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Adaptive traits in plants for salinity stress tolerance: A critical review

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Abstract

Soil salinity negatively affects plants at multiple levels, inducing ionic and metabolic imbalances that directly affect growth and productivity. Plants counter salinity stress through a combination of adaptive traits that facilitate cellular ion homeostasis and prevent excessive sodium (Na^+) accumulation or its detrimental effects. This review provides in-depth information focusing on plant salinity tolerance mechanisms. The Na^+-exclusion, xylem loading, and Na^+-vacuolar sequestration by compartmentalization are primarily achieved by the set of antiporters (HKT1, NHX1, NHX2, and SOS1) located at the root cell plasma membrane, xylem parenchyma, and the tonoplast. Plants regulate Na^+ xylem loading to restrict Na^+ translocation to aerial tissues, mediated by SOS1 and HKT1. Cellular compartmentalization is regulated by both Na^+/H^+ and K^+/H^+ antiporters, which maintain ion homeostasis. Osmoregulation in cells is achieved with the help of both organic osmolytes (proline, glycine betaine, sugars, polyols, etc.) and inorganic ions (Na^+, K^+, Ca^{2+}), which counter salt-induced osmotic stress. However, oxidative stress is mitigated by various enzymatic antioxidant proteins (SOD, CAT, POD, APX, GR, DHAR) and non-enzymatic antioxidant molecules (e.g., vitamin C, glutathione, etc.). Apart from that, the roles of various hormones, for instance, abscisic acid, ethylene, salicylic acid, jasmonates, brassinosteroids, auxins, gibberellins, and cytokinins are discussed at length in this review.

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Introduction

"No toxic substance restricts plant growth more than does salt" (Zhu, 2002). According to the latest data released by the FAO, the global area of salt-affected soils has reached 1,381 million ha, which is equivalent to 10.7% of the global land (FAO and UN, 2024). Previously, salt-affected lands were estimated at ~830-950 million ha (Ruan et al., 2010), which means that there has been a 35% increase in soil salinity across the globe (~ 2.3% annually) over the last 15 years. Likewise, Pakistan is losing 40,000 ha annually due to soil salinization, and a total of 5.7 Mha has been lost (IAEA, 2024). It is pertinent to mention that the dominant ions in salt-affected soils include Na^+, K^+, Ca^{2+}, Mg^{2+}, Cl^-, HCO_3^-, and SO_4^{2-} (Koull and Chehma, 2016). In contrast, most cash crops are glycophytes that cannot survive NaCl concentrations over 50 mM (Navarro-Torre et al., 2023). Therefore, soil salinity impairs crop productivity and decreases the profitability of most of the glycophytic cash crops, leading to considerable economic losses (Nicolas et al., 2023).

Soil salinity interferes with plant physiological functioning at all levels and during every developmental stage (Atta et al., 2023). First and foremost, salt-induced osmotic stress inhibits cellular expansion by reducing turgor pressure (Taiz and Zeiger, 2010; Colin et al., 2023). Moreover, hyperosmolality reduces soil matric potential, thereby reducing water uptake by seeds or plant roots

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(Tedeschi et al., 2017). Seed germination is the most crucial stage of plant development and one of the most susceptible stages to salinity stress. Even the seed germination of halophytes is inhibited by salinity stress (Hadi et al., 2018). This inhibition of germination is primarily linked to salt-induced osmotic stress, which inhibits seed water uptake and imbibition (Chartzoulakis and Klapaki, 2000; Munns and Tester, 2008; Khan et al., 2022). At the leaf level, salinity stress causes damage to the chloroplast envelope and disintegration of thylakoids, directly affecting photosynthetic light-harvesting complexes (Stefanov et al., 2016). Moreover, salinity stress can enhance chlorophyllase activity (the enzyme involved in chlorophyll breakdown) and alter chlorophyll biosynthesis by inhibiting 5-ALA biosynthesis (Santos, 2004; Li et al., 2024). Consequently, salinity induces instability in the chlorophyll protein complex, reduces *PSII* efficiency, and causes a reduction in the *Fv/Fm* ratio, contributing to photoinhibition (Lichtenthaler et al., 2005; Chaves et al., 2009; Shu et al., 2012). Moreover, leaf photosynthetic activity is severely affected by salinity stress because of disturbed plant water relations, reducing overall carbon dioxide fixation (Kim et al., 2010; Tardieu et al., 2011; Hnilickova et al., 2021; Wang et al., 2024).

In addition to these salinity-induced effects, the most prominent is the induction of ion toxicity, also known as sodium toxicity, within cells. Although Na is a beneficial element for some plants (halophytes), it is extremely toxic to glycophytes. Higher levels of Na inside the cells cause ion disequilibrium, which disturbs cell metabolism (Teakle and Tyerman, 2010; Körner et al., 2025). Both Na^+ and K^+ compete at the HKT site, but higher soil Na^+ concentrations result in high Na^+ uptake and subsequent vascular transport to the leaves, causing ion toxicity and physiological disturbance (Hasegawa et al., 2000; Alemán et al., 2009; Taiz and Zeiger, 2010; Hasegawa, 2013; Song et al., 2024; Wang et al., 2024b). This ultimately causes growth reduction in crops, including cereals (Lin and Kao, 2001). It is pertinent to mention that ion toxicity also results in oxidative stress through enhanced production of reactive oxygen species (ROS). Salinity-induced production of superoxide anion (O_2^-) has been reported inside the thylakoid membrane and singlet oxygen ($^1O_2$) production at PSII, and salt-induced overproduction of hydrogen peroxide (H_2O_2) and hydroxyl radical ($^{\bullet}OH$) within the chloroplasts via the Fenton reaction and Haber-Wiess reaction (Wagner et al., 2004; Mittler et al., 2011; Jian et al., 2025). The overproduction of ROS is extremely dangerous because it causes membrane damage, electrolyte leakage, DNA damage, protein oxidation, and photosynthetic pigment degradation (Pamplona, 2008; Ashraf, 2009; Tanoua et al., 2009; Sachdev et al., 2023; Rao et al., 2025). The overall result of these physio-biochemical changes is evident in the form of compromised yield and productivity losses in various cash crops, including wheat (Iqbal and Ashraf, 2013; Koevoets et al., 2016; Shafiq et al., 2021), rice (Zheng et al., 2023; Meng et al., 2025), sugarcane (Khan et al., 2022), maize (Liao et al., 2024), sorghum (Yang et al., 2025; Fu et al., 2025), barley (Bouhraoua et al., 2025; Sreesaeng et al., 2025), and cotton (Xiao et al., 2023; Ma et al., 2024; Li et al., 2025).

In the current review, we have discussed at length multiple physio-biochemical and molecular processes involved in salinity-stressed plants and how far these processes can enable such plants to adapt to salinity stress.

Adaptive plant traits that contribute to salinity tolerance

In this section, special emphasis is given to the adaptive plant mechanisms that contribute to salinity stress tolerance. Various plant species belonging to different families and ecological niches display a wide range of characteristics that assist them in surviving salt stress, which are discussed here (**Figure 1**).

1. Sodium exclusion: The first line of defense

As previously mentioned, Na^+ above certain limits becomes toxic; therefore, its concentration must be regulated efficiently to avoid metabolic distress. All plants, including halophytes, exhibit various mechanisms to exclude Na^+ from their shoots (Munns and Tester, 2008; Munns et al., 2020). The Na^+-exclusion is a highly desirable trait for breeding salt-tolerant crops (Assaha et al., 2017; Ismail and Horie, 2017; Garcia-Daga et al., 2025). This is achieved by a combination of membrane transporters, viz. High-Affinity Potassium (K^+) transporter 1 (HKT1), Na^+/H^+ exchanger (NHX1 and NHX2), and an SOS1 antiporter, part of the Salt-Overly Sensitive (SOS) pathway, function to maintain Na^+ below the permissible limits. The specific roles of these membrane transporters are discussed here in detail.

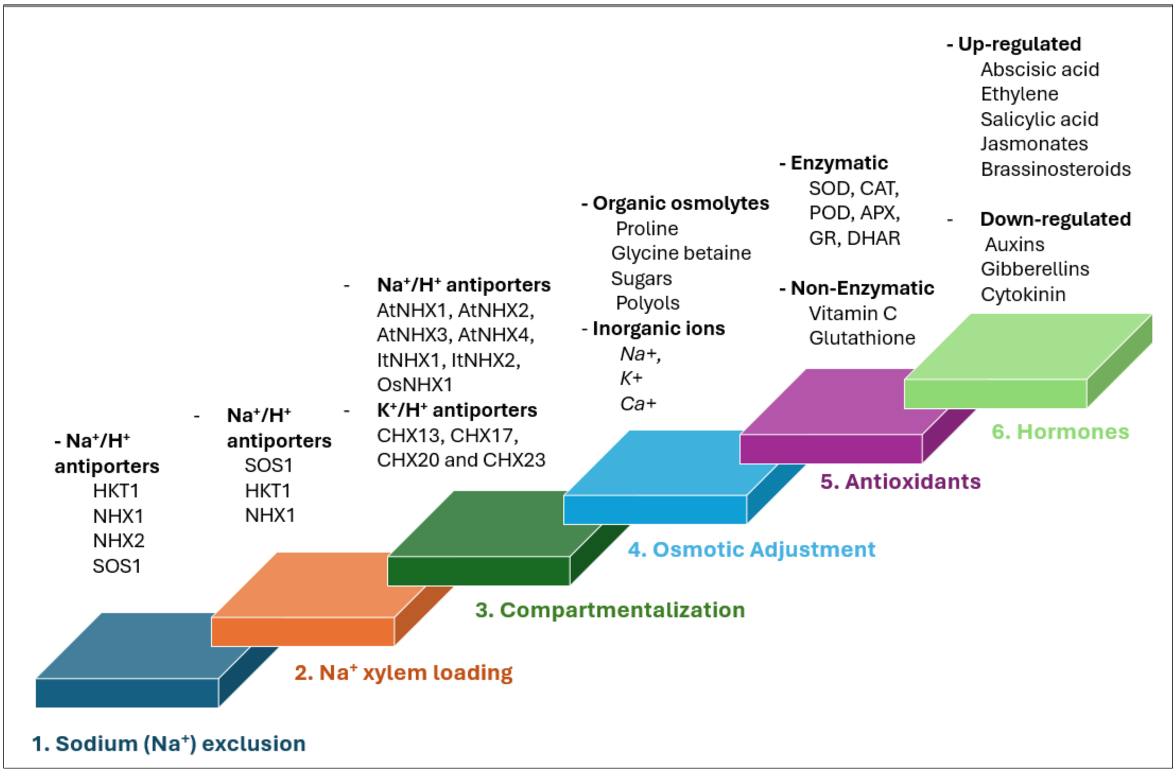

Figure 1: A schematic diagram representing different adaptive traits in plants for salinity tolerance. 1. Sodium exclusion 2. Na^+ xylem loading 3. Compartmentalization 4. Osmotic adjustment 5. Antioxidants 6. Hormones. HKT1, High-Affinity Potassium (K^+) transporter 1; NHX1 and NHX2, Na^+/H^+ exchangers; SOS1, Salt-Overly Sensitive (SOS) 1.

High-Affinity Potassium (K^+) transporter 1 (HKT1) was the first HKT discovered in wheat and is an HKT protein that acts as a Na^+ channel responsible for Na^+ exclusion (Uozumi et al., 2022; Wang et al., 2024a). The HKT1 is a uniporter that regulates Na^+ levels in different plant species. It is pertinent that HKT1 is found in all plants; however, HKT2 transporters are specific to monocots (Platten et al., 2006; Riedelsberger et al., 2021). Additionally, the activity of HKT1 is highly regulated and tissue-specific, and its localization in the vascular bundle (either xylem or phloem) predominantly determines its physiological role (reviewed by Garcia-Daga et al., 2025). In *Arabidopsis thaliana*, AtHKT1;1 mediates Na^+ secretion from the stelar apoplast and xylem into root xylem parenchyma cells, thereby reducing Na^+ transport to shoots. However, the *athkt1;1* knockout mutant failed to stop Na^+ transport to the shoots, even under non-saline conditions (Rus et al., 2006). Nonetheless, *HKT1* is variably expressed in the root and shoot tissues of *Arabidopsis thaliana,* and accessions with lower *HKT1* expression levels in the roots exhibit higher Na^+ concentrations in the shoots, and vice versa (Baxter et al., 2010). Studies have also reported that HKT1 might control Na^+ accumulation in reproductive tissues, contributing to viable seed production under salinity stress (An et al., 2017). Similarly, HKT1-mediated regulation of shoot Na^+ content has been reported in wheat (Munns et al., 2012; Byrt et al., 2014), maize (Zhang et al., 2018), rice (Kobayashi et al., 2017; Shohan et al., 2019), barley (Houston et al., 2020), tomato (Jaime-Pérez et al., 2017; Romero-Aranda et al., 2020), and berries, including grapes and blueberries (Song et al., 2024).

Na^+ exclusion can also be achieved through Na^+ compartmentalization in the vacuole with the help of both NHX1 and NHX2, which are Na^+/H^+ exchangers located at the tonoplast (Liu et al., 2017; Zhang et al., 2025a). A Na^+/H^+ transporter located at the root cell plasma membrane has also been reported, which is expressed by the *SOS1* gene, and its role in K^+ homeostasis has been proposed (Blumwald et al., 2000; Wang et al., 2017). Similarly, overexpression of halophytic *NHX1* in *Arabidopsis thaliana* confers salt stress tolerance via Na^+ exclusion and cytosolic K^+ retention (Liu et al., 2017). Likewise, overexpression of *NHX1* in transgenic plants, viz. *Vigna radiata*, *Nicotiana tabacum*, and *Panicum virgatum* have been shown to have enhanced salt tolerance linked with Na^+-exclusion (Sahoo et al., 2016; Zhang et al., 2017b; Huang et al., 2017). Above all, salt tolerance in plants has been linked to their ability to exclude sodium (Wang et al., 2017; Chen et al., 2024; An et al., 2025; Shabala et al., 2025).

1.a. Xylem loading: Control of Na^+ transport to shoots

Interestingly, Na^+ exclusion cannot contribute to salinity tolerance alone, and it works along with other mechanisms to induce salt tolerance. In the halophytic grass species *Puccinellia tenuiflora,* the co-expression of *SOS1*, *HKT1;5,* and *NHX1* contributed to Na^+ efflux and K^+ retention (Zhang et al., 2017b). Therefore, the control of Na^+ transport into the xylem is another prominent phenomenon by which plants achieve ion homeostasis and eliminate excessive Na^+.

Na^+ ions enter plant roots via pressure-driven bulk flow (Taiz and Zeiger, 2010), and plant roots tend to avoid ion toxicity by transporting excess Na^+ into the shoots via xylem vessels during xylem loading (Shabala et al., 2010; Shabala et al., 2025). It takes place at the interface of xylem parenchyma by specific ion transporters, including Na^+/H^+, Na^+-permeable non-selective cation channels, and Na^+: K^+: Cl^- cotransporters (Zhu et al., 2017; Ishikawa and Shabala, 2019). Studies have also suggested that the expression of *SOS1* mediates Na^+ xylem loading (Shi et al., 2002; Shabala and Mackay, 2011; Assaha et al., 2025). Transgenic plants overexpressing Na^+-efflux transporters have high root-to-shoot Na^+ transport (Zhang et al., 2017b). Whereas, the HKT is believed to be involved in Na^+-retrieval or xylem unloading (Munns and Tester 2008; Horie et al., 2009). This controlled Na^+ transport to plant aboveground tissues prevents metabolic disruption and ion toxicity in the root cells (Läuchli et al., 2008; Zhang et al., 2025b). In agreement, elevated Na^+ concentrations in the xylem tissue of barley genotypes have been recorded and explained based on the involvement of inorganic ions for osmotic adjustment (Shabala et al. 2010; Bose et al. 2014; Zeng et al., 2015), which serve as a cheap osmotica as energetic costs are lower (Ishikawa and Shabala, 2019). Therefore, Na^+ xylem loading and its sequestration in vacuoles, along with K^+ retention, could serve as a faster and more efficient strategy to maintain ion homeostasis. It has also been reported that when sufficient Na^+ is sequestered in the vacuoles of mesophyll cells, xylem Na^+ loading and transport are stopped to maintain manageable concentrations of Na^+ (Bose et al. 2014; Zhu et al., 2017).

An alternate viewpoint is that the ability to transport fewer Na^+ ions to shoots is a desirable trait for salinity tolerance (Munns and Tester, 2008). For example, when salt-sensitive rice and salt-tolerant barley were exposed to salinity stress, there was a sharp increase in the Na^+ concentration in the xylem sap of barley, whereas the Na^+ levels in the xylem sap of rice remained low. The researchers concluded that rapid Na^+-xylem loading contributes to the upregulation of adaptive responses, leading to salinity tolerance (Ishikawa and Shabala, 2019). A third opinion is that under moderate salinity stress, *SOS1* expression actively mediates Na^+ xylem loading, as *sos1* mutants exhibit less Na^+ accumulation (Shi et al., 2000). At higher salinity levels, Na^+ entry into the xylem is a passive process. Above all, the Na^+ fraction in the xylem of *Arabidopsis* could range between 5-9 mM when plants were exposed to 100 mM NaCl for two days (Shi et al., 2002; Horie et al., 2006). Moreover, plant salinity tolerance is closely associated with the ability to transport, compartmentalize, and mobilize Na^+ ions, and its radial transport into the xylem tissue enables homeostatic control (Apse and Blumwald, 2007; Hu et al., 2025; Tibesigwa et al., 2025).

1.b. Compartmentalization: The cellular detoxification

Cells cope with toxic levels of Na^+ entering the cytosol via vacuolar sequestration. The cost of pumping Na^+ ions into the vacuole is only 10% compared to that of the *de novo* synthesis of 1 mol of organic osmolytes (Shabala and Shabala, 2011). Therefore, the removal of excessive Na^+ ions inside the cells is achieved by Na^+ vacuolar sequestration mediated by NHX transporters located in the tonoplast (Wu et al., 2018). These intracellular NHX transporters comprise subclass 1 of cation/proton antiporters, which include both Na^+/H^+ and K^+/H^+ antiporters (Wang and Wu, 2013). These Na^+/H^+ antiporters include AtNHX1, AtNHX2, AtNHX3, AtNHX4, ItNHX1, ItNHX2, and OsNHX1 (Gierth and Mäser, 2007), whereas there are some K^+/H^+ antiporters, including CHX13, CHX17, CHX20, and CHX23 from the CPA2 family, that participate in K^+ homeostasis (Ren et al., 2013; Wu et al., 2021). In this context, the upregulation of the *NHX1* gene in *Arabidopsis*, barley, and alfalfa has been reported under salt stress (Gaxiola et al., 1999; Adem et al., 2014; Sandhu et al., 2017). Likewise, overexpression of *AtNHX1* enhanced Na^+ vacuolar sequestration and contributed to K^+ homeostasis and plant growth under saline conditions (Rodríguez-Rosales et al., 2009; Leidi et al., 2010; Bassil et al., 2011; Liu et al., 2025). Similarly, overexpression of NHX1 improved salt tolerance in *Arabidopsis* (Apse et al., 1999), rice (Chen et al., 2007), and tobacco (Gouiaa et al., 2012).

Apart from NHX1, the role of SOS1 (also known as Na^+/H^+ exchanger or NHX7) transporter is significant for Na^+-vacuolar sequestration in plants. In this context, the Si application enhanced *NHX1* and *SOS1* expression in zucchini, which enhanced salt stress tolerance (Zhang et al., 2024). Recently, using cryo-imaging, Ramakrishna et al. (2025) confirmed that SOS1 is involved in Na^+-vacuolar transport and subsequent sequestration in *Arabidopsis* root meristematic cells (Ramakrishna et al., 2025). Moreover, they reported concentration-dependent Na^+-accumulation patterns, revealing that low external Na^+ levels led to its accumulation in the cell walls, whereas high Na^+ concentrations caused SOS1 accumulation as the late endosomes and prevacuoles and their localization in the plasma membrane and tonoplast (Ramakrishna et al., 2025). The internalization of SOS1 proteins into the tonoplast under salt stress has also been confirmed in *Arabidopsis* and is involved in Na^+ compartmentalization (Liu et al., 2025). Additionally, the subcellular localization of SOS1 at vacuolar and plasma membranes has also been reported in the salt-tolerant species *Salicornia bigelovii* (Salazar et al. 2024). Hence, it is now proposed that under salt stress, SOS1 has a dual role in Na^+ vacuolar compartmentalization and its extrusion to the apoplast (Qi and Qiu, 2025; Ramakrishna et al., 2025).

2. Osmotic adjustment

Adaptation to salinity is achieved at multiple levels, and one of the most fundamental adaptive traits is osmotic adjustment. The synthesis of compatible solutes in response to osmotic shock is achieved, and both organic and inorganic components contribute to osmotic adjustment in the cells and tissues under salinity stress. Plants exposed to salt stress can experience several-fold increases in the amounts of organic osmolytes (Sakamoto and Murata 2000; Amiri et al., 2024). However, the energetic costs associated with osmotic adjustment are also very high. Raven (1985) reported that for the synthesis of 1 mole of compatible solutes, around 40-60 moles of ATP are required. Nonetheless, these osmolytes are synthesized and retained inside the cytosol to balance the cell's osmotic potential under salinity stress (Flowers and Colmer, 2008; Kaur et al., 2024). These include proline, glycine betaine, sugars, and polyols, which do not interfere with cellular metabolic pathways (Ruffino et al., 2010; Shabala and Shabala, 2011). Increased synthesis of dehydrin proteins under salt stress has also been reported (Rorat, 2006; Brini et al., 2007; Zhang et al., 2025c). Most importantly, osmotic adjustment is not solely reliant on organic components; rather, the incorporation of inorganic ions plays a significant role in ionic balance, making it a two-way strategy. The retention of inorganic ions has been reported in both glycophytes and halophytes (Flowers and Colmer, 2008; Shabala and Shabala, 2011; Shabala and Mackay, 2011; Hasegawa, 2013).

The retention of inorganic ions, particularly K^+, provides additional support for osmotic adjustment in plants under salt and drought stress (Iannucci et al., 2002; Shafiq et al., 2015; Hammami et al., 2017). Potassium (K) is a macronutrient for plants, which is essentially involved in protein synthesis, enzyme activation, regulation of membrane potential, regulation of stomata, and photosynthesis (Gattward et al., 2012; Adams and Shin, 2014; Shabala, 2017; Ameen et al., 2024). The retention of K^+ in the mesophyll cells of halophytes enhances salinity tolerance (Percey et al., 2016). Under salinity stress, cytosolic K^+ levels contribute to ion homeostasis, and the Na^+/K^+ ratio is a determinant of salt tolerance (Shabala and Cuin, 2007; Cuin et al., 2009; Barragán et al., 2012; Shabala, 2017; Choi et al., 2024). It has also been reported that the overexpression of *AhNHX1*, a K^+/H^+ antiporter, improved K^+ retention in tobacco and *Arabidopsis*, conferring salt tolerance (Zhang et al., 2017a; Liu et al., 2017).

In addition to K^+, Ca^{2+} ions play a significant role in regulating plant stress responses under salt stress. The calcium (Ca) ions are essentially required for the activation of various cellular enzymes and the regulation of ion transport (Pikor et al., 2024). In addition, the Ca^{2+} ions also contribute to osmotic adjustments through regulation of gene expression. For example, the application of Ca^{2+} alleviated salinity stress in multiple crops, including *Vicia faba* (Morgan et al., 2017), rice (Rahman et al., 2016), brinjal, chilli, and soybean (Baba et al., 2017).

3. Antioxidants

The role of reactive oxygen species (ROS) as secondary messengers in many signal transduction pathways has already been proven, such as modulating gene expression, hormonal pathways, and programmed cell death (when necessary) (Zhang et al., 2016; Bhattacharjee, 2019; Liao et al., 2025; Lindsay and Rhodes, 2025). These ROS include singlet oxygen ($^1O_2$), superoxide ($O_2^{\bullet -}$), hydrogen peroxide (H_2O_2), and the hydroxyl radical ($^\bullet OH$). Among ROS, H_2O_2 is the most stable and mobile ROS; it triggers antioxidant gene expression, activates the MAPK cascade, and communicates stress signals between cells and tissues within the plant (Yang and Guo, 2018; Porter et al., 2025). Early ROS burst (mainly H_2O_2) under salinity stress is necessary to initiate the downstream defense response, as it helps initiate the defense gene expression and activate ion transporters, e.g., SOS1 and NHX1 (Zhang et al., 2016). Furthermore, it also regulates osmolyte production for metabolic homeostasis. Excessive accumulation of ROS becomes harmful, as high or prolonged ROS levels cause lipid peroxidation, DNA damage, protein oxidation, dysfunctional chloroplasts and mitochondria, and cell death at extreme conditions (Li et al., 2022; Ombale et al., 2025). This happens when ROS production outpaces scavenging capacity, resulting in an overwhelmed antioxidant defense system, such as in salt-sensitive genotypes.

The ROS are both signaling agents and toxins, and this is known as the ROS paradox. A balanced ROS-antioxidant homeostasis is the key adaptive strategy for tolerant species and/or genotypes. To keep ROS levels under control to survive under salt stress, plants utilize both enzymatic and non-enzymatic antioxidative mechanisms. Although these antioxidants alone are not completely sufficient to overcome salinity stress, rather they should work in coordination with other salinity adaptive mechanisms such as ion transporters, osmolyte production, and hormone regulation signaling.

3.a. *Enzymatic antioxidants*

Enzymatic antioxidative enzymes involve enzymes that directly detoxify ROS. Under salinity stress, plants mediate a complex response involving multiple classes of antioxidants. Major categories of enzymes involve superoxide dismutases, peroxidases, catalases, glutathione system enzymes, ascorbate-glutathione cycle enzymes, and thiol-related enzymes (Foyer and Kunert, 2024). Each category contributes differently under salinity stress (Rajput et al., 2021). For instance, superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX) act directly on ROS, while glutathione reductase (GR) and dehydroascorbate reductase (DHAR) maintain reductant pools. Additionally, peroxiredoxins and peroxidase (POD) modulate ROS signaling.

Superoxide anion scavengers include dismutase (SOD), which converts O_2^- into H_2O_2, and is the first line of defense against oxidative stress. Peroxidases include ascorbate peroxidase (APX), guaiacol peroxidase (POD), and class III peroxidases. They reduce H_2O_2 using electron donors (ascorbic acid, phenolics) into water, as APX uses ascorbate to convert H_2O_2 into water. They detoxify H_2O_2 in chloroplasts, cytosol, and apoplasts and are involved in stress signaling and cell wall strengthening. Catalase (CAT) converts H_2O_2 into water and oxygen without requiring a reductant and is active mostly in peroxisomes (Yemelyanov et al., 2022). It is critical for eliminating in peroxisomes, especially under stress conditions. Enzymes from the glutathione system, such as glutathione reductase (GR) and glutathione peroxidase (GPX), maintain the GSH pool and detoxify lipid peroxidases and H_2O_2. They sustain cellular redox homeostasis, which is essential for the glutathione-ascorbate cycle under saline conditions (Zheng et al., 2021; Foyer and Kunert, 2024). Furthermore, enzymes in the ascorbate-glutathione (AsA-GSH) cycle regenerate ascorbate from oxidized forms using NAD(P)H or GSH, including monodehydroascorbate reductase (MDHAR) and dehydroascorbate reductase (DHAR). Under salinity stress, they maintain ascorbate levels for APX function, which is critical for detoxification of H_2O_2 and oxidative balance. Thiol-related enzymes, such as peroxiredoxins (PRX), thioredoxins (TRX), and glutaredoxins (GRX), reduce H_2O_2, lipid peroxides, or protein disulfides using thiol donors and protect proteins and membranes from oxidative damage under salt stress (Van Breusegem and Mittler, 2023).

Under salt stress, genes encoding antioxidant enzymes are upregulated by specific transcription factors, which recognize stress-responsive *cis*-elements in the promoter regions of these genes. Key transcription factor families include NAC, DREB (Dehydration-Responsive Element Binding proteins), and CBF (C-repeat Binding Factor). These TFs are widely implicated in abiotic stress signaling (Chen et al., 2021; Zhao et al., 2023). NAC (NAM, ATAF1/2, and CUC2) proteins bind to the NAC recognition sequences (NACRS) and activate the expression of antioxidant genes such as *SOD, APX*, and *GR*, leading to enhanced ROS scavenging (Hu et al., 2006; Wang et al., 2022; Gupta et al., 2024). DREB transcription factors, particularly those in the DREB1/CBF subfamily, regulate genes containing DRE/CRT (dehydration-responsive element/C-repeat) motifs. These TFs induce expression of *SOD, CAT*, and other redox-related genes, thereby increasing oxidative stress tolerance (Agarwal et al., 2006; Singh and Laxmi, 2020; Zhao et al., 2023). CBF transcription factors, often overlapping with DREB, regulate salt-inducible genes, including those related to ROS detoxification and osmotic adjustment, such as APX and peroxiredoxins (Zhao et al., 2023). bZIP (Basic Leucine Zipper) family, especially the ABA-responsive subfamily (e.g., ABF/AREB), modulates the expression of antioxidant and stress-responsive genes under salt-induced abscisic acid (ABA) signaling (Fujita et al., 2005; Li et al., 2022; Gupta et al., 2024). For instance, AREB1 is known to activate CAT and DHAR (dehydroascorbate reductase) expression.

The role of antioxidants is manifested by studying antioxidant mutants. These transgenic plants showed higher photosynthesis rate, better root/shoot biomass, and reduced electrolyte leakage and lipid peroxidation (Tavleeva et al., 2022; Sharma et al., 2023). For instance, transgenic rice overexpressing the *katE* gene of *E. coli* showed 150% higher expression of catalase (Moriwaki et al., 2008). These transgenic rice plants under salinity stress showed remarkable tolerance and survived successfully under 50-250 mM NaCl treatments, at which wild-type plants could not survive (Moriwaki et al., 2008; Prodhan et al., 2008). Similarly, other studies showing higher expressions of catalase in rice (Nagamiya et al., 2007) and *Cynobacterium synechococcus* sp. (Kaku et al., 2000) showed improved growth and salinity tolerance (Zhang et al., 2021). The upregulation of these transcription factors under salt stress enhances the plant's ROS-scavenging capacity, maintaining cellular redox homeostasis and protecting against oxidative damage (Singh et al., 2022). Higher expression of superoxide dismutase showed enhanced salinity tolerance. For instance, Cu/Zn SOD overexpression in *Nicotiana tabacum* (Lee et al., 2013) and *Oryza sativa* (Prashanth et al., 2008) has shown improved germination rate and chloroplast integrity under salinity and oxidative stress (Wang et al., 2022). The other isoforms of SOD were less studied, but their overexpression, such as Fe-SOD (Van Camp et al., 1996) and Mn-SOD (Wang et al., 2004), also improved salinity tolerance in target plants. Similarly, *Arabidopsis* plants overexpressing peroxisomal *APX* from the *Puccinellia tenuiflora* showed high salinity tolerance (Guan et al., 2015). *APX* transgenes under 150 and 175 mM NaCl showed improved chlorophyll content, less lipid peroxidation, and less H_2O_2 content under exogenous application of H_2O_2. Overexpression of cytosolic *AtAPX1* increased catalase and GPX activities, improving salinity tolerance in Indian mustard by reducing ROS and membrane damage (Saxena et al., 2020; Ali et al., 2023).

Additionally, transgenic antioxidant lines exhibited several effects that enhanced salinity tolerance. Notably, many transgenic lines demonstrated 20–40% increases in photosynthetic rate, improved chlorophyll retention, and increased shoot/root biomass under salt stress compared to the wild type (Hasanuzzaman et al., 2021; Rajput et al., 2021; Cao et al., 2023). Transgenics often had 25-35% greater root/shoot dry weight and plant height due to improved stress resilience and growth maintenance (Hasanuzzaman et al., 2021). Lower electrolyte leakage and malondialdehyde contents were consistently observed, indicating reduced lipid peroxidation and membrane damage (Saxena et al., 2020). Some studies reported up to 50% higher survival, though exact figures vary depending on enzyme, genotype, and NaCl concentration (Hasanuzzaman et al., 2021).

3.b. *Non-enzymatic systems*

Plants also utilize non-enzymatic antioxidants to scavenge ROS and protect cellular components. Important non-enzymatic antioxidants include ascorbic acid, tocopherols, carotenoids, flavonoids, proline, and polyamines (Ashraf, 2009). Ascorbate (vitamin C) is a potent antioxidant that directly reacts with ROS, neutralizing them and preventing oxidative damage. Ascorbate also participates in the ascorbate-glutathione cycle, which is essential for detoxifying H_2O_2 (Foyer and Kunert, 2024). Overexpression of ascorbic acid in transgenic potato showed improved tolerance to oxidative stress under salinity stress by overproducing glutathione and activating glyoxalase enzyme (Upadhyaya et al., 2011). Under salinity stress, plants accumulate proline, a multi-functional amino acid that acts as an osmoprotectant and antioxidant (Targino et al., 2025). Proline helps maintain cell turgor and protects cellular structures from high salt concentrations (Koc et al., 2024). It also scavenges ROS (Zulfiqar and Ashraf, 2023), stabilizes the quaternary structures of proteins and membranes (Wright et al., 2025), and contributes to osmotic adjustment (Zuo et al., 2022). Proline accumulation is regulated by stress-responsive genes such as *P5CS* (Δ^1-pyrroline-5-carboxylate synthetase), *ProDH*, and *P5CR* (pyrroline-5-carboxylate reductase), which are transcriptionally modulated under salt stress (Tavakoli et al., 2016). Overexpression of *P5CS* has been associated with improved salinity tolerance in several transgenic plants, including *Arabidopsis*, tobacco, sugarcane, cotton, and rice (Hmida-Sayari et al., 2005; Guerzoni et al., 2014; Sellamuthu et al., 2024).

Polyamines (PAs), a group of low-molecular-weight aliphatic amines, including putrescine (Put), spermidine (Spd), and spermine (Spm), have been shown to have protective roles in plants under salt stress. They help stabilize membranes, scavenge free radicals, and modulate ion channel activity. One of the primary effects of salinity stress is ion imbalance (*i.e.*, the accumulation of Na^+ ions and the depletion of K^+ ions). At the same time, PAs help maintain ion homeostasis by regulating the activity of ion transporters such as H^+-ATPases and Na^+/H^+ antiporters (Xu et al., 2024). Exogenous application of Spd improved K^+/Na^+ ratio in wheat and rice under salt stress by modulating the expression of ion transporter genes (Paul and Roychoudhury, 2017; Shokri et al., 2024). PAs contribute to osmotic adjustment by stabilizing membrane structures and macromolecules under osmotic stress. Studies have shown that Spm and Spd reduce H_2O_2 and malondialdehyde (MDA) levels in salt-stressed plants, indicating reduced oxidative damage (Nahar et al., 2016; Zhou et al., 2019). Polyamines as signaling molecules regulate the expression of stress-responsive genes, including those involved in ABA signaling, ion transport, and ROS detoxification. Transcriptome studies have revealed that exogenous PAs modulate transcription factors such as DREB, NAC, and WRKY under salinity stress

(Takahashi and Kakehi, 2010; Paul and Roychoudhury, 2017). Rice mutant overexpressing the anthocyanidin synthase gene, a gene involved in the flavonoid pathway, increased antioxidative potential (Reddy et al., 2007).

4. Hormonal regulation

Plants adapt to salinity stress through hormonal regulation in a complex process. Phytohormones have a crucial role in salinity adaptation through modulating growth, development, and stress-responsive processes in tissue-specific and stage-dependent manners. These hormones act as signaling molecules, influencing plant responses to salinity at morphological, physiological, biochemical, and molecular levels (Ghosh et al., 2025; Mahajan, 2025; Waheed et al., 2025).

Abscisic acid (ABA) is a central hormone in salinity stress response. Under salinity, ABA regulates stomatal closure to reduce water loss and adjusts root architecture for water use (Yun et al., 2024). ABA can influence ion transport through ABI2 and PYL5, affecting calcium cascades and potassium retention. ABA can also regulate the production of ROS by acting through OST1 and ABI4 to influence RBOHF and RBOHD (Yun et al., 2024). During salinity stress, ABA synthesis is upregulated via key biosynthetic enzymes such as 9-*cis*-epoxycarotenoid dioxygenase (NCED) (Woo et al., 2011; Molinari et al., 2020). *NCED* overexpression enhanced dehydration stress resilience in AtNCED3-transgenics plants, showing improved root growth and photosynthetic efficiency. The mutants with low AtNCED3 were hypersensitive to salinity stress (Woo et al., 2011).

Ethylene (ET) plays a dual role in salinity tolerance as its effect can be both protective and deleterious. Its production is induced by salt stress and ET signaling pathways, including receptors like ERS1 and ETR1 (Wang et al., 2025). Mutants deficient in these signaling actors display heightened salt sensitivity, highlighting ethylene's protective role (Wang et al., 2008; Wilson et al., 2014). Ethylene often interacts with GA biosynthesis pathways, enabling morphological responses such as shoot elongation under stress conditions. The role of ET signaling and its temporal regulation in salt adaptation mechanisms is evidenced by recent transcriptomic analyses in the semi-halophyte (*Mesembryanthemum crystallinum*), which reveal that extended exposure to 0.4 M NaCl alters the circadian expression rhythms of important ethylene biosynthesis genes, *ACS6* and *ACO1* (Gieniec et al., 2024). Increased ET production in polyploid plants has been shown to enhance ROS scavenging by activating the transcription of genes involved in antioxidant defense (Song et al., 2025).

Salicylic acid (SA) and jasmonic acid (JA) predominantly contribute to salinity stress tolerance, with nuanced context-specific roles (Jayakannan et al., 2015; Farhangi-Abriz and Ghassemi-Golezani, 2018; Atta et al., 2023). JA is involved in guard cell and aquaporin regulation (Luo et al., 2019). It also regulates ROS levels by acting through antioxidant enzymes and MYC2 to influence VTC/GSH, involved in both ROS generation and elimination (Yuan et al., 2017; Song et al., 2021). SA contributes to maintaining redox homeostasis and osmoprotection under saline conditions (Atta et al., 2023; Aizaz et al., 2024). It acts through NPR1 to regulate Na^+ flux in plant cells, contributing to overall ion balance (Yun et al., 2024). SA also influences key antioxidant enzymes in the ROS-elimination process (Karimi et al., 2025; Song et al., 2025). Many recent studies have reported that the foliar, soil, and seed priming treatments with SA impart salinity tolerance via improvement in pigment biosynthesis, K^+/Na^+ ratio, antioxidative capacity, improved PSII light utilization efficiency, and osmotic adjustment (Karimi et al., 2025; Ma et al., 2025; Song et al., 2025).

Gibberellins (GA) levels generally decline under salt stress, an effect mediated in part by ABA-related DELLA protein accumulation; mutants lacking DELLAs show heightened salt sensitivity, underscoring DELLA's protective function (Waadt et al., 2022). Whereas, the cytokinins (CKs) signaling is downregulated under salt, potentiating enhanced ABA responsiveness, particularly via interplays involving SnRK2 kinases and type-A/B ARR transcription factors (Waadt et al., 2022). CKs initiate a signaling cascade involving ARR1/12, which affects HKT1, leading to Na^+ accumulation in plant cells. CKs can also act on ABI4, impacting other components in the ion-transport network (Yun et al., 2024). The brassinosteroids (BRs) contribute to stress resilience, notably in mitigating chlorophyll degradation and improving growth under salinity as observed in BR-treated rice seeds. Recent studies on BR showed that the exogenous application of EBR (24-epibrassinolide) significantly alleviated salt-induced damage in pepper and tea (Jin et al., 2024; Zhang et al., 2024). In pepper seedlings, foliar EBR treatment boosts photosynthetic efficiency, osmolyte production (including proline, soluble sugars, and glycine betaine). It enhances antioxidant defenses, while reducing ROS and Na^+ accumulation and upregulating stress-responsive genes like HKT1, NHX6, and SOS1 (Jin et al., 2024). Similarly, in tea plants, BR application mitigates salt-induced lipid peroxidation, elevates levels of photosynthetic pigments, soluble proteins, proline, and flavonoids, and strengthens antioxidant enzyme activities (Zhang et al., 2024). At the molecular level, BR signaling components such as AtBRI1, BIN2, and

BES1 are upregulated under salt stress, underscoring their involvement in stress adaptation networks (Ahmar et al., 2025).

Auxins, while having a major role in growth regulation, also play a significant role in salinity stress adaptation by interacting with other hormones, especially through modulating root development and gravitropic responses (Ghosh et al., 2025). Auxin signaling is often suppressed in root regions under salinity stress, which hinders the development of lateral roots. However, plants compensate for impaired auxin via the transcription factor LBD16, which can drive lateral root formation (Zhang et al., 2023). Moreover, ZAT6 acts as an alternative upstream activator of LBD16 under saline conditions, ensuring lateral root development (Zhang et al., 2024). It acts through auxin response factor 2 (ARF2) to influence high-affinity K^+ transporter gene 5 (*HAK5*), which is involved in potassium uptake (Zhao et al., 2016; Verma et al., 2022), and guard cell outward rectifying channel (GORK), responsible for potassium efflux (Kopic, 2024). This fine-tunes potassium levels in plant cells by regulating both uptake and efflux mechanisms. Auxins can also modulate ROS production through ARF5-RSL4, influencing RBOHC/J (Mangano et al., 2017; Yun et al., 2024).

Overall, hormonal regulation is a key adaptation mechanism in plants under salinity stress, involving a complex interplay of ABA, auxins, cytokinins, SA, and JA to regulate ion transport, ROS homeostasis, and stress-related gene expression (Waheed et al., 2024). Furthermore, no hormone acts in isolation; rather, hormonal crosstalk forms a regulatory web that enables plants to fine-tune responses. For instance, the ABA/GA/CK triangle coordinates stomatal behavior, growth modulation, and osmotic homeostasis (Waadt et al., 2022). Similarly, SA and JA interplay with redox signaling and antioxidant defenses (He, 2025). Ghosh et al. (2025) highlight how, under saline conditions, multiple hormones, including ABA, ethylene, jasmonates, GAs, SA, BRs, melatonin, and auxins, coordinate during seed germination and early seedling development. These hormones integrate signals that determine whether growth proceeds or is arrested during salt stress. In conclusion, hormones formulate a dynamic and context-sensitive network to regulate salinity tolerance where ABA functions as a master stress regulator, ET and SA/JA reinforce adaptive responses, and GA, CK, BRs, and auxins fine-tune growth and development.

Morphological adaptations

Other than the physiological adaptations, the structural adaptations often contribute to salinity stress tolerance. Plants develop deeper roots to grow away from high salinity and to forage for water and nutrients (Zou et al., 2021). Moreover, the deposition of suberin restricts salt entry into the roots (de Silva et al., 2021). For example, in halophytes, the development of endodermal barriers in the vascular system restricts salt movement (Flowers et al., 2010; Bose et al., 2023). At the shoot level, the reduction in leaf size and leaf area under salinity stress lowers transpiration (Parida and Das, 2005). Leaves of halophytes are succulent and store more water and accumulate more salt within vacuoles (Rozema and Schat, 2013; Flowers and Colmer, 2015). An increased trichome density has also been reported among plants under salinity stress (Shabala and Mackay, 2011; Shabala et al., 2022). Both *Atriplex* and *Tamarix* possess salt glands that release salt as crystals (Yuan et al., 2016).

Conclusions and Prospects

The current review mainly highlights some key physio-biochemical and molecular traits primarily involved in plant salinity tolerance, including Na^+-exclusion, xylem loading and Na^+-vacuolar sequestration, osmoregulation, antioxidants, and hormonal regulation. The roles of various antiporters HKT1, NHX1, NHX2, and SOS1 are therefore imperative for ion homeostasis, whereas organic osmolytes (proline, glycine betaine, sugars, polyols) and inorganic ions (Na^+, K^+, Ca^{2+}) participate in osmoregulation. Both enzymatic and non-antioxidant compounds help mitigate oxidative stress, and hormones facilitate the regulation of key physiological processes. Based on this information, future studies should involve screening crop species and wild relatives for superior combinations of these traits to enhance salt tolerance. By using CRISPR-Cas9 and other advanced gene editing approaches, breeding programs could focus on the development of genotypes expressing HKTI, SOS1, and NHX, thereby exhibiting better ion homeostasis under salt stress. Lastly, high-throughput plant phenotyping approaches could help in identifying salt-tolerant genotypes.

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References

Adams, E., Shin, R. (2014). Transport, signaling, and homeostasis of potassium and sodium in plants. *Journal of Integrative Plant Biology* 56(3):231-249. https://doi.org/10.1111/jipb.12159

Adem, G., Roy, S.J., Zhou, M., Bowman, J.P., Shabala, S. (2014). Evaluating contribution of ionic, osmotic and oxidative stress components towards salinity tolerance in barley. *BMC Plant Biology* 14:113. https://doi.org/10.1186/1471-2229-14-113

Agarwal, P.K., Agarwal, P., Reddy, M.K., Sopory, S.K. (2006). Role of DREB transcription factors in abiotic and biotic stress tolerance in plants. *Plant Cell Reports* 25(12):1263-1274.

Ahmar, S., Shafique, M.S., Rapacz, M., Pociecha, E. (2025). Elucidating the role of brassinosteroid signaling genes and their promoters in Arabidopsis revealed regulatory mechanisms in plant development and responses to different abiotic stresses. *BMC Plant Biology* 25(1):970.

Aizaz, M., Mahmood, A., Shahid, M.A., Khan, A.H., Javed, M.T. (2024). Hormonal cross-talk in plants under salinity stress: Molecular mechanisms and adaptive strategies. *Biology* 13(9):673. https://doi.org/10.3390/biology13090673

Alemán, F., Nieves-Cordones, M., Martínez, V., Rubio, F. (2009). Potassium/sodium steady-state homeostasis in *Thellungiella halophila* and *Arabidopsis thaliana* under long-term salinity conditions. *Plant Science* 176(6):768-774. https://doi.org/10.1016/j.plantsci.2009.03.006

Ali, A., Raza, A., Mehmood, S., Hussain, S., Habib, M. (2023). Engineering antioxidant defense for improving salinity tolerance in crops: Recent advances and future perspectives. *Frontiers in Plant Science* 14*:*1175629. https://doi.org/10.3389/fpls.2023.1175629

Ameen, M., Akhtar, J., Anwar-ul-Haq, M., Abbasi, G.H., Ali, M. et al. (2024). Potassium in plants: Possible functions, mechanisms and proteomics under abiotic environmental stress. *In* "*Metals and Metalloids in Plant Signaling.* (T. Aftab ed.). pp. 73-110. Springer. https://doi.org/10.1007/978-3-031-59024-5_4

Amiri, H., Banakar, M.H., Gavyar, P.H.H. (2024). Polyamines: New plant growth regulators promoting salt stress tolerance in plants. *Journal of Plant Growth Regulation* 43(12):4923-4940. https://doi.org/10.1007/s00344-024-11345-4

An, D., Chen, J.G., Gao, Y.Q., Li, X., Chao, D.Y. (2017). *AtHKT1* drives adaptation of *Arabidopsis thaliana* to salinity by reducing floral sodium content. *PLOS Genetics* 13(10):e1007086. https://doi.org/10.1371/journal.pgen.1007086

An, M., Huang, X., Long, Y., Wang, Y., Tan, Y. et al. (2025). Salt tolerance evaluation and key salt-tolerant traits at germination stage of upland cotton. *Frontiers in Plant Science* 15*:*1489380. https://doi.org/10.3389/fpls.2024.1489380

Apse, M.P., Aharon, G.S., Snedden, W.A., Blumwald, E. (1999). Salt tolerance conferred by overexpression of a vacuolar Na^+/H^+ antiport in *Arabidopsis. Science* 285(5431):1256-1258. https://doi.org/10.1126/science.285.5431.1256

Ashraf, M. (2009). Biotechnological approach of improving plant salt tolerance using antioxidants as markers. *Biotechnology Advances* 27(1):84-93. https://doi.org/10.1016/j.biotechadv.2008.09.003

Assaha, D.V., Mekawy, A.M.M., Liu, L., Saneoka, H., Ueda, A. (2025). The role of *SOS1* and *HKT* transporters in Na^+ exclusion in huckleberry under saline conditions. *Tropical Plant Biology* 18*(*1):59. https://doi.org/10.1007/s12042-024-09358-0

Assaha, D.V., Ueda, A., Saneoka, H., Al-Yahyai, R., Yaish, M.W. (2017). The role of Na^+ and K^+ transporters in salt stress adaptation in glycophytes. *Frontiers in Physiology* 8:509. https://doi.org/10.3389/fphys.2017.00509

Atta, K., Mondal, S., Gorai, S., Singh, A.P., Kumari, A. et al. (2023). Impacts of salinity stress on crop plants: Improving salt tolerance through genetic and molecular dissection. *Frontiers in Plant Science* 14:1241736. https://doi.org/10.3389/fpls.2023.1241736

Atta, R.S., Abdelhamid, M.T., Dawood, M.G. (2023). Role of salicylic and jasmonic acids in mitigating salinity stress in plants: Physiological and biochemical perspectives. *Plant Growth Regulation* 111(2):233-248. https://doi.org/10.1007/s10725-023-01005-7

Baba, T., Sato, Y., Katsube, Y., Kuroda, C., Fujiyama, H. (2017). Relationship between plant responses to high Na and ameliorative effects of supplemental K and Ca. *Journal of Plant Nutrition* 40(1):33-39. https://doi.org/10.1080/01904167.2016.1201493

Barragán, V., Leidi, E.O., Andrés, Z., Rubio, L., De Luca, A. et al. (2012). Ion exchangers *NHX1* and *NHX2* mediate active potassium uptake into vacuoles to regulate cell turgor and stomatal function in *Arabidopsis. The Plant Cell* 24(3):1127-1142. https://doi.org/10.1105/tpc.111.095273

Bassil, E., Tajima, H., Liang, Y.C., Ohto, M.A., Ushijima, K. et al. (2011). The Arabidopsis Na^+/H^+ antiporters *NHX1* and *NHX2* control vacuolar pH and K^+ homeostasis to regulate growth, flower development, and reproduction. *The Plant Cell* 23(9):3482-3497. https://doi.org/10.1105/tpc.111.089581

Baxter, I., Brazelton, J.N., Yu, D., Huang, Y.S., Lahner, B. et al. (2010). A coastal cline in sodium accumulation in *Arabidopsis thaliana* is driven by natural variation of the sodium transporter AtHKT1;1. *PLOS Genetics* 6(11):e1001193. https://doi.org/10.1371/journal.pgen.1001193

Bhattacharjee, S. (2019). ROS and oxidative stress: origin and implication. In "Reactive Oxygen Species in Plant Biology*"*. (S. Bhattacharjee, ed.). pp. 1-31. Springer Nature, New Delhi, India. https://doi.org/10.1007/978-81-322-3941-3_1

Blumwald, E., Aharon, G.S., Apse, M.P. (2000). Sodium transport in plant cells. *Biochimica et Biophysica Acta (BBA) - Biomembranes* 1465(1-2):140-151. https://doi.org/10.1016/S0005-2736(00)00135-8

Bose, J., Shabala, L., Pottosin, I. (2023). Halophytes as new model plant species for salt tolerance strategies. *Frontiers in Plant Science* 14*:*11423 https://doi.org/10.3389/fpls.2023.1142310

Bose, J., Shabala, L., Pottosin, I., Zeng, F., Velarde-Buendía, A.M. et al. (2014). Kinetics of xylem loading, membrane potential maintenance, and sensitivity of K^+-permeable channels to reactive oxygen species: Physiological traits that differentiate salinity tolerance between pea and barley. *Plant, Cell & Environment* 37(3):589-600. https://doi.org/10.1111/pce.12180

Bouhraoua, S., Ferioun, M., Boussakouran, A., Belahcen, D., Srhiouar, N. et al. (2025). Physio-biochemical responses and yield performance of North African barley genotypes submitted to moderate and severe salinity. *Cereal Research Communications* 53(1):337-353. https://doi.org/10.1007/s42976-024-00520-8

Brini, F., Hanin, M., Lumbreras, V., Amara, I., Khoudi, H. et al. (2007). Overexpression of wheat dehydrin *DHN-5* enhances tolerance to salt and osmotic stress in *Arabidopsis thaliana. Plant Cell Reports* 26(11):2017-2026. https://doi.org/10.1007/s00299-007-0412-x

Byrt, C.S., Xu, B., Krishnan, M., Lightfoot, D.J., Athman, A. et al. (2014). The Na^+ transporter, TaHKT1;5-D, limits shoot Na^+ accumulation in bread wheat. *The Plant Journal* 80(3):516-526. https://doi.org/10.1111/tpj.12651

Cao, Y.H., Ren, W., Gao, H.J., Lü, X.P., Zhao, Q. et al. (2023). HaASR2 from *Haloxylon ammodendron* confers drought and salt tolerance in plants. *Plant Science* 328:111572.

Chartzoulakis, K., Klapaki, G. (2000). Response of two greenhouse pepper hybrids to NaCl salinity during different growth stages. *Scientia Horticulturae* 86(3):247-260. https://doi.org/10.1016/S0304-4238(00)00147-3

Chaves, M.M., Flexas, J., Pinheiro, C. (2009). Photosynthesis under drought and salt stress: Regulation mechanisms from whole plant to cell. *Annals of Botany* 103(4):551-560. https://doi.org/10.1093/aob/mcn125

Chen, C., Li, Y., Wang, Y. (2021). Transcriptional control of antioxidant defense by stress-responsive transcription factors under salt stress. *Plant Science* 311*:*111008. https://doi.org/10.1016/j.plantsci.2021.111008

Chen, C., Yu, W., Xu, X., Wang, Y., Wang, B. et al. (2024). Research advancements in salt tolerance of Cucurbitaceae: From salt response to molecular mechanisms. *International Journal of Molecular Sciences 25*(16):9051. https://doi.org/10.3390/ijms25169051

Chen, H., An, R., Tang, J.H., Cui, X.H., Hao, F.S. et al. (2007). Over-expression of a vacuolar Na^+/H^+ antiporter gene improves salt tolerance in an upland rice. *Molecular Breeding* 19(3):215-225. https://doi.org/10.1007/s11032-006-9058-6

Choi, M.S., Kim, J.H., Jang, C.S. (2024). Rice H2-type RING E3 ligase gene, *OsSIRH2-3*, positively regulates salt tolerance by maintaining Na^+/K^+ homeostasis. *Journal of Plant Biology 67*(4):283-298. https://doi.org/10.1007/s12374-024-09418-8

Colin, L., Ruhnow, F., Zhu, J.K., Zhao, C., Zhao, Y. et al. (2023). The cell biology of primary cell walls during salt stress. *The Plant Cell* 35(1):201-217. https://doi.org/10.1093/plcell/koac292

Cuin, T.A., Tian, Y., Betts, S.A., Chalmandrier, R., Shabala, S. (2009). Ionic relations and osmotic adjustment in durum and bread wheat under saline conditions. *Functional Plant Biology* 36(12):1110-1119. https://doi.org/10.1071/FP09051

de Silva, N.D.G., Murmu, J., Chabot, D., Hubbard, K., Ryser, P. et al. (2021). Root suberin plays important roles in reducing water loss and sodium uptake in *Arabidopsis thaliana*. *Metabolites* 11(11):735. https://doi.org/10.3390/metabo11110735

Farhangi-Abriz, S., Ghassemi-Golezani, K. (2018). How can salicylic acid and jasmonic acid mitigate salt toxicity in soybean plants? *Ecotoxicology and Environmental Safety* 147:1010-1016. https://doi.org/10.1016/j.ecoenv.2017.09.070

Flowers, T.J., Colmer, T.D. (2008). Salinity tolerance in halophytes. *New Phytologist* 179(4):945-963. https://doi.org/10.1111/j.1469-8137.2008.02531.x

Flowers, T.J., Colmer, T.D. (2015). Plant salt tolerance: Adaptations in halophytes. *Annals of Botany* 115(3):327-331. https://doi.org/10.1093/aob/mcu267

Flowers, T.J., Galal, H.K., Bromham, L. (2010). Evolution of halophytes: Multiple origins of salt tolerance in land plants. *Functional Plant Biology* 37(7):604-612. https://doi.org/10.1071/FP09269

Food and Agriculture Organization (FAO). United Nations (UN). (2024). FAO launches first major global assessment of salt-affected soils in 50 years. FAO Newsroom. https://www.fao.org/newsroom/detail/fao-launches-first-major-global-assessment-of-salt-affected-soils-in-50-years/en

Foyer, C.H., Kunert, K. (2024). The ascorbate-glutathione cycle coming of age. *Journal of Experimental Botany* 75*(*9):2682-2699. https://doi.org/10.1093/jxb/erae123

Fu, E., Myrans, H., Gleadow, R.M. (2025). Saline irrigation improves survival of forage sorghum but limits growth and increases toxicity. *Plant Biology* 27(3):401-409. https://doi.org/10.1111/plb.13622

Fujita, Y., Fujita, M., Shinozaki, K., Yamaguchi-Shinozaki, K. (2005). ABA-mediated transcriptional regulation in response to osmotic stress in plants. *Journal of Plant Research* 118(3):175-186.

Garcia-Daga, S., Roy, S.J., Gilliham, M. (2025). Redefining the role of sodium exclusion within salt tolerance. *Trends in Plant Science* 30(1):12-25. https://doi.org/10.1016/j.tplants.2024.09.002

Gattward, J.N., Almeida, A.A.F., Souza, J.O., Gomes, F.P., Kronzucker, H.J. (2012). Sodium-potassium synergism in *Theobroma cacao*: Stimulation of photosynthesis, water-use efficiency and mineral nutrition. *Physiologia Plantarum* 146(3):350-362. https://doi.org/10.1111/j.1399-3054.2012.01621.x

Gaxiola, R.A., Rao, R., Sherman, A., Grisafi, P., Alper, S.L. et al. (1999). The *Arabidopsis thaliana* proton transporters, *AtNhx1* and *Avp1*, can function in cation detoxification in yeast. *Proceedings of the National Academy of Sciences* 96(4):1480-1485. https://doi.org/10.1073/pnas.96.4.1480

Ghosh, S., Biswas, S., Maiti, S. (2025). Plant hormone-mediated adaptive traits under salinity stress: Advances and prospects. *Plant Growth Regulation* 111(1):1-18. https://doi.org/10.1007/s10725-025-01305-7

Gieniec, M., Miszalski, Z., Rozpądek, P., Jędrzejczyk, R. J., Czernicka, M. et al. (2024). How the ethylene biosynthesis pathway of semi-halophytes is modified with prolonged salinity stress occurrence? *International Journal of Molecular Sciences* 25(9):4777. https://doi.org/10.3390/ijms25094777

Gierth, M., Mäser, P. (2007). Potassium transporters in plants - Involvement in K^+ acquisition, redistribution and homeostasis. *FEBS Letters* 581(12):2348-2356. https://doi.org/10.1016/j.febslet.2007.03.035

Gouiaa, S., Khoudi, H. (2019). Expression of V-PPase proton pump, singly or in combination with a NHX1 transporter, in transgenic tobacco improves copper tolerance and accumulation. *Environmental Science and Pollution Research* 26(36):37037-37045. https://doi.org/10.1007/s11356-019-06694-7

Guan, Q., Wang, Z., Wang, X., Takano, T., Liu, S. (2015). A peroxisomal APX from *Puccinellia tenuiflora* improves the abiotic stress tolerance of transgenic *Arabidopsis thaliana* through decreasing of H_2O_2 accumulation. *Journal of Plant Physiology* 175:183-191.

Guerzoni, J.T.S., Belintani, N.G., Moreira, R.M.P., Hoshino, A.A., Domingues, D.S. et al. (2014). Stress-induced Δ1-pyrroline-5-carboxylate synthetase (P5CS) gene confers tolerance to salt stress in transgenic sugarcane. *Acta Physiologiae Plantarum* 36(9):2309-2319.

Gupta, K., Singh, A., Pandey, A., Mishra, V. (2024). Transcriptional regulation of antioxidant defense in plants under salt stress: Role of NAC, DREB, and bZIP factors. *Plant Physiology and Biochemistry* 205*:*107200. https://doi.org/10.1016/j.plaphy.2024.107200

Hadi, S.M.S., Ahmed, M.Z., Hameed, A., Khan, M.A., Gul, B. (2018). Seed germination and seedling growth responses of toothbrush tree (*Salvadora persica* Linn.) to different interacting abiotic stresses. *Flora* 243:45-52. https://doi.org/10.1016/j.flora.2018.04.002

Hammami, Z., Gauffreteau, A., Belhaj Fraj, M., Sahli, A., Jeuffroy, M.H. et al. (2017). Predicting yield reduction in improved barley (*Hordeum vulgare* L.) varieties and landraces under salinity using selected tolerance traits. *Field Crops Research* 211:10-18. https://doi.org/10.1016/j.fcr.2017.06.014

Hasanuzzaman, M., Raihan, M.R.H., Masud, A.A.C., Rahman, K., Nowroz, F. et al. (2021). Regulation of reactive oxygen species and antioxidant defense in plants under salinity. *International Journal of Molecular Sciences* 22(17):9326.

Hasegawa, P.M. (2013). Sodium (Na^+) homeostasis and salt tolerance of plants. *Environmental and Experimental Botany* 92:19-31. https://doi.org/10.1016/j.envexpbot.2012.07.001

Hasegawa, P.M., Bressan, R.A., Zhu, J.K., Bohnert, H.J. (2000). Plant cellular and molecular responses to high salinity. *Annual Review of Plant Biology* 51:463-499. https://doi.org/10.1146/annurev.arplant.51.1.463

He, L., Zhang, Q., Liu, Y. (2025). Hormonal regulation of salinity tolerance: Integrative signaling pathways in plants. *Plant Signaling & Behavior* 20(1):2479513. https://doi.org/10.1080/15592324.2025.2479513

Hmida-Sayari, A., Gargouri-Bouzid, R., Bidani, A., Jaoua, L., Savouré, A. et al. (2005). Overexpression of Δ1-pyrroline-5-carboxylate synthetase increases proline production and confers salt tolerance in transgenic potato plants. *Plant Science* 169(4):746-752.

Hnilickova, H., Kraus, K., Vachova, P., Hnilicka, F. (2021). Salinity stress affects photosynthesis, malondialdehyde formation, and proline content in *Portulaca oleracea* L. *Plants* 10(5):845. https://doi.org/10.3390/plants10050845

Horie, T., Hauser, F., Schroeder, J.I. (2009). HKT transporter-mediated salinity resistance mechanisms in *Arabidopsis* and monocot crop plants. *Trends in Plant Science* 14(12):660-668. https://doi.org/10.1016/j.tplants.2009.08.009

Houston, K., Qiu, J., Wege, S., Hrmova, M., Oakey, H. et al. (2020). Barley sodium content is regulated by natural variants of the Na^+ transporter *HvHKT1;5. Communications Biology* 3(1):258. https://doi.org/10.1038/s42003-020-0989-y

Hu, Y., Wang, D., Zhang, X., Lv, X., Li, B. (2025). Current progress in deciphering the molecular mechanisms underlying plant salt tolerance. *Current Opinion in Plant Biology 83:*102671. https://doi.org/10.1016/j.pbi.2025.102671

Huang, Y., Guan, C., Liu, Y., Chen, B., Yuan, S. et al. (2017). Enhanced growth performance and salinity tolerance in transgenic switchgrass via overexpressing vacuolar Na^+ $(K^+)/H^+$ antiporter gene (*PvNHX1*). *Frontiers in Plant Science* 8:458. https://doi.org/10.3389/fpls.2017.00458

Iannucci, A., Russo, M., Arena, L., Di Fonzo, N., Martiniello, P. (2002). Water deficit effects on osmotic adjustment and solute accumulation in leaves of annual clovers. *European Journal of Agronomy* 16(2):111-122. https://doi.org/10.1016/S1161-0301(01)00122-1

International Atomic Energy Agency (IAEA) (2024). “Pakistan Shares IAEA Soil Salinization Solutions Through South-South Cooperation”. *IAEA News Centre.* https://doi.org/10.1016/S1161-0301(01)00122-1

Iqbal, M., Ashraf, M. (2013). Gibberellic acid mediated induction of salt tolerance in wheat plants: Growth, ionic partitioning, photosynthesis, yield and hormonal homeostasis. *Environmental and Experimental Botany* 86:76-85. https://doi.org/10.1016/j.envexpbot.2012.07.006

Ishikawa, T., Shabala, S. (2019). Control of xylem Na^+ loading and transport to the shoot in rice and barley as a determinant of differential salinity stress tolerance. *Physiologia Plantarum* 165(3):619-631. https://doi.org/10.1111/ppl.12756

Ismail, A.M., Horie, T. (2017). Genomics, physiology, and molecular breeding approaches for improving salt tolerance. *Annual Review of Plant Biology* 68:405-434. https://doi.org/10.1146/annurev-arplant-042916-040949

Jaime-Pérez, N., Pineda, B., García-Sogo, B., Atares, A., Athman, A. et al. (2017). The sodium transporter encoded by the *HKT1;2* gene modulates sodium/potassium homeostasis in tomato shoots under salinity. *Plant, Cell & Environment* 40(4):658-671. https://doi.org/10.1111/pce.12883

Jayakannan, M., Bose, J., Babourina, O., Rengel, Z., Shabala, S. (2015). Salicylic acid in plant salinity stress signalling and tolerance. *Plant Growth Regulation* 76(1):25-40. https://doi.org/10.1007/s10725-015-0028-z

Jiang, L., Xiao, M., Huang, R., Wang, J. (2025). The regulation of ROS and phytohormones in balancing crop yield and salt tolerance. *Antioxidants* 14*(*1):63. https://doi.org/10.3390/antiox14010063

Jin, Y., Yang, P., Li, J., Yang, Y., Yang, R. et al. (2024). Brassinosteroids alleviate salt stress by enhancing sugar and glycine betaine in pepper (*Capsicum annuum* L.). *Plants* 13(21):3029. https://doi.org/10.3390/plants13213029

Kaku, N., Hibino, T., Tanaka, Y., Ishikawa, H., Araki, E. et al. (2000). Effects of overexpression of *Escherichia coli katE* and *bet* genes on the tolerance for salt stress in a freshwater cyanobacterium *Synechococcus* sp. PCC 7942. *Plant Science* 159(2):281-288. https://doi.org/10.1016/S0168-9452(00)00353-8

Karimi, M.R., Sabokdast, M., Korang Beheshti, H., Abbasi, A.R., Bihamta, M.R. (2025). Seed priming with salicylic acid enhances salt stress tolerance by boosting antioxidant defense in *Phaseolus vulgaris* genotypes. *BMC Plant Biology* 25(1):489. https://doi.org/10.1186/s12870-025-04889-8

Kaur, G., Sanwal, S.K., Kumar, A., Pundir, R.K., Yadav, M. et al. (2024). Role of osmolytes dynamics in plant metabolism to cope with salinity induced osmotic stress. *Discover Agriculture* 2(1):59. https://doi.org/10.1007/s44279-024-00059-6

Khan, I., Muhammad, A., Chattha, M.U., Skalicky, M., Bilal Chattha, M. et al. (2022). Mitigation of salinity-induced oxidative damage, growth, and yield reduction in fine rice by sugarcane press mud application. *Frontiers in Plant Science* 13:840900. https://doi.org/10.3389/fpls.2022.840900

Khan, M.O., Irfan, M., Muhammad, A., Ullah, I., Nawaz, S. et al. (2022). A practical and economical strategy to mitigate salinity stress through seed priming. *Frontiers in Environmental Science* 10*:*991977. https://doi.org/10.3389/fenvs.2022.991977

Kim, T.H., Böhmer, M., Hu, H., Nishimura, N., Schroeder, J.I. (2010). Guard cell signal transduction network: Advances in understanding abscisic acid, CO_2, and Ca^{2+} signaling. *Annual Review of Plant Biology* 61:561-591. https://doi.org/10.1146/annurev-arplant-042809-112226

Kobayashi, N.I., Yamaji, N., Yamamoto, H., Okubo, K., Ueno, H. et al. (2017). *OsHKT1;5* mediates Na^+ exclusion in the vasculature to protect leaf blades and reproductive tissues from salt toxicity in rice. *The Plant Journal* 91(4):657-670. https://doi.org/10.1111/tpj.13595

Koc, Y.E., Aycan, M., Mitsui, T. (2024). Self-defense mechanism in rice to salinity: proline. *J* 7(1):103-115. https://doi.org/10.3390/j7010006

Koevoets, I.T., Venema, J.H., Elzenga, J.T.M., Testerink, C. (2016). Roots withstanding their environment: Exploiting root system architecture responses to abiotic stress to improve crop tolerance. *Frontiers in Plant Science* 7:1335. https://doi.org/10.3389/fpls.2016.01335

Kopic, E. (2024). "On the physiological role of post-translational regulation of the *Arabidopsis* guard cell outward rectifying potassium channel GORK". Doctoral dissertation, Universität Würzburg.

Körner, T., Zinkernagel, J., Röhlen-Schmittgen, S. (2025). Plant growth and metabolic responses of tomato varieties to salinity stress after thermopriming. *Stresses* 5(2):27. https://doi.org/10.3390/stresses5020027

Koull, N., Chehma, A. (2016). Soil characteristics and plant distribution in saline wetlands of Oued Righ, northeastern Algeria. *Journal of Arid Land* 8(6):948-959. https://doi.org/10.1007/s40333-016-0058-z

Läuchli, A., James, R.A., Huang, C.X., McCully, M., Munns, R. (2008). Cell-specific localization of Na^+ in roots of durum wheat and possible control points for salt exclusion. *Plant, Cell & Environment* 31(11):1565-1574. https://doi.org/10.1111/j.1365-3040.2008.01864.x

Lee, Y.P., Ahmad, R., Lee, H.S., Kwak, S.S., Shafqat, M.N. et al. (2013). Improved tolerance of Cu/Zn superoxide dismutase and ascorbate peroxidase expressing transgenic tobacco seeds and seedlings against multiple abiotic stresses. *International Journal of Agriculture and Biology* 15(4):725-730.

Leidi, E.O., Barragán, V., Rubio, L., El-Hamdaoui, A., Ruiz, M.T. et al. (2010). The *AtNHX1* exchanger mediates potassium compartmentation in vacuoles of transgenic tomato. *The Plant Journal* 61(3):495-506. https://doi.org/10.1111/j.1365-313X.2009.04073.x

Li, S., Liu, S., Zhang, Q., Cui, M., Zhao, M. et al. (2022). The interaction of ABA and ROS in plant growth and stress resistances. *Frontiers in Plant Science* 13:1050132. https://doi.org/10.3389/fpls.2022.1050132

Li, W., Zhang, C., Zou, M., Lai, H., Javed, T. et al. (2025). Optimizing irrigation salinity for cotton production through cotton yield and fiber quality and water use efficiency in arid regions. *Industrial Crops and Products* 233:121375. https://doi.org/10.1016/j.indcrop.2025.121375

Li, X., Chen, Z., Wang, P., Zhang, H. (2022). The AREB/ABF-bZIP transcription factor network regulates salt-induced antioxidant responses through ABA signaling. *Environmental and Experimental Botany* 196*:*104799. https://doi.org/10.1016/j.envexpbot.2021.104799

Li, X., Zhang, W., Niu, D., Liu, X. (2024). Effects of abiotic stress on chlorophyll metabolism. *Plant Science* 342*:*112030. https://doi.org/10.1016/j.plantsci.2024.112030

Liao, Q., Ding, R., Du, T., Kang, S., Tong, L. et al. (2024). Stomatal conductance modulates maize yield through water use and yield components under salinity stress. *Agricultural Water Management* 294:108463. https://doi.org/10.1016/j.agwat.2024.108463

Liao, R., Wang, L., Zeng, J., Tang, X., Huang, M. et al. (2025). Reactive oxygen species: Orchestrating the delicate dance of platelet life and death. *Redox Biology* 75*:*103489. https://doi.org/10.1016/j.redox.2025.103489

Lichtenthaler, H.K., Langsdorf, G., Lenk, S., Buschmann, C. (2005). Chlorophyll fluorescence imaging of photosynthetic activity with the flash-lamp fluorescence imaging system. *Photosynthetica* 43(3):355-369. https://doi.org/10.1007/s11099-005-0060-8

Lin, C.C., Kao, C.H. (2001). Relative importance of Na^+, Cl^-, and abscisic acid in NaCl induced inhibition of root growth of rice seedlings. *Plant and Soil* 237(1):165-171. https://doi.org/10.1023/A:1013380329776

Lindsay, R.T., Rhodes, C.J. (2025). Reactive oxygen species (ROS) in metabolic disease - Don't shoot the metabolic messenger. *International Journal of Molecular Sciences* 26(6):2622. https://doi.org/10.3390/ijms26062622

Liu, G., Yu, X., Zeng, Y., Li, B., Wang, R. et al. (2025). SOS2-FREE1 regulates *SOS1* tonoplast sorting to promote Na^+ compartmentalization in vacuole during salt stress response. *Journal of Integrative Plant Biology* 67(2):301-315. https://doi.org/10.1111/jipb.13622

Liu, H.S., Liu, Q., Hepworth, S.R., Li, P.Q., Huang, J. et al. (2025). *ZxNHX1* from a xerophyte outperforms *AtNHX1* in sequestering Na^+ into vacuoles to enhance plant stress resistance and yield. *Plant Biotechnology Journal* 23*(*5):1124-1138. https://doi.org/10.1111/pbi.14322

Liu, X., Cai, S., Wang, G., Wang, F., Dong, F. et al. (2017). Halophytic *NHXs* confer salt tolerance by altering cytosolic and vacuolar K^+ and Na^+ in *Arabidopsis* root cell. *Plant Growth Regulation* 82(2):333-351. https://doi.org/10.1007/s10725-017-0263-6

Luo, Z., Kong, X., Zhang, Y., Li, W., Zhang, D. et al. (2019). Leaf-derived jasmonate mediates water uptake from hydrated cotton roots under partial root-zone irrigation. *Plant Physiology* 180(3):1660-1676. https://doi.org/10.1104/pp.19.00315

Ma, Y., Wang, Z., Zhou, B., Yang, W., Wang, Y. (2025). Salicylic acid improving salinity tolerance by enhancing photosynthetic capacity, osmotic adjustment and maintenance of Na^+/K^+ homeostasis in faba bean seedlings. *Chemical and Biological Technologies in Agriculture* 12(1):89. https://doi.org/10.1186/s40538-025-00489-4

Ma, Z., Zhu, Y., Liu, J., Li, Y., Zhang, J. et al. (2024). Multi-objective optimization of saline water irrigation in arid oasis regions: Integrating water-saving, salinity control, yield enhancement, and CO_2 emission reduction for sustainable cotton production. *Science of the Total Environment* 912:169672. https://doi.org/10.1016/j.scitotenv.2023.169672

Mahajan, R., Kumar, P., Sharma, S. (2025). Abscisic acid and its regulation of salinity tolerance in crop plants. *Environmental and Experimental Botany* 212:105653. https://doi.org/10.1016/j.envexpbot.2025.105653

Mangano, S., Denita-Juarez, S.P., Choi, H.S., Marzol, E., Hwang, Y. et al. (2017). Molecular link between auxin and ROS-mediated polar growth. *Proceedings of the National Academy of Sciences* 114(20):5289-5294. https://doi.org/10.1073/pnas.1701536114

Meng, T., Wang, L., Zhu, W., Zhu, G., Wei, H. et al. (2025). Root morpho-physiological characteristics and yield formation of rice under combined salinity-drought stress. *Journal of Agronomy and Crop Science* 211(2):e70026. https://doi.org/10.1111/jac.12622

Mittler, R., Vanderauwera, S., Suzuki, N., Miller, G., Tognetti, V.B. et al. (2011). ROS signaling: The new wave? *Trends in Plant Science* 16(6):300-309. https://doi.org/10.1016/j.tplants.2011.03.007

Molinari, M.D.C., Fuganti-Pagliarini, R., Marin, S.R.R., Ferreira, L.C., Barbosa, D.D.A. et al. (2020). Overexpression of *AtNCED3* gene improved drought tolerance in soybean in greenhouse and field conditions. *Genetics and Molecular Biology* 43(3):e20190292. https://doi.org/10.1590/1678-4685-GMB-2019-0292

Morgan, S.H., Lindberg, S., Maity, P.J., Geilfus, C.M., Plieth, C. et al. (2017). Calcium improves apoplastic-cytosolic ion homeostasis in salt-stressed *Vicia faba* leaves. *Functional Plant Biology* 44(5):515-524. https://doi.org/10.1071/FP16290

Moriwaki, T., Yamamoto, Y., Aida, T., Funahashi, T., Shishido, T. et al. (2008). Overexpression of the *Escherichia coli* catalase gene, *katE*, enhances tolerance to salinity stress in the transgenic indica rice cultivar, BR5. *Plant Biotechnology Reports* 2(1):41-46. https://doi.org/10.1007/s11816-008-0046-7

Munns, R., James, R.A., Xu, B., Athman, A., Conn, S.J. et al. (2012). Wheat grain yield on saline soils is improved by an ancestral Na^+ transporter gene. *Nature Biotechnology* 30(4):360-364. https://doi.org/10.1038/nbt.2120

Munns, R., Passioura, J.B., Colmer, T.D., Byrt, C.S. (2020). Energy costs of salt tolerance in crop plants. *New Phytologist* 225(3):1072-1090. https://doi.org/10.1111/nph.15864

Munns, R., Tester, M. (2008). Mechanisms of salinity tolerance. *Annual Review of Plant Biology* 59:651-681. https://doi.org/10.1146/annurev.arplant.59.032607.092911

Nagamiya, K., Motohashi, T., Nakao, K., Prodhan, S. H., Hattori, E. et al. (2007). Enhancement of salt tolerance in transgenic rice expressing an *Escherichia coli* catalase gene, *kat E*. *Plant Biotechnology Reports* 1(1):49-55.

Nahar, K., Hasanuzzaman, M., Rahman, A., Alam, M.M., Mahmud, J.A. et al. (2016). Polyamines confer salt tolerance in mung bean (*Vigna radiata* L.) by reducing sodium uptake, improving nutrient homeostasis, antioxidant defense, and methylglyoxal detoxification systems. *Frontiers in Plant Science* 7:1104.

Navarro-Torre, S., Garcia-Caparrós, P., Nogales, A., Abreu, M.M., Santos, E. et al. (2023). Sustainable agricultural management of saline soils in arid and semi-arid Mediterranean regions through halophytes, microbial and soil-based technologies. *Environmental and Experimental Botany* 212:105397. https://doi.org/10.1016/j.envexpbot.2023.105397

Nicolas, F., Kamai, T., Ben-Gal, A., Ochoa-Brito, J., Daccache, A. et al. (2023). Assessing salinity impacts on crop yield and economic returns in the Central Valley. *Agricultural Water Management* 287:108463. https://doi.org/10.1016/j.agwat.2023.108463

Ombale, S., Bhatt, M., Tiwari, A.K., Sharma, A., Tiwari, B.S. (2025). Cellular nitro-oxidative burden and survival through regulated cell death in the plants. *Protoplasma* 262*(*3):1-14. https://doi.org/10.1007/s00709-025-01989-8

Pamplona, R. (2008). Membrane phospholipids, lipoxidative damage and molecular integrity: A causal role in aging and longevity. *Biochimica et Biophysica Acta (BBA) - Biomembranes* 1777(10):1249-1262. https://doi.org/10.1016/j.bbamem.2008.07.003

Parida, A.K., Das, A.B. (2005). Salt tolerance and salinity effects on plants: A review. *Ecotoxicology and Environmental Safety* 60(3):324-349. https://doi.org/10.1016/j.ecoenv.2004.06.010

Paul, S., Roychoudhury, A. (2017). Seed priming with spermine and spermidine regulates the expression of diverse groups of abiotic stress-responsive genes during salinity stress in the seedlings of indica rice varieties. *Plant Gene* 11:124-132. https://doi.org/10.1016/j.plgene.2017.04.004

Percey, W.J., Shabala, L., Wu, Q., Su, N., Breadmore, M.C. et al. (2016). Potassium retention in leaf mesophyll as an element of salinity tissue tolerance in halophytes. *Plant Physiology and Biochemistry* 109:346-354. https://doi.org/10.1016/j.plaphy.2016.10.011

Pikor, D., Hurła, M., Słowikowski, B., Szymanowicz, O., Poszwa, J. et al. (2024). Calcium ions in the physiology and pathology of the central nervous system. *International Journal of Molecular Sciences* 25(23):13133. https://doi.org/10.3390/ijms252313133

Platten, J.D., Cotsaftis, O., Berthomieu, P., Bohnert, H., Davenport, R.J. et al. (2006). Nomenclature for HKT transporters, key determinants of plant salinity tolerance. *Trends in Plant Science* 11(8):372-374. https://doi.org/10.1016/j.tplants.2006.06.001

Porter, T.K., Sánchez-Velázquez, G., Strano, M.S. (2025). The role of basal H_2O_2 concentration in ROS stress signaling waveforms *in planta. ACS Agricultural Science & Technology* 5(3):112-125. https://doi.org/10.1021/acsagscitech.5c00022

Prashanth, S.R., Sadhasivam, V., Parida, A. (2008). Overexpression of cytosolic copper/zinc superoxide dismutase from a mangrove plant *Avicennia marina* in indica rice var Pusa Basmati-1 confers abiotic stress tolerance. *Transgenic Research* 17:281-291. https://doi.org/10.1007/s11248-007-9099-6

Prodhan, S.H., Hossain, A., Nagamiya, K., Komamine, A., Morishima, H. (2008). Improved salt tolerance and morphological variation in indica rice (*Oryza sativa* L.) transformed with a catalase gene from *E. coli*. *Plant Tissue Culture and Biotechnology* 18(1):57-63.

Qi, Y., Qiu, Q.S. (2025). Dual roles of *SOS1*: Na^+ extrusion and vacuolar compartmentation. *Plant Communications* 6(1):100678. https://doi.org/10.1016/j.xplc.2025.100678

Rahman, A., Mostofa, M.G., Nahar, K., Hasanuzzaman, M., Fujita, M. (2016). Exogenous calcium alleviates cadmium-induced oxidative stress in rice (*Oryza sativa* L.) seedlings by regulating the antioxidant defense and glyoxalase systems. *Brazilian Journal of Botany* 39(2):393-407. https://doi.org/10.1007/s40415-016-0264-0

Rajput, V.D., Harish, Singh, R.K., Verma, K.K., Sharma, L. et al. (2021). Recent developments in enzymatic antioxidant defence mechanism in plants with special reference to abiotic stress. *Biology* 10(4):267. https://doi.org/10.3390/biology10040267

Ramakrishna, P., Gámez-Arjona, F.M., Bellani, E., Martin-Olmos, C., Escrig, S. et al., (2025). Elemental cryo-imaging reveals *SOS1*-dependent vacuolar sodium accumulation. *Nature* 637(8048):1228-1233. https://doi.org/10.1038/s41586-025-04389-1

Rao, M.J., Duan, M., Zhou, C., Jiao, J., Cheng, P. et al. (2025). Antioxidant defense system in plants: Reactive oxygen species production, signaling, and scavenging during abiotic stress-induced oxidative damage. *Horticulturae* 11(5):477. https://doi.org/10.3390/horticulturae11050477

Raven, J.A. (1985). Regulation of pH and generation of osmolarity in vascular plants - A cost-benefit analysis in relation to efficiency of use of energy, nitrogen and water. *New Phytologist* 101(1):25-77. https://doi.org/10.1111/j.1469-8137.1985.tb02816.x

Reddy, A.M., Reddy, V.S., Scheffler, B.E., Wienand, U., Reddy, A.R. (2007). Novel transgenic rice overexpressing anthocyanidin synthase accumulates a mixture of flavonoids leading to an increased antioxidant potential. *Metabolic Engineering* 9(1):95-111.

Ren, X.L., Qi, G.N., Feng, H.Q., Zhao, S., Zhao, S.S. et al. (2013). Calcineurin B-like protein *CBL10* directly interacts with *AKT1* and modulates K^+ homeostasis in *Arabidopsis. The Plant Journal* 74(2):258-266. https://doi.org/10.1111/tpj.12123

Riedelsberger, J., Miller, J.K., Valdebenito-Maturana, B., Piñeros, M.A., González, W. et al. (2021). Plant HKT channels: An updated view on structure, function and gene regulation. *International Journal of Molecular Sciences* 22(4):1892. https://doi.org/10.3390/ijms22041892

Rodríguez-Rosales, M.P., Gálvez, F.J., Huertas, R., Aranda, M.N., Baghour, M. et al. (2009). Plant NHX cation/proton antiporters. *Plant Signaling & Behavior* 4(4):265-276. https://doi.org/10.4161/psb.4.4.7919

Romero-Aranda, M.R., Espinosa, J., González-Fernández, P., Jaime-Pérez, N., Carvajal, M. et al. (2020). Na^+ transporter *HKT1;2* reduces flower Na^+ content and considerably mitigates the decline in tomato fruit yields under saline conditions. *Plant Physiology and Biochemistry* 154:341-352. https://doi.org/10.1016/j.plaphy.2020.05.036

Rorat, T. (2006). Plant dehydrins - Tissue location, structure and function. *Cellular and Molecular Biology Letters* 11(4):536-556. https://doi.org/10.2478/s11658-006-0044-0

Rozema, J., Schat, H. (2013). Salt tolerance of halophytes, research questions reviewed in the perspective of saline agriculture. *Environmental and Experimental Botany* 92:83-95. https://doi.org/10.1016/j.envexpbot.2012.08.004

Ruan, C.J., Teixeira da Silva, J.A., Mapper, S., Qin, P., Lutts, S. (2010). Halophyte improvement for a salinized world. *Critical Reviews in Plant Sciences* 29(6):329-359. https://doi.org/10.1080/07352689.2010.524517

Ruffino, A.M.C., Rosa, M., Hilal, M., González, J.A., Prado, F.E. (2010). The role of cotyledon metabolism in the establishment of quinoa (*Chenopodium quinoa*) seedlings growing under salinity. *Plant and Soil* 326(1-2):213-224. https://doi.org/10.1007/s11104-009-9998-9

Rus, A., Baxter, I., Muthukumar, B., Gustin, J., Lahner, B. et al. (2006). Natural variants of *AtHKT1* enhance Na^+ accumulation in two wild populations of *Arabidopsis. PLOS Genetics* 2(12):e210. https://doi.org/10.1371/journal.pgen.0020210

Sachdev, S., Ansari, S.A., Ansari, M.I. (2023). "*Reactive Oxygen Species in Plants*". Springer. https://doi.org/10.1007/978-3-031-31129-8

Sahoo, D.P., Kumar, S., Mishra, S., Kobayashi, Y., Panda, S.K. et al. (2016). Enhanced salinity tolerance in transgenic mungbean overexpressing *Arabidopsis* antiporter (*NHX1*) gene. *Molecular Breeding* 36(10):144. https://doi.org/10.1007/s11032-016-0566-8

Sakamoto, A., Murata, N. (2002). The role of glycine betaine in the protection of plants from stress: Clues from transgenic plants. *Plant, Cell & Environment* 25(2):163-171. https://doi.org/10.1046/j.0016-8025.2001.00790.x

Sandhu, D., Cornacchione, M.V., Ferreira, J.F.S., Suarez, D.L. (2017). Variable salinity responses of 12 alfalfa genotypes and comparative expression analyses of salt-response genes. *Scientific Reports* 7:42958. https://doi.org/10.1038/srep42958

Santos, C.V. (2004). Regulation of chlorophyll biosynthesis and degradation by salt stress in sunflower leaves. *Scientia Horticulturae* 103(1):93-99. https://doi.org/10.1016/j.scienta.2004.04.009

Saxena, S.C., Salvi, P., Kamble, N.U., Joshi, P.K., Majee, M. et al. (2020). Ectopic overexpression of cytosolic ascorbate peroxidase gene (*Apx1*) improves salinity stress tolerance in *Brassica juncea* by strengthening antioxidative defense mechanism. *Acta Physiologiae Plantarum* 42(4):45. https://doi.org/10.1007/s11738-020-3032-5

Sellamuthu, G., Tarafdar, A., Jasrotia, R.S., Chaudhary, M., Vishwakarma, H. et al. (2024). Introgression of Δ1-pyrroline-5-carboxylate synthetase (PgP5CS) confers enhanced resistance to abiotic stresses in transgenic tobacco. *Transgenic Research* 33(3):131-147.

Shabala, S. (2017). Signalling by potassium: Another second messenger to add to the list? *Journal of Experimental Botany* 68(15):4003-4007. https://doi.org/10.1093/jxb/erx238

Shabala, S., Bose, J., Hedrich, R. (2022). Salt glands: Evolution, structure, and function. *Annual Review of Plant Biology* 73:559-584. https://doi.org/10.1146/annurev-arplant-070221-020457

Shabala, S., Chen, X., Yun, P., Zhou, M. (2025). Salinity tolerance in wheat: Rethinking the targets. *Journal of Experimental Botany* 76(12):eraf152. https://doi.org/10.1093/jxb/eraf152

Shabala, S., Cuin, T.A. (2007). Potassium transport and plant salt tolerance. *Physiologia Plantarum* 133(4):651-669. https://doi.org/10.1111/j.1399-3054.2007.01008.x

Shabala, S., Mackay, A. (2011). Ion transport in halophytes. *Advances in Botanical Research* 57:151-187. https://doi.org/10.1016/B978-0-12-387692-8.00005-9

Shabala, S., Shabala, L. (2011). Ion transport and osmotic adjustment in plants and bacteria. *Biomolecular Concepts* 2(5):407-419. https://doi.org/10.1515/BMC.2011.032

Shabala, S., Shabala, S., Cuin, T. A., Pang, J., Percey, W. et al. (2010). Xylem ionic relations and salinity tolerance in barley. *The Plant Journal* 61(5):839-853. https://doi.org/10.1111/j.1365-313X.2009.04110.x

Shafiq, F., Batool, H., Raza, S.H., Hameed, M. (2015). Effect of potassium nitrate seed priming on allometry of drought-stressed cotton (*Gossypium hirsutum* L.). *Journal of Crop Science and Biotechnology* 18(3):195-204. https://doi.org/10.1007/s12892-015-0034-8

Shafiq, F., Iqbal, M., Ali, M., Ashraf, M.A. (2021). Fullerenol regulates oxidative stress and tissue ionic homeostasis in spring wheat to improve net-primary productivity under salt-stress. *Ecotoxicology and Environmental Safety* 211:111901. https://doi.org/10.1016/j.ecoenv.2021.111901

Shafiq, F., Raza, S.H., Bibi, A., Khan, I., Iqbal, M. (2018). Influence of proline priming on antioxidative potential and ionic distribution and its relationship with salt tolerance of wheat. *Cereal Research Communications* 46(2):286-299. https://doi.org/10.1556/0806.46.2018.019

Sharma, R., Jha, P., Dubey, A., Shanker, A.K. (2023). Antioxidant defense mechanisms and genetic engineering approaches for salinity tolerance in plants. *Environmental and Experimental Botany* 209:105977. https://doi.org/10.1016/j.envexpbot.2022.105977

Shi, H., Quintero, F.J., Pardo, J.M., Zhu, J.K. (2002). The putative plasma membrane Na^+/H^+ antiporter *SOS1* controls long-distance Na^+ transport in plants. *The Plant Cell* 14(2):465-477. https://doi.org/10.1105/tpc.010371

Shohan, M.U.S., Sinha, S., Nabila, F.H., Dastidar, S.G., Seraj, Z.I. (2019). *HKT1;5* transporter gene expression and association of amino acid substitutions with salt tolerance across rice genotypes. *Frontiers in Plant Science* 10:1420. https://doi.org/10.3389/fpls.2019.01420

Shokri, G., Amiri, J., Barin, M. (2024). Spermidine mitigates salt stress in grapevine with alterations in physicochemical properties and nutrient composition. *Journal of Plant Nutrition and Soil Science* 187(4):516-532.

Shorning, B.Y., Smirnova, E.G., Yaguzhinsky, L.S., Vanyushin, B.F. (2000). Necessity of superoxide production for development of etiolated wheat seedlings. *Biochemistry* 65(12):1357-1361.

Shu, S., Guo, R., Sun, J., Yuan, Y. (2012). Effects of salt stress on the structure and function of the photosynthetic apparatus in *Cucumis sativus* and its protection by exogenous putrescine. *Physiologia Plantarum* 146(3):285-296. https://doi.org/10.1111/j.1399-3054.2012.01623.x

Singh, D., Laxmi, A. (2020). Transcriptional regulation of ROS scavenging enzymes by NAC and DREB TFs during abiotic stress. *Journal of Experimental Botany* 71(21):6694-6708. https://doi.org/10.1093/jxb/eraa375

Singh, P., Kumar, R., Verma, R.K. (2022). Transcriptional regulation of ROS homeostasis and antioxidant defense under salt stress: Recent advances. *Plant Stress* 5:100101. https://doi.org/10.1016/j.stress.2022.100101

Song, H., Cao, Y., Zhao, X., Zhang, L. (2024). Na^+-preferential ion transporter *HKT1;1* mediates salt tolerance in blueberry. *Plant Physiology* 194(1):511-529. https://doi.org/10.1093/plphys/kiad584

Song, R.F., Li, T.T., Liu, W.C. (2021). Jasmonic acid impairs *Arabidopsis* seedling salt stress tolerance through *MYC2*-mediated repression of *CAT2* expression. *Frontiers in Plant Science* 12:730228. https://doi.org/10.3389/fpls.2021.730228

Song, X., Zhang, M., Wang, T.T., Duan, Y.Y., Ren, J. et al. (2025). Polyploidization leads to salt stress resilience via ethylene signaling in citrus plants. *New Phytologist* 246(1):176-191. https://doi.org/10.1111/nph.19722

Sreesaeng, J., Qiu, C.W., Zhang, S., Shi, S.H., Wang, Q.Q. et al. (2025). Evaluation of high potential-yielding naked barley genotypes under saline-alkaline soil condition. *Journal of Agronomy and Crop Science* 211(3):e70066. https://doi.org/10.1111/jac.12666

Stefanov, M., Yotsova, E., Rashkov, G., Ivanova, K., Markovska, Y. et al. (2016). Effects of salinity on the photosynthetic apparatus of two *Paulownia* lines. *Plant Physiology and Biochemistry* 101:54-59. https://doi.org/10.1016/j.plaphy.2016.01.018

Taiz, L., Zeiger, E. (2010). “Plant Physiology”. (5th ed.). Sinauer Associates.

Takahashi, T., Kakehi, J. (2010). Polyamines: ubiquitous polycations with unique roles in growth and stress responses. *Annals of Botany* 105(1):1-6. https://doi.org/10.1093/aob/mcp259

Tanou, G., Molassiotis, A., Diamantidis, G. (2009). Hydrogen peroxide- and nitric oxide-induced systemic antioxidant prime-like activity under NaCl-stress and stress-free conditions in citrus plants. *Journal of Plant Physiology* 166(17):1904-1913. https://doi.org/10.1016/j.jplph.2009.06.012

Tardieu, F., Granier, C., Muller, B. (2011). Water deficit and growth. Co-ordinating processes without an orchestrator? *Current Opinion in Plant Biology* 14(3):283-289. https://doi.org/10.1016/j.pbi.2011.02.002

Targino, V.A., Dias, T.J., Sousa, V.F.D.O., Silva, M.D.M., da Silva, A.J. et al. (2025). Growth, gas exchange, and phytochemical quality of nasturtium (*Tropaeolum majus* L.) subjected to proline concentrations and salinity. *Plants* 14(3):301. https://doi.org/10.3390/plants14030301

Tavakoli, M., Poustini, K., Alizadeh, H. (2016). Proline accumulation and related genes in wheat leaves under salinity stress. *Journal of Agricultural Science and Technology* 18(3):707-716.

Tavleeva, M.M., Belykh, E.S., Rybak, A.V., Rasova, E.E., Chernykh, A.A. et al. (2022). Effects of antioxidant gene overexpression on stress resistance and malignization *in vitro* and *in vivo*: a review. *Antioxidants* 11(12):2316. https://doi.org/10.3390/antiox11122316

Teakle, N.L., Tyerman, S.D. (2010). Mechanisms of Cl^- transport contributing to salt tolerance. *Plant, Cell & Environment* 33(4):566-589. https://doi.org/10.1111/j.1365-3040.2009.02060.x

Tedeschi, A., Zong, L., Huang, C.H., Vitale, L., Volpe, M.G. et al. (2017). Effect of salinity on growth parameters, soil water potential and ion composition in *Cucumis melo* cv. Huanghemi in North-Western China. *Journal of Agronomy and Crop Science* 203(1):41-55. https://doi.org/10.1111/jac.12186

Tibesigwa, D.G., Zhuang, W., Matola, S.H., Zhao, H., Li, W. et al. (2025). Molecular insights into salt stress adaptation in plants. *Plant, Cell & Environment* 48*(*3):1-18. https://doi.org/10.1111/pce.14822

Uozumi, N., Kim, E.J., Rubio, F., Yamaguchi, T., Muto, S. et al. (2000). The *Arabidopsis HKT1* gene homolog mediates inward Na^+ currents in *Xenopus laevis* oocytes and Na^+ uptake in *Saccharomyces cerevisiae. Plant Physiology* 122(4):1249-1260. https://doi.org/10.1104/pp.122.4.1249

Upadhyaya, C.P., Venkatesh, J., Gururani, M.A., Asnin, L., Sharma, K. et al. (2011). Transgenic potato overproducing L-ascorbic acid resisted an increase in methylglyoxal under salinity stress via maintaining higher reduced glutathione level and glyoxalase enzyme activity. *Biotechnology Letters* 33(11):2297-2307. https://doi.org/10.1007/s10529-011-0684-7

Van Breusegem, F., Mittler, R. (2023). “*Oxidative Stress Responses in Plants”.* Vol. 105. Elsevier.

Van Camp, W., Capiau, K., Van Montagu, M., Inze, D., Slooten, L. (1996). Enhancement of oxidative stress tolerance in transgenic tobacco plants overproducing Fe-superoxide dismutase in chloroplasts. *Plant Physiology* 112:1703-1714. https://doi.org/10.1104/pp.112.4.1703

Verma, S., Negi, N.P., Pareek, S., Mudgal, G., Kumar, D. (2022). Auxin response factors in plant adaptation to drought and salinity stress. *Physiologia Plantarum* 174(3):e13714. https://doi.org/10.1111/ppl.13714

Waadt, R., Seller, C., Schroeder, J.I. (2022). Integration of ABA, GA, and cytokinin signaling in salinity stress responses. *Frontiers in Plant Science* 13:959212. https://doi.org/10.3389/fpls.2022.959212

Wagner, D., Przybyla, D., op den Camp, R., Kim, C., Landgraf, F. et al. (2004). The genetic basis of singlet oxygen-induced stress responses of *Arabidopsis thaliana. Science* 306(5699):1183-1185. https://doi.org/10.1126/science.1103178

Waheed, A., Xu, Y., Khan, A. (2024). Systems biology approaches to decipher hormonal signaling networks in salt stress tolerance. *Plant Physiology and Biochemistry* 211:1083https://doi.org/10. https://doi.org/10.1016/j.plaphy.2024.108310

Waheed, A., Zhao, Y., Chen, L. (2025). Hormonal regulation of mitochondrial metabolism under salt stress. *Current Plant Biology* 33:100499. https://doi.org/10.1016/j.cpb.2025.100499

Wang, H., Zhang, L., Chen, Y., Liu, Q. (2022). NAC transcription factors enhance salt tolerance by modulating ROS scavenging and antioxidant gene expression in wheat. *BMC Plant Biology* 22(413): https://doi.org/10.1186/s12870-022-03893-5

Wang, J., Li, Y., Zhu, Y., Liu, X., Zhang, X. et al. (2024). Structures and ion transport mechanisms of plant high-affinity potassium transporters. *Molecular Plant* 17(3):409-422. https://doi.org/10.1016/j.molp.2023.12.012

Wang, N., Qi, H., Qiao, W., Shi, J., Xu, Q. et al. (2017). Cotton (*Gossypium hirsutum* L.) genotypes with contrasting K^+/Na^+ ion homeostasis: Implications for salinity tolerance. *Acta Physiologiae Plantarum* 39(3):77-87. https://doi.org/10.1007/s11738-017-2379-8

Wang, X., Chen, Z., Sui, N. (2024a). Sensitivity and responses of chloroplasts to salt stress in plants. *Frontiers in Plant Science* 15*:*1374086. https://doi.org/10.3389/fpls.2024.1374086

Wang, X., Liu, Y., Li, H., Chen, L. (2022). Role of SOD isoforms in salinity tolerance: Insights from transgenic and mutant studies. *BMC Plant Biology* 22*:*502. https://doi.org/10.1186/s12870-022-03893-5

Wang, X., Shen, X., Qu, Y., Zhang, H., Wang, C. et al. (2024b). Structural insights into ion selectivity and transport mechanisms of *Oryza sativa HKT2;1* and HKT2;2/1 transporters. *Nature Plants* 10(4):633-644. https://doi.org/10.1038/s41477-024-01651-w

Wang, X., Wen, H., Suprun, A., Zhu, H. (2025). Ethylene signaling in regulating plant growth, development, and stress responses. *Plants* 14(3):309. https://doi.org/10.3390/plants14030309

Wang, Y., Wang, T., Li, K., Li, X. (2008). Genetic analysis of involvement of *ETR1* in plant response to salt and osmotic stress. *Plant Growth Regulation* 54(3):261-269. https://doi.org/10.1007/s10725-007-9248-1

Wang, Y., Ying, Y., Chen, J., Wang, X. (2004). Transgenic *Arabidopsis* overexpressing Mn-SOD enhanced salt-tolerance. *Plant Science* 167(4):671-677. https://doi.org/10.1016/j.plantsci.2004.03.032

Wilson, R.L., Kim, H., Bakshi, A., Binder, B.M. (2014). The ethylene receptors *ETHYLENE RESPONSE1* and *ETHYLENE RESPONSE2* have contrasting roles in seed germination of *Arabidopsis* during salt stress. *Plant Physiology* 165(3):1353-1366. https://doi.org/10.1104/pp.114.241695

Woo, D.H., Park, H.Y., Kang, I.S., Lee, S.Y., Moon, B.Y. et al. (2011). *Arabidopsis lenc1* mutant displays reduced ABA accumulation by low *AtNCED3* expression under osmotic stress. *Journal of Plant Physiology* 168(2):140-147. https://doi.org/10.1016/j.jplph.2010.06.014

Wu, H. (2018). Plant salt tolerance and Na^+ sensing and transport. *The Crop Journal* 6(3):215-225. https://doi.org/10.1016/j.cj.2017.11.003

Wu, L., Wu, M., Liu, H., Gao, Y., Chen, F. et al. (2021). Identification and characterisation of monovalent cation/proton antiporters (CPAs) in *Phyllostachys edulis* and the functional analysis of *PheNHX2* in *Arabidopsis thaliana. Plant Physiology and Biochemistry* 164:205-221. https://doi.org/10.1016/j.plaphy.2021.04.034

Xiao, C., Ji, Q., Zhang, F., Li, Y., Fan, J. et al. (2023). Effects of various soil water potential thresholds for drip irrigation on soil salinity, seed cotton yield and water productivity of cotton in northwest China. *Agricultural Water Management* 279:108172. https://doi.org/10.1016/j.agwat.2023.108172

Xu, J., Sui, C., Ge, J., Ren, R., Pang, Y. et al. (2024). Exogenous spermidine improved the salinity-alkalinity stress tolerance of grapevine (*Vitis vinifera*) by regulating antioxidant system, Na^+/K^+ homeostasis and endogenous polyamine contents. *Scientia Horticulturae* 326:112725. https://doi.org/10.1016/j.scienta.2023.112725

Yang, W., Zhao, Y., Zhang, R., Wang, L., Yang, Y. et al. (2025). Two-five organic substitution of nitrogen with manure reduces yield-scaled footprint and enhances net ecosystem carbon budget of sorghum production in saline-alkali soils. *Environmental Technology & Innovation* 34:104212. https://doi.org/10.1016/j.eti.2025.104212

Yang, Y., Guo, Y. (2018). Elucidating the molecular mechanisms mediating plant salt-stress responses. *New Phytologist* 217(2):523-539. https://doi.org/10.1111/nph.14920

Yemelyanov, V.V., Lastochkin, V.V., Prikaziuk, E.G., Chirkova, T.V. (2022). Activities of catalase and peroxidase in wheat and rice plants under conditions of anoxia and post-anoxic aeration. *Russian Journal of Plant Physiology* 69(6):117. https://doi.org/10.1134/S1021443722602019

Yuan, F., Leng, B., Wang, B. (2016). Progress in studying salt secretion from the salt glands in recretohalophytes: How do plants secrete salt? *Frontiers in Plant Science* 7:977. https://doi.org/10.3389/fpls.2016.00977

Yuan, L.B., Dai, Y.S., Xie, L.J., Yu, L.J., Zhou, Y. et al. (2017). Jasmonate regulates plant responses to postsubmergence reoxygenation through transcriptional activation of antioxidant synthesis. *Plant Physiology* 173(3):1864-1876. https://doi.org/10.1104/pp.16.01803

Yun, P., Kaya, C., Shabala, S. (2024). Hormonal and epigenetic regulation of root responses to salinity stress. *The Crop Journal* 12(5):1309-1320. https://doi.org/10.1016/j.cj.2024.03.005

Zeng, Y., Li, L., Yang, R., Yi, X., Zhang, B. (2015). Contribution and distribution of inorganic ions and organic compounds to the osmotic adjustment in *Halostachys caspica* response to salt stress. *Scientific Reports* 5(1):13639. https://doi.org/10.1038/srep13639

Zhang, H., Zhu, J., Gong, Z., Zhu, J.K. (2021). Abiotic stress responses in plants. *Nature Reviews Genetics* 22:104-119. https://doi.org/10.1038/s41576-020-00335-2

Zhang, M., Cao, Y., Wang, Z., Wang, Z.Q., Shi, J. et al. (2018). A retrotransposon in an *HKT1* family sodium transporter causes variation of leaf Na$^+$ exclusion and salt tolerance in maize. *New Phytologist* 217(3):1161-1176. https://doi.org/10.1111/nph.14882

Zhang, M., Pan, M., Li, H., Liu, B., Qiao, S. et al. (2025b). Plant survival strategies under heterogeneous salt stress: Remodeling of root architecture, ion dynamic balance, and coordination of metabolic homeostasis. *Plant and Soil* 498(1-2):1-40. https://doi.org/10.1007/s11104-025-06589-0

Zhang, M., Smith, J.A.C., Harberd, N.P., Jiang, C. (2016). The regulatory roles of ethylene and reactive oxygen species (ROS) in plant salt stress responses. *Plant Molecular Biology* 91(6):651-659. https://doi.org/10.1007/s11103-016-0488-1

Zhang, R., Wang, G., Luo, S., Li, L., Mu, T. et al. (2024). Silicon promotes Na$^+$ compartmentalization and mineral uptake in zucchini seedlings to maintain physiological homeostasis and alleviate salt stress. *Journal of Plant Growth Regulation* 43(1):1-13. https://doi.org/10.1007/s00344-023-11159-w

Zhang, W.D., Wang, P., Bao, Z., Ma, Q., Duan, L. et al. (2017b). *SOS1*, *HKT1;5*, and *NHX1* synergistically modulate Na$^+$ homeostasis in the halophytic grass *Puccinellia tenuiflora. Frontiers in Plant Science* 8:576. https://doi.org/10.3389/fpls.2017.00576

Zhang, W.W., Meng, J.J., Xing, J.Y., Yang, S., Guo, F. et al. (2017a). The K$^+$/H$^+$ antiporter *AhNHX1* improved tobacco tolerance to NaCl stress by enhancing K$^+$ retention. *Journal of Plant Biology* 60(3):259-267. https://doi.org/10.1007/s12374-016-0570-x

Zhang, X., Xia, X., Sun, Y., Wang, R., Liang, K. et al. (2025c). Identification of dehydrin family genes in three *Medicago* species and insights into their tolerant mechanism to salt stress. *Plant Cell Reports* 44(1):4. https://doi.org/10.1007/s00299-024-03244-5

Zhang, X.M., Wu, G.Q., Wei, M., Kang, H.X. (2025a). Overexpression of *BvNHX1*, a novel tonoplast Na$^+$/H$^+$ antiporter gene from sugar beet (*Beta vulgaris*), confers enhanced salt tolerance in transgenic tobacco. *Journal of Plant Biochemistry and Biotechnology* 34(1):211-223. https://doi.org/10.1007/s13562-024-00895-z

Zhang, Y., Li, Y., de Zeeuw, T., Duijts, K., Kawa, D. et al. (2024). Root branching under high salinity requires auxin-independent modulation of *LATERAL ORGAN BOUNDARY DOMAIN 16* function. *The Plant Cell* 36(4):899-918. https://doi.org/10.1093/plcell/koae005

Zhang, Y., Li, Y., de Zeeuw, T., Duijts, K., Kawa, D. et al. (2023). Root branching in salt requires auxin-independent modulation of *LBD16* function. *bioRxiv* 04:https://doi.org/10.1101/2023.04.12.536587

Zhang, Z., Ma, X., Tang, D., Chen, Y., Chen, G. et al. (2024). Effects of brassinosteroid on the physiological changes on two varieties of tea plants under salt stress. *International Journal of Molecular Sciences* 25(24):13445. https://doi.org/10.3390/ijms252413445

Zhao, S., Zhang, M.L., Ma, T.L., Wang, Y. (2016). Phosphorylation of *ARF2* relieves its repression of transcription of the K$^+$ transporter gene *HAK5* in response to low potassium stress. *The Plant Cell* 28(12):3005-3019. https://doi.org/10.1105/tpc.16.00684

Zhao, Y., Wang, X., Li, J., Zhang, S. (2023). CBF/DREB transcription factors integrate ROS homeostasis and osmotic adjustment during salinity stress in *Arabidopsis* and rice. *Frontiers in Plant Science* 14:1187421. https://doi.org/10.3389/fpls.2023.1187421

Zheng, C., Liu, C., Liu, L., Tan, Y., Sheng, X. et al. (2023). Effect of salinity stress on rice yield and grain quality: A meta-analysis. *European Journal of Agronomy* 144:126765.

Zheng, J., Fang, C., Ru, L., Sun, N., Liu, Y. et al. (2021). Role of glutathione-ascorbate cycle and photosynthetic electronic transfer in alternative oxidase-manipulated waterlogging tolerance in watermelon seedlings. *Horticulturae* 7(6):130. https://doi.org/10.3390/horticulturae7060130

Zhou, Y., Diao, M., Chen, X., Cui, J., Pang, S. et al. 2019. Application of exogenous glutathione confers salinity stress tolerance in tomato seedlings by modulating ions homeostasis and polyamine metabolism. *Scientia Horticulturae* 250:45-58. https://doi.org/10.1016/j.scienta.2019.02.026

Zhu, J.K. (2002). Salt and drought stress signal transduction in plants. *Annual Review of Plant Biology* 53:247-273. https://doi.org/10.1146/annurev.arplant.53.091401.143329.

Zhu, M., Zhou, M., Shabala, L., Shabala, S. (2017). Physiological and molecular mechanisms mediating xylem Na$^+$ loading in barley in the context of salinity stress tolerance. *Plant, Cell & Environment* 40(7):1009-1020. https://doi.org/10.1111/pce.12727

Zou, Y., Zhang, Y., Testerink, C. (2021). Root dynamic growth strategies in response to salinity. *Plant, Cell & Environment* 45(3): 695-704. https://doi.org/10.1111/pce.14205

Zulfiqar, F., Ashraf, M. (2023). Proline alleviates abiotic stress induced oxidative stress in plants. *Journal of Plant Growth Regulation* 42(8):4629-4651. https://doi.org/10.1007/s00344-022-10839-3

Zuo, S., Zuo, Y., Gu, W., Wei, S., Li, J. (2022). Exogenous proline optimizes osmotic adjustment substances and active oxygen metabolism of maize embryo under low-temperature stress and metabolomic analysis. *Processes* 10(7):1388. https://doi.org/10.3390/pr10071388