjustment, and antioxidant defense systems, researchers can identify key genes and regulatory pathways involved in salt tolerance. This understanding opens up avenues for genetic engineering and breeding approaches to introduce these salt tolerance traits into conventional crops. Furthermore, the genetic diversity present in halophytes offers a vast pool of potential genes and alleles that can be incorporated into crop plants. By harnessing this genetic variation, researchers can develop crop varieties with improved salt

tolerance, enabling them to thrive in saline environments and expanding agricultural land usability. The application of halophyte-derived knowledge and techniques can also aid in the reclamation of salt-affected soils. By utilizing organic and inorganic amendments, as well as beneficial soil microorganisms identified in halophytes, it is possible to improve soil properties, such as bulk density, aggregate stability, hydraulic conductivity, and pH, while reducing electrical conductivity and exchangeable sodium percentage.

REFERENCES

- ACHARD, P.; H. CHENG, L. DE GRAUWE, J. DECAT, H. SCHOUTTETEN, T. MORITZ, D. VAN DER STRAETEN, J. PENG, AND N.P. HARBERD. 2006. Integration of plant responses to environmentally activated phytohormonal signals. *Science* 311: 91–94.
- AFZAL, M., S.E.S. HINDAWI, S.S. ALGHAMDI, H.H. MIGDADI, M.A. KHAN, M.U. HASNAIN, M. ARSLAN, M. HABIB UR RAHMAN, AND M. SOHAIB. 2023. Potential breeding strategies for improving salt tolerance in crop plants. *Journal of Plant Growth Regulation* 42: 3365–3387.
- AHMAD, P., C.A. JALEEL, M. A. SALEM, G. NABI, AND S. SHARMA. 2010. Roles of enzymatic and nonenzymatic antioxidants in plants during abiotic stress. *Critical Reviews in Biotechnology* 30(3): 161–175.
- AHMAD, R., C. J. LIM, AND S.-Y. KWON. 2013. Glycine betaine: a versatile compound with great potential for gene pyramiding to improve crop plant performance against environmental stresses. *Plant Biotechnology Reports* 7:49–57.
- APSE, M.P. AND E. BLUMWALD. 2002. Engineering salt tolerance in plants. *Current Opinion in Biotechnology* 13:146-150.
- ARORA, S., P. PATEL. M. VANZA, AND G.G. RAO. 2014. Isolation and characterization of endophytic bacteria colonizing halophyte and other salt tolerant plant species from coastal Gujarat. *African Journal of Microbiology Research* 8: 1779–1788.
- ASHRAF, M., AND M. R. FOOLAD. 2007. Roles of glycine betaine and proline in improving plant abiotic stress resistance. *Environmental and Experimental Botany* 59(2): 206–216.
- AUGE, R.M., H.D. TOLER, AND A.M. SAXTON. 2015. Arbuscular mycorrhizal symbiosis alters stomatal conductance of host plants more under drought than under amply watered conditions: a meta-analysis. *Mycorrhiza* 25: 13–24.
- AZEEM, M., K. PIRJAN, M. QASIM, A. MAHMOOD, T. JAVED, H. MUHAMMAD, S. YANG, R. DONG, B. ALI, AND M. RAHIMI. 2023. Salinity stress improves antioxidant potential by modulating physio-biochemical responses in *Moringa oleifera* Lam. *Scientific Reports* 13: 2895.
- BABU, S., R. PRASANNA, N. BIDYARANI, AND R. SINGH, 2015. Analysing the colonisation of

- inoculated cyanobacteria in wheat plants using biochemical and molecular tools. *Journal of Applied Phycology* 27:327–338.
- BARRERO, J.M., P.L. RODRIGUEZ, V. QUESADA, P. PIQUERAS, M.R. PONCE, J.L. MICOL. 2006. Both abscisic acid (ABA)-dependent and ABA-independent pathways govern the induction of NCED3, AAO3 and ABA1 in response to salt stress. *Plant, Cell & Environment* 29: 2000–2008.
- BEN AHMED C., B. BEN ROUINA, S. SENSOY, M. BOUKHRISS, AND F. BEN ABDULLAH. 2010. Exogenous proline effects on photosynthetic performance and antioxidant defense system of young olive tree. *Journal of Agricultural and Food Chemistry* 58(7): 4216–4222.
- BOHNERT, H.J., D. E. NELSON, AND R. G. JENSEN. 1995. Adaptations to environmental stresses. *Plant Cell* 7(7): 1099–1111.
- BORSANI, O., V. VALPUESTA, AND J. BOTELLA. 2003. Developing salt tolerant plants in a new century: a molecular biology approach. *Plant Cell, Tissue Organ Culture* 73:101–115.
- BOURSIAC, Y., CHEN, S., LUU, D.T., SORIEUL, M., VAN, DEN, DRIES, N., AND C. MAUREL, 2005. Early effects of salinity on water transport in *Arabidopsis* roots. Molecular and cellular features of aquaporin expression. *Plant Physiology* 139, 790–805.
- BROOKBANK, B.P., J. PATEL, S. GAZZARRINI, AND E. NAMBARA. 2021. Role of basal ABA in plant growth and development. *Genes* 12: 1936.
- CAI, S., G. CHEN, Y. WANG, Y. HUANG, D.B. MARCHANT, Y. WANG, Q. YANG, F. DAI, A. HILLS, P.J. FRANKS, E. NEVO, D.E. SOLTIS, P.S. SOLTIS, E. SESSA, P.G. WOLF, D. XUE, G. ZHANG, B.J. POGSON, M.R. BLATT, Z.-H. CHEN. 2017. Evolutionary conservation of ABA signaling for stomatal closure. *Plant Physiology* 174: 732–747.
- CAO, J., X. LI, X. KONG, R. ZED, AND L. DONG. 2012. Using alfalfa (*Medicago sativa*) to ameliorate salt-affected soils in Yingda irrigation district in Northwest China. *Acta Ecologica Sinica* 32: 68–73.
- CELLIER, F., G. CONÉJÉRO, L. RICAUD, D.T. LUU, M. LEPETIT, F. GOSTI, AND F. CASSE. 2004. Characterization of AtCHX17, a member of the cation/H⁺ exchangers, CHX family, from *Arabidopsis thaliana* suggests a role in K⁺ homeostasis. *The Plant Journal* 39:834–46
- CHANG, W., X. SUI, X.X. FAN, T.T. JIA, AND F.Q. SONG. 2018. Arbuscular mycorrhizal symbiosis modulates antioxidant response and ion distribution in salt-stressed *Elaeagnus angustifolia* seedlings. *Frontiers in Microbiology* 9: 652.
- CHA-UM, S., AND C. KIRDMANEE. 2010. Effect of glycinebetaine on proline, water use, and photosynthetic efficiencies, and growth of rice seedlings under salt stress. *Turkish Journal of Agriculture and Forestry* 34 (6): 517–527.
- CHAUMONT, F., AND S.D. TYERMAN. 2014. Aquaporins: highly regulated channels controlling plant water relations. *Plant Physiology* 164, 1600–1618.
- CHEN, K., G.J. LI, R.A. BRESSAN, C.P. SONG, J.K. ZHU, AND Y. ZHAO. 2020. Abscisic acid dynamics, signaling, and functions in plants. *Journal of Integrative Plant Biology* 62: 25–54.
- CHINNUSAMY, V., A. JAGENDORF, AND J.K. ZHU. 2005. Understanding and improving salt tolerance in plants. *Crop Science* 45: 437–448.
- DABBOUS, A., R. BEN SAAD, F. BRINI, A. FARHAT-KHEMEKHEM, W. ZORRIG, C. ABDELY, AND K. BEN HAMED. 2017. Over-expression of a subunit E1 of a vacuolar H⁺-ATPase gene (*Lm VHA-E1*) cloned from the halophyte *Lobularia maritima* improves the tolerance of *Arabidopsis thaliana* to salt and osmotic stresses. *Environmental and Experimental Botany* 137: 128–141.
- DAGAR, J.C., K. LAL, J. RAM, M. KUMAR, S.K. CHAUDHARI, R.K. YADAV, S. AHAMAD, G. SINGH, AND A. KAUR. 2016. Eucalyptus geometry in agroforestry on waterlogged saline soils influences plant and soil traits in North-West India. *Agriculture, Ecosystem & Environment* 233: 33–42.
- DALIAKOPOULOS, I.N., I.K. TSANIS, A.G. KOUTROULIS, N. KOURGIALAS, E.A. VAROUCHAKIS, G.P. KARATZAS, AND C.J. RITSEMA, 2016. The threat of soil salinity: A European scale review. *Science of the Total Environment* 573: 727–739.
- DEOLU-AJAYI, A.O., A.J. MEYER, M.A. HARING, M.M. JULKOWSKA, AND C. TESTERINK. 2019. Genetic loci associated with early salt stress responses of roots. *iScience* 21:458–73
- DIETZ, K.J., N. TAVAKOLI, C. KLUGE, T. MIMURA, S.S. SHARMA, G.C. HARRIS, A.N. CHARDONNENS, AND D. GOLLDACK. 2001. Significance of the Vtype ATPase for the adaptation to stressful growth conditions and its regulation on the molecular and biochemical level. *Journal of Experimental Botany* 52(363):1969–1980.
- EL-SHINTINAWY, F., AND M. N. EL-SHOUBAGY. 2001. Alleviation of changes in protein metabolism in NaCl-stressed wheat seedlings by thiamine. *Biologia Plantarum* 44(4): 541–545.
- ESMAEILI, N., G. SHEN, AND H. ZHANG. 2022. Genetic manipulation for abiotic stress resistance traits in crops. *Front. Plant Sci.* 13: 1011985.
- FENG, P., X. SUN, X. LIU, Y. LI, Q. SUN, H. LU, M. LI, X. DING, AND Y. DONG. 2022. Epigenetic regulation of plant tolerance to salt stress by histone acetyltransferase GsMYST1 from wild soybean. *Frontiers in Plant Science* 13: 860056.
- GEETHA, S., A. VASUKI, P.J. SELVAM, R. SARASWATHI, S.L. KRISHNAMURTHY, M. DHASARATHAN, G. THAMODHARAN, AND M. BASKAR. 2021. Development of sodicity tolerant rice varieties through marker assisted

- backcross breeding. *Electronic Journal of Plant Breeding* 8: 1013–1031.
- GENG, X., S. CHEN, E. YILAN, W. ZHANG, H. MAO, A. QIQIGE, Y. WANG, Z. QI, AND X. LIN. 2020. Overexpression of a tonoplast Na⁺/H⁺ antiporter from the halophytic shrub *Nitraria sibirica* improved salt tolerance and root development in transgenic poplar. *Tree Genetics and Genomes* 16: 1–14.
- GUO, R., L. ZHAO, K. ZHANG, H. LU, N. BHANBHRO, AND C. YANG. 2021. Comparative genomics and transcriptomics of the extreme halophyte *Puccinellia tenuiflora* provides insights into salinity tolerance differentiation between halophytes and glycophytes. *Frontiers in Plant Science* 12: 767.
- HALL, D., A.R. EVANS, H.J. NEWBURY, AND J. PRITCHARD. 2006. Functional analysis of CHX21: a putative sodium transporter in *Arabidopsis*. *Journal of Experimental Botany* 57:1201–1210
- HAN, B. W. XU, N. AHMED, A. YU, Z. WANG, AND A. LIU. 2020. Changes and associations of genomic transcription and histone methylation with salt stress in castor bean. *Plant & Cell Physiology* 61: 1120–1133.
- HAN, Z.-J., Y. SUN, M. ZHANG, AND J.-T. ZHAI. 2020. Transcriptomic profile analysis of the halophyte *Suaeda rigida* response and tolerance under NaCl stress. *Scientific Reports* 10: 1–10.
- HASEGAWA, P. M., R.A. BRESSAN, J.-K. ZHU, AND H.J. BOHNERT. 2000. Plant cellular and molecular responses to high salinity. *Annual Review of Plant Biology* 51: 463–499.
- HASEGAWA, P.M. 2013. Sodium (Na⁺) homeostasis and salt tolerance of plants. *Environmental and Experimental Botany* 92:19–31.
- HIMABINDU, Y., T. CHAKRADHAR, M.C. REDDY, A. KANYGIN, K.E. REDDING, AND T. CHANDRASEKHAR. 2016. Salt-tolerant genes from halophytes are potential key players of salt tolerance in glycophytes. *Environmental and Experimental Botany* 124: 39–63.
- HOQUE, M. A., M. N. A. BANU, Y. NAKAMURA, Y. SHIMOISHI, AND Y. MURATA. 2008. Proline and glycinebetaine enhance antioxidant defense and methylglyoxal detoxification systems and reduce NaCl-induced damage in cultured tobacco cells. *Journal of Plant Physiology* 165(8): 813–824.
- HOSSAIN, M. A., S. MUNEMASA, M. URAJI, Y. NAKAMURA, I. C. MORI, AND Y. MURATA. 2011. Involvement of endogenous abscisic acid in methyl jasmonate-induced stomatal closure in *Arabidopsis*. *Plant Physiology* 156(1): 430–438.
- HSIEH, T.H., C.W. LI, R.C. SU, C.P. CHENG, SANJAYA, Y.C. TSAI, AND M.T. CHAN. 2010. A tomato bZIP transcription factor, SIAREB, is involved in water deficit and salt stress response. *Planta* 2010; 231(6):1459–73
- HUSSAIN, N., Y. SOHAIL, N. SHAKEEL, M. JAVED, H. BANO, H.S. GUL, Z.U. ZAFAR, I.F.Z. HASSAN, A. GHAFAR, H.-U. ATHAR, AND R. AJAJ. Role of mineral nutrients, antioxidants, osmotic adjustment and PSII stability in salt tolerance of contrasting wheat genotypes. *Scientific Reports* 12: 12677.
- IGLESIAS, M.J.; M.C. TERRILE, D. WINDELS, M.C. LOMBARDO, C.G. BARTOLI, F. VAZQUEZ, M. ESTELLE, AND C.A. CASALONGUÉ. 2014. MiR393 regulation of auxin signaling and redox-related components during acclimation to salinity in *Arabidopsis*. *PLoS ONE* 9: e107678.
- ISMAIL, A.M., AND T. HORIE. 2017. Genomics, physiology, and molecular breeding approaches for improving salt tolerance. *Annual Review of Plant Biology* 68: 405–434.
- J.MARTINEZ-ATIENZA, X. JIANG, B. GARCIADREBLAS, I. MENDOZA, J.-K. ZHU, J. M. PARDO, F. J. QUINTERO. 2007. Conservation of the salt overly sensitive pathway in rice. *Plant Physiology* 143(2):1001–1012.
- JESUS, J. M., A.S. DANKO, A. FIUZA, AND M.-T. BORGES. 2015. Phytoremediation of salt-affected soils: a review of processes, applicability, and the impact of climate change. *Environmental Science and Pollution Research* 22: 6511–6525.
- JIANG, K., J. MOE-LANGE, L. HENNET, AND L.J. FELDMAN. 2016. Salt stress affects the redox status of *Arabidopsis* root meristems. *Frontiers in Plant Science* 7: 81.
- JIN, T., Y. SUN, R. ZHAO, Z. SHAN, J. GAI, AND Y. LI. 2019. Overexpression of peroxidase gene GsPRX9 confers salt tolerance in soybean. *International Journal of Molecular Science* 20: 3745.
- KALDENHOFF, R., M. RIBAS CARBO, J.F. SANS, C. LOVISOLO, M. HECKWOLF, AND N. UEHLEIN. 2008. Aquaporins and plant water balance. *Plant, Cell & Environment* 31: 658–666.
- KARLOVA, R.M D. BOER, S. HAYES, AND C. TESTERINK. 2021. Root Plasticity under Abiotic Stress. *Plant Physiology* 187: 1057–1070.
- KEREPESI, I., AND G. GALIBA. 2000. Osmotic and salt stress-induced alteration in soluble carbohydrate content in wheat seedlings. *Crop Science* 40(2): 482–487.
- KHAN, M.A., I.A. UNGAR, AND A.M. SHOWALTER. 2000. Effects of sodium chloride treatments on growth and ion accumulation of the halophyte *haloxylon recurvum*. *Communications in Soil Science and Plant Analysis* 31(17-18): 2763–2774.
- KONG, L. Y. LIU, X. WANG, AND C. CHANG. 2020. Insight into the role of epigenetic processes in abiotic and biotic stress response in wheat and barley. *International Journal of Molecular Science* 21: 1480.
- KOYRO, H.-W., L. WEGMANN, H. LEHMANN AND H. LIETH. 1997. Physiological mechanisms and morphological adaptation of *Laguncularia racemosa* to high salinity. In: H. Lieth, A. Hamdy

- and H.-W. Koyro (Eds.), Water management, salinity and pollution control towards sustainable irrigation in the mediterranean region: Salinity problems and halophyte use 51-78. Technomack Publ., Bari.
- KRZYWIŃSKA, E., M. BUCHOLC, A. KULIK, A. CIESIELSKI, M. LICHOCKA, J. DĘBSKI, A. LUDWIKÓW, M. DADLEZ, P.L. RODRIGUEZ, AND G. DOBROWOLSKA. 2106 Phosphatase ABI1 and okadaic acid-sensitive phosphoprotein phosphatases inhibit salt stress-activated SnRK2. 4 kinase. *BMC Plant Biology* 16: 136.
- KU, Y.S., M. SINTAHA, M.Y. CHEUNG, AND H.M. LAM. 2018. Plant hormone signaling crosstalks between biotic and abiotic stress responses. *International Journal of Molecular Sciences* 19: 3206.
- LEIGH, R. 1997. The solute composition of the vacuoles. *Advances in Botanical Research* 25:253-295.
- LI, H., Q. ZHAO, AND H. HUANG. 2019. Current states and challenges of salt-affected soil remediation by cyanobacteria. *Science of the Total Environment* 669: 258-272.
- MAGOME, H., S. YAMAGUCHI, A. HANADA, Y. KAMIYA, AND K. ODA. 2008. The DDF1 transcriptional activator upregulates expression of a gibberellin-deactivating gene, *GA2ox7*, under high-salinity stress in *Arabidopsis*. *The Plant Journal* 56: 613-626.
- MATYSIK, J., A. ALIA, B. BHALU, AND P. MOHANTY. 2002. Molecular mechanisms of quenching of reactive oxygen species by proline under stress in plants. *Current Science* 82(5):525-532.
- MAUREL, C., AND P. NACRY. 2020. Root Architecture and Hydraulics Converge for Acclimation to Changing Water Availability. *Nature Plants* 6: 744-749.
- MENG, D., AND W. FRICKE. 2017. Changes in root hydraulic conductivity facilitate the overall hydraulic response of rice (*Oryza sativa* L.) cultivars to salt and osmotic stress. *Plant Physiology and Biochemistry* 113: 64-77.
- MINHAS, P.S., R.K. YADAV, AND A. BALI. 2020b. Perspectives on reviving waterlogged and saline soils through plantation forestry. *Agriculture Water Management* 232: 106063.
- MISHRA, V.K., S.K. JHA, T. DAMODARAN, Y. P. SINGH, S. SRIVASTAVA, D.K. SHARMA, AND J. PRASAD. 2019. Feasibility of coal combustion fly ash alone and in combination with gypsum and green manure for reclamation of degraded sodic soils of the Indo-Gangetic Plains: A mechanism evaluation. *Land Degradation & Development* 30: 1300-1312.
- NGUYEN, N.H., C. JUNG, AND J.J. CHEONG. 2019. Chromatin remodeling for the transcription of type 2C protein phosphatase genes in response to salt stress. *Plant Physiology and Biochemistry* 141: 325-331.
- NISHA, R., B. KIRAN, A. KAUSHIK, AND C.P. KAUSHIK. 2018. Bioremediation of salt affected soils using cyanobacteria in terms of physical structure, nutrient status and microbial activity. *International Journal of Environmental Science and Technology* 15: 571-580.
- NIU, N.X., R.A. BRESSAN, P. M. HASEGAWA, AND J. M. PARDO. 1995. Ion homeostasis in NaCl stress environments. *Plant Physiology* 109(3):735-742.
- NOUNJAN, N., P. T. NGHIA, AND P. THEERAKULPISUT. 2012. Exogenous proline and trehalose promote recovery of rice seedlings from salt-stress and differentially modulate antioxidant enzymes and expression of related genes. *Journal of Plant Physiology* 169(6): 596-604.
- NOUNJAN, N., P. T. NGHIA, AND P. THEERAKULPISUT. 2012. Exogenous proline and trehalose promote recovery of rice seedlings from salt-stress and differentially modulate antioxidant enzymes and expression of related genes. *Journal of Plant Physiology* 169(6):596-604.
- OHTA, H. 2002. Introduction of a Na⁺/H⁺ antiporter gene from *Atriplex gmelina* confers salt tolerance to rice. *FEBS Letters* 532:279-282.
- OHTA, M., Y. GUO, U. HALFTER, AND J.K. ZHU. 2003. A novel domain in the protein kinase SOS2 mediates interaction with the protein phosphatase 2C ABI2. *Proceedings of the National Academy of Sciences of the United States of America* 100: 11771-11776.
- PARIDA, A.K., A.B. DAS, AND P. MOHANTY. 2004. Investigations on the antioxidative defence responses to NaCl stress in a mangrove, *Bruguiera parviflora*: differential regulations of isoforms of some antioxidative enzymes. *Plant Growth Regulation* 42(3): 213-226.
- Qadir, m., a.d. Noble, s. Schubert, r.j. Thomas, a. Arslan. 2006. Sodicy-induced land degradation and its sustainable management: Problems and prospects. *Land Degradation and Development* 17:661-676.
- QAMER, Z., M.T. CHAUDHARY, X. DU, L. HINZE, M.T. AZHAR. 2021. Review of oxidative stress and antioxidative defense mechanisms in *Gossypium hirsutum* L. in response to extreme abiotic conditions. *Journal of Cotton Research* 4: 9.
- RAHMAN, S., H. MIYAKE, AND Y. TAKEOKA. 2002. Effects of exogenous glycinebetaine on growth and ultrastructure of salt-stressed rice seedlings (*Oryza sativa* L.). *Plant Production Science* 5(1): 33-44.
- RAM, J., J.C. DAGAR, K. LAL, G. SINGH, O.P. TOKY, R.S. TANWAR, S.R. DAR, AND K. MUKESH, 2011. Biodrainage to combat water logging, increase farm productivity and sequester carbon in canal command area of north-west India. *Current Science* 100: 1673-1680.
- ROSSI, F., H. LI, Y. LIU, AND R. DE PHILIPPIS. 2017. Cyanobacterial inoculation (cyanobacterisation): perspectives for the development of a

- standardized multifunctional technology for soil fertilization and desertification reversal. *Earth-Science Reviews* 171: 28–43.
- ROY, S. 2016. Function of MYB domain transcription factors in abiotic stress and epigenetic control of stress response in plant genome. *Plant Signaling & Behavior* 11(1):e1117723.
- SANDERS, D. 2000. Plant biology: the salty tale of Arabidopsis. *Current Biology* 10(13):R486–R488.
- SARKER, U., AND S. OBA. 2020. The response of salinity stress-induced *A. tricolor* to growth, anatomy, physiology, non-enzymatic and enzymatic antioxidants. *Frontiers in Plant Science* 11: 559876.
- SAXENA, S. C., H., KAUR, P., VERMA, B. P., PETLA, V. R., ANDUGULA, AND M. MAJEE. 2013. Osmo-protectants: potential for crop improvement under adverse conditions. In: *Plant acclimation to environmental stress* 197–232. Springer, New York, NY, USA.
- SCHROEDER, J.I. E. DELHAIZE, W. B. FROMMER, M. L. GUERINOT, M. J. HARRISON, L. HERRERA-ESTRELLA, T. HORIE, L.V. KOCHEAN, R. MUNNS, N. K. NISHIZAWA, Y.-F. TSAY AND D. SANDERS. 2013. Using membrane transporters to improve crops for sustainable food production. *Nature* 497: 60–66.
- SERRANO, R., J.M. MULET, G. RIOS, J.A. MARQUEZ, I.F. DE LARRINOA, M.P. LEUBE, I. MENDIZABAL, A. PASCUAL-AHUIR, M. PROFIT, R. ROS, AND C. MONTESINOS . 1999. A glimpse of the mechanisms of ion homeostasis during salt stress. *Journal of Experimental Botany* 50: 1023–1036.
- SHABALA, S., AND T.A. CUIN. 2008. Potassium transport and plant salt tolerance. *Physiologia Plantarum* 133:651–69.
- SHI, H., F. J. QUINTERO, J. M. PARDO, AND J.-K. ZHU. 2002. The putative plasma membrane Na⁺/H⁺ antiporter SOS1 controls longdistance Na⁺ transport in plants. *Plant Cell* 14(2):465–477.
- SHI, H., M. ISHITANI, C. KIM, AND J.-K. ZHU. 2000. The Arabidopsis thaliana salt tolerance gene SOS1 encodes a putative Na⁺/H⁺ antiporter. *Proceedings of the National Academy of Sciences of the United States of America* 97(12):6896–6901.
- SINGH, J.S., 2015. Plant-microbe interactions: a viable tool for agricultural sustainability. *Applied Soil Ecology* 92: 45–46.
- SINGH, V., AND D.V. SINGH. 2015. Cyanobacteria modulated changes and its impact on bioremediation of saline-alkaline soils. *Bangladesh Journal of Botany* 44 (4): 653–658.
- SINGH, Y. P., S. ARORA, V. K. MISHRA, H. DIXIT, AND R.K. GUPTA. 2018. Effect of organic and inorganic amendments on amelioration of sodic soil and sustaining rice (*Oryza sativa*)-wheat (*Triticum aestivum*) productivity. *The Indian Journal of Agricultural Sciences* 88: 1455-1462
- SINGROHA, G., S. KUMAR, O.P. GUPTA, G.P. SINGH, AND P. SHARMA. 2022. Uncovering the epigenetic marks involved in mediating salt stress tolerance in plants. *Frontiers in Genetics* 13: 811732.
- STEUDLE, E., AND C.A. PETERSON. 1998. How does water get through roots? *Journal of Experimental Botany* 49: 775-788.
- SUNDHA, P., N. BASAK, A.K. RAI, R.K. YADAV, P.C. SHARMA, AND D.K. SHARMA. 2020. Can conjunctive use of gypsum, city waste composts and marginal quality water rehabilitate saline-sodic soils? *Soil and Tillage Reserach* 200:104608.
- SWAPNIL, P., AND A.K. RAI. 2018. Physiological responses to salt stress of salt-adapted and directly salt (NaCl and NaCl + Na₂SO₄ mixture)-stressed cyanobacterium *Anabaena fertilissima*. *Protoplasma*. 255: 963–976.
- TAHIR, M.A., T. AZIZ, M. FAROOQ, AND G. SARWAR. 2012. Siliconinduced changes in growth, ionic composition, water relations, chlorophyll contents and membrane permeability in two saltstressed wheat genotypes,” *Archives of Agronomy and Soil Science* 58 (3): 247–256.
- TAKAHASHI, F., T. SUZUKI, Y. OSAKABE, S. BETSUYAKU, Y. KONDO, N. DOHMAE, H. FUKUDA, K.Y. SHINOZAKI, AND K., SHINOZAKI, 2018. A small peptide modulates stomatal control via abscisic acidin long-distance signalling. *Nature* 556: 235-238.
- THOMAS, J. C., M. SEPAHI, B. ARENDALL, AND H. J. BOHNERT. 1995. Enhancement of seed germination in high salinity by engineeringmannitol expression in Arabidopsis thaliana. *Plant, Cell and Environment* 18(7): 801–806.
- UMEZAWA, T., N. SUGIYAMA, M. MIZOGUCHI, S. HAYASHI, F. MYOUGA, K. YAMAGUCHI-SHINOZAKI, Y. ISHIHAMA, T. HIRAYAMA, AND K. SHINOZAKI, 2009. Type 2C protein phosphatases directly regulate abscisic acid-activated protein kinases in Arabidopsis. *Proceedings of the National Academy of Sciences of the United States of America* 106: 17588–17593.
- VAN OOSTEN, M.J., A. SHARKHUU, G. BATELLI, R.A. BRESSAN, AND MAGGIO, A. 2013.The Arabidopsis thaliana mutant air1 implicates SOS3 in the regulation of anthocyanins under salt stress. *Plant Molecular Biology* 83: 405–415.
- VERMA, V., P. RAVINDRAN, AND P.P. KUMAR. 2016. Plant hormone-mediated regulation of stress responses. *BMC Plant Biology* 16: 86.
- WALLENDER, W.W., AND K.K. TANJI. 2011. Nature and extent of agricultural salinity and sodicity. In: W.W. Wallender and K.K. Tanji (Eds.), *Agricultural Salinity Assessment and Management*; American Society of Civil Engineers, New York, NY, USA.
- WANG, B., U. L'UTTGE, AND R. RATAJCZAK. 2001. Effects of salt treatment and osmotic stress on V-ATPase and V-PPase in leaves of the halophyte Suaeda salsa. *Journal of Experimental Botany* 52 (365): 2355–2365.
- WANG, M.; L. QIN, C. XIE, W. LI, J. YUAN, L. KONG, W. YU, G. XIA, AND S. LIU. 2014. Ind-

- uced and constitutive DNA methylation in a salinity-tolerant wheat introgression line. *Plant & Cell Physiology* 55: 1354–1365.
- XIANG, D., AND L. MAN. 2018. EhEm1, a novel Em-like protein from *Eutrema halophilum*, confers tolerance to salt and drought stresses in rice. *Molecular Breeding* 38: 17.
- YANG, G.; YU, L.; ZHANG, K.; ZHAO, Y.; GUO, Y.; AND C.A. GAO. 2017. ThDREB gene from *Tamarix hispida* improved the salt and drought tolerance of transgenic tobacco and *T. hispida*. *Plant Physiology and Biochemistry* 113: 187–197.
- YE, W., T. WANG, W. WEI, S. LOU, F. LAN, S. ZHU, Q. LI, G. JI, C. LIN, X. WU, AND L. MA. 2020. The full-length transcriptome of *Spartina alterniflora* reveals the complexity of high salt tolerance in monocotyledonous halophyte. *Plant and Cell Physiology* 61: 882–896.
- YOUSEFIRAD, S., H. SOLTANLOO, S.S. RAMEZANPOUR, K. ZAYNALINEZHAD, AND V. SHARIATI. 2018. Salt oversensitivity derived from mutation breeding improves salinity tolerance in barley via ion homeostasis. *Biologia Plantarum* 62: 775–785.
- YUNG, W.S., M.W. LI, C.C. SZE, Q. WANG, AND H.M. LAM. 2021. Histone modifications and chromatin remodelling in plants in response to salt stress. *Physiologia Plantarum* 173: 1495–1513.
- ZHAO, S. Q. ZHANG, M. LIU, H. ZHOU, C. MA, P. WANG. 2021. Regulation of plant responses to salt stress. *International Journal of Molecular Sciences* 22: 4609.
- ZHU, J.-K. 2003. Regulation of ion homeostasis under salt stress. *Current Opinion in Plant Biology* 6 (5): 441–445.
- ZHU, J.K. 2016. Abiotic stress signaling and responses in plants. *Cell* 167: 313–324.
- ZHU, X., F. SONG, S. LIU, AND F. LIU. 2016. Role of arbuscular mycorrhiza in alleviating salinity stress in wheat (*Triticum aestivum* L.) grown under ambient and elevated CO₂. *Journal of Agronomy and Crop Science* 202: 486–496.
- VALERIO, J., KLOOS, M., SIKORSKI, M., MIL-LS, G., BIEL-EKI, J., KIRKWOOD, H., KIM, C., DE WIJN, R., LORENZEN, K., XAVIER, P.L., RAHMANI, A., GELISIO, L., YEFANOV, O., MANCUSO, A.P., CHAPMAN, H.N., CRICK-MORE, N., RIZKALLAH, P.J., BERRY, C., OBERTHÜR, D. 2022. Structure of the *Lysinibacillus sphaericus* Tpp49Aa1 pesticidal protein elucidated from natural crystals using MHz-SFX. *Biorxiv preprint* doi: <https://doi.org/10.1-101/2022.01.14.476343>.
- WIRTH, M.C., PARK, H.W., WALTON, W.E., FEDERICI, B.A., PARK, H.W. 2007. Co-expression of the receptor for *Bacillus thuringiensis* Cry11Aa toxin increases mortality in *Culex quinquefasciatus* larvae challenged with *Bacillus sphaericus* binary toxin. *Journal of Invertebrate Pathology*, 94(1): 37–44.
- YAHYA, G., EBADA, A., KHALAF, E.M., MANSOUR, B., NOUH, N.A., MOSBAH, R.A., SABER, S., MOUSTAFA, M., NEGM, S., EL-SOKKARY, M.M.A., EL-BAZ, A.M. 2021. Soil-Associated *Bacillus* Species: A reservoir of bioactive compounds with potential therapeutic activity against human pathogens. *Microorganisms*, 24:9(6):1131.
- YI, H.Y., CHOWDHURY, M., HUANG, Y.D., YU, X.Q. 2014. Insect antimicrobial peptides and their applications. *Applied Microbiology and Biotechnology*, 98(13): 5807–5822
- YUAN, Z. 2002. *Bacillus sphaericus*: Mechanism and Application as a Mosquito Larvicide. In K. Tanada, H.K. Kaya (Eds.), *Advances in Microbial Control of Insect Pests* (pp. 41–69). Springer.
- ZAYED, A. B., SZUMLAS, D. E., HANAFI, H. A., FRYAUFF, D. J., MOSTAFA, A. A., ALLAM, K. M., BROGDON, W. G. 2006. Use of bioassay and microplate assay to detect and measure insecticide resistance in field populations of *Culex pipiens* from filariasis endemic areas of Egypt. *Journal of the American Mosquito Control Association*, 22(3):473–482.
- ZHANG, R., WANG, W., WANG, Y., LEI, Z., WANG, L. 2017. Dynamic changes in the expression of antimicrobial peptides in innate immune defense of *Anopheles gambiae* (Diptera: Culicidae) larvae against Gram-positive bacteria. *Journal of Medical Entomology*, 54(5):1272–1279.

استكشاف الآليات الفسيولوجية والجزئية لتكيف النباتات الملحية مع البيئات عالية الملوحة: الآثار المترتبة على تحسين مقاومه النبات للملوحة

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الملخص العربي

تشكل ملوحة التربة تحديا كبيرا للانتاج الزراعى في جميع أنحاء العالم وذلك للتأثير السلبى لملوحة التربة على انتاج معظم المحاصيل الزراعية. لذا كان لابد من تسليط الضوء على بعض أنواع النباتات التى لها القدرة على تحمل تركيزات عالية من الملوحة، المعروفة باسم النباتات الملحية، حيث لوحظ تكيفها فى البيئات شديدة الملوحة عن طريق تطور او استخدام آليات فسيولوجية وجزئية. تستخدم النباتات الملحية آليات لتنظيم التوازن الأيونى، والحفاظ على التوازن الأسموزى، وتقليل فقدان الماء عن طريق تراكم المواد المذابة المتوافقة، مثل البرولين والجليسين ، او التخلص من الأيونات السامة فى الفجوات وكذلك ايضا تستخدم مضادات للأكسدة. كما ان النباتات الملحية تتميز على المستوى الجزيئى بامتلاكها جينات مقاومة للملوحة العالية. إن تسخير المعرفة المكتسبة من آليات تكيف النباتات الملحية يمكن أن يوفر أفقا واعدة لتحسين تحمل الملوحة للمحاصيل ذات الأهمية الاقتصادية حيث يمكن استخدام أساليب الهندسة الوراثية لتعزيز الجينات الرئيسية لتحمل الملح فى الأنواع غير الملحية. ولذلك، فإن دراسة الآليات الفسيولوجية والجزئية لتحمل الملح فى النباتات الملحية توفر رؤى قيمة حول الاستراتيجيات التى تستخدمها النباتات للتكيف والازدهار فى البيئات عالية الملوحة. ويمكن تسخير المعرفة المكتسبة من هذه الدراسات لتعزيز قدرة نباتات المحاصيل غير الملحية على تحمل الملوحة، وبالتالي المساهمة فى الزراعة المستدامة فى المناطق المتضررة من الملوحة.