DECODING PLANT RESILIENCE: INNOVATIVE MECHANISMS OF RESPONSE TO SALINITY STRESS

PRABAKARAN, C.[1] – KALAIAVANI, R.[2*] – SABAPATHY, M.[3] – RAJESH, M.[4] – PRABU, P. C.[1]

[1]*Department of Environmental Sciences, Tamil Nadu Agricultural University, Coimbatore, India*

[2]*Department of Computer Sciences, National College, Trichy, India*

[3]*Department of Veterinary and Animal Sciences, ICAR-KVK, Thiruvarur, India*

[4]*Department of Plant Pathology, Tamil Nadu Agricultural University, Coimbatore, India*

**Corresponding author*
e-mail: kalaivanics@nct.ac.in

(Received 10th Feb 2025; accepted 17th Sep 2025)

Abstract. Soil salinity is a major global problem. Poor irrigation, improper land use, and excessive fertilizer use are the main causes. Salt accumulation stunts plant growth, disrupts plant functions, and threatens global food security. High levels of sodium (Na^+) and chloride (Cl^-) disrupt plant cells. These ions interfere with important processes like seed germination and photosynthesis. In severe cases, salinity can damage plant tissues and cause plant death. Plants adapt to salinity by balancing ions, removing salts, and producing protective compounds. Scientists use genomics to study salt-tolerant genes. They use proteomics to analyze proteins involved in salt tolerance. This review explores plants' response to salinity stress, highlighting salt-tolerant genes. It also summarizes recent research. Understanding salt tolerance can help develop stronger crops. These crops can improve farming in saline, arid, and semi-arid regions.

Keywords: *soil sodicity, salt stress, ion homeostasis, osmoprotectants, genomic advances, proteomic research*

Introduction

Soil salinization is a major global challenge. It affects 1100 million hectares, covering 7% of Earth's surface. Natural processes and human activities cause this problem. Salinity impacts 20% of irrigated land, with 60% of these soils being sodic (Negacz et al., 2022; Singh, 2022; Cui et al., 2025). Atmospheric deposition, rising sea levels, saltwater intrusion, and high temperatures cause primary salinization. Human activities trigger secondary salinization. Poor irrigation, excessive fertilizer use, and intensive cropping worsen the issue. Poor irrigation depletes freshwater, increasing soil salt. High salt levels degrade farmland. These problems reduce crop productivity, especially in arid and semi-arid regions, bring salt to the surface due to excessive irrigation (Hopmans et al., 2021; Kaushal et al., 2025).

Soil salinization has been a problem for centuries and has worsened in the last five decades. It affects major farming areas. The Yellow River Basin in China and the San Joaquin Valley in California have increased salinity due to excessive irrigation, poor drainage, and low rainfall. In Australia, the Murray-Darling Basin suffers from salinity as rising groundwater brings salt to the surface. These issues reduce soil fertility and harm crops (Teng et al., 2025). The Yellow River Delta in China is a coastal saline-alkali region with soil salinity ranging from 0.2 to 4.6 g kg^{-1} (Wang et al., 2025b). California's San Joaquin Valley, a key agricultural area, relies on saline groundwater for irrigation because freshwater is scarce (Kramer et al., 2025).

DOI: http://dx.doi.org/10.15666/aeer/2402_21152142

The primary cause of soil salinization is the buildup of water-soluble salts. These salts include sodium (Na^+), potassium (K^+), chloride (Cl^-), and sulfate (SO_4^{2-}). They accumulate in the root zone. This buildup creates osmotic stress. As a result, plant roots struggle to absorb water (Stavi et al., 2021; Qin et al., 2025). The presence of these salts results in hyperionic stress, which can be harmful to plant cells. Na^+ and Cl^- are the main contributors to salinity. Too much exchangeable Na^+ causes sodicity. Early life forms adapted to saline conditions. This suggests that salt tolerance has been an evolutionary factor. Ancient cells first emerged in primordial oceans. These oceans had salt levels like or higher than today's seas. Some terrestrial plants can tolerate mild to moderate salinity. Halophytes, or salt-tolerant plants, can survive in saline environments. Some even thrive in such conditions. In contrast, most cultivated plants, classified as glycophytes, are sensitive to salinity (Foronda, 2022).

Key food crops, such as tomatoes and rice, are vulnerable to salt stress. The harmful effects of salinity begin with short-term osmotic stress. Over time, ion accumulation leads to toxicity in plant tissues (Ullah et al., 2021). Osmotic stress starts when salt uptake increases. This lowers water potential in the root zone. As a result, disrupt water conductivity. which hinders plant growth (Abbasi et al., 2016). Prolonged exposure to high salinity causes toxic ions like Na^+, Cl^-, and SO_4^{2-} to accumulate. These ions interfere with nutrient absorption. They also damage plant cells and tissues (Isayenkov and Maathuis, 2019). Salinity causes physiological and biochemical effects. These include stunted growth, chlorosis, and reduced seed germination. It also impairs photosynthesis and induces oxidative stress. Salinity disrupts plant cell function. It causes electrolyte leakage and damages cell membranes. This reduces cell stability and impairs physiological processes (Ji et al., 2022; Hannachi et al., 2022). Salinity effects are most severe at the reproductive stage (Rafaliarivony et al., 2023). In the past two decades, researchers have studied the impact of salinity on plants. They have also explored ways to reduce its effects.

Improving salt tolerance in crops is essential for farming, ecosystems, and food supply. Conventional breeding and genetic engineering have improved salt tolerance. Understanding how plants adapt to salinity helps develop ways to reduce stress. This review explains how salinity harms plant growth. It describes key adaptations like osmotic regulation, ion balance, antioxidant defense, and hormones. It highlights ways to improve salt tolerance, including breeding, biotechnology, microbes, and biostimulants. Finally, it suggests studying new technologies and sustainable farming to reduce salinity (*Figs. 1* and *2*).

Types and sources of soil salinity

Soil salinity comes from natural (primary) and human-induced (secondary) causes. Primary salinity happens due to geological and climatic factors. It is common in dry regions where high evaporation leaves salts in the soil. Human activities like excessive irrigation and poor drainage cause secondary salinity. These practices raise water tables and deposit salts in the root zone.

There are different types of soil salinity. Irrigation-induced salinity comes from improper irrigation. Dryland salinity occurs in non-irrigated areas due to rising water tables. Sodic soil contains excess sodium, which damages soil structure and reduces crop growth. Natural salinity comes from slow environmental processes. Rocks break down over time. They release salts like sodium, calcium, magnesium, and potassium (Muhammad et al., 2024). Coastal areas face seawater intrusion and salt-laden winds. In some regions, saline groundwater rises to the surface when evaporation is high (Tang et al., 2024). While these processes occur, human activities make soil salinity worse.

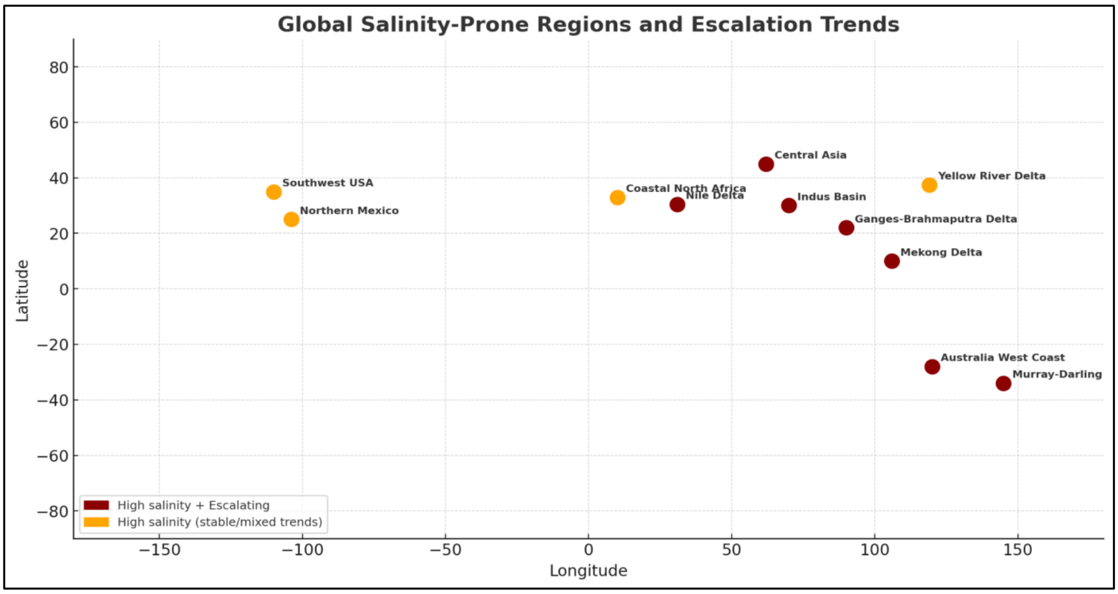

Figure 1. *World map schematic showing salinity-prone regions and their escalation trends over the past decades*

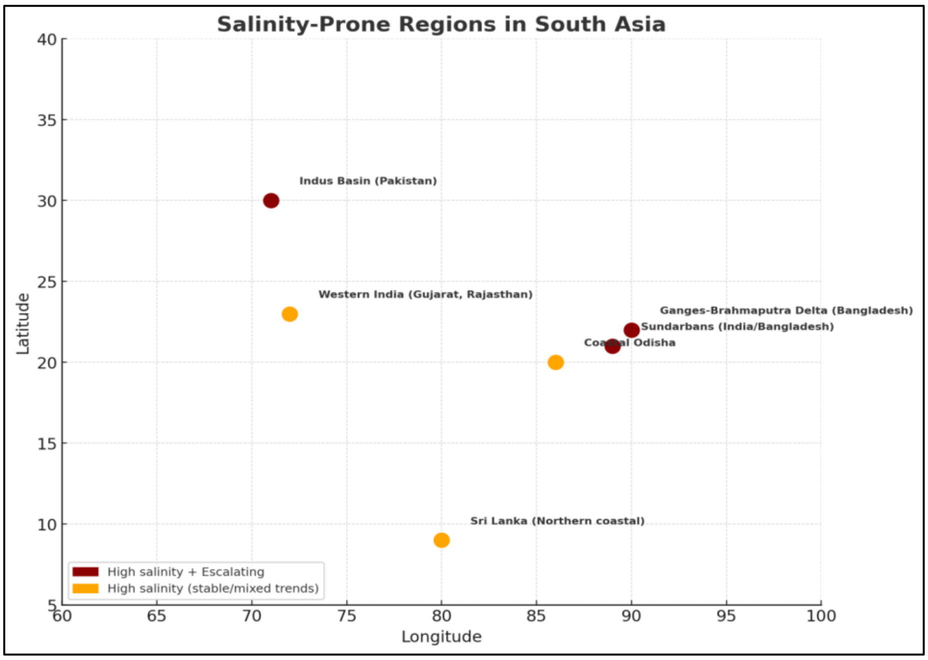

Figure 2. *South Asia salinity map showing major affected regions*

Human activities like farming and industry add more salts to the soil. Poor-quality irrigation water, excessive fertilizers, and deforestation disrupt the natural water cycle. This raises water tables and increases salt buildup. Industrial and urban wastewater also adds salts to the soil and groundwater.

Proper irrigation, soil treatments, and sustainable land management help reduce soil salinity. These methods stop land degradation. They also protect food production, ecosystems, and the environment (Tarolli et al., 2024).

Effects of salinity on soil fertility

Under non-saline conditions, plant growth depends on nutrient availability. It follows a "generalized dose–response curve" in the root zone. But, salt stress disrupts nutrient uptake. This disruption occurs due to nutrient deficiency or toxicity. Nutrient acquisition becomes difficult under salinity. The main challenge is competition between essential nutrients and dominant salt ions. Na^+ and Cl^- are the most dominant salt ions. Their presence often leads to deficiencies of Ca^{2+}, K^+, and Mg^{2+}. Salt stress affects essential nutrients like nitrogen, phosphorus, and potassium. These interactions are complex. Nitrogen is an important component of plant cellular structures. Salinity affects nitrogen uptake. Excessive Cl^- uptake interferes with nitrogen assimilation. This interference happens due to Cl^-/NO_3^- antagonism. Phosphorus is essential for photosynthesis, storage, and energy transfer. Saline soils reduce its uptake. This reduction is more severe in the presence of excess Cl^- and SO_4^{2-}. Increased ionic strength and low solubility of Ca-P compounds likely cause this. Potassium is necessary for protein synthesis and water balance. Under saline conditions, K^+ competes with Na^+ for uptake. Na^+ and K^+ have similar molecular properties. Na^+ can replace K^+ at uptake sites. But, Na^+ cannot perform K^+'s cellular functions. High Na^+ levels reduce K^+ and Ca^{2+} concentrations. This reduction worsens nutrient imbalances.

Effects of salinity stress on plants

Physiological and biochemical effects of salinity

Water balance

When plants face salt stress, they take in salt ions, which build up in their cells and upset their water balance. High salt levels make it harder for plants to hold onto water, causing water to leave their cells. This lowers pressure inside the cells, making it difficult for the plant to function properly.

A study on *Corchorus olitorius* (a leafy green plant can tolerate drought but is sensitive to high salt levels, which affect its water balance and growth) found that salt stress reduced water content, water intake, and transpiration (Sheldon et al., 2017). Later research confirmed these effects (Campos et al., 2025). How much water a plant loses depends on the salt levels in the soil. To survive, plants adjust by lowering their internal water potential to maintain cell pressure (Gu et al., 2025).

Normally, water moves from the soil into plant roots through spaces between cells (the apoplastic pathway). This happens because of natural pressure differences. But when salt stress reduces transpiration, water takes a different route, moving from one cell to another through membranes instead (Swetha et al., 2025). Too much salt changes how water moves, affecting plant growth and health.

Nutrient absorption

Cassava (*Manihot esculenta*) and maize (*Zea mays*) are staple food crops. Salinity affects these plants by disturbing nutrient balance. It also reduces crop yield and increases toxicity (Betzen et al., 2019; Nadeem et al., 2025).

Light reaction

Photosynthesis is a fundamental process in plants. It converts solar energy into chemical energy. Yet, salt stress affects photosynthesis. It disrupts chlorophyll biosynthesis (Qin et al., 2020). It also alters enzymatic activity (Al-Hinai et al., 2022). Additionally, it causes stomatal closure, which reduces CO_2 availability (Orzechowska et al., 2021). Salt stress also damages the photosynthetic apparatus (Zahra et al., 2022; Lu et al., 2023; Chen et al., 2025).

Chlorophyll content declines under saline conditions. Increased oxidation and chlorophyll degradation cause accumulation of reactive oxygen species (ROS). It triggers the process. The extent of chlorophyll reduction depends on salinity levels (Tomaskinova et al., 2025).

Salt stress inhibits the electron transport chain. This inhibition leads to pseudocyclic electron transport. Pseudocyclic electron transport produces excessive ROS (Zahra et al., 2021). ROS damages photosynthetic proteins. It also disrupts the photosystem complex (Huihui et al., 2020).

Short-term exposure to high salinity changes chloroplast ultrastructure. It induces thylakoid swelling and starch accumulation (Goussi et al., 2018). Many studies have examined the effects of salt stress on different plant species. They include *Solanum melongena, Portulaca oleracea, Oryza sativa,* and *Jatropha curcas*. Research shows that low salinity levels reduce photosynthetic efficiency. Moderate to high salt concentrations cause severe damage to the chloroplast structure. Moderate to high salt concentrations are harmful to plants. They damage photosynthetic machinery (Wang et al., 2018; Hnilickova et al., 2021; Hannachi et al., 2022; Ahmadzai et al., 2025) (*Table 1*).

Table 1. *Impact of salinity on different growth stages: vegetative vs. reproductive*

Factor	Vegetative stage (early growth)	Reproductive stage (flowering & seed formation)
Water uptake	Reduced due to osmotic stress, causing dehydration (Şekerci et al., 2025)	Further reduced, affecting flower and seed formation (Singh et al., 2025)
Growth	Poor seed germination, Stunted growth, smaller leaves, and shorter stems (Afonso et al., 2025)	Poor fruit/grain development, lower seed production (Samineni et al., 2005)
Photosynthesis	Reduced due to leaf damage and stomatal closure (Huang et al., 2025)	Lower food production, affecting fruit and seed growth (Kumar et al., 2025)
Leaf condition	Yellowing (chlorosis) and leaf drying (necrosis) (Sevgi et al., 2025)	Older leaves may die, reducing energy for reproduction (Alvan et al., 2025)
Flowering	May be delayed but not completely stopped (Mondal et al., 2025)	Fewer flowers develop, leading to lower yields (Zhang et al., 2025a)
Pollen & seed formation	Not affected much at this stage (Wang et al., 2025a)	Pollen viability drops, leading to poor seed set (Kanneri et al., 2025)
Fruit/grain yield	No immediate effect on yield, as plants are still growing (Reta et al., 2025)	Major impact—smaller fruits, lower grain weight, poor quality (Yan et al., 2025)
Recovery potential	Possible if salinity stress is removed in time (Siddique et al., 2025)	Very low; damage is usually permanent (Wei et al., 2025)

Salt stress, like other abiotic stressors, inhibits plant growth. Plant type, growth stage, and salt level determine growth inhibition. In response to salinity, plants often grow slowly to survive stressful conditions. It leads to reduced yield and biomass (Yousefi et al., 2025).

Salt stress can weaken key cell cycle genes like cyclins and cyclin-dependent kinases. This leads to a decrease in the number of meristematic cells. As a result, the plant fails to absorb water and nutrients (Peduzzi et al., 2024).

In *Arabidopsis*, salt stress slows root growth by inhibiting cyclin-dependent kinase (CDK) activity. This reduces the number of dividing cells and leads to a smaller meristem. Some plants stop growing under salt stress, while others keep growing. These plants may die (Vazquez-Rivera et al., 2025).

At the reproductive stage pollen viability increases the economic yield. Salt range increases pollen viability percentage in salt tolerant species (Nazish et al., 2025) (*Fig. 3*).

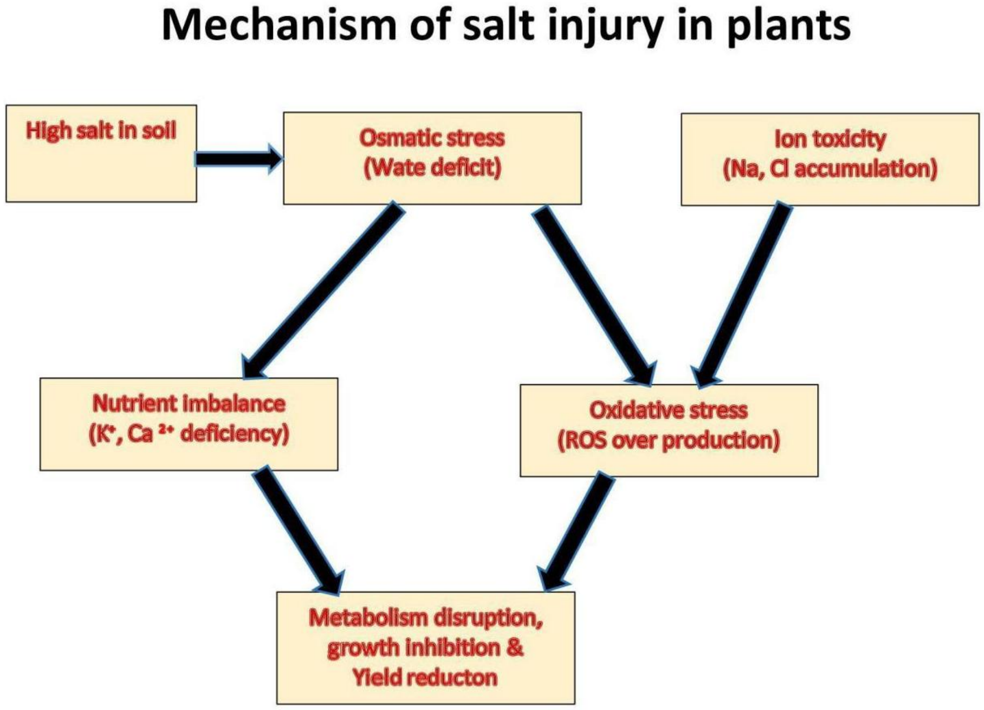

Figure 3. *Mechanisms of plant response to salinity*

Osmotic and ionic regulation

Salinity stress disrupts ionic balance in plants. This affects important physiological processes. These processes include cellular metabolism, photosynthesis, and root architecture. The disruption happens due to reduced nutrient uptake. Plants have developed mechanisms to counteract these effects. They regulate intracellular ion homeostasis. This regulation happens through controlled ion influx and compartmentalization (Chang et al., 2025; Xu et al., 2025a).

Mechanisms of ion homeostasis

Ion homeostasis is a dynamic process. It requires energy to maintain a balance between essential and toxic ions. Both glycophytes and halophytes are vulnerable to sodium (Na$^+$)

accumulation. Excess Na^+ in the cytoplasm can harm cellular function. Sodium uptake occurs at the root–soil interface. Non-selective cation channels ease this uptake. These channels include cyclic nucleotide-gated channels (CNGCs) and glutamate receptors (GLRs). High-affinity potassium transporters (HKTs) contribute to Na^+ uptake. Aquaporins also play a role in Na^+ transport (Liu et al., 2025a).

Translocation and compartmentalization of Na^+

Once absorbed, Na^+ moves from the roots to the shoots. It first travels via the apoplastic pathway. Then, it enters the root epidermis symplast. The plant loads it into the xylem tracheids. The highest Na^+ accumulation occurs in the leaf blades. This is where its toxic effects are most severe (Fu et al., 2025).

Plant strategies to reduce Na^+ toxicity

Plants use several strategies to reduce Na^+ toxicity. They *restrict Na^+ influx* by regulating root uptake. This limits excessive sodium entry into the cytoplasm. They *enhance Na^+ exclusion* by expelling sodium from cells. This helps maintain ionic balance. They *compartmentalize Na^+ into vacuoles* to reduce its toxicity. This protects metabolic processes. By combining these strategies, plants improve their resistance to salt stress. This helps them grow and survive in saline conditions (He et al., 2025).

Salt sensitive (SOS) genes and high-affinity potassium transporters (HKTs) in salt tolerance

Plants use various strategies to combat salinity stress. The Salt Overly Sensitive (SOS) signaling pathway in *Arabidopsis thaliana* is well known. This pathway involves three key genes: SOS1, SOS2, and SOS3 (Yang et al., 2025). SOS1 plays a key role in ion homeostasis by regulating Na^+/H^+ exchange across the plasma membrane. This antiporter removes Na^+ ions. It exchanges them for protons, preventing toxic sodium buildup in the cytoplasm. Physiological studies confirm SOS1's role in Na^+ transport and efflux. Genetic and biochemical studies provide further support. Parenchyma cells at the xylem/symplast boundary express the gene. This helps retrieve Na^+ from xylem sap. Overexpressing SOS1 improves salt stress tolerance. Rice is a staple food crop. *Oryza sativa* (rice) is a model organism for studying monocot plant biology. It is also used for genome sequencing and agronomy. Rice plays a key role in crop improvement. Researchers have observed this in these plants (*Arabidopsis*, tobacco, and rice) (Shahzad et al., 2022; Liang et al., 2025).

Another key mechanism for salt tolerance involves High-Affinity Potassium Transporters (HKTs). This family of monovalent cation transporters helps exclude Na^+ ions from sensitive shoot tissues (Ullah et al., 2025)

- HKTs mediate Na^+/K^+ transport, preventing excessive sodium accumulation and promoting potassium uptake. Some HKTs also facilitate Mg^{2+} and Ca^{2+} permeability (Liu et al., 2025).
- Four M-P-M (Membrane-Pore-Membrane) repeats in HKTs determine ion selectivity. Researchers classify HKTs into two types based on these structural features.
  - HKT1-type transports Na^+. It prevents Na^+ accumulation in shoot tissues by unloading it from xylem sap. It also sequesters Na^+ into xylem parenchyma cells (Yanez-Dominguez et al., 2025).

- HKT2-type functions as a Na^+/K^+ symporter. It balances the uptake of these ions based on cellular needs. HKTs regulate Na^+ exclusion to enhance salt tolerance. They help plants maintain ion balance, supporting growth and survival in saline conditions (Govindan et al., 2024).

Role of proton pumps in salt tolerance

Plants use different mechanisms to maintain cytosolic Na^+ balance. They either sequester excess Na^+ into vacuoles or export it from the cytosol. Plants use different mechanisms to maintain cytosolic Na^+ balance. They either sequester excess Na^+ into vacuoles or export it from the cytosol. These processes prevent salt stress damage. They rely on membrane proton pumps, ion transporters, and channels.

Key proton pumps in salt stress tolerance

(1) Plasma membrane H^+-ATPase (P-type H^+ ATPase)

- Embedded in the *plasma membrane* as a homodimer.
- Functions in *secondary active transport,* driving ion movement across membranes.
- It also helps maintain turgor pressure. Additionally, it supports cell wall expansion and regulates intracellular pH.

(2) Vacuolar H^+-ATPase (V-ATPase)

- Composed of two major subcomplexes:
  - *V_0 complex* (membrane-integral proton transporter).
  - *V_1 complex* (ATP hydrolysis-driven energy provider).
- It acts as an eco-enzyme, especially under salt stress. It drives H^+ into vacuoles to establish an electro-chemical gradient.

(3) Vacuolar H^+-Pyrophosphatase (H^+-PPase)

- Utilizes *inorganic pyrophosphate (PPi)* as an energy source instead of ATP.
- It creates a strong proton motive force (PMF) across the vacuolar membrane. This drives secondary transporters to sequester Na^+ into vacuoles.
- In *Arabidopsis thaliana*, type-1 H^+-PPase (AtVHP1 or AVP1) localizes specifically to the vacuolar membrane (Uzun et al., 2025; Fu et al., 2022).

Under salinity stress, H^+-ATPases and H^+-PPases generate proton motive force (PMF). Na^+/H^+ and K^+/H^+ antiporters harness this energy to store Na^+ in vacuoles. They help maintain a high cytosolic K^+/Na^+ ratio (He et al., 2025).

Scientists have studied AVP1 overexpression in various plants. These include *Arabidopsis*, creeping bentgrass, cotton, peanut, and barley. It improves salt tolerance (Esmaeili et al., 2021; Xu et al., 2025b). Proton pumps regulate ion compartmentalization. As a result, they are key targets for genetic and biotechnological strategies. These approaches aim to improve salt tolerance in crops.

Antioxidant defense system and oxidative stress

Reactive oxygen species (ROS) cause oxidative stress in plants. Plants have developed adaptive mechanisms to withstand salinity stress. They undergo morphological, physiological, biochemical, and molecular changes. Salt tolerance depends on cytoplasmic ion regulation. This includes ion homeostasis and compartmentalization. It also involves osmotic and enhanced antioxidant metabolism. Antioxidant metabolism helps remove ROS. This process supports plant survival under salinity stress (Yu et al., 2020; Nawaz et al., 2025).

Salt stress causes excessive production of reactive oxygen species (ROS). ROS have strong oxidative properties. They damage membrane lipids, proteins, and nucleic acids. This leads to metabolic dysfunction. Plants have a defense system to reduce oxidative damage. This system includes enzymatic and nonenzymatic antioxidants.

Enzymatic and nonenzymatic antioxidants

Enzymatic antioxidants help protect plants. These antioxidants comprise superoxide dismutase (SOD), catalase (CAT), peroxidase (POX), and ascorbate peroxidase (APX) (Rao et al., 2025). Nonenzymatic antioxidants include glutathione (GSH), ascorbates (ASC), and carotenoids. These antioxidants work together to remove ROS. Mitochondria and chloroplasts produce ROS. SOD is the first line of defense. It converts superoxide radicals into oxygen and hydrogen peroxide. This reduces the formation of toxic hydroxyl radicals. POX and CAT break down hydrogen peroxide. This prevents cellular damage under salt stress (Kozlov et al., 2024).

Studies show a strong link between salt tolerance and antioxidant activity. Salt-tolerant plants have higher antioxidant levels. Research on *A. tricolor* plants showed this effect. A salt-tolerant variety (VA14) had increased levels of SOD, ascorbate, and APX. These antioxidants helped remove ROS. Salt stress damages membranes. This damage increases malondialdehyde (MDA) levels. Lipid peroxidation causes MDA accumulation. In wheat, salt-tolerant genotypes produced less MDA. This reduced oxidative damage (Hussain et al., 2022).

Genetic and metabolic contributions to salt tolerance

The peroxidase gene *GsPRX9* from wild soybean improves salt tolerance. Overexpression of this gene strengthens the antioxidant response. Secondary metabolites also help plants adapt to salt stress. Anthocyanins are an example of these metabolites. In *Arabidopsis*, the *air1* mutant gene prevents anthocyanin production. Without anthocyanins, plants fail to respond to salt stress. This shows the role of anthocyanins in oxidative stress regulation. Antioxidant enzymes, nonenzymatic molecules, and pigments reduce oxidative damage. They help plants survive under salt stress. These mechanisms improve plant resilience (Balasubramaniam et al., 2023).

Hormonal regulation and signaling pathways

Phytohormones are essential regulatory molecules in plants. They control growth, development, and responses to stress. There are nine well-known groups of plant hormones. Each hormone plays a unique but connected role in salt stress adaptation (Chen et al., 2020). Some hormones respond to stress. These include abscisic acid (ABA), ethylene, salicylic acid (SA), and jasmonic acid (JA). Other hormones promote growth and development. These include auxins, gibberellins (GA), cytokinins, brassinosteroids (BRs), and strigolactones (SLs). Plant responses to stress depend on hormone interactions. No single hormone controls stress adaptation alone.

Abscisic acid (ABA) and salt stress

ABA plays a key role in helping plants survive salt stress. It triggers a signaling cascade that controls gene expression. When plants face salt stress, ABA levels rise. This increase activates a kinase cascade. The cascade controls stomatal closure. As a result, plants regulate water balance and osmotic homeostasis. ABA signaling depends on specific protein kinases. These include SnRK2.2, SnRK2.3, and SnRK2.6. These kinases activate transcription factors. These transcription factors regulate genes that improve salt tolerance (Zhao et al., 2021). ABI1 protein reduces salt tolerance. ABI1 inhibits SnRK2 kinases. This inhibition affects primary root growth. Salt stress increases ABA production. Several enzymes help produce ABA. These include zeaxanthin oxidase (ZEP) and 9-cis-epoxycarotenoid dioxygenase (NCED). ABA biosynthesis follows the MEP pathway. The Ca^{2+} and salt overly sensitive (SOS) pathways work with ABA signaling. They prevent excessive activation of SOS2. This coordination fine-tunes the plant's response to salt stress.

Auxins, gibberellins (GA), and cytokinins in salt stress

Salt stress affects auxin transport and signaling. It reduces polar auxin transport. It also lowers auxin levels in roots. As a result, plants downregulate auxin-related genes. These genes include *TRANSPORT INHIBITOR RESPONSE 1* and *AUXIN SIGNALING F-BOX*. Lower auxin signaling slows root growth. GA levels also change under salt stress. Plants reduce GA signaling to improve salt tolerance. The DELLA protein SLR1 helps regulate GA signaling. Reduced GA levels after germination improve salt tolerance. Cytokinins usually promote cell division and differentiation. But, they react differently under salt stress. Losing the *isopentenyl transferase (IPT)* enzyme improves salt tolerance. Overexpression of *cytokinin oxidase (CKX)* also enhances salt tolerance (Singroha et al., 2022). Foliar application of gibberellin and cytokinin at $50\,mg\,L^{-1}$ enhances growth, yield, and salt tolerance in faba bean under saline conditions (El-Beltagi et al., 2025).

Ethylene and salt stress

Ethylene is a key stress hormone. It accumulates under salt stress. Ethylene affects many important physiological processes. Ethylene signaling influences salt tolerance. Mutations in ethylene receptors ETR1 and EIN4 increase salt tolerance. Yet, mutations in EIN2 and EIN3 make plants more sensitive to salt stress. Ethylene also interacts with other plant hormones, and together they help regulate how plants respond to salinity stress (Riyazuddin et al., 2020). These findings highlight the importance of phytohormones in salt stress adaptation. Phytohormones help balance plant growth and stress responses.

Process of plant salt tolerance development

The process of plant salt tolerance development is multi-layered, involving sensing, signaling, gene regulation, and physiological adaptation. Plants first encounter high salt in soil (Na^+, Cl^-), which causes osmotic stress (reduced water uptake) and ionic stress (toxic Na^+ accumulation). Stress is sensed by membrane receptors, ion transporters, and mechanosensitive channels (Wang et al., 2022). Stress perception triggers signaling cascades, including: Calcium signaling → cytosolic Ca^{2+} spikes act as early messengers. Reactive oxygen species (ROS) → moderate ROS act as signals, while excess must be detoxified. Mitogen-activated protein kinases (MAPKs) → phosphorylate proteins and activate transcription factors (Signal Transduction). Signal pathways activate stress-responsive transcription factors: DREB, NAC, bZIP, MYB, WRKY families. These regulate salt-responsive genes involved in ion transport, osmolyte biosynthesis, and antioxidant defense. Epigenetic modifications (DNA methylation, histone modifications, small RNAs) fine-tune expression and enable stress memory (Gene Regulation). Plants restrict *Na^+ entry* and compartmentalize excess Na^+ into vacuoles. *SOS1* (Salt Overly Sensitive 1) exports Na^+ out of the cell. *NHX1* sequesters Na^+ into vacuoles. *HKT1* prevents Na^+ accumulation in shoots. *K^+ retention* is maintained to balance cellular metabolism (*ion homeostasis*). Plants synthesize *compatible solutes (osmolytes)* like proline, glycine betaine, sugars, and polyols. These stabilize proteins, membranes, and maintain water balance (*osmotic adjustment*). Salt stress generates oxidative stress (ROS). Plants activate enzymatic antioxidants (SOD, CAT, APX, POD) and non-enzymatic antioxidants (ascorbate, glutathione, carotenoids, flavonoids) (*antioxidant defense*). Abscisic acid (ABA) regulates stomatal closure and stress gene expression. Ethylene, salicylic acid (SA), jasmonic acid (JA), gibberellins (GA), cytokinins (CK) modulate stress responses via crosstalk (Hormonal Regulation). Improved water-use efficiency, controlled stomatal conductance, and adjusted root/shoot architecture. Some halophytes develop salt glands or succulent tissues for salt exclusion or dilution (Physiological and Developmental Adaptation) (Liu et al., 2025b) (*Fig. 4*).

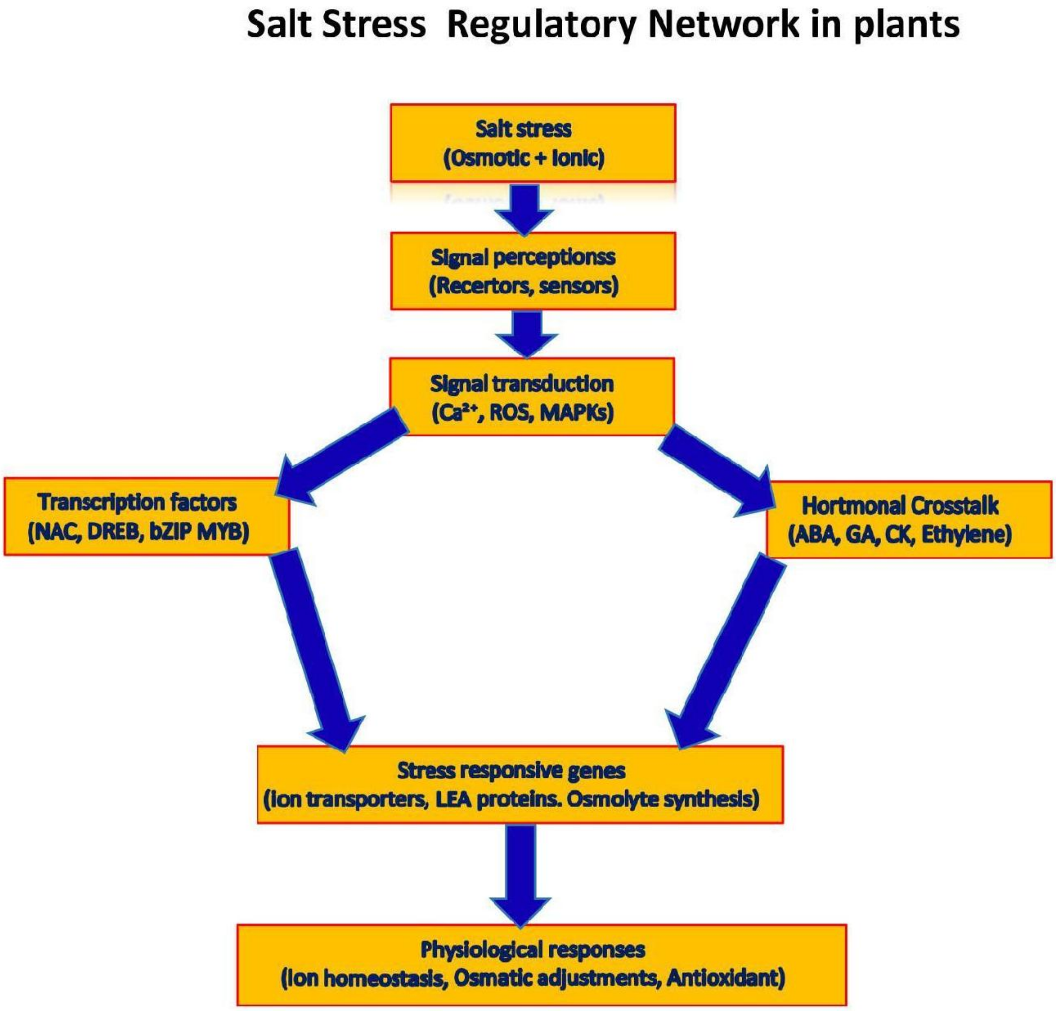

Figure 4. *Strategies for enhancing salt tolerance in crops*

Conventional breeding approaches

Researchers have studied crop breeding for salinity tolerance. This subject has been reviewed periodically (Haque et al., 2021; Guo et al., 2022; Afzal et al., 2023). Conventional breeding methods help develop salt-tolerant varieties. These methods include hybridization, selection, polyploidy, and introgression. Wild relatives of crops provide salt-tolerant genes. Using these genes increases genetic variation for salt tolerance improvement.

But, conventional breeding faces challenges. Many crop species have limited genetic variation. The process is labor-intensive and time-consuming. It may transfer undesirable genes along with beneficial traits. The outcomes are often unpredictable. Conventional breeding cannot introduce non-native traits. Reproductive barriers prevent transferring useful alleles from different species.

Another challenge is evaluating genetic materials under optimal conditions. This method may overlook salt-tolerant traits. Plants respond to abiotic stress at various growth stages. This complexity makes it difficult to select for salt-stress tolerance (Yousefirad et al., 2018).

Molecular breeding approaches

To address the challenges of conventional breeding, alternative breeding strategies are available. Mutational breeding (Geetha et al., 2021) introduces genetic variations for salt tolerance. Double haploid production speeds up breeding programs. Marker-assisted breeding (Turki et al., 2023) allows precise selection of salt-tolerant traits. These methods help develop crops with better resistance to salinity stress.

QTL mapping and marker-assisted selection for salt tolerance

Quantitative trait loci (QTL) mapping and marker-assisted selection (MAS) improve plant breeding by enabling selection based on genotype rather than solely phenotype, thereby often reducing time and labor. These methods can be more efficient than traditional phenotypic screening—especially when traits are heritable and markers closely linked to causative loci—but their success depends on stable marker-trait associations and adequate marker density. Molecular techniques (PCR-based markers, SNP arrays, etc.) help identify and track genetic markers, reducing the time needed for genotype screening and limiting—but not eliminating—environmental effects and genotype × environment interactions. Salt tolerance is a complex trait controlled by multiple QTLs. Many of these show additive effects; some also show dominance or epistasis (Nakhla et al., 2021).

In rice, several quantitative trait loci (QTLs) influence salinity tolerance, particularly during the *reproductive phase*, which is critical for maintaining grain yield under salt stress. The *Saltol* QTL, although mainly effective at the *seedling stage*, is among the best characterized: it helps maintain a high K^+/Na^+ ratio and reduces Na^+ accumulation in shoots. For instance, Saltol was introgressed into Pusa44 and Sarjoo52, resulting in near-isogenic lines that show lower salt injury scores and favorable Na^+/K^+ ratios under seedling-stage salinity (Krishnamurthy et al., 2020).

In tomato (*Solanum lycopersicum*), recent meta-analyses and genome studies have uncovered QTLs and allelic variation associated with fruit yield and reproductive traits under salinity. For example, a Meta-QTL study grouped *60 of 85 productivity-linked QTLs* into 12 robust *productivity-MQTLs*, some of which (e.g. *MQTL4.2*, *MQTL1.2*) co-localize fruit yield QTLs operating under saline conditions, affecting fruit set, fruits per truss, and flower number (Asins and Carbonell, 2024). Another recent study via GWAS identified a major QTL that controls sodium accumulation in leaf tissue, with *SlHKT1.2* implicated. Variation in this transporter may help limit ion toxicity and thus contribute indirectly to maintenance of yield under high salinity. Additionally, wild tomato *S. pimpinellifolium* accession 'LA0480' demonstrates superior yield-related performance under salt stress compared to the cultivated line *Heinz 1706*, primarily via maintaining fruit number. Genomic analyses revealed expansion of stress-related pathways (e.g. inositol metabolism) in 'LA0480', offering promising candidate genes for introgression (Hereil et al., 2024).

In maize (*Zea mays*), recent studies have identified several QTLs and genes contributing to salinity tolerance, particularly through Na^+ exclusion and ion homeostasis. For example, *ZmNC3/ZmHKT1;2* is a HKT1-family transporter with a teosinte-derived allele (SNP947-G) that significantly reduces shoot Na^+ accumulation by withdrawing Na^+ from root xylem sap, enhancing salt tolerance (Zhang et al., 2023). Similarly, *ZmHAK4* (also known as *ZmNC2*) accounts for approximately *11%* of the variation in shoot Na^+ content and functions in shoot Na^+ exclusion by acting in the root stele to retrieve Na^+ from xylem sap. A linkage mapping study in mature, field-grown maize identified the major QTL *qSPH1* on chromosome 1, which explains ~31.24% of phenotypic variance for plant height under saline conditions (across three seasons), indicating a stable, environment-insensitive locus. More recent work shows that *ZmSnRK2.10*, a kinase, enhances salt tolerance by phosphorylating *ZmHAK4*, boosting its activity. Natural variation in *ZmHAK11* promoter also influences shoot Na^+ accumulation (minor effect, ~7.5%) and contributes to salt tolerance (Zhang et al., 2025b). These validated loci represent promising targets for marker-assisted breeding, though their effects on yield under saline stress in adult plants (grain yield) require further field validation across developmental stages.

Nax2 from the diploid relative *Triticum monococcum* has substantially improved salt tolerance. The candidate gene at the Nax2 locus, *TmHKT1;5-A*, encodes a Na^+-selective transporter in root xylem parenchyma cells that removes Na^+ from the xylem sap, thereby reducing shoot Na^+ accumulation and preserving ion homeostasis. Field trials on saline soils show that durum wheat lines carrying Nax2 yield about *25% more grain* compared to near-isogenic lines lacking the locus, with no significant yield penalty under non-saline conditions.

In another study, researchers created a genetic linkage map for *Brassica napus*. The map included 532 molecular markers covering 1341.1 cM. They identified a candidate gene, Bra003640, associated with salt tolerance (Farooq et al., 2021) of high-density SNP and InDel markers, and improved genotyping platforms—have greatly enhanced DNA marker technology. Over the past two decades, these tools have enabled the construction of dense linkage and physical maps in many crop species, increasing resolution and accuracy. Marker-assisted selection (MAS) based on tightly linked or functional markers allows early-stage screening of genotypes, reducing time and cost compared to phenotypic selection. While MAS reduces reliance on phenotype in early generations and avoids some environmental noise, environmental effects and genotype × environment interactions remain important for validating trait performance in field conditions.

Genetic engineering and biotechnology

Transgenic approaches for salt resistance

Scientists have identified many salt stress-related genes. They used recombinant DNA technology and genomic studies. Some genes encode proteins involved in plant growth and metabolism under stress. Other genes encode regulatory proteins, such as transcription factors. Transcription factors control multiple target genes by binding to specific DNA sequences (Qamer et al., 2021). Several transcription factor families contribute to salt tolerance. These families include ERF/AP2, bZIP, WRKY, NAC, MYB, and C2H2 zinc finger proteins (C2H2-ZFP). Different Brassica genotypes showed the upregulation of genes involved in the SOS pathway. These genes include SOS1, SOS2, and SOS3. SOS1 is a plasma membrane Na^+/K^+ antiporter. SOS2 is a protein kinase. SOS3 is a calcium-binding protein. The NHX1 gene, which encodes a vacuolar Na^+/K^+ antiporter, is also upregulated under salt stress. Similarly, salt-stressed rice genotypes showed increased expression of OsHKT, OsNHX, and OsSOS1. These genes help maintain Na^+/K^+ balance (Pramanik et al., 2021).

A key strategy for engineering salt tolerance is gene manipulation. These genes regulate ion homeostasis. Genes controlling water uptake, transport, and compartmentalization also play a role. Overexpressing genes encoding transporters or antiporters in root tissues reduces excessive ion uptake. Scientists modified proton pumps. They also modified Na^+/H^+ antiporters. Scientists modified potassium transporters to improve salt tolerance. Yet, single-gene overexpression is often insufficient for high salt tolerance. Transgenic plants overexpressing AtNHX1, SOS1/AVP1 tolerated only 100–150 mM NaCl (Long et al., 2020). To improve salt tolerance, researchers have explored co-overexpression strategies. Transgenic plants co-overexpressing AVP1 and SOS1 tolerated up to 200–250 mM NaCl. Similarly, plants co-overexpressing AVP1 and OsSIZ1/AVP1 and PP2A-C5 showed higher salt tolerance. Transgenic Arabidopsis plants overexpressing AVP1, AtCLCc, and PP2A-C5 tolerated 300 mM NaCl. These findings highlight the effectiveness of multi-gene strategies in improving salt tolerance (Esmaeili et al., 2021).

Genetic engineering

In tomato (*Solanum lycopersicum*), transgenic lines overexpressing the BADH (betaine aldehyde dehydrogenase) gene show increased accumulation of glycine betaine and improved physiological performance under salinity in greenhouse or controlled-environment conditions (higher chlorophyll retention, osmotic balance). However, strong field trials demonstrating fruit yield improvement under saline soils are scarce.

In wheat, some transgenic approaches—e.g. overexpressing NHX-family antiporters—have exhibited improved salt tolerance and increased yield in saline-alkali soils under controlled experimental conditions. Still, as with tomato, robust multi-season, field-scale yield data for specific transgenes like *SbNHX1* is limited in recent literature. Transgenic Arabidopsis lines showed markedly higher glycine betaine accumulation; reduced leaf damage (lower relative electrical conductivity under salt stress); longer root growth under 100-150 mM NaCl; better survival and growth during germination and seedling stages (Sun et al., 2019).

CRISPR and gene-editing technologies

Genome editing technologies have emerged as powerful tools. These tools help in engineering salt tolerance in plants. CRISPR/Cas is one such genome editing technology. These technologies go beyond traditional transgenic approaches. CRISPR-based modifications have altered structural genes. They have also modified regulatory genes and cis-regulatory elements. These changes impact salt stress responses in plants. Scientists inserted a 60 bp translational enhancer at the SOS1 locus in rice. This insertion increased salt tolerance in rice. CRISPR/Cas9-mediated knockout of the barley HVP10 gene disrupted ion homeostasis. This disruption led to excessive Na^+ accumulation in shoots. Customized nucleases allow precise modifications for crop improvement. Zinc-finger nucleases (ZFNs) and TALENs are examples of these nucleases. These tools help improve crop traits.

Small RNA-mediated gene silencing is also an effective tool for engineering salt tolerance. This includes microRNAs (miRNAs) and RNA interference (RNAi) technology. RNAi silences target genes. It controls gene expression with precision. It does this without disrupting the expression of other essential genes. Computational tools help identify stress-responsive miRNAs and their regulatory targets. For example, miR172a in soybean is shown to enhance salt tolerance. This miRNA also contributes to long-distance stress signaling. Engineered plants with miR172a can survive under severe salt stress conditions. Yet, applying genetic engineering strategies in the field remains a challenge. Further research needs to understand the complexity of salt tolerance. Scientists must also study the regulatory networks that control salt signaling. Species-specific variations in salt tolerance need more investigation. Genome-editing technologies continue to advance. These technologies hold great potential for developing salt-tolerant crops. Salt-tolerant crops can withstand harsh environmental conditions. They can also contribute to global food security.

Agronomic strategies for alleviating salt stress in plants

Endogenous phytohormones play a crucial role in modulating plant responses to salinity stress. Key hormones help enhance salt tolerance. These hormones include abscisic acid (ABA) and auxin. They also include salicylic acid (SA) and jasmonic acid (JA). Other important hormones are cytokinins, gibberellins, ethylene, and brassinosteroids (BR). These hormones regulate various stress-related pathways. Many salinity-responsive genes become active under salt stress. Transcription factors are also upregulated in response to salt stress. These genetic changes help plants adapt to saline environments.

Role of compatible organic solutes in salt stress alleviation

Plants respond to salt stress by accumulating compatible organic solutes. These solutes include proline, soluble sugars, glycine betaine, and polyols. These compounds have low molecular weight. They act as osmoprotectants. They help with intracellular osmotic change. They detoxify reactive oxygen species (ROS). They protect membrane integrity. They do this without disrupting cellular metabolism.

Glycine betaine

Glycine betaine is a quaternary ammonium compound. It accumulates significantly under dehydration and salt stress conditions. It is synthesized in the chloroplast. It plays a crucial role in osmotic adjustment of the thylakoid membrane. This helps maintain photosynthetic efficiency. Genetic engineering approaches have shown its potential in enhancing salt tolerance. Overexpression of the betaine aldehyde dehydrogenase gene in transgenic tobacco improved salt tolerance. This gene was taken from *Suaeda liaotungensis*. Similarly, scientists introduced the choline oxidase gene from *Arthrobacter globiformis* into Indica rice. This modification enabled rice to withstand salt stress up to 150 mM. The gene helped convert choline into glycine betaine. Apart from genetic modifications, exogenous application of glycine betaine improves salt tolerance. It has been effective in crops like *Phaseolus vulgaris L.* and *Dalbergia odorifera*. It reduces Na^+ uptake. It enhances K^+ absorption. Thereby maintaining a favorable K^+/Na^+ ratio (Cisse et al., 2021).

Proline

Proline is an important osmolyte and antioxidant. It accumulates in plants under salinity stress and helps maintain cell turgor. An increase in proline content is a key sign of a plant's response to salinity stress. It serves as a well-known physiological marker.

Salinity stress activates genes involved in proline biosynthesis. This leads to increased proline accumulation in plant cells. The enzyme Pyrroline-5-carboxylate synthetase (P5CS) catalyzes the first step of proline biosynthesis. Its isoform, P5CS1, plays a key role in salt-induced proline accumulation.

Studies in *Arabidopsis thaliana* show that P5CS1 is essential for salt stress tolerance. Knocking out P5CS1 makes plants more sensitive to salt stress (Jamil et al., 2018). Additionally, applying proline to *Capsicum annuum L.* helps mitigate salinity's inhibitory effects. This improves plant growth and yield (Balasubramaniam et al., 2022).

In desert plants like *Pancratium maritimum L.*, proline accumulation enhances antioxidative enzyme activity. It also increases the production of stress-protective dehydrin proteins. This helps improve salt tolerance (Singh et al., 2022).

Soluble sugars and polyols

Soluble sugars, such as glucose, sucrose, and trehalose, help plants tolerate salt stress. They protect soluble enzymes from toxicity. High intracellular inorganic ions can be harmful.

Trehalose, in particular, has a reversible water absorption capacity. This property shields molecules from osmotic damage (Liang et al., 2018). Transgenic *Arabidopsis* plants overexpressing the wheat gene *TaSST* show higher soluble sugar content. These plants exhibit better salt tolerance under NaCl treatment than wild-type plants.

Researchers inserted the enzyme mannitol-1-phosphate dehydrogenase (mt/D) into *Indica* rice. This enzyme originates from *E. coli*. This modification increased mannitol accumulation and enhanced salt tolerance (Byrt et al., 2017).

Understanding how specific osmolytes help plants withstand salt stress is essential. These insights help develop salt-tolerant crops. They offer promising solutions for sustainable agriculture in saline environments.

Multi-omics perspectives on salt-stress tolerance: the role of epigenetic regulation

In recent years, researchers have studied transcriptional responses to salt stress. They aim to identify key signaling pathways and regulatory proteins. The proteins help with stress adaptation. Epigenetics refers to gene expression regulation through heritable covalent modifications in chromatin architecture. It plays a crucial role in making transcription more accessible. Major epigenetic components regulate genes and maintain genome stability. These include DNA methylation, histone modifications, histone variants, and noncoding RNAs (ncRNAs). DNA methylation is one of the most studied epigenetic modifications. It involves adding a methyl group to the 5' position of cytosine in CG, CHG, and CHH sequence contexts. Here, H represents A, T, or C. Changes in DNA methylation patterns occur under saline conditions. These changes affect gene expression. For example, in wheat, *TaFLS1* is a salt-stress-responsive gene. Its promoter region showed lower methylation levels in a salt-tolerant cultivar. This suggests that DNA methylation regulates salt tolerance.

Histone proteins also undergo various covalent modifications. These include acetylation, methylation, phosphorylation, sumoylation, and ubiquitination. Specific histone-modifying enzymes mediate these changes. Such modifications play a key role in regulating gene expression under salt stress. A recent study (Feng et al., 2022) explored histone acetylation. Researchers discovered that GsMYST1 is a histone acetyltransferase in wild soybean. It undergoes phosphorylation by GsSnRK1 kinase. This process leads to the acetylation of histone H4 on stress-responsive genes. As a result, salt tolerance improves (Han et al., 2020).

Histone methylation is another important epigenetic process. It alters histone hydrophobicity and creates binding sites for regulatory proteins. In castor bean, methylation at *H3K4me3* and *H3K27me3* regulates the transcription of *RSM1*. This gene plays a critical role in ABA-mediated salt-stress signaling (Yung et al., 2021).

Beyond histone modifications, chromatin remodeling plays an essential role in modulating gene expression. Histone-DNA interactions change over time. These changes control the accessibility of transcriptional machinery to genomic regions (Nguyen et al., 2019).

Chromatin remodeling factors (CHR) include several ATPase subfamilies. These subfamilies are SWI/SNF, Imitation Switch (ISWI), and Chromodomain-Helicase-DNA-binding (CHD). CHRs facilitate ATP-dependent chromatin remodeling. They also regulate post-translational histone modifications (Yung et al., 2021).

In the *brm-3* mutant, the expression of ABA-related *PP2C* genes (*ABI1, ABI2,* and *HAI1*) increased after NaCl treatment. This suggests that the *brm-3* mutation affects the regulation of these genes. It may make them more active under salt stress. This finding suggests that BRAHMA (BRM) is a chromatin-remodeling ATPase. It suppresses these genes under salt stress (Haque et al., 2021).

Recent advancements in epigenetic research provide new insights. “Understanding these regulatory mechanisms could improve crop resilience to salt stress. Leveraging genome-editing technologies may further enhance this process”.

As researchers explore epigenetics, they may develop innovative strategies for crop breeding. These strategies could increase salt tolerance and boost agricultural productivity.

Integrated multi-omics discoveries

Genomics + transcriptomics identified candidate salt tolerance genes in rice (e.g., *OsHKT1;5*). Proteomics + metabolomics integration helped ROS detoxification and osmolyte synthesis (central to stress resilience). Antioxidants and osmolytes are key for stress survival. Epigenomics + transcriptomics uncovered stress memory mechanisms, guiding breeding strategies (*Fig. 5*).

Plant growth-promoting microbes (PGPMs)

Plant growth-promoting microbes (PGPMs), including plant growth-promoting rhizobacteria (PGPR), endophytes, and arbuscular mycorrhizal fungi (AMF), enhance plant salt tolerance through various mechanisms. PGPR such as *Halomonas alkaliantarcticae* M23 and *Bacillus halotolerans* KKD1 improve ion homeostasis by increasing the K^+/Na^+ ratio and reducing Na^+ uptake in plants like maize and wheat (Liu et al., 2025c). They also promote osmotic adjustment by stimulating the accumulation of osmolytes like betaine and proline. Additionally, PGPMs enhance antioxidant defense by boosting the activity of enzymes such as superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD), thereby mitigating oxidative stress. They regulate hormonal balance by modulating levels of abscisic acid (ABA), salicylic acid (SA), and jasmonic acid (JA), which are crucial for stress responses. Furthermore, PGPMs produce exopolysaccharides (EPS) that bind Na^+ in the rhizosphere, reducing its uptake by plants Bohrium. AMF-like *Rhizophagus intraradices* improve nutrient uptake, especially P, K, and micronutrients, and enhance water absorption under saline conditions. They also induce systemic tolerance by priming plants for better stress responses through modulation of gene expression and signaling pathways (Hidri et al., 2025). Collectively, PGPMs mitigate salt stress by regulating ion balance, enhancing osmotic and antioxidant defenses, modulating phytohormones, producing EPS, and improving nutrient acquisition via symbiosis, thereby supporting better growth, yield, and resilience in saline environments.

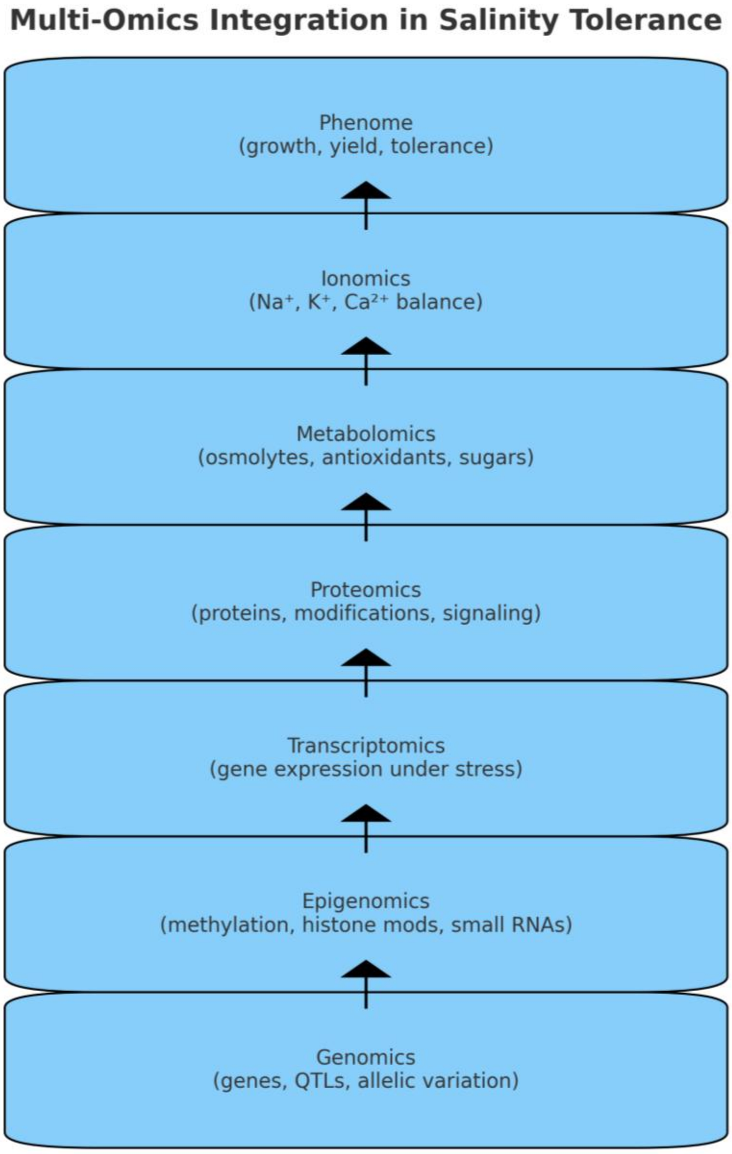

Figure 5. *Flowchart showing how different omics layers build upon each other to explain salinity tolerance—from genome (potential) all the way to phenome (observed tolerance)*

In *maize*, *Halomonas alkaliantarcticae* M23 improved tolerance via K^+/Na^+ balance, antioxidant enzyme upregulation, and ABA regulation. In *wheat*, *Bacillus halotolerans* KKD1 and other halotolerant PGPRs improved seedling growth, reduced Na^+ uptake, increased betaine, and improved morphological traits under salt stress. In salt-affected facultative halophyte *Sulla carnosa*, *Rhizophagus intraradices* AMF dramatically increased biomass, nutrient uptake, limited Na^+ accumulation and modulated stress hormone levels (*Fig. 6*).

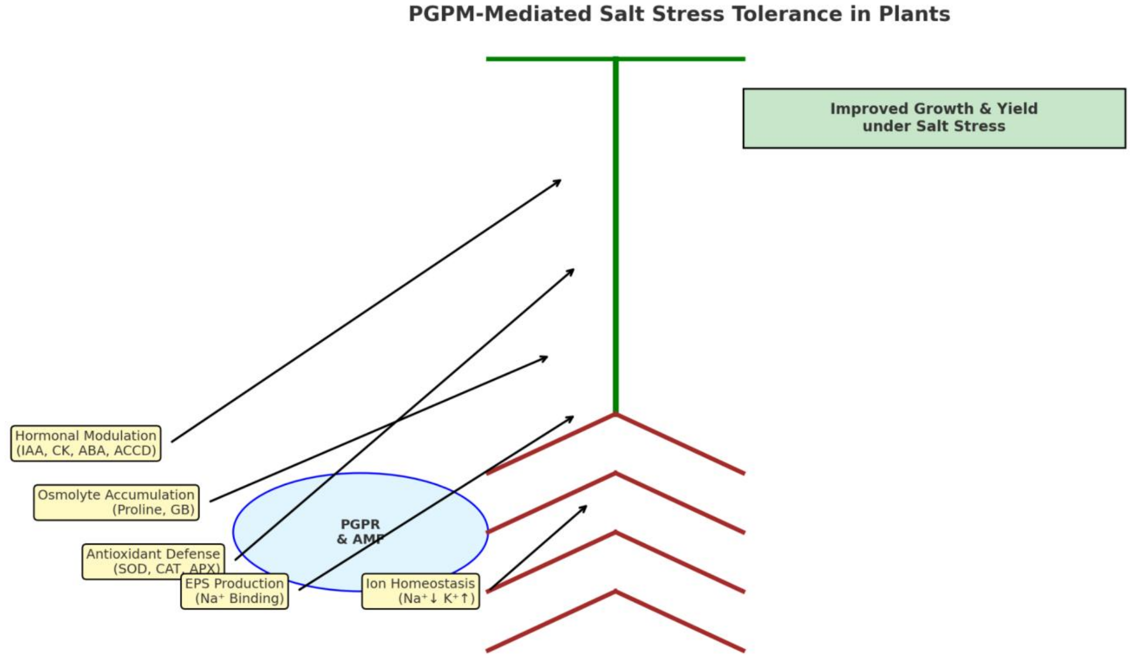

Figure 6. *PGPM mediated salt stress in plants*

Use of biofertilizers

Biofertilizers are microorganisms that enhance nutrient availability and improve plant health. Nitrogen-fixing bacteria (*Rhizobium, Azospirillum, Azotobacter*) → improve nitrogen supply under saline soils. Phosphate solubilizing microbes (*Pseudomonas, Bacillus, Aspergillus*) → increase phosphorus availability. Potassium solubilizing bacteria (*Frateuria aurantia*) → improve K^+ availability, balancing Na^+. Arbuscular mycorrhizal fungi (AMF) improve water/nutrient uptake. They also enhance Na^+ exclusion, and regulate osmolytes. For example, *Rhizobium* inoculation in chickpea improved nodulation and yield under saline conditions.

Use of biostimulants

Biostimulants are substances or microorganisms (other than nutrient fixing organisms). Plant growers apply these to enhance growth, nutrient uptake, and stress tolerance. Humic and Fulvic acids Improve nutrient uptake, stimulate root growth. Seaweed extracts (Ascophyllum nodosum, Sargassum spp.) are rich in hormones, polysaccharides, and antioxidants. Improve chlorophyll content, osmolyte levels, and antioxidant activity. *Protein hydrolysates & amino acids* Supply building blocks for stress proteins. Enhance osmotic regulation and metabolism. *Microbial biostimulants*

(*Trichoderma*, *Bacillus*) enhance root vigor, induce systemic tolerance, and modulate hormones. *Silicon and Chitosan-based biostimulants* Strengthen cell walls, reduce Na^+ toxicity, enhance antioxidant defense. Seaweed extract helps tomato plants build up proline and antioxidant activity during stress. Maintain *ion homeostasis* (low Na^+, high K^+). Enhance *antioxidant activity* to combat ROS. Stimulate *root growth* for better water/nutrient uptake. Improve *yield and quality* in saline soils. Provide a *sustainable alternative* to chemical inputs.

Concluding remarks and future perspectives

In the past ten years, researchers have learned more about how plants react to salt stress. They have also studied the mechanisms behind salt tolerance. These mechanisms involve complex interactions at the genetic, cellular, and physiological levels. Key processes help plants survive salt stress. These include ion balance and ion movement control. Water regulation is also important. Antioxidant activity protects cells. Hormone signaling helps plants respond to stress. Transgenic approaches, gene editing technologies, and computational tools have helped develop salt-tolerant plants. Despite these advancements, several challenges remain. Scientists must improve multi-omics methods. These include genomic, transcriptomic, proteomic, and metabolomic studies. This refinement will help identify key pathways that regulate salinity tolerance. We do not understand ion transport across membranes completely. Signal detection is also not completely clear. Long-distance signaling needs more research. Researchers need more insights into root-to-shoot communication under salt stress. We still lack knowledge about ion uptake. Ion exclusion is not understood completely. Scientists need to study ion storage. Ion transport in major crops needs more research. The role of hormonal crosstalk in salt-stress responses requires further investigation. Future research should focus on unraveling the regulatory networks involved in salt tolerance. It is important to ensure that improved crops keep high agronomic value. Bridging fundamental discoveries with field-based applications is critical for developing resilient crop varieties. These crops must thrive in saline environments. Integrating advanced breeding technologies, genome editing, and systems biology may enhance crop productivity. This integration could also improve sustainability in salt-affected regions. Looking ahead, a multidisciplinary approach is essential. It should combine genetics, epigenetics, bioinformatics, and agronomic practices. This approach will help address salt stress and improve crop productivity. Collaboration between researchers, policymakers, and farmers will be crucial. These efforts will help translate scientific discoveries into practical solutions. Innovative technologies and sustainable agricultural practices can support global food security. These strategies will create strong crops. The crops will survive salty soil. They will also endure climate change.

REFERENCES

[1] Abbasi, H., Jamil, M., Haq, A., Ali, S., Ahmad, R., Malik, Z., Parveen, Z. (2016): Salt stress manifestation on plants, mechanism of salt tolerance and potassium role in alleviating it: a review. – Zemdirb. Agric. 103: 229-238.

[2] Afonso, P., Castro, I., Carvalho, M. (2025): Salt-resilient cowpeas: early identification through growth parameters and gene expression at germination stage. – Int. J. Mol. Sci. 26: 1892. https://doi.org/10.3390/ijms26051892.

[3] Afzal, M., Hindawi, S. E. S., Alghamdi, S. S., Migdadi, H. H., Khan, M. A., Hasnain, M. U., Arslan, M., Habibur Rahman, M., Sohaib, M. (2023): Potential breeding strategies for improving salt tolerance in crop plants. – J. Plant Growth Regul. 42: 3365-3387.

[4] Ahmadzai, A. S., Hu, C., Zhang, C., Li, Y. (2025) Mechanisms of anthocyanin-mediated salt stress alleviation and cellular homeostasis in plants. – Plant Growth Regul. 105: 655-673 https://doi.org/10.1007/s10725-025-01298-3.

[5] Al-Hinai, M. S., Ullah, A., Al-Rajhi, R. S., Farooq, M. (2022): Proline accumulation, ion homeostasis and antioxidant defence system alleviates alt stress and protect carbon assimilation in bread wheat genotypes of Omani origin. – Environ. Exp. Bot. 193: 104687.

[6] Alvan, H. A., Jabbarzadeh, Z., Fard, J. R., Noruzi, P. (2025): Selenium foliar application alleviates salinity stress in sweet william (*Dianthus barbatus* L.) by enhancing growth and reducing oxidative damage. – Sci Rep 15: 5570. https://doi.org/10.1038/s41598-025-89463-6.

[7] Asins, M. J., Carbonell, E. A. (2024): Meta-QTL and candidate gene analyses of agronomic salt tolerance and related traits in an RIL population derived from Solanum pimpinellifolium. – International Journal of Molecular Sciences 25(11): 6055. https://doi.org/10.3390/ijms25116055.

[8] Balasubramaniam, T., Wijewardene, I., Hu, R., Shen, G., Zhang, J., Zhang, H. (2022): Co-over expression of AVP1, PP2A-C5, and AtCLCc in *Arabidopsis thaliana* greatly increases tolerance to salt and drought stresses. – Environ. Exp. Bot. 200: 104934.

[9] Balasubramaniam, T., Shen, G., Esmaeili, N., Zhang, H. (2023): plants' response mechanisms to salinity stress. – Plants 12(12): 2253.

[10] Betzen, B. M., Smart, C. M., Maricle, K. L., Cle, B. R. (2019): Effects of increasing salinity on photosynthesis and plant water potential in Kansas salt marsh species. – Trans. Kans. Acad. Sci. 122: 49-58.

[11] Byrt, C. S., Zhao, M., Kourghi, M., Bose, J., Henderson, S. W., Qiu, J., Gilliham, M., Schultz, C., Schwarz, M., Ramesh, S. A., Yool, A., Tyerman, A. (2017): Non-selective cation channel activity of aquaporin AtPIP2;1 regulated by $Ca^{2+}$and pH. – Plant Cell Environ. 40: 802-815.

[12] Campos, W. V., Filho, J. T., São José, A. R. (2025): African mahogany under saline stress: an analysis of the transpiration response at different salinity levels. – Plants (Basel) 21 14(5): 666. DOI: 10.3390/plants14050666.

[13] Chang, J., Wang, Y., Chu, J., Huang, Y., Ling, Y., Jiang, X. (2025): Comparative salt stress responses in two turnip cultivars: insights into ion homeostasis, osmotic regulation, and antioxidant capacity. – Hortic. Environ. Biotechnol. https://doi.org/10.1007/s13580-024-00673-9.

[14] Chen, K., Li, G. J., Bressan, R. A., Song, C. P., Zhu, J. K., Zhao, Y. (2020): Abscisic acid dynamics, signaling, and functions in plants. – J. Integr. Plant Biol. 62: 25-54.

[15] Chen, X., Liu, X., Cong, Y., Jiang, Y., Zhang, J., Yang, Q., Liu, H. (2025): Melatonin alleviates photosynthetic injury in tomato seedlings subjected to salt stress via OJIP chlorophyll fluorescence kinetics. – Plants 14: 824. https://doi.org/10.3390/plants14050824.

[16] Cisse, E. H. M., Miao, L. F., Yang, F., Huang, J. F., Li, D. D., Zhang, J. (2021): Gly Betaine surpasses melatonin to improve salt tolerance in *Dalbergia odorifera*. – Front. Plant Sci. 12: 588847.

[17] Cui, G., Liu, Y., Li, X., Wang, S., Qu, X., Wang, L., Tong, S., Zhang, M., Li, X., Zhang, W. (2025): Impacts of groundwater storage variability on soil salinization in a semi-arid agricultural plain. – Geoderma 454: 117162. https://doi.org/10.1016/j.geoderma.2024.117162.

[18] El-Beltagi, H. S., El-Nady, F. M., Ismail, A. M., Abomarzoka, E. A. E., El-Mogy, M. M., Metwaly, M. M. S. (2025): Foliar application of exogenous gibberellin or cytokinin mitigates salinity stress on faba bean (Vicia fabaL.). – Not Bot Horti Agrobo 53(2):14579.

[19] Esmaeili, N., Cai, Y., Tang, F., Zhu, X., Smith, J., Mishra, N., Hequet, E., Ritchie, G., Jones, D., Shen, G., Payton, P., Zhang, H. (2021): Towards doubling fibre yield for cotton in the semiarid agricultural area by increasing tolerance to drought, heat and salinity simultaneously. – Plant Biotechnol. J. 19: 462-476.

[20] Esmaeili, N., Shen, G., Zhang, H. (2022): Genetic manipulation for abiotic stress resistance traits in crops. – Front. Plant Sci. 13: 1011985.

[21] Farooq, M., Park, J. R., Jang, Y. H., Kim, E. G., Kim, K. M. (2021): Rice cultivars under salt stress Show differential expression of genes related to the regulation of Na^+/K^+ balance. – Front. Plant Sci. 12: 680131.

[22] Feng, P., Sun, X., Liu, X., Li, Y., Sun, Q., Lu, H., Li, M., Ding, X., Dong, Y. (2022): Epigenetic regulation of plant tolerance to salt stress by histone acetyl transferase GsMYST1 from wild soybean. – Front. PlantSci. 13: 860056.

[23] Foronda, D. A. (2022): Reclamation of a saline-sodic soil with organic amendments and leaching. – Environ. Sci. Proc. 16: 56.

[24] Fu, E., Myrans, H. and 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.70009.

[25] Fu, L., Wu, D., Zhang, X., Xu, Y., Kuang, L., Cai, S., Zhang, G., Shen, Q. (2022): Vacuolar H^+ pyrophosphatase HVP10 enhances salt tolerance via promoting Na^+ translocation into root vacuoles. – Plant Physiol.188: 1248-1263.

[26] Geetha, S., Vasuki, A., Selvam, P. J., Saraswathi, R., Krishnamurthy, S. L., Dhasarathan, M., Thamodharan, G., Baskar, M. (2021): Development of sodicity tolerant rice varieties through marker assisted backcross breeding. – Electron. J. Plant Breed. 8: 1013-1031.

[27] Goussi, R., Manaa, A., Derbali, W., Cantamessa, S., Abdelly, C., Barbato, R. (2018): Comparative analysis of salt stress, duration and intensity, on the chloroplast ultrastructure and photosynthetic apparatus in *Thellungiella salsuginea*. – J. Photochem. Photobiol. BBiol. 183: 275-287.

[28] Govindan, G., Harini, P., Alphonse, V. and Parani, M. (2024): From swamp to field: how genes from mangroves and its associates can enhance crop salinity tolerance. – Molecular Biology Reports 51(1): 598.

[29] Gu, H., He, Z., Lu, Z., Liao, S., Zhang, Y., Li, X., Cong, R., Ren, T., Lu, J. (2025): Growth and survival strategies of oilseed rape (*Brassica napus* L.) leaves under potassium deficiency stress: trade-offs in potassium ion distribution between vacuoles and chloroplasts. – 121(4): e70009. https://doi.org/10.1111/tpj.70009.

[30] Guo, J., Shan, C., Zhang, Y., Wang, X., Tian, H., Han, G., Zhang, Y., Wang, B. (2022) Mechanisms of salt tolerance and molecular breeding of salt-tolerant ornamental plants. – Front. Plant Sci. 13: 854116.

[31] Han, B., Xu, W., Ahmed, N., Yu, A., Wang, Z., Liu, A. (2020): Changes and associations of genomic transcription and histone methylation with salt stress in castor beans. – Plant Cell Physiology 61: 1120-1133.

[32] Han, L., Yang, M., Xu, B., Dai, L., Huang, Y., Wang, W., Pan, J., Abdel-Motaal, H., Wang, Y. (2025): Identification and functional analysis of a novel single-transmembrane Na+/H+ antiporter SATP1, in Pseudidiomarina sediminum: characterization of its key Na+ binding site. – International Journal of Biological Macromolecules 308(4): 142670. https://doi.org/10.1016/j.ijbiomac.2025.142670.

[33] Hannachi, S., Steppe, K., Eloudi, M., Mechi, L., Bahrini, I., Van Labeke, M. C. (2022): Salt stress induced changes in photosynthesis and metabolic profiles of one tolerant ('Bonica') and one sensitive ('Black beauty') eggplant cultivars (*Solanum melongena* L.). – Plants 11: 590.

[34] Haque, M. A., Rafii, M. Y., Yusoff, M. M., Ali, N. S., Yusuff, O., Datta, D. R., Anisuzzaman, M., Ikbal, M. F. (2021): Advanced breeding strategies and future perspectives of salinity tolerance in rice. – Agronomy 11: 1631.

[35] He, X., Zhu, J., Gong, X., Zhang, D., Li, Y., Zhang, X., Zhao, X. and Zhou, C. (2025). Advances in deciphering the mechanisms of salt tolerance in Maize. – Plant Signaling and Behavior 20(1): 2479513.

[36] Hereil, A., Guillaume, M., Duboscq, R., Carretero, Y., Pelpoir, E., Bitton, F., Giraud, C., Karlova, R., Testerink, C., Stevens, R., Causse, M. (2024): Characterisation of a major QTL for sodium accumulation in tomato grown in high salinity. – Plant Cell Environ. 47(12):5089-5103. DOI: 10.1111/pce.15082.

[37] Hidri, R., Zorrig, W., Debez, A., Mahmoud, O. M., Zamarreño, A. M., García-Mina, J. M., Nait Mohamed, S., Abdelly, C., Azcon, R., Aroca, R. (2025): Role of *Rhizophagus intraradices* in Mitigating Salt Stress of *Sulla carnosa* Through Modulating Plant Hormones (ABA, SA, and JA) and Nutrient Profile. – Biology (Basel). 14(4):341. DOI: 10.3390/biology14040341.

[38] Hnilickova, H., Kraus, K., Vachova, P., Hnilicka, F. (2021): Salinity stress affects photosynthesis, malondialdehyde formation, and proline content in *Portulaca oleracea* L. – Plants 10: 845.

[39] Hopmans, J. W., Qureshi, A. S., Kisekka, I., Munns, R., Grattan, S. R., Rengasamy, P., Ben-Gal, A., Assouline, S., Javaux, M., Minhas, P. S., Raats, P. A. C., Skaggs, T. H., Wang, G., De Jong van Lier, Q., Jiao, H., Lavado, R. S., Lazarovitch, N., Li, B., Taleisnik, E. (2021): Critical knowledge gaps and research priorities in global soil salinity. – Adv. Agron. 169: 1-191.

[40] Huang, S., Wu, P., Yang, X., Li, W., Zhou, W., Xie, Y., Meng, X., Li, Z., Xu, Z., Jin, N., Jin, L., Wang, S., Lyu, J., Yu, J. (2025): Enhancing saline-alkali tolerance in cucumber seedlings: the role of exogenous melatonin in redox homeostasis and stomatal function. – Plant Stress 15: 100789. https://doi.org/10.1016/j.stress.2025.100789.

[41] Huihui, Z., Yue, W., Xin, L., Guoqiang, H., Yanhui, C., Zhiyuan, T., Jieyu, S., Nan, X., Guangyu, S. (2020): Chlorophyll synthesis and the photo protective mechanism in leaves of mulberry (*Morus alba* L.) seedlings under NaCl and $NaHCO_3$ stress revealed by TMT-based proteomics analyses. – Ecotoxicol. Environ. Saf 190: 110164.

[42] Hussain, N., Sohail, Y., Shakeel, N., Javed, M., Bano, H., Gul, H. S., Zafar, Z. U., Hassan, I. F., Ghaffar, A., Athar, H. U., Ajaj, R. (2022): Role of mineral nutrients, antioxidants, osmotic adjustment and PS II stability in salt tolerance of contrasting wheat genotypes. – Sci. Rep. 12: 12677.

[43] Isayenkov, S. V., Maathuis, F. J. (2019): Plant salinity stress: many unanswered questions remain. – Front. PlantSci. 10: 80.

[44] Jamil, M., Kharal, M. A., Ahmad, M., Abbasi, G. H., Nazli, F., Hussain, A., Akhtar, M. F. U. Z. (2018) Inducing salinity tolerance in red pepper (*Capsicum annuum* L.) through exogenous application of proline and L-tryptophan. – Soil Environ. 37: 160-168.

[45] Ji, X., Tang, J., Zhang, J. (2022): Effects of salt stress on the morphology growth physiological parameters of *Juglans microcarpa* L. Seedl. –Plants 11:2381.

[46] Kanneri, A., Saraladevi, R. M., Rasack, R. V., JayanthikumariI, V. P. (2025): Comprehensive Analysis of Pollen Viability, in vitro Germination, and Self-incompatibility in Hamelia patens Jacq. Pollen. – International Journal of Horticultural Science and Technology 12(1):145-156. doi: 10.22059/ijhst.2024.372736.782

[47] Kaushal, S. S., Shelton, S. A., Mayer, P. M., Kellmayer, B., Utz, R. M., J. E., Reimer, Baljunas, J., Bhide, S. V., Mon, A., Rodriguez-Cardona, B. M., Grant, S. B., Newcomer-Johnson, T. A., Malin, J. T., Shatkay, R. R., Collison, D. C., Papageorgiou, K., Escobar, J., Rippy, M. A., Likens, G. E., Najjar, R. G., Mejia, A. I., Lassiter, A., Li, M., Chant, R. J. (2025): Freshwater faces a warmer and saltier future from headwaters to coasts: climate risks, saltwater intrusion, and biogeochemical chain reactions. – Biogeochemistry 168: 31. https://doi.org/10.1007/s10533-025-01219-6.

[48] Kozlov, V. A., Javadov, S., Sommer, N. (2024): Cellular ROS and antioxidants: physiological and pathological role. – Antioxidants 13(5): 602.

[49] Kramer, I., Peleg, N., Mau, Y. (2025): Climate change shifts risk of soil salinity and land degradation in water-scarce regions. – Agricultural Water Management 307: 109223. https://doi.org/10.1016/j.agwat.2024.109223.

[50] Krishnamurthy, S. L., Pundir, P., Warraich, A. S., Rathor, S., Lokeshkumar, B. M., Singh, N. K., Sharma, P. C. (2020): Introgressed saltol QTL lines improves the salinity tolerance in rice at seedling stage. – Front Plant Sci. 11:833. DOI: 10.3389/fpls.2020.00833.

[51] Kumar, S., Saxena, V., Sopory, S. K., Sanan-Mishra, N. (2025): miRNAs: A Low-Cost Solution to Enhance Rice Yield Under Salinity Stress. – – In: Goswami, K. et al. (eds.) Non-Coding RNAs for crop Improvement: Concepts and Applications. Springer Nature, Singapore, pp. 283-306.

[52] Liang, L., Liu, X., Guo, L., Wang, L., Zhao, Y., Wu, Y., Chen, Y., Liu, W. and Gao, G. (2025): Beyond salt tolerance: SOS1-13's pivotal role in regulating the immune response to *Fusarium oxysporum* in *Solanum phureja*. – Frontiers in Plant Science 16:1553348.

[53] Liang, W., Ma, X., Wan, P., Liu, L. (2018): Plant salt-tolerance mechanism: a review. – Biochem. Biophys. Res. Commun 495: 286-291.

[54] Liu, H., Pan, L., Ahmad, I., Bai, Y., Shen, S., Shi, R., Xu, T., Sun, Y., Gao, Y., Kang, B., Lu, Y., Wang, X. (2025b): Study on the mechanism of exogenous CaCl2 regulating cell growth and development to alleviate salt tolerance of alfalfa (Medicago sativa). – Frontiers in Plant Science 16:1565723.

[55] Liu, J., Zhao, X., Niu, Y., Ren, Y., Wang, M., Han, B., Wang, C., Ma, H. (2025c): Plant growth-promoting rhizobacteria Halomonas alkaliantarcticae M23 promotes the salt tolerance of maize by increasing the K+/Na+ ratio, antioxidant levels, and ABA levels and changing the rhizosphere bacterial community. – BMC Plant Biol. 25(1):727. DOI: 10.1186/s12870-025-06765-7.

[56] Liu, X., Shi, L., Bai, H., Wang, J., Yu, A., Liu, A. and Li, P. (2025a): Comparative analysis of HKTs in six poplar species and functional characterization of PyHKTs in stress-affected tissues. – BMC genomics 26(1):18.

[57] Long, L., Zhao, J. R., Guo, D. D., Ma, X. N., Xu, F. C., Yang, W. W., Gao, W. (2020): Identification of NHXs in Gossypium species and the positive role of *GhNHX$_1$* in salt tolerance. – BMC Plant Biol. 20: 147.

[58] Lu, C.; Li, L.; Liu, X.; Chen, M.; Wan, S.; Li, G. (2023): salt stress inhibits photosynthesis and destroys chloroplast structure by downregulating chloroplast development-related genes in *Robinia pseudoacacia* seedlings. – Plants 12: 1283. https://doi.org/10.3390/plants12061283.

[59] Mondal, S., Vaughn, R., Septiningsih, E. M., Singh, R. K., Thomson, M. J. (2025): Identification of QTLs for reproductive stage salinity tolerance in rice using a cross between CSR 28 and BRRI dhan 28. – Crop Science 65(1): e70014. https://doi.org/10.1002/csc2.70014.

[60] Muhammad, M., Waheed, A., Wahab, A., Majeed, M., Nazim, M., Liu, Y. H., Li, L., Li, W. (2024): Soil salinity and drought tolerance: an evaluation of plant growth, productivity, microbial diversity, and amelioration strategies. – Plant Stress 11: 100319. https://doi.org/10.1016/j.stress.2023.100319.

[61] Nadeem, M., Anwar-Ul-Haq, M., Xin, X., Shohag, M. J. I., Ayub, M. A., Ahmad, W., He, Z. (2025): Exogenous application of silica and nano silica particles improves nutrient acquisition and growth of maize (*Zea mays* L.) under saline and water deficit conditions. – Communications in Soil Science and Plant Analysis. https://doi.org/10.1080/00103624.2025.2480126.

[62] Nakhla, W. R., Sun, W., Fan, K., Yang, K., Zhang, C., Yu, S. (2021): Identification of QTLs for salt tolerance at the germination and seedling stages in rice. – Plants 10: 428.

[63] Nazish, M., Kamal, A., Zafar, M., Ahmad, M., Shah, G. M., Alkahtani, J., Rahman, K. U., Elshikh, M. S., Razak, S. A., Naseem, M. T., Zaman, W. (2025): Pollen patterns and morphological variability unraveling taxonomic relevance and evolutionary relationship in salt-tolerant species. – Genet Resources and Crop Evolution 72: 5979-5996.

https://doi.org/10.1007/s10722-024-02316-5.

[64] Negacz, K., Malek, Z., Vos, A. D., Vellinga, P. (2022): Saline soils worldwide: identifying the most promising areas for saline agriculture. – Journal of Arid Environments 203: 104775.

[65] Nguyen, N. H., Jung, C., Cheong, J. J. (2019) Chromatin remodeling for the transcription of type 2C protein phosphatase genes in response to salt stress. – Plant Physiol. Biochem. 141: 325-331.

[66] Orzechowska, A., Trtílek, M., Tokarz, K. M., Szymanska, R., Niewiadomska, E., Rozpa˛ dek, P., Wator, K. (2021): Thermal analysis of stomatal response under salinity and highlight. – Int. J. Mol. Sci. 22: 4663.

[67] Peduzzi, A., Piacentini, D., Brasili, E., Rovere, F. D., Patriarca, A., D'Angeli, S., Altamura, M. M., Falasca, G. (2024): Salt stress alters root meristem definition, vascular differentiation and metabolome in Sorghum bicolor (L.) genotypes. – Environmental and Experimental Botany 226: 105876. https://doi.org/10.1016/j.envexpbot.2024.105876.

[68] Pramanik, D., Shelake, R. M., Kim, M. J., Kim, J. Y. (2021): CRISPR-mediated engineering across the central dogma in plant biology for basic research and crop improvement. – Mol. Plant 14: 127-150.

[69] Qamer, Z., Chaudhary, M. T., Du, X., Hinze, L., Azhar, M. T. (2021): Review of oxidative stress and antioxidative defense mechanisms in *Gossypium hirsutum* L. in response to extreme abiotic conditions. – J. Cotton Res. 4: 9.

[70] Qin, C., Ahanger, M. A., Zhou, J., Ahmed, N., Wei, C., Yuan, S., Ashraf, M., Zhang, L. (2020): Beneficial role of acetylcholine in chlorophyll metabolism and photosynthetic gas exchange in *Nicotiana benthamiana* seedlings under salinity stress. – Plant Biol. 22: 357-365.

[71] Qin, Z., Nie, T., Wang, Y., Zheng, H., Tong, C., Wang, J., Wang, R., Hou, H. (2025): The characteristics and driving factors of soil salinisation in the irrigated area on the southern bank of the Yellow River in Inner Mongolia: assessment of the Donghaixin irrigation district. – Agriculture 15:566. https://doi.org/10.3390/agriculture15050566.

[72] Rafaliarivony, S., Ranarijaona, H. L. T., Rasoafalimanana, M., Radanielina, T., Wissuwa, M. (2023): Evaluation of salinity tolerance of lowland rice genotypes at the reproductive stage. – African Journal of Agricultural Research 19(10): 945-961.

[73] Rao, M. J., Duan, M., Zhou, C., Jiao, J., Chang, P., Yang, L., Wei, W., Shen, Q., Ji, P., Yang, Y., Conteh, O., Yan, Yuan, H., Rauf, A., Ai, Zheng, B. (2025): Antioxidant Defense system in plants: reactive oxygen species production, signaling, and scavenging During Abiotic Stress-Induced Oxidative Damage. – Horticulturae 11(5):11050477.

[74] Reta, B. G., Habite, W. (2025): Optimizing tomato yield in saline-sodic soils with gypsum and mulching techniques near Lake Abaya, Ethiopia. – Applied and Environmental Soil Science 2025(1): 4199651.

[75] Riyazuddin, R., Verma, R., Singh, K., Nisha, N., Keisham, M., Bhati, K. K., Kim, S. T., Gupta, R. (2020): Ethylene: a master regulator of salinity stress tolerance in plants. – Biomolecules 10(6):959.

[76] Samineni, S., Gummadi, S., Thushar, S., Khan, D. N., Gkanogiannis, A., Becerra Lopez-Lavalle, L. A., Singh, R. K. (2025): Exploring Proso millet resilience to abiotic stresses: high-yield potential in desert environments of the Middle East. – Agronomy 15: 165. https://doi.org/10.3390/agronomy15010165.

[77] Şekerci, K., Higashitani, N., Ozgur, R., Higashitani, A., Turkan, I., Uzilday, B. (2025): Gene expression and mucilage adaptations to salinity in germination of extreme halophyte *Schrenkiella parvula* seeds. – International Journal of Biological Macromolecules 308(4): 142670. https://doi.org/10.1016/j.plaphy.2025.109517.

[78] Sevgi, B., Leblebici, S. (2025): Exogenous sucrose alleviates salt stress in sunflower (*Helianthus annuus* L.) and canola (*Brassica napus* L.) by modulating osmotic adjustment and antioxidant defense system. – Physiol Mol Biol Plants. https://doi.org/10.1007/s12298-025-01571-9.

[79] Shahzad, B., Shabala, L., Zhou, M., Venkataraman, G., Solis, C. A., Page, D., Chen, Z. H., Shabala, S. (2022). Comparing essentiality of SOS1-mediated Na^+ exclusion in salinity tolerance between cultivated and wild rice species. – Int. J. Mol. Sci. 23: 9900.

[80] Sheldon, A. R., Dalal, R. C., Kirchhof, G., Kopittke, P. M., Menzies, N. W. (2017). The effect of salinity on plant-available water. – Plant Soil 418: 477-491.

[81] Siddique, M. A., Egdane, J., Bagunu, E., Quick, W. P., Diaz, M. G., Henry, A. (2025): Optimizing a protocol for salinity recovery during seedling stage in rice. – agriRxiv 2025: 20250010676.

[82] Singh, A. (2022): Soil salinity: a global threat to sustainable development. – Soil Use Manag. 38: 39-67.

[83] Singh, N., Maurya, V., Gupta, K., Sharma, I., Sharma, A., Kumar, R. (2025): Salt stress and its eco-friendly management using biostimulants in grain legumes: a review. – Discov Agric 3: 13 https://doi.org/10.1007/s44279-024-00150-y.

[84] Singh, P., Choudhary, K. K., Chaudhary, N., Gupta, S., Sahu, M., Tejaswini, B., Sarkar, S. (2022): Salt stress resilience in plants mediated through osmolyte accumulation and its crosstalk mechanism with phytohormones. – Front. PlantSci. 13: 1006617.

[85] Singroha, G., Kumar, S., Gupta, O. P., Singh, G. P., Sharma, P. (2022): Uncovering the epigenetic marks involved in mediating salt stress tolerance in plants. – Front. Genet. 13: 811732.

[86] Stavi, I., Thevs, N., Priori, S. (2021): Soil salinity and sodicity in drylands: a review of causes, effects, monitoring, and restoration measures. – Front. Environ. Sci. 330: 712831.

[87] Sun, Y., Liu, X., Fu, L., Qin, P., Li, T., Ma, X., Wang. X. (2019): Overexpression of *TaBADH* increases salt tolerance in *Arabidopsis*. – Canadian Journal of Plant Science 99(4): 546-555. https://doi.org/10.1139/cjps-2018-0190.

[88] Swetha, R., Sridhanya, V. M., Varanavasiappan, S., Kumar, K. K., Kokiladevi, E., Ravichandran, V., Ramalingam, J., Sudhakar, D., Arul, L. (2025): Root apoplastic barrier mechanism: an adaptive strategy to protect against salt stress. – Mol Biol Rep 52: 56. https://doi.org/10.1007/s11033-024-10171-x.

[89] Tang, H., Du, L., Xia, C., Luo, J. (2024): Bridging gaps and seeding futures: a synthesis of soil salinization and the role of plant-soil interactions under climate change. – iScience 23;27(9):110804. DOI: 10.1016/j.isci.2024.110804.

[90] Tarolli, P., Luo, J., Park, J., Barcaccia, G., Masin, R. (2024): Soil salinization in agriculture: mitigation and adaptation strategies combining nature-based solutions and bioengineering. – iScience 27(2): 108830. https://doi.org/10.1016/j.isci.2024.108830.

[91] Teng, J., Chiew, F. H. S., Zheng, H., Yang, A., Penton, D. J., Ticehurst, C., Marvanek, S., Vaze, J., Khanam, F., Post, D. A., Pollino, C. (2025). Floodplain inundation in the Murray–Darling Basin under current and future climate conditions. – Sci Rep 15: 8917. https://doi.org/10.1038/s41598-025-93670-6.

[92] Tomaškinová, J., Tomaškin, J., Drimal, M., Bellido, J. (2025): The Impact of abiotic environmental stressors on fluorescence and chlorophyll content in *Glycine max* (L.) Merrill. – Agronomy 15: 263. https://doi.org/10.3390/agronomy15020263.

[93] Turki, N., Shehzad, T., Harrabi, M., Okuno, K. (2023): Mapping novel QTLs for tolerance to salt stress at the late vegetative stage in durum wheat (*Triticumdurum* L.). – J. King Saud Univ. Sci. 35: 102506.

[94] Ullah, A., Bano, A., Khan, N. (2021): Climate change and salinity effects on crops and chemical communication between plants and plant growth-promoting microorganisms under stress. – Front. Sustain. Food Syst. 5: 618092.

[95] Ullah, M. A., Abdullah-Zawawi, M. R., Razalli, I. I. Sukiran, N. L., Uddin, M. I. Zainal, Z. (2025): Overexpression of rice High-affinity Potassium Transporter gene *OsHKT1;5* improves salinity and drought tolerance in Arabidopsis. – Mol Biol Rep 52: 40. https://doi.org/10.1007/s11033-024-10130-6.

[96] Uzun, H. D., Malysenko, E., Justesen, B. H., Pomorski, T. G. (2025): Functional reconstitution of plant plasma membrane H+-ATPase into giant unilamellar vesicles. – Sci Rep 15: 8541. https://doi.org/10.1038/s41598-025-92663-9.

[97] Vázquez-Rivera, D., Huerta-Venegas, P. I., Raya-González, J., Peña-Uribe, C. A., Lopez-Bucio, J. S., García-Pineda, E., López-Bucio, J., Campos-García, J., Reyes de la Cruz, H. (2025): BX517, an inhibitor of the mammalian phospholipid-dependent kinase 1 (PDK1), antagonizes sucrose-induced plant growth and represses the target of rapamycin (TOR) signaling and the cell cycle through WEE1 kinase in *Arabidopsis thaliana*. – Journal of Plant Physiology 304:154386. https://doi.org/10.1016/j.jplph.2024.154386.

[98] Wang, C. F., Han, G. L., Yang, Z. R., Li, Y. X., Wang, B. S. (2022): Plant salinity sensors: current understanding and future directions. – Front Plant Science 13:859224.
DOI: 10.3389/fpls.2022.859224.

[99] Wang, L., Liu, Y., Li, D., Feng, S., Yang, J., Zhang, J., Zhang, J., Wang, D., Gan, Y. (2019): Improving salt tolerance in potato through over expression of AtHKT1 gene. – BMC Plant Biol. 19: 357.

[100] Wang, W., Chi, M., Liu, S., Zhang, Y., Song, J., Xia, G., Liu, S. (2025a): TaGPAT6 enhances salt tolerance in wheat by synthesizing cutin and suberin monomers to form a diffusion barrier. – Journal of Integrative Plant Biology 67(2): 208-225.

[101] Wang, W., Li, Y., Li, G., Fang, Y., Xu, H. (2025b): Effects of surface water irrigation on fertility and properties of agricultural soil in the above ground segment of the Yellow River downstream. – Water Air Soil Pollut 236: 77. https://doi.org/10.1007/s11270-024-07722-0.

[102] Wang, X., Wang, W., Huang, J., Peng, S., Xiong, D. (2018): Diffusion conductance to CO_2 is the key limitation to photosynthesis in salt-stressed leaves of rice (*Oryza sativa*). – Physiol. Plant. 163: 45-58.

[103] Wei, J., Liu, M., Zhao, D., Du, P., Yan, L., Liu, D., Shi, Q., Yang, C., Qin, G., Gong, B. (2025): Melatonin confers saline-alkali tolerance in tomato by alleviating nitrosative damage and *S*-nitrosylation of H+-ATPase 2. – The Plant Cell 37(2): koaf035.
https://doi.org/10.1093/plcell/koaf035.

[104] Xu, H., Chen, H., Halford, N. G., Xu, R., He, T., Yang, B., Zhou, L., Guo, H., Liu, C. (2025a): Ion homeostasis and coordinated salt tolerance mechanisms in a barley (*Hordeum vulgare* L.) doubled haploid line. – BMC Plant Biol 25: 52. https://doi.org/10.1186/s12870-024-06033-0.

[105] Xu, Q., Zhang, X., Zhao, R., Li, S., Liesche, J. (2025b): UBIQUITIN-CONJUGATING ENZYME34 mediates pyrophosphatase AVP1 turnover and regulates abiotic stress responses in Arabidopsis. – Plant Physiology 197(2): kiaf015.
https://doi.org/10.1093/plphys/kiaf015.

[106] Yan, H. K., Zhang, C. C., Nai, G. J., Ma, L., Lai, Y., Pu, Z. H., Ma, S. Y. and Li, S. (2025): Microbial Inoculant GB03 Increased the yield and quality of grape fruit under salt-alkali stress by changing rhizosphere microbial communities. – Foods 14(5): 711.

[107] Yanez-Dominguez, C., Macedo-Osorio, K., Lagunas-Gomez, D., Torres-Cifuentes, D., Castillo-Gonzalez, J., Zavala, G., Pantoja, O. (2025): The chloroplast-located HKT transporter plays an important role in fertilization and development in Physcomitrium patens. – The Plant Journal 121(3): e17253.

[108] Yang, D., Ha, Y., Lee, M. M. and Nam, K. H. (2025): Salt overly sensitive components differentially regulate seed germination and seedling growth under saline conditions in Arabidopsis. – Journal of Plant Biology 69: 49-69.

[109] Yousefi, F., Soltani, F., Hassandokht, M. (2025): Morphological, physiological, and biochemical changes of eggplant (*Solanum melongena* L.) in response to salinity stress. – Sci Rep 15: 24385. https://doi.org/10.1038/s41598-025-09901-3.

[110] Yousefirad, S., Soltanloo, H., Ramezanpour, S. S., Zaynalinezhad, K., Shariati, V. (2018) Salt over sensitivity derived from mutation breeding improves salinity tolerance in barley via ion homeostasis. – Biol. Plant. 62: 775-785.

[111] Yu, Z., Duan, X., Luo, L., Dai, S., Ding, Z., Xia, G. (2020): How plant hormones mediate salt stress responses. – Trends Plant Sci. 25: 1117-1130.

[112] Yung, W. S., Li, M. W., Sze, C. C., Wang, Q., Lam, H. M. (2021): Histone modifications and chromatin remodeling in plants in response to salt stress. – Physiol. Plant. 173: 1495-1513.

[113] Zahra, N., Wahid, A., Shaukat, K., Hafeez, M. B., Batool, A., Hasanuzzaman, M. (2021): Oxidative stress tolerance potential of milk thistle ecotypes after supplementation of different plant growth-promoting agents under salinity. – Plant Physiol. Biochem. 166: 53-65.

[114] Zahra, N., Al Hinai, M. S., Hafeez, M. B., Rehman, A., Wahid, A., Siddique, K. H., Farooq, M. (2022): Regulation of photosynthesis under salt stress and associated tolerance mechanisms. – Plant Physiol. Biochem. 178: 55-69.

[115] Zhang, M., Li, Y., Liang, X., Lu, M., Lai, J., Song, W., Jiang, C. (2023): A teosinte-derived allele of an HKT1 family sodium transporter improves salt tolerance in maize. – Plant Biotechnol. J. 21(1):97-108. DOI: 10.1111/pbi.13927.

[116] Zhang, M., Zhou, X., Wang, L., Liang, X., Liu, X., Jiang, C. (2025b): A SnRK2-HAK regulatory module confers natural variation of salt tolerance in maize. – Nat. Commun. 16(1):4026. DOI: 10.1038/s41467-025-59332-x.

[117] Zhang, X., Li, H., Liu, H., Wang, J., Qiang, X. (2025a): Response of tomato quality parameters to water deficit under soil salinity and simulation based on stem water potential. – Horticulturae 11(2): 114.

[118] Zhao, S., Zhang, Q., Liu, M., Zhou, H., Ma, C., Wang, P. (2021): Regulation of plant responses to salt stress. – Int. J. Mol. Sci. 22: 4609.