Advances in Agriculture and Biology (2026) 9(1): 1-24
DOI: https://doi.org/10.63072/aab.26001
https://aabinternational.com/
ISSN: 3079-174X

REVIEW PAPER

From salt stress to climate resilience: Recent advances in plant responses, molecular regulation, and sustainable strategies for salinity tolerance

Abdullah[1], Izhar Muhammad[2], Sartaj Aziz[3], Shah Zaib[4], Aneesa Gul[5] and Sohail Ahmad Jan[6]

[1]State Key Laboratory of Herbage Improvement and Grassland Agro-ecosystems, College of Ecology, Lanzhou University, Lanzhou, 730000, China
[2]School of Biotechnology, Jiangnan University, Wuxi, China
[3] College of Life Science, Guizhou University Guiyang, China
[4]CAS Key Laboratory of Environmental and Applied Microbiology, Chengdu Institute of Biology, Chinese Academy of Sciences, China
[5]College of Horticulture, Guangdong Ocean University, Guangdong, China
[6]Department of Bioinformatics and Biosciences, Capital University of Science and Technology, Islamabad, Pakistan

*Corresponding author's email: abdullah2026@lzu.edu.cn

Abstract

Soil salinity is one of the most severe abiotic stresses limiting agricultural productivity worldwide, and its adverse impacts are expected to intensify under climate change, sea-level rise, and unsustainable land-use practices. Excessive accumulation of soluble salts disrupts plant water relations, ion homeostasis, nutrient acquisition, photosynthesis, and cellular metabolism, ultimately resulting in substantial reductions in crop growth and yield. Unlike earlier reviews that focus mainly on physiological and ionic responses or on a single technology, this review integrates molecular regulation, genome editing, plant–microbe–soil interactions, and digital phenotyping within the context of climate-driven soil salinization and critically evaluates how far each approach has progressed from laboratory proof of concept toward field application. First, epigenetic regulation, microRNAs, and long non-coding RNAs fine-tune ion transport, antioxidant defense, and osmotic adjustment and contribute to stress memory, while multi-omics and genetic mapping studies have identified ion transporters such as HKT1, SOS1 and NHX as breeding targets. Second, CRISPR/Cas editing of salt-responsive genes has improved salt tolerance in crops such as rice and tomato, but most evidence is restricted to seedling-stage and controlled-environment studies, and effects on yield are rarely tested. Third, salt-adapted plant growth-promoting rhizobacteria, arbuscular mycorrhizal fungi, and synthetic microbial communities improve plant performance, although survival, colonization, and consistency under field conditions remain major limitations. Fourth, hyperspectral, thermal, and chlorophyll fluorescence imaging combined with machine learning enable early, non-destructive screening of salt-tolerant genotypes. Long-term salinity management requires salt-tolerant plants, better soil, water and nutrient management, and field testing. Key research priorities include field trials, combining multi-omics data, assessing growth and yield in genetically modified plants, and developing reliable microbial inoculants. Together, these findings provide a framework for developing resilient cropping systems that maintain productivity in increasingly saline environments and support global food security. © 2026 The Author(s)

Keywords: Climate resilience, CRISPR/Cas genome editing, Digital phenotyping, Multi-omics, Plant–microbe–soil interactions, Salinity stress, Sustainable salinity management

Citation: Abdullah, Muhammad, I., Aziz, S., Zaib, S., Gul, A., & Jan, S. A. (2026). From salt stress to climate resilience: Recent advances in plant responses, molecular regulation, and sustainable strategies for salinity tolerance. *Advances in Agriculture and Biology, 9*(1), 1–24. https://doi.org/10.63072/aab.26001

Introduction

Salinity is one of the most detrimental abiotic stresses affecting plant growth and productivity by inducing ionic imbalance, osmotic stress, and excessive accumulation of reactive oxygen species (ROS), which collectively impair cellular metabolism and physiological functions. Recent studies have demonstrated that several physiological, biochemical, and molecular mechanisms contribute to enhancing plant tolerance to saline conditions. Among these, melatonin has emerged as an effective stress-mitigating molecule that promotes Osmo protectant accumulation and antioxidant enzyme activity, limits sodium (Na^+) accumulation, and improves membrane stability, relative water content (RWC), and the K^+/Na^+ ratio under salt stress (Hussain et al., 2023). Despite considerable advances in understanding physiological responses to salinity, the development of highly salt-tolerant crop varieties remains challenging because salinity tolerance is controlled by complex genetic networks and is strongly influenced by phenotypic variability (Li et al., 2023).

Recent advances in molecular biology have significantly improved our understanding of the genetic basis of salinity tolerance. Numerous quantitative trait loci (QTLs) associated with salt tolerance have been identified, revealing the involvement of genes responsible for ion homeostasis, osmotic adjustment, and oxidative stress mitigation. Among these, the Salt Overly Sensitive (SOS) signaling pathway has been recognized as a key regulatory mechanism controlling Na^+ efflux and root-to-shoot ion transport, thereby maintaining ionic balance and enhancing plant adaptation to saline environments (Cao et al., 2023).

The application of plant growth regulators has also been recognized as an effective strategy for alleviating the adverse effects of salinity. Exogenous application of salicylic acid (SA) has been reported to improve plant biomass and growth under saline conditions by reducing Na^+ uptake and enhancing the K^+/Na^+ ratio. These physiological adjustments contribute to improved ionic homeostasis, better metabolic activity, and enhanced tolerance to salt-induced stress (Mutlu-Durak et al., 2023). In addition to conventional approaches, nanotechnology has emerged as a promising tool for improving plant resilience to salinity stress. The combined application of zinc oxide nanoparticles (ZnO-NPs) and 24-epibrassinolide (EBL) has been shown to enhance plant growth, leaf area, relative water content, chlorophyll concentration, and photosynthetic efficiency under saline conditions. Furthermore, these treatments reduce Na^+ accumulation, lower the Na^+/K^+ ratio, and alleviate oxidative stress, resulting in enhanced physiological performance and greater tolerance to salinity (Seleiman et al., 2023). Salinity management also requires consideration of soil characteristics and the nature of saline stress. Soil and irrigation water salinity continue to pose significant threats to global agricultural productivity and food security.

Studies have demonstrated that alkaline salinity causes more severe physiological damage than neutral salinity because elevated soil pH restricts nutrient availability, disrupts membrane integrity, and intensifies stress responses. Therefore, integrated management strategies, including biological interventions and chemical amendments, have been recommended to improve soil health, enhance plant resilience, and sustain agricultural productivity under saline conditions (Ondrasek et al., 2022). Several authoritative reviews have summarized the physiological and ionic basis of salinity tolerance (Munns & Tester, 2008), highlighted the questions that remain unanswered (Isayenkov & Maathuis, 2019), and described how plants sense, signal, and adapt to soil salinity (van Zelm et al., 2020; Zhao et al., 2020). However, these reviews generally treat molecular regulation, genome editing, plant–microbe–soil interactions, digital phenotyping, and climate-driven soil salinization as separate topics, and they rarely assess how mature each approach is for field use. A specific knowledge gap therefore remains it is unclear how recent advances in epigenetic and non-coding RNA regulation, multi-omics, genome editing, microbiome-based interventions, and phenotyping can be combined to support salinity management under a changing climate, and where the evidence is still limited to laboratory or greenhouse conditions. This review addresses that gap in three ways. First, it links molecular discoveries to breeding and agronomic applications. Second, it distinguishes experimentally demonstrated results from proposed applications. Third, it connects these strategies to climate-related processes, such as sea-level rise, altered precipitation, and secondary salinization, that determine where and how salinity will intensify. The scope of this review is deliberately weighted toward recent advances. Greatest attention was given to (i) molecular regulation, including epigenetic mechanisms, microRNAs, long non-coding RNAs, and multi-omics approaches (ii) CRISPR/Cas genome editing (iii) the root microbiome and plant–microbe–soil interactions (iv) digital phenotyping and artificial intelligence and (v) the influence of climate change on soil salinization. Physiological responses, nutrient management, and biostimulants are summarized more briefly to provide the background needed to interpret these advances. Much of the physiological evidence discussed is derived from maize and other cereals, and the extent to which conclusions can be generalized to other crops is noted where relevant.

Review Methodology

Literature for this review was collected from Scopus, Web of Science, PubMed, and Google Scholar. The search covered publications mainly from 2000 to 2026, although seminal earlier studies were included where they established key concepts. Search terms were combined with Boolean operators and included “salinity stress”, “salt tolerance”, “soil salinization”, “climate change”, “epigenetic”, “microRNA”, “long non-coding RNA”, “multi-omics”, “CRISPR/Cas”, “genome editing”, “PGPR”, “arbuscular mycorrhizal fungi”, “root microbiome”, “digital phenotyping”, “hyperspectral imaging”, and “machine learning”. Peer-reviewed research articles, reviews, book chapters, and authoritative institutional reports (e.g., FAO and IPCC) were considered. Studies were selected if they (i) addressed plant responses to salinity or salinity-related soil processes, (ii) provided experimental or quantitative evidence or a critical synthesis, and (iii) were published in English. Conference abstracts, non-peer-reviewed sources, and studies without a clear experimental description were excluded. Titles and abstracts were screened first, followed by full-text assessment, and duplicate records were removed.

Genotypic variation and physiological approaches for enhancing salinity tolerance

Salinity tolerance varies considerably among plant genotypes owing to differences in their physiological, biochemical, and genetic characteristics. Comparative evaluation of diverse genotypes under saline conditions has demonstrated significant variation in germination, growth, biomass accumulation, and photosynthetic performance. Salinity generally causes substantial reductions in root and shoots growth, fresh biomass, germination percentage, and photosynthetic pigments; however, tolerant genotypes exhibit relatively lower reductions than susceptible ones. Based on their performance under salt stress, genotypes can be classified into salt-tolerant, moderately tolerant, and highly sensitive categories, providing valuable genetic resources for crop improvement and breeding programs (Zia et al., 2022). Salt-tolerant genotypes generally exhibit greater capacity to maintain K^+ uptake while restricting Na^+

accumulation, highlighting selective ion transport and maintenance of ionic balance as key mechanisms underlying salinity tolerance. These characteristics provide valuable selection criteria for breeding programs aimed at improving crop performance under saline environments (Akram et al., 2010). The major mechanisms associated with salinity tolerance and the physiological approaches used to enhance plant performance under salt stress are summarized in Fig. 1.

Genotypic differences in salinity tolerance are particularly evident during the germination and early seedling stages, where salinity adversely affects seed germination, seedling establishment, and morphological development. Significant genotype × environment interactions have been reported, indicating that the response to salinity depends largely on the genetic background of individual genotypes. In general, shoot growth is more severely affected than root growth under saline conditions, while tolerant genotypes maintain superior growth and vigor compared with susceptible ones (Masuda et al., 2021). Similar seedling-stage differences were reported among four maize cultivars grown hydroponically (Alam et al., 2018). The identification of genomic regions associated with salinity tolerance has significantly advanced the understanding of plant adaptation to saline environments. Quantitative trait loci (QTLs) associated with salt tolerance have been identified and are considered valuable targets for marker-assisted selection and genetic improvement of stress tolerance in crop plants (Luo et al., 2017). Screening of diverse genotypes has further confirmed significant variation in salinity tolerance based on physiological and morphological characteristics, including chlorophyll content, leaf number, shoot length, leaf area, dry matter accumulation, and proline content. Salt-tolerant genotypes consistently exhibit superior growth and physiological performance compared with susceptible genotypes under saline conditions, highlighting the importance of genotype selection in salinity management (Billah et al., 2017). Early-stage screening based on morphological, physiological and biochemical characteristics has therefore been recognized as an effective approach for identifying salt-tolerant germplasm and supporting breeding programs aimed at improving salinity tolerance (Ahmed et al., 2012).

Biostimulants have emerged as promising eco-friendly approaches for alleviating salinity-induced damage in plants. Commercial biostimulants improve salt tolerance by reducing Na^+ accumulation, minimizing oxidative damage, preserving photosynthetic pigments, and promoting greater shoot growth and biomass production. These physiological improvements contribute to enhanced plant performance under saline environments and highlight the potential of biostimulants as sustainable tools for salinity management (Amato & Del Buono, 2021). In recent years, protein hydrolysate-based biostimulants have gained increasing attention for improving plant resilience to abiotic stresses. These biostimulants enhance stress tolerance primarily by stimulating root development, increasing nitrogen uptake efficiency, and improving antioxidant defense mechanisms. Their application has been shown to alleviate the adverse effects of salinity and nutrient deficiency, resulting in improved seedling growth and greater physiological adaptability under stressful environmental conditions (Trevisan et al., 2019).

Silicon (Si) supplementation has also been widely recognized for its protective role against salt stress. Exogenous application of silicon enhances plant growth, biomass accumulation, RWC, stomatal conductance, and photosynthetic efficiency while strengthening the antioxidant defense system through increased activities of superoxide dismutase (SOD), peroxidase (POD), ascorbate peroxidase (APX), and catalase (CAT). Moreover, silicon effectively reduces oxidative stress by lowering the accumulation of malondialdehyde (MDA) and hydrogen peroxide (H_2O_2), thereby protecting cellular structures from oxidative damage (Ali et al., 2020). Melatonin has also been identified as an effective regulator of plant responses to salinity stress. Exogenous melatonin application enhances osmotic adjustment, maintains ion homeostasis by reducing Na^+ accumulation and promoting K^+ uptake, and alleviates oxidative damage through stimulation of both enzymatic antioxidants (SOD, CAT, and POD) and non-enzymatic antioxidant systems. These integrated physiological responses substantially improve plant adaptation to saline environments (Ren et al., 2020). Interpretation of these studies requires caution because findings are not always consistent across crops and experimental conditions. Genotype rankings often differ between hydroponic and soil experiments, between seedling and reproductive stages, and between short-term and long-term exposure, because the osmotic and ionic components of stress contribute differently at each stage (Munns & Tester, 2008; Negrão et al., 2017). Likewise, the benefits reported for biostimulants, silicon, and melatonin vary with dose, application method (seed priming, foliar spray, or root application), crop species, and salinity level, and many of these studies were conducted on maize seedlings under controlled conditions. For this reason, results from individual studies are compared throughout this review with attention to the species, developmental stage, and salinity regime used.

Physiological and biochemical responses of plants to salinity stress

Salinity is one of the most destructive abiotic stresses limiting agricultural productivity worldwide, particularly during seed germination and early seedling establishment, which are the most sensitive stages of plant development. Excessive accumulation of sodium (Na^+) and chloride (Cl^-) ions delays germination by disrupting water uptake and interfering with the absorption of essential mineral nutrients, including nitrogen (N), potassium (K), calcium (Ca), and magnesium (Mg). These nutritional imbalances impair physiological processes, reduce photosynthetic efficiency through stomatal closure and chlorophyll degradation, and ultimately decrease carbon fixation, grain formation, and crop yield (Farooq et al., 2015). Salinity-induced physiological damage is closely associated with reductions in RWC, membrane stability, chlorophyll concentration, transpiration rate, and, under severe stress, antioxidant capacity. The response of antioxidant enzymes to salinity is not uniform: the activities of CAT, POD, and SOD may increase or decrease depending on the plant species, genotype, tissue, and the severity and duration of stress (Gill & Tuteja, 2010). Under mild to moderate salinity, tolerant genotypes typically up-regulate these enzymes, which limit ROS accumulation and lipid peroxidation. Under severe or

prolonged salinity, enzyme activities often decline or fail to keep pace with ROS production, which leads to oxidative damage, membrane injury, and growth inhibition, and this decline is generally more pronounced in sensitive genotypes (Miller et al., 2010; Abbasi et al., 2014).

Plant adaptation to salinity is regulated through complex physiological and molecular signaling networks. Among various signaling molecules, abscisic acid (ABA) serves as a central phytohormone that coordinates stress perception, metabolic regulation, and developmental processes. ABA-mediated signaling integrates osmotic stress responses with primary metabolism, enabling plants to adjust their physiological activities and improve survival under saline and drought conditions (Golldack et al., 2014). Based on their evolutionary adaptation to saline environments, plants are broadly classified as halophytes and glycophytes. While halophytes possess specialized mechanisms that enable them to thrive in highly saline habitats, most economically important crop species are glycophytes and therefore exhibit limited tolerance to salt stress. Combined with drought and water scarcity, soil salinity has become a major environmental constraint causing an estimated 20–50% reduction in the productivity of many important crops worldwide (Shrivastava & Kumar, 2015). Plant responses to salinity involve a wide range of physiological, biochemical, and anatomical adaptations aimed at minimizing stress-induced damage. Salinity causes osmotic stress and ionic toxicity, prompting plants to regulate ion transport, modify their metabolism, alter anatomical structures, and accumulate compatible solutes such as glycine betaine for osmotic adjustment. Understanding these integrated adaptive mechanisms is essential for developing effective strategies to improve crop performance under saline environments (Rasool et al., 2013). Seed priming techniques have also proven effective in improving plant establishment under stressful environments. Hydropriming enhances seed imbibition, accelerates germination, and improves seedling establishment by promoting early metabolic activation before exposure to saline conditions, making it a simple and cost-effective strategy for improving plant performance under abiotic stress (Bayat et al., 2012).

Salinity affects plants in two overlapping phases. The early osmotic phase begins within minutes to hours of exposure, when the lowered soil water potential reduces water uptake and cell expansion, closes stomata, and slows leaf growth largely independently of the amount of salt accumulated in the shoot (Munns, 2002; Munns & Tester, 2008). The later, ionic phase develops over days to weeks as Na^+ and Cl^- accumulate in transpiring leaves beyond the capacity for vacuolar compartmentalization, causing toxicity, premature senescence of older leaves, and loss of photosynthetic area (Munns & Tester, 2008). The distinction matters because tolerance to the osmotic phase and tolerance to ion toxicity are controlled by different mechanisms and can be combined in breeding (Munns, 2005; Munns & Tester, 2008). Species and genotypes differ markedly in how they handle these two phases. Halophytes tolerate high salinity through efficient Na^+ compartmentalization in vacuoles, salt excretion or sequestration in specialized structures, and accumulation of compatible solutes, whereas most crops are glycophytes in which these mechanisms are limited (Flowers & Colmer, 2008). Among cereals, rice is generally more sensitive than bread wheat, barley is among the most tolerant, and durum wheat is less tolerant than bread wheat largely because of weaker Na^+ exclusion from leaves (Munns & Tester, 2008). Within species, tolerant genotypes typically restrict Na^+ transport to shoots and maintain K^+ retention. For example, the tolerant rice genotype Pokkali and the sensitive genotype IR29 show contrasting transcriptional responses to salinity at the vegetative stage (Walia et al., 2005), and salt-tolerant maize lines remove Na^+ and retain K^+ more effectively than sensitive lines (Gao et al., 2016).

Salinity-induced growth reduction is closely tied to the coupling between stomatal behavior and photosynthesis. In the early phase, stomatal closure restricts CO_2 diffusion and lowers stomatal conductance, which reduces carbon assimilation; during the ionic phase, accumulation of Na^+ and Cl^- in leaves additionally impairs chlorophyll content and photochemical efficiency, so that non-stomatal limitations increasingly dominate (Chaves et al., 2009). Reduced carbon gain, together with the energy cost of osmotic adjustment and ion exclusion, limits leaf expansion and biomass accumulation, although growth is often inhibited before photosynthesis per unit leaf area is affected because cell expansion is more sensitive to water deficit than carbon assimilation (Munns & Tester, 2008). For example, exogenous Ca^{2+} alleviated Na^+-induced phytotoxicity in wheat seedlings in association with improved photosynthetic characteristics (Zhang et al., 2023).

Salinity stress perception and signal transduction networks

Salinity tolerance begins with the rapid perception of osmotic and ionic disturbances at the plasma membrane. Within minutes of salt exposure, plants detect changes in membrane tension and extracellular sodium concentrations through specialized membrane-associated proteins and mechanosensitive channels. These early events trigger transient increases in cytosolic calcium (Ca^{2+}), which functions as a universal secondary messenger initiating downstream stress responses. Calcium signals are decoded by calcium-binding proteins, including calmodulins (CaMs), calcineurin B-like proteins (CBLs), and calcium-dependent protein kinases (CDPKs), which activate multiple phosphorylation cascades responsible for stress adaptation. Recent evidence indicates that the intensity and frequency of calcium oscillations determine the specificity of downstream responses, allowing plants to distinguish salinity from other abiotic stresses (Waheed et al., 2024). Following stress perception, several protein kinase families, particularly mitogen-activated protein kinases (MAPKs) and sucrose non-fermenting 1-related protein kinases (SnRKs), coordinate transcriptional reprogramming and metabolic adjustment. These signaling pathways regulate hundreds of stress-responsive genes involved in ion transport, osmolyte biosynthesis, antioxidant metabolism, hormone signaling, and cellular protection. The activation of these signaling networks enables plants to rapidly adjust growth patterns, conserve energy, and maintain cellular homeostasis under prolonged saline conditions (Waheed et al., 2024) (Fig. 2).

An equally important component of salinity signaling involves ROS. Rather than functioning solely as harmful molecules, controlled ROS production acts as an essential

signaling mechanism that regulates stress-responsive gene expression (Mishra et al., 2026). Crosstalk between ROS, nitric oxide (NO), hydrogen sulfide (H_2S), and calcium signaling establishes an integrated communication network that coordinates antioxidant defense, osmotic adjustment, and ion transport (Anee et al., 2025; Corpas et al., 2026). Maintaining an appropriate balance between ROS production and detoxification has therefore emerged as a critical determinant of plant survival under saline environments (dos Reis et al., 2026). Recent studies have further demonstrated that salinity signaling is regulated through extensive hormonal interactions. Instead of acting independently, abscisic acid (ABA), ethylene, brassinosteroids, auxins, cytokinins, jasmonates, salicylic acid, and melatonin function as interconnected signaling molecules that collectively regulate root architecture, stomatal conductance, osmotic adjustment, antioxidant metabolism, and stress-responsive gene expression. This complex hormonal crosstalk enables plants to optimize growth while simultaneously activating defense mechanisms under saline conditions (Raza et al., 2022; Ali et al., 2026).

The interactions among these hormones follow recognizable patterns rather than acting additively. ABA accumulates rapidly under salinity and promotes stomatal closure, osmolyte synthesis, and expression of stress-responsive genes, but it also restrains growth, partly by suppressing lateral root emergence (Ryu & Cho, 2015; Yu et al., 2020). Growth-promoting pathways are in turn repressed: salinity reduces gibberellin levels, which stabilizes DELLA growth repressors and slows growth while enhancing survival (Achard et al., 2006). Ethylene, jasmonates, and salicylic acid interact with ABA signaling in a context-dependent manner, and the outcome (synergistic or antagonistic) depends on tissue, stress intensity, and developmental stage (Ryu & Cho, 2015; Yu et al., 2020). Cytokinins and auxins modulate the balance between roots and shoot growth, and brassinosteroids can in some contexts counteract part of the growth inhibition imposed by ABA. Such crosstalk allows plants to trade growth for survival under severe stress, and it explains why manipulating a single hormone pathway may improve tolerance while compromising growth or yield.

Epigenetic regulation of salinity tolerance

Salinity tolerance is a complex trait that is regulated not only by genetic variation but also by epigenetic mechanisms that alter gene expression without changing the underlying DNA sequence. Epigenetic regulation enables plants to rapidly perceive and respond to saline environments by activating or repressing stress-responsive genes through reversible molecular modifications. Unlike genetic mutations, epigenetic changes are dynamic and can be induced by environmental stresses, allowing plants to adapt more efficiently to fluctuating saline conditions. In recent years, epigenetic regulation has emerged as one of the most promising areas of plant stress biology because it provides new opportunities for developing stress-resilient crops through epigenetic breeding and molecular engineering (Bibi et al., 2024; Shilpa et al., 2024).

One of the most extensively studied epigenetic mechanisms is DNA methylation, which involves the addition of a methyl group to cytosine residues within the DNA molecule. Under salinity stress, plants undergo substantial alterations in DNA methylation patterns that regulate the expression of numerous stress-responsive genes. Hypermethylation generally suppresses gene expression, whereas hypomethylation activates genes involved in antioxidant defense, ion transport, osmotic adjustment, and hormonal signaling. Recent genome-wide methylation studies have identified numerous salt-responsive methylation sites that are strongly associated with improved tolerance in several crop species (Sen et al., 2024; Yuan et al., 2025). Another important epigenetic mechanism involves histone modifications, including histone acetylation, methylation, phosphorylation, and ubiquitination. Histones are proteins around which DNA is tightly wrapped, and chemical modifications of these proteins alter chromatin structure and accessibility of genes to the transcriptional machinery. Histone acetylation generally relaxes chromatin, promoting transcription of stress-responsive genes, whereas histone deacetylation leads to chromatin condensation and gene repression. Similarly, specific histone methylation marks either activate or silence genes associated with salinity adaptation. These reversible modifications regulate genes involved in ion homeostasis, antioxidant metabolism, osmolyte biosynthesis, and hormonal signaling, thereby enhancing plant adaptability under saline conditions (Yung et al., 2021; Zhang et al., 2024a). Specific examples illustrate the biological significance of these modifications. In rice, salt-tolerant and salt-sensitive varieties differ in the flexibility of their methylomes under salinity, which suggests that the capacity to remodel DNA methylation contributes to tolerance (Ferreira et al., 2015). Histone modifications at stress-responsive loci likewise alter chromatin accessibility and transcription under salt stress (Yung et al., 2021). These examples indicate that epigenetic marks are not merely correlates of stress but may provide semi-stable regulatory variation that could be exploited in breeding; however, the causal contribution of most individual marks to crop tolerance has not yet been demonstrated experimentally.

Epigenetic regulation also contributes to the phenomenon of stress memory, whereby plants exposed to a previous episode of salinity respond more rapidly and effectively to subsequent stress events. Stress-induced epigenetic modifications, including DNA methylation and histone modifications may persist even after the stress is removed; enabling plants to retain a molecular "memory" of earlier stress exposure. This epigenetic memory facilitates faster activation of defense mechanisms during recurring salinity events and may even be transmitted to subsequent generations, although the stability of transgenerational inheritance varies among plant species (Lämke & Bäurle, 2017). The integration of epigenetics with modern omics technologies, including transcriptomics, methylomics, proteomics, metabolomics, and single-cell sequencing, has significantly advanced our understanding of plant adaptation to saline environments (Roychowdhury et al., 2023; Ali et al., 2026; Kaur et al., 2026). These approaches enable researchers to identify epigenetic markers associated with salinity tolerance and reveal complex regulatory networks controlling stress-responsive genes. Such knowledge is expected to accelerate the development of stress-resilient crop varieties through marker-assisted selection,

epigenome editing, and precision breeding approaches (Dakal et al., 2025 Yuan et al., 2025).

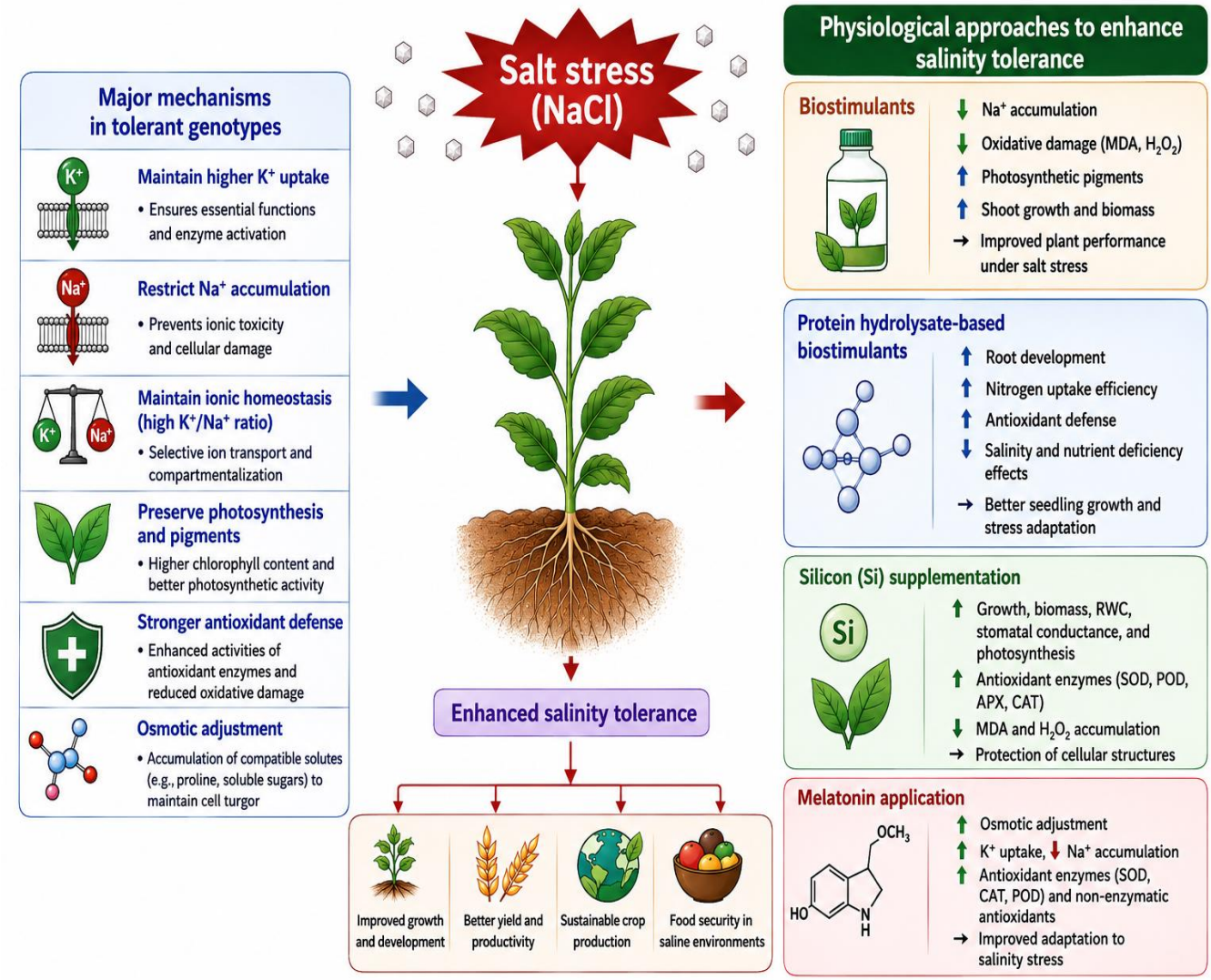


Fig. 1 Schematic representation of the major physiological mechanisms underlying salinity tolerance and physiological approaches for improving plant performance under salt stress. Salt-tolerant genotypes maintain higher K^+ uptake, restrict Na^+ accumulation, sustain a favorable K^+/Na^+ ratio, preserve photosynthetic activity, enhance osmotic adjustment, and strengthen antioxidant defenses, thereby reducing oxidative damage. Physiological approaches, including biostimulants, protein hydrolysate-based biostimulants, silicon supplementation, and melatonin application, further promote root development, nutrient acquisition, osmotic regulation, ion homeostasis, photosynthetic performance, and antioxidant protection.

MicroRNAs in salinity stress responses

MicroRNAs are endogenous, single-stranded RNA molecules approximately 20–24 nucleotides in length that regulate gene expression through sequence-specific degradation of messenger RNA (mRNA) or inhibition of protein translation. Under salinity stress, the expression of numerous miRNAs is either induced or suppressed, resulting in rapid adjustment of stress-responsive metabolic and physiological pathways. Because a single miRNA can regulate multiple target genes simultaneously, these molecules serve as master regulators of stress adaptation (Yang et al., 2022). One of the primary functions of miRNAs during salinity stress is the regulation of ion homeostasis.

Several miRNAs influence the expression of Na^+ and K^+ transporter genes, thereby maintaining cellular ionic balance and minimizing sodium toxicity. Proper regulation of ion transport systems ensures reduced Na^+ accumulation in the cytoplasm while promoting potassium retention, which is essential for enzyme activity, protein synthesis, and osmotic regulation (Fang et al., 2026). MicroRNAs also regulate the antioxidant defense system by modulating genes encoding antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), and peroxidase (POD). Through these regulatory pathways, plants maintain

reactive oxygen species (ROS) homeostasis, thereby reducing oxidative damage to membranes, proteins, and nucleic acids.

Certain miRNAs additionally influence the biosynthesis of osmoprotectants, including proline, glycine betaine, and soluble sugars, which contribute to osmotic adjustment and cellular protection under saline conditions (Chu et al., 2026). Specific miRNA and lncRNA examples illustrate how these regulatory layers operate. In Arabidopsis, salinity induces members of the miR169 family, which transiently repress NF-YA transcription factor genes (Zhao et al., 2009). miR398 targets Cu/Zn superoxide dismutase transcripts, and its stress-dependent repression increases SOD expression, linking miRNA regulation directly to antioxidant defense (Zhu et al., 2011), although the direction of its change under salinity differs among species. In rice, osa-miR393 is responsive to salinity and alkaline stress and targets auxin-signaling genes, yet its overexpression increased sensitivity to these stresses, showing that induction of a miRNA does not necessarily indicate a positive contribution to tolerance (Gao et al., 2011). Small-RNA sequencing in chrysanthemum likewise identified salt-responsive miRNAs and their predicted targets (Nai et al., 2023). Among lncRNAs, DRIR is induced by drought, salt, and ABA in Arabidopsis, and its overexpression enhanced tolerance to both stresses (Qin et al., 2017); more broadly, lncRNAs act as miRNA target mimics, chromatin regulators, and transcriptional scaffolds (Das et al., 2023). Most functional evidence, however, comes from Arabidopsis and a few crops, and validation of salt-responsive non-coding RNAs in major crops under field salinity is still scarce.

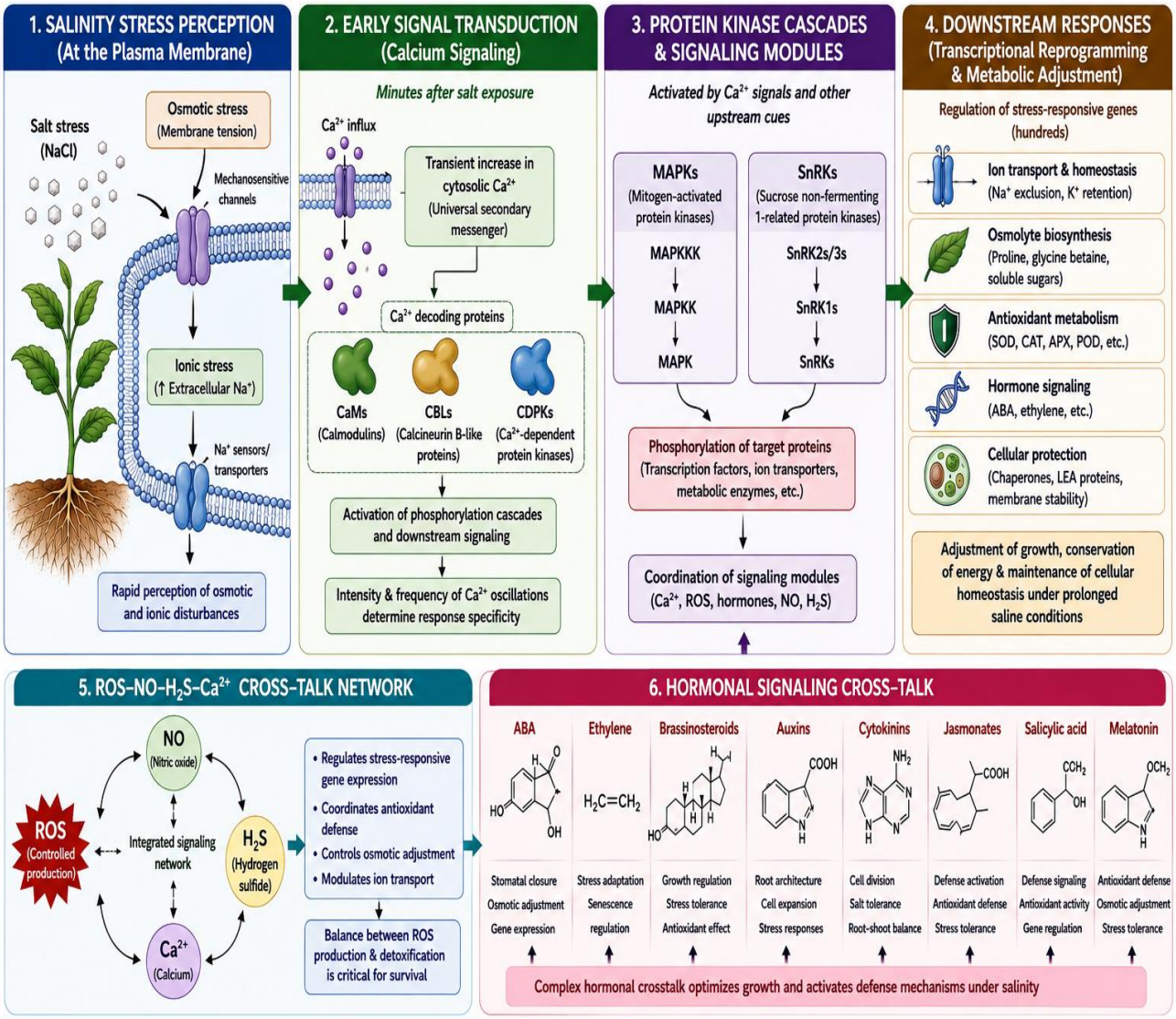


Fig. 2 Salinity stress perception and signal transduction networks in plants. Salinity-induced osmotic and ionic disturbances are perceived at the plasma membrane, triggering transient increases in cytosolic Ca^{2+} that are decoded by calmodulins (CaMs), calcineurin B-like proteins (CBLs), and calcium-dependent protein kinases (CDPKs). These calcium-dependent signals activate downstream protein kinase cascades, particularly mitogen-activated protein kinases (MAPKs) and sucrose non-fermenting 1-related protein kinases (SnRKs), which regulate stress-responsive gene expression and metabolic adjustment. Reactive oxygen species (ROS), nitric oxide (NO), and hydrogen sulfide (H_2S) interact with Ca^{2+} signaling to coordinate antioxidant defense, osmotic adjustment, and ion transport. These interconnected signaling networks facilitate cellular homeostasis, stress adaptation, and salinity tolerance. Schematic diagram was prepared by the authors based on Yu et al. (2020); Waheed et al. (2024).

Transcriptomics, proteomics, metabolomics, and ionomics in salinity research

The rapid advancement of omics technologies has revolutionized the understanding of plant responses to salinity stress by enabling comprehensive analyses of genes, proteins, metabolites, and mineral elements involved in stress adaptation. Unlike conventional physiological studies, which investigate a limited number of traits, omics approaches provide a holistic understanding of the complex molecular networks that regulate salinity tolerance. The integration of transcriptomics, proteomics, metabolomics, and ionomics has revealed numerous stress-responsive pathways, regulatory genes, signaling molecules, and metabolic adjustments that collectively enhance plant survival under saline environments. These technologies have become indispensable tools for identifying candidate genes, molecular markers, and biochemical pathways that can be exploited in breeding programs and biotechnological interventions aimed at developing salt-tolerant crops (Jana et al., 2022; Alrajeh et al., 2024).

Transcriptomics is the large-scale analysis of the complete set of RNA transcripts expressed in plant cells under specific environmental conditions. The development of high-throughput RNA sequencing (RNA-Seq) has enabled researchers to identify thousands of genes that are differentially expressed in response to salinity stress. Transcriptomic analyses have demonstrated that salinity induces profound changes in the expression of genes involved in ion transport, osmotic regulation, antioxidant defense, hormone biosynthesis, photosynthesis, carbohydrate metabolism, and signal transduction. These coordinated transcriptional responses enable plants to maintain cellular homeostasis while minimizing salt-induced damage (Srivastava et al., 2026). Among the most important genes identified through transcriptomic studies are those encoding SOS (Salt Overly Sensitive) pathway proteins, NHX (Na^+/H^+ antiporters), HKT transporters, aquaporins, calcium-dependent protein kinases (CDPKs), mitogen-activated protein kinases (MAPKs), and various transcription factors, including NAC, WRKY, MYB, DREB, bZIP, and bHLH families. These genes regulate sodium exclusion, potassium retention, osmotic adjustment, reactive oxygen species (ROS) detoxification, and hormonal signaling. Comparative transcriptomic studies between salt-tolerant and salt-sensitive genotypes have further identified regulatory networks that explain differences in stress adaptations and provide valuable targets for molecular breeding (Fu et al., 2024).

Although transcriptomics provides information on gene expression, protein abundance does not always correlate directly with transcript levels because proteins undergo post-transcriptional and post-translational modifications. Proteomics, therefore, offers a more direct understanding of cellular responses by identifying proteins whose abundance or activity changes during salinity stress. Proteomic studies have revealed that salt stress alters proteins associated with photosynthesis, ATP synthesis, carbon metabolism, antioxidant defense, protein folding, membrane transport, and stress signaling. Increased accumulation of heat shock proteins (HSPs), late embryogenesis abundant (LEA) proteins, chaperones, antioxidant enzymes, and ion transport proteins contribute to cellular protection against osmotic and oxidative stress. In contrast, proteins associated with photosynthetic carbon fixation often decline under severe salinity, reflecting reduced photosynthetic capacity. Recent quantitative proteomic techniques, including iTRAQ, TMT labeling, and LC-MS/MS, have substantially improved the identification of salt-responsive proteins and their functional interactions (Alrajeh et al., 2024).

Metabolomics involves the comprehensive analysis of low-molecular-weight metabolites that represent the final products of cellular metabolism. Because metabolites directly reflect physiological status, metabolomics provides valuable insights into biochemical adjustments occurring during salinity stress. Exposure to salinity induces significant accumulation of compatible solutes such as proline, glycine betaine, trehalose, raffinose, sucrose, glucose, fructose, polyamines, amino acids, and organic acids. These metabolites contribute to osmotic adjustment, stabilization of proteins and cellular membranes, detoxification of reactive oxygen species, and maintenance of cellular turgor. In addition, salinity stimulates the biosynthesis of numerous secondary metabolites, including phenolic compounds, flavonoids, anthocyanins, alkaloids, and terpenoids, which function as antioxidants and protect plants against oxidative damage. Metabolomic analyses have also revealed substantial reprogramming of primary metabolic pathways, including glycolysis, the tricarboxylic acid (TCA) cycle, amino acid metabolism, and lipid metabolism, enabling plants to optimize energy production and stress adaptation (Carrera et al., 2021; Zhu et al., 2023).

Ionomics is the systematic study of the complete mineral nutrient composition (ionome) of plants and has become an essential approach for investigating ionic regulation under salinity stress (Ali et al., 2021). Since excessive accumulation of sodium (Na^+) and chloride (Cl^-) disrupts nutrient balance, ionomic analyses help identify mechanisms responsible for maintaining ionic homeostasis. Salt-tolerant plants typically exhibit reduced Na^+ accumulation together with greater retention of essential nutrients such as potassium (K^+), calcium (Ca^{2+}), magnesium (Mg^{2+}), phosphorus (P), sulfur (S), iron (Fe), zinc (Zn), manganese (Mn), and copper (Cu) (Gupta & Huang, 2014; Chakraborty et al., 2018). Maintenance of a high K^+/Na^+ ratio is considered one of the most reliable physiological indicators of salinity tolerance because potassium is essential for enzyme activation, protein synthesis, photosynthesis, and stomatal regulation (Assaha et al., 2017). Modern analytical techniques such as inductively coupled plasma mass spectrometry (ICP-MS), ICP-optical emission spectrometry (ICP-OES), X-ray fluorescence spectroscopy, and laser ablation imaging have enabled highly accurate quantification and spatial mapping of mineral nutrients in plant tissues, providing new insights into ion transport and compartmentalization during salinity stress (Salt et al., 2008).

CRISPR/Cas genome editing for developing salt-tolerant crops

Genome editing technologies, particularly CRISPR/Cas systems, have transformed functional genomics and crop improvement (Haider et al., 2026). However, current applications are largely restricted to modifying individual

genes (Kaniganti et al., 2026). Because salinity tolerance is a polygenic trait, future breeding efforts should focus on multiplex genome editing, enabling simultaneous modification of multiple stress-responsive genes involved in ion homeostasis, osmotic regulation, antioxidant defense, hormone signaling, and root development (Osei-Wusu et al., 2025). The integration of CRISPR/Cas technologies with genomic selection, genome-wide association studies (GWAS), speed breeding, and artificial intelligence-assisted breeding platforms will substantially accelerate the development of salt-tolerant cultivars (Rai, 2022). In addition, greater emphasis should be placed on improving transformation efficiency and regeneration protocols for crop species that remain difficult to edit genetically.

Salinity stress is a complex trait controlled by numerous genes involved in ion transport, osmotic regulation, antioxidant defense, hormonal signaling, and stress-responsive transcriptional networks. Conventional breeding has successfully improved salinity tolerance in several crops; however, progress is often slow because of the polygenic nature of salt tolerance, long breeding cycles, and the influence of environmental factors on trait expression. The advent of Clustered Regularly Interspaced Short Palindromic Repeats (CRISPR)/CRISPR-associated protein (Cas) genome editing technology has revolutionized plant breeding by enabling precise, efficient, and targeted modification of genes associated with salinity tolerance. Unlike traditional transgenic approaches, CRISPR/Cas allows the introduction of specific genetic changes without necessarily incorporating foreign DNA, making it one of the most promising tools for developing climate-resilient crops (Kumar et al., 2023; Mohamed et al., 2024). The CRISPR/Cas system is derived from the adaptive immune system of bacteria and archaea, where it functions to defend against invading viruses and plasmids. In plants, the technology utilizes a guide RNA (gRNA) to direct the Cas nuclease, most commonly Cas9 or Cas12a (Cpf1), to a specific DNA sequence. The nuclease creates a double-stranded break at the target site, which is subsequently repaired by endogenous cellular mechanisms, including non-homologous end joining (NHEJ) or homology-directed repair (HDR). These repair processes generate targeted gene knockouts, insertions, deletions, or precise nucleotide substitutions, enabling modification of genes controlling salinity tolerance (Kumar et al., 2023). Fig. 3 combines approaches that have been experimentally demonstrated for salt tolerance, such as knockout of negative regulators, with approaches that remain proposed or emerging, such as multiplex, base, and prime editing of several salinity-related loci and artificial intelligence-assisted breeding; the latter should not be interpreted as established practice.

Oxidative stress is a major consequence of salinity, leading to excessive accumulation of ROS that damage proteins, lipids, and nucleic acids. Genome editing of genes that regulate antioxidant capacity (such as those encoding SOD, CAT, APX, and enzymes of glutathione metabolism) and the biosynthesis of compatible osmolytes (proline, glycine betaine, trehalose, and soluble sugars) is a logical strategy, because greater antioxidant activity and osmoprotectant accumulation could reduce oxidative damage and improve osmotic adjustment (Kesawat et al., 2023). It is important, however, to distinguish demonstrated results from proposed applications. The experimentally demonstrated examples of genome-edited salt tolerance described below mostly involve regulatory or signaling genes rather than direct editing of antioxidant enzymes or osmolyte biosynthesis genes, and evidence that editing the latter pathways improves salt tolerance in crops remains limited; much of the support for these pathways comes from transgenic overexpression or mutant studies. Systematic surveys of CRISPR/Cas applications for salt tolerance (Sun et al., 2026) should therefore be read with this distinction in mind.

Experimentally validated examples are now available. In rice, CRISPR/Cas9-targeted mutagenesis of OsRR22, which encodes a B-type response regulator involved in cytokinin signaling, generated mutants with enhanced salinity tolerance at the seedling stage (Zhang et al., 2019); the same gene had previously been identified as the cause of salt tolerance in a rice mutant by MutMap (Takagi et al., 2015). In tomato, CRISPR/Cas9-based precise excision of domain(s) of SlHyPRP1, a negative regulator of salt-stress responses, produced lines with improved salt tolerance (Tran et al., 2021). These examples share a common strategy, namely knocking out or truncating negative regulators of the salt response, which is more tractable with current tools than increasing the activity of positive regulators. Genes shown as targets in Fig. 3 (for example SOS1, HKT1;5, NHX1, and AKT1) are therefore best regarded as candidate targets unless editing has been shown to improve tolerance.

Genome editing also has important limitations. Off-target cleavage at sequences resembling the guide RNA target can introduce unintended mutations, and its frequency depends on guide design and the nuclease variant used, so high-fidelity nucleases, careful guide selection, and sequencing-based verification are recommended (Zhang et al., 2019). Transformation and regeneration remain bottlenecks because many elite cultivars and several crop species are recalcitrant to tissue culture and Agrobacterium-mediated transformation, which restricts genotype choice and can generate somaclonal variation (Altpeter et al., 2016). Because salt tolerance is polygenic and strongly influenced by the environment, an edit that improves seedling survival in a growth chamber may not improve yield in the field; multi-location, multi-season field trials under realistic salinity heterogeneity are needed before edited lines can be considered useful (Roy et al., 2014; Negrão et al., 2017). The regulatory status of genome-edited crops also differs among countries and may affect adoption. Whether edits improve salt tolerance without penalizing growth, development, or yield is a central question. Many salt-responsive genes also function in development or in responses to other stresses, so loss-of-function edits can have pleiotropic effects, and removing a negative regulator of stress responses may trade growth under non-stress conditions for tolerance. Reports of edited rice and tomato lines have largely emphasized seedling-stage tolerance under controlled conditions, and data on agronomic traits and yield under both saline and non-saline field conditions are scarce. Claims that edited lines improve salt tolerance without yield penalties should therefore be regarded as unproven until multi-season field data are available.

Genome editing also differs from conventional breeding and marker-assisted selection (MAS) in its benefits and limitations. Conventional breeding for salt tolerance has

delivered cultivars but is slow because tolerance is polygenic, phenotyping is difficult, and linkage drag accompanies introgression from wild relatives (Collard & Mackill, 2008; Roy et al., 2014). MAS accelerates selection for known QTL or alleles, such as OsHKT1;5 in rice, and does not involve transformation, but it depends on previously mapped loci with stable effects, and its gains are limited by marker–trait associations and population-specific allele effects (Collard & Mackill, 2008). Genome editing can modify a target gene directly in an elite background without linkage drag and can create new allelic variation, which makes it faster for loci that are already validated; its limits are its dependence on prior gene knowledge, the difficulty of editing many small-effect loci simultaneously, regeneration bottlenecks, and variable regulatory acceptance. The approaches are therefore complementary: MAS and genomic selection are best suited to improving the polygenic background, whereas genome editing is best suited to precise modification of defined large-effect or regulatory loci (Roy et al., 2014).

Root microbiome dynamics under salinity stress

Salinity profoundly influences the composition, diversity, and metabolic activity of root-associated microbial communities. Elevated concentrations of sodium (Na^+) and chloride (Cl^-) alter soil physicochemical properties, including pH, osmotic potential, nutrient availability, and oxygen diffusion, thereby changing the abundance of beneficial microorganisms in the rhizosphere. Although severe salinity may reduce overall microbial diversity, it simultaneously enriches salt-adapted microbial taxa capable of surviving under extreme environmental conditions. These halotolerant microorganisms possess specialized physiological and metabolic traits that enable them to support plant growth despite high salt concentrations (Han et al., 2023). Root exudates, consisting of sugars, amino acids, organic acids, phenolic compounds, flavonoids, and secondary metabolites, play a central role in shaping microbial community composition. Under saline conditions, plants modify both the quantity and composition of root exudates, selectively recruiting beneficial microorganisms that enhance stress tolerance. This dynamic communication between plant roots and microorganisms establishes a highly coordinated biological system that promotes plant adaptation to salinity (Qiu et al., 2026).

The evidence on how salinity shapes root microbial communities are not entirely consistent. Several studies report reduced richness and a shift toward halotolerant taxa, whereas others find little change in diversity but marked changes in community composition, and the microbial response differs between salt-tolerant and salt-sensitive genotypes of the same crop (Han et al., 2023). Such discrepancies reflect differences in salinity type and level, soil texture, crop species, the compartment sampled (bulk soil, rhizosphere, or endosphere), and sequencing methods. In addition, most studies are descriptive and based on amplicon sequencing, which shows correlations but does not prove that enriched taxa cause tolerance; causal tests with isolates or synthetic communities are rare. Likewise, plant-mediated recruitment (the “cry for help” concept) is inferred largely from enrichment patterns, and whether recruited microbes provide a benefit large enough to improve yield under field salinity is still uncertain (Trivedi et al., 2020). Root exudates influence recruitment through several mechanisms. Sugars and organic acids serve as carbon sources and chemoattractants that favor fast-growing colonizers, whereas flavonoids, coumarins, and other secondary metabolites act as signals or selective antimicrobials that favor specific taxa (Trivedi et al., 2020; Vives-Peris et al., 2020). Under salinity, changes in the amount and composition of exudates, together with altered soil osmotic potential, change which microbes can colonize the root zone. However, most evidence comes from correlative metabolite–microbiome studies, and the specific exudate compounds that recruit beneficial microbes under salinity in crops remain largely unidentified.

Plant growth-promoting rhizobacteria (PGPR)

Among root-associated microorganisms, PGPR have been extensively investigated for their ability to mitigate salinity stress. These beneficial bacteria improve plant performance through multiple direct and indirect mechanisms. They synthesize phytohormones such as indole-3-acetic acid (IAA), gibberellins, cytokinins, and abscisic acid, which stimulate root development and improve water and nutrient uptake. Many PGPR also produce 1-aminocyclopropane-1-carboxylate (ACC) deaminase, an enzyme that lowers stress-induced ethylene production, thereby preventing inhibition of root growth under saline conditions (Backer et al., 2018). In addition, PGPR improves nutrient availability through biological nitrogen fixation, phosphate solubilization, potassium mobilization, and siderophore production, enhancing the acquisition of essential mineral nutrients even in salt-affected soils. Many strains also stimulate antioxidant enzyme activities, increase compatible solute accumulation, regulate ion transport, and improve membrane stability, collectively enhancing plant tolerance to osmotic and ionic stress (Singh et al., 2023).

Specific strains illustrate these effects. *Bacillus amyloliquefaciens* SQR9 improved salt tolerance of maize when inoculated into the rhizosphere (Chen et al., 2016). Pseudomonas putida UW4, which produces ACC deaminase, promoted the growth of canola in the presence of salt (Cheng et al., 2007). *Bacillus subtilis* GB03 conferred salt tolerance in Arabidopsis through tissue-specific regulation of the sodium transporter HKT1 (Zhang et al., 2008). Salt-tolerant PGPR has been identified for many other crops (Egamberdieva et al., 2019). It is useful to distinguish directly from indirect mechanisms. Direct mechanisms act on plant nutrition and hormone balance: biological nitrogen fixation, phosphate solubilization, siderophore production, and synthesis of IAA and other phytohormones (Glick, 2012). Indirect mechanisms help plants tolerate salinity by modifying stress physiology: ACC deaminase activity that lowers ethylene, exopolysaccharide production that binds Na^+ and improves soil aggregation, induction of antioxidant enzymes and compatible solutes, regulation of ion transporters, and induced systemic tolerance (Backer et al., 2018; Egamberdieva et al., 2019). In practice the two categories overlap, because improved nutrient uptake also supports osmotic adjustment, and few studies separate them experimentally; mutant strains lacking a specific

trait are needed to show which mechanism is responsible for an observed improvement in tolerance.

Arbuscular mycorrhizal fungi (AMF) represent another major component of the root microbiome that contributes significantly to salinity tolerance (Abdallah et al., 2025). AMF establishes symbiotic associations with plant roots, extending their hyphal networks into surrounding soil and thereby increasing the absorption of water and mineral nutrients, particularly phosphorus (P), zinc (Zn), and other immobile elements (Wahab et al., 2023; Samanta et al., 2025). Mycorrhizal colonization also enhances osmotic adjustment, antioxidant defense, chlorophyll synthesis, and photosynthetic efficiency while reducing Na^+ accumulation and maintaining a favorable K^+/Na^+ ratio under saline conditions (Nie et al., 2024). Similarly, endophytic bacteria and fungi, which inhabit internal plant tissues without causing disease, enhance stress tolerance through the production of phytohormones, osmoprotectants, antimicrobial compounds, and antioxidant metabolites. These microorganisms also induce systemic tolerance by activating stress-responsive genes involved in ion homeostasis, ROS detoxification, and hormone signaling pathways. Recent advances have shifted from the application of single microbial strains toward the development of synthetic microbial communities (SynComs). These designer microbial consortia consist of carefully selected beneficial microorganisms with complementary physiological functions (Ameen et al., 2024). Compared with single inoculants, SynComs provide greater stability, broader functional diversity, and improved establishment under field conditions. They simultaneously promote nutrient acquisition, suppress pathogens, improve soil structure, enhance antioxidant capacity, and maintain ionic balance, thereby providing superior protection against salinity stress (Compant et al., 2024). Microbiome engineering also includes manipulation of root exudation patterns, soil amendments that favor beneficial microbial populations, microbial seed coatings, biofertilizers, and microbial encapsulation technologies. These approaches enhance colonization efficiency and improve the persistence of beneficial microorganisms under adverse environmental conditions.

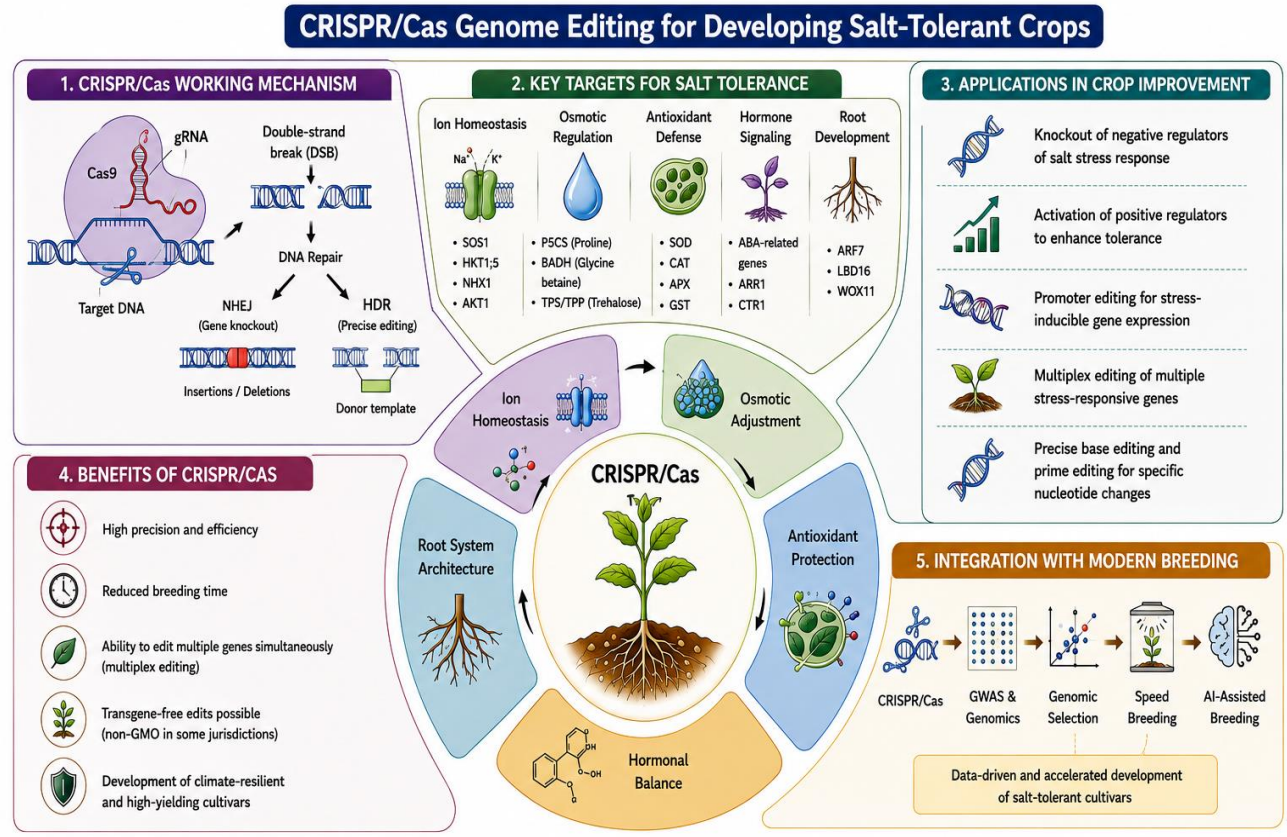


Fig. 3 Schematic representation of CRISPR/Cas genome editing for developing salt-tolerant crops. CRISPR/Cas enables targeted modification of genes involved in ion homeostasis, osmotic regulation, antioxidant defense, hormone signaling, and root development. Integration with GWAS, genomic selection, speed breeding, and artificial intelligence-assisted breeding can accelerate the development of salt-tolerant and climate-resilient crops.

Plant–microbe–soil interactions in salt-affected soils

Salinity affects not only plant physiology but also the intricate biological interactions occurring within the soil ecosystem. The plant–microbe–soil continuum functions as an integrated system in which plant roots, soil physicochemical properties, and diverse microbial communities continuously interact to influence nutrient cycling, water availability, soil structure, and stress adaptation. In salt-affected soils, these interactions become increasingly important because they determine the capacity of plants to maintain growth and productivity under adverse environmental conditions (Chen et al., 2026). Recent research has shifted from studying individual microorganisms to understanding the entire rhizosphere ecosystem, recognizing that plant resilience depends on coordinated interactions among plants, microorganisms, and soil processes rather than on any single biological component (Jacoby et al., 2017; Liu et al., 2025). Soil salinity substantially alters the physical, chemical, and biological characteristics of agricultural soils. Excessive accumulation of soluble salts increases osmotic potential, reducing water availability to plants even when soil moisture appears adequate. High concentrations of sodium ions also promote clay dispersion, resulting in deterioration of soil structure, reduced aggregate stability, increased bulk density, and decreased porosity. Consequently, water infiltration, aeration, and root penetration become severely restricted. In saline-sodic soils, elevated pH further decreases the availability of essential nutrients such as phosphorus, iron, zinc, manganese, and copper, thereby intensifying nutrient deficiencies and reducing crop productivity (Qadir et al., 2007). Salinity also influences soil biochemical processes by suppressing microbial respiration, enzyme activities, and organic matter decomposition. Reduced activities of enzymes such as dehydrogenase, urease, phosphatase, β-glucosidase, and catalase limit nutrient mineralization and decrease the availability of nitrogen, phosphorus, and carbon required for plant growth. Consequently, maintaining biological activity within saline soils has become a major objective of sustainable soil management (Han et al., 2023).

The rhizosphere, the narrow zone of soil surrounding plant roots, represents one of the most biologically active ecosystems on Earth. Plant roots continuously release root exudates consisting of carbohydrates, amino acids, organic acids, sugars, vitamins, flavonoids, phenolic compounds, and signaling molecules that regulate microbial recruitment and activity (Habtemariam, 2026). Under salinity stress, both the composition and quantity of these exudates change substantially. These modifications selectively recruit salt-tolerant and plant-beneficial microorganisms capable of enhancing stress adaptation while suppressing opportunistic pathogens. This selective recruitment illustrates the concept of the "cry for help" hypothesis, whereby stressed plants actively reshape their rhizosphere microbiome to attract beneficial microorganisms that improve nutrient acquisition, regulate hormonal balance, and enhance stress tolerance (Kumar et al., 2023; Yusuf et al., 2025). Recent metagenomic studies indicate that root exudates function not merely as nutrient sources but also as molecular signals governing microbial communication, colonization, and functional specialization within saline environments (Liu et al., 2025). Beneficial microbial communities perform essential ecological functions that sustain plant growth under saline conditions. They participate in decomposition of organic matter, biological nitrogen fixation, phosphorus solubilization, sulfur oxidation, potassium mobilization, and micronutrient cycling. Through these processes, microorganisms improve nutrient availability despite the reduced mobility of many essential elements in saline soils (Maciel-Rodríguez et al., 2025). Recent ecological studies demonstrate that microbial interaction networks, rather than individual microbial species, determine ecosystem stability under salinity stress. Highly connected microbial communities exhibit greater functional redundancy, allowing nutrient cycling and soil biological activity to continue even when environmental conditions become unfavorable. Keystone microorganisms act as central regulators within these ecological networks, maintaining microbial diversity and promoting resilience against salinity-induced disturbances (Banerjee et al., 2018).

Soil organic matter plays a fundamental role in mediating plant–microbe–soil interactions under salinity stress. Organic matter improves soil aggregation, increases water-holding capacity, enhances cation exchange capacity, and provides carbon substrates that support microbial growth. Microbial decomposition of organic residues generates humic substances and extracellular polysaccharides that improve soil structure and reduce sodium-induced dispersion (Luo et al., 2026). Furthermore, improved microbial activity enhances soil carbon sequestration, contributing not only to soil fertility but also to climate change mitigation. Recent studies have shown that maintaining healthy microbial communities promotes long-term stabilization of soil organic carbon while simultaneously improving salinity tolerance through enhanced nutrient availability and improved soil physical properties (Lehmann et al., 2020). Recent research has revealed that plant roots continuously communicate with surrounding microorganisms through a complex exchange of chemical signals. Beneficial microorganisms produce lipochitooligosaccharides, volatile organic compounds (VOCs), quorum-sensing molecules, siderophores, and extracellular polysaccharides, which influence plant development and activate stress-responsive signaling pathways. These microbial signals stimulate induced systemic resistance (ISR) and enhance plant immune responses without causing disease. Simultaneously, plants regulate microbial colonization through secretion of flavonoids, coumarins, and antimicrobial peptides that selectively enrich beneficial microorganisms while restricting pathogenic populations. This bidirectional molecular communication establishes a dynamic and mutually beneficial relationship that becomes particularly important under saline conditions (Trivedi et al., 2020).

Digital phenotyping and hyperspectral imaging for salinity detection

The increasing severity of soil salinization and climate change has accelerated the development of digital phenotyping and hyperspectral imaging (HSI) technologies for rapid, non-destructive, and high-throughput assessment of plant responses to salinity stress. Traditional methods for evaluating salinity tolerance rely on destructive measurements, including biomass

determination, ion analysis, chlorophyll estimation, and biochemical assays. Although these techniques provide accurate physiological information, they are labor-intensive, time-consuming, and unsuitable for screening thousands of breeding lines. Digital phenotyping has emerged as a transformative approach that integrates advanced imaging technologies, sensors, robotics, artificial intelligence (AI), and automated data analysis to continuously monitor plant growth, morphology, physiology, and stress responses under controlled and field conditions. These technologies enable precise quantification of plant traits throughout the entire life cycle and have become indispensable tools for modern crop improvement programs (Furbank & Tester, 2011; He et al., 2024a).

Digital phenotyping refers to the automated acquisition and analysis of plant characteristics using imaging systems and environmental sensors (Devi & Rana, 2026). Modern phenotyping platforms employ visible (RGB) imaging, thermal infrared imaging, fluorescence imaging, hyperspectral imaging, LiDAR (Light Detection and Ranging), X-ray computed tomography (CT), magnetic resonance imaging (MRI), and three-dimensional (3D) imaging to evaluate plant performance under saline conditions (Lee et al., 2018) (Table 1). These systems provide continuous measurements of plant architecture, leaf morphology, canopy development, biomass accumulation, root architecture, water status, and photosynthetic performance without damaging plant tissues. Automated phenotyping platforms equipped with conveyor systems, robotic arms, drones (unmanned aerial vehicles; UAVs), and field-based sensor networks have significantly increased the efficiency of salinity screening (Omari et al., 2020; Abebe et al., 2023). Compared with conventional phenotyping, these systems minimize human error, improve reproducibility, and enable simultaneous evaluation of thousands of genotypes under diverse environmental conditions. Consequently, digital phenotyping has become a critical component of precision agriculture and climate-resilient crop breeding (Araus et al., 2022). The enormous amount of data generated by digital phenotyping platforms has necessitated the application of artificial intelligence (AI) and machine learning (ML) algorithms for automated image processing and decision-making. Advanced computational models, including convolutional neural networks (CNNs), deep learning, random forest, support vector machines (SVMs), and gradient boosting algorithms, are increasingly employed to classify stress severity, predict salinity tolerance, identify spectral signatures, and estimate physiological traits directly from imaging data. AI-driven image analysis substantially improves the speed and accuracy of salinity assessment by extracting complex patterns that are difficult to detect through conventional statistical approaches. Integration of imaging data with environmental variables, genomic information, and multi-omics datasets further enhances predictive accuracy and accelerates the identification of superior genotypes for breeding programs (Singh et al., 2018).

Among modern imaging technologies, hyperspectral imaging (HSI) has gained considerable attention because of its ability to detect physiological changes before visible symptoms appear. Unlike conventional RGB cameras, which record only three spectral bands (red, green, and blue), hyperspectral sensors collect hundreds of narrow spectral bands across the visible, near-infrared (NIR), and short-wave infrared (SWIR) regions of the electromagnetic spectrum (Sarić et al., 2022). This detailed spectral information enables identification of subtle biochemical and physiological changes associated with salinity stress. Salinity alters leaf pigment composition, cellular water content, membrane integrity, internal leaf structure, and photosynthetic activity, all of which modify spectral reflectance patterns. Hyperspectral imaging can therefore identify stress-induced changes in chlorophyll concentration, carotenoid content, water status, osmotic adjustment, and nutrient imbalance long before reductions in growth become apparent. Early detection enables timely implementation of management strategies and improves the efficiency of breeding programs by facilitating rapid identification of salt-tolerant genotypes (Mishra et al., 2017). Thermal imaging has become another valuable tool for assessing salinity stress because leaf temperature is closely associated with stomatal conductance and transpiration. Under saline conditions, stomatal closure reduces transpiration, causing an increase in leaf surface temperature. Infrared thermal cameras can accurately detect these temperature changes, providing indirect information regarding plant water status, stomatal regulation, and stress severity. Similarly, chlorophyll fluorescence imaging enables evaluation of photosystem II (PSII) efficiency, electron transport, and photochemical performance. Salinity-induced damage to the photosynthetic apparatus reduces fluorescence parameters such as Fv/Fm, indicating impairment of photosynthetic efficiency. These measurements provide sensitive indicators of physiological stress before visible symptoms become apparent and are widely used in both laboratory and greenhouse experiments (Zhang et al., 2024b).

Practical applications illustrate how these tools are used to identify tolerant genotypes. In Arabidopsis, high-throughput non-destructive imaging of image-derived growth and physiological traits was used to dissect components of salinity tolerance (Awlia et al., 2016). In rice, a diverse panel was phenotyped with automated non-invasive imaging under salinity, and association analysis of the image-derived traits revealed loci associated with salinity tolerance (Al-Tamimi et al., 2016). Hyperspectral reflectance combined with machine-learning algorithms such as partial least squares regression, random forest, or support vector machines can be calibrated against measured traits such as leaf Na^+ content or biomass to rank genotypes before visible symptoms appear (Mishra et al., 2017; Singh et al., 2018). Applying these technologies under field conditions is considerably harder than in controlled-environment platforms. Variation in soil type, moisture, and salinity within a field produces spatial heterogeneity that can mask genotype differences, and soil background, shadows, wind, changing illumination, and cloud cover reduce the quality and repeatability of spectral and thermal data. Canopy reflectance also changes with growth stage, so a model trained on seedlings may not transfer to flowering plants, and the signatures of salinity overlap with those of drought, nutrient deficiency, and disease, which complicates attribution (Araus & Cairns, 2014; Tardieu et al., 2017). Machine-learning models trained on one crop, location, or season often generalize poorly, so calibration with ground-truth

measurements of soil electrical conductivity and plant ion content, multi-environment training data, and standardized protocols are needed. Cost, data storage, and the technical skills required for processing also limit use in breeding programs in the regions where salinity is most severe.

Climate change, sea-level rise, and secondary soil salinization

Climate change has emerged as one of the most significant drivers of soil salinization, posing a serious threat to global agricultural sustainability and food security. Although salinity has traditionally been considered a localized problem associated with arid and semi-arid regions, recent evidence indicates that climate change is accelerating the expansion of salt-affected lands across diverse agroecosystems. Rising global temperatures, altered precipitation patterns, prolonged droughts, increasing evapotranspiration, sea-level rise, and extreme weather events collectively intensify both primary (natural) and secondary (human-induced) soil salinization. Consequently, millions of hectares of productive agricultural land are gradually becoming unsuitable for crop cultivation, necessitating the development of climate-resilient management strategies (Intergovernmental Panel on Climate Change [IPCC], 2023; Food and Agriculture Organization of the United Nations [FAO], 2024).

Climate change directly influences the hydrological cycle, resulting in substantial modifications to soil water balance and salt dynamics. Rising temperatures increase evaporation from soil surfaces and transpiration from vegetation, leading to greater upward movement of saline groundwater through capillary action (Lei et al., 2026; Wang et al., 2026). As water evaporates, dissolved salts remain in the upper soil layers, gradually increasing salt concentrations within the crop root zone. This process is particularly severe in arid and semi-arid regions where evaporation greatly exceeds precipitation (He et al., 2024b). Changes in rainfall patterns further exacerbate salinity problems. In many regions, declining annual rainfall reduces the natural leaching of salts below the root zone, while prolonged droughts decrease freshwater availability for irrigation. Conversely, short periods of intense rainfall often fail to remove accumulated salts because rapid surface runoff limits effective infiltration (Amouyal et al., 2026). Consequently, climate change alters both the accumulation and redistribution of salt within agricultural soils, increasing the frequency and severity of salinity stress (IPCC, 2023). Climate change also modifies groundwater recharge and water table dynamics. Reduced recharge during prolonged dry periods may be followed by excessive irrigation, causing fluctuations in groundwater levels that promote secondary salinization. In areas with shallow saline groundwater, rising water tables transport dissolved salts upward into the rooting zone, significantly reducing soil fertility and crop productivity (Lekshmy & Achari, 2026).

Sea-level rise and coastal salinization

One of the most visible consequences of climate change is global sea-level rise, resulting primarily from thermal expansion of seawater and accelerated melting of glaciers and polar ice sheets. Coastal agricultural regions are particularly vulnerable because rising sea levels facilitate the intrusion of seawater into rivers, estuaries, coastal aquifers, and agricultural lands. Saltwater intrusion contaminates freshwater resources used for irrigation and drinking, increasing soil salinity even in previously productive coastal areas. Agricultural soils subjected to repeated tidal inundation accumulate excessive concentrations of sodium and chloride ions, which degrade soil structure, reduce nutrient availability, and impair crop growth. In addition, saline groundwater increasingly replaces freshwater aquifers, making irrigation more difficult and expensive. Low-lying coastal deltas, which represent some of the world's most productive agricultural regions, are especially susceptible to sea-level rise. Repeated coastal flooding associated with tropical cyclones, storm surges, and extreme rainfall events accelerate salt deposition on agricultural land. Recovery of these soils often requires several years because natural rainfall alone is frequently insufficient to remove accumulated salts (Nicholls et al., 2021).

Secondary soil salinization

Unlike primary salinization, which develops naturally through geological and climatic processes, secondary salinization results primarily from human activities that disturb the natural water and salt balance of soils (Tarolli et al., 2024). It has become one of the most serious forms of land degradation because it develops rapidly and is closely linked to agricultural practices. One of the major causes of secondary salinization is inappropriate irrigation management. Irrigation water often contains dissolved salts, even when considered suitable for agriculture (Batool et al., 2026). Continuous irrigation without adequate drainage allows these salts to accumulate progressively within the root zone. The problem becomes particularly severe where evaporation rates are high, and rainfall is insufficient to leach salts from the soil profile. Poor drainage systems further aggravate salt accumulation by preventing excess irrigation water from leaving agricultural fields. Waterlogged conditions promote upward movement of saline groundwater through capillary rise, concentrating salts near the soil surface (Liu et al., 2024). In many irrigated regions, inadequate drainage has transformed formerly productive land into saline or saline-sodic soils with greatly reduced agricultural value (Zhao et al., 2025). Groundwater overexploitation also contributes to secondary salinization. Excessive pumping lowers freshwater tables, allowing saline groundwater or seawater to move inland and contaminate irrigation supplies. This process is becoming increasingly common in coastal agricultural regions where freshwater demand continues to increase because of population growth and agricultural intensification (Ramya & Vishnumolakala, 2025).

Additional anthropogenic factors contributing to secondary salinization include deforestation, removal of deep-rooted vegetation, inappropriate fertilizer application, industrial wastewater discharge, mining activities, and urban expansion. These activities alter natural hydrological processes and accelerate the movement and accumulation of salt within agricultural landscapes (FAO, 2024).

Impacts on soil health and ecosystem functioning

Climate-driven salinization affects not only crops but also the entire soil ecosystem. Elevated salt concentrations reduce microbial diversity, suppress enzymatic activities, alter nutrient cycling, and decrease organic matter decomposition. Beneficial microorganisms involved in nitrogen fixation, phosphorus solubilization, and organic matter mineralization become less abundant, resulting in reduced soil fertility (Shu et al., 2026). Salinity also deteriorates soil physical properties by dispersing clay particles and destroying stable aggregates. Consequently, infiltration rates decline, bulk density increases, soil aeration decreases, and root penetration becomes more difficult. These physical changes further reduce crop productivity while increasing susceptibility to erosion and desertification. At the ecosystem level, progressive salinization reduces biodiversity, alters vegetation composition, decreases carbon sequestration, and weakens ecosystem resilience. Natural ecosystems, wetlands, and coastal habitats are increasingly threatened by saline intrusion associated with climate change (FAO, 2024).

Climate change and the effectiveness of salinity management strategies

Climate change influences not only the extent of salinization but also how well management options work. Projections suggest that primary soil salinization may increase in many regions as warming and altered precipitation raise evaporative demand and reduce leaching (Corwin, 2021; Hassani et al., 2021). Consequently, practices that depend on leaching and drainage become less reliable where rainfall is declining or irregular and freshwater is scarce, and they can themselves aggravate salinization if saline drainage water or groundwater is not managed (Machado & Serralheiro, 2017; Corwin, 2021). Higher temperatures also raise crop water requirements and the salt load delivered with irrigation water, which narrows the margin of tolerance of existing cultivars, and co-occurring drought and heat stress may limit the benefit of a single trait such as Na^+ exclusion. In coastal zones, sea-level rise and saltwater intrusion increase salinity in both soil and irrigation water, so that salt-tolerant crops become a necessary component of adaptation rather than an optional one (Lesk et al., 2022; Su et al., 2025). Under these conditions, strategies that increase soil organic matter and water-holding capacity, microbial and nutrient management that sustains plant function under combined stresses, and genotypes selected under multi-stress field conditions are expected to be more robust than measures that address salinity alone, although long-term evidence under projected climate scenarios is still limited (Mazhar et al., 2022).

Mechanisms of salinity-induced growth reduction and salt tolerance

Salinity is a major environmental constraint that adversely affects plant growth and productivity by disrupting water and nutrient uptake from the root zone. Excessive accumulation of sodium (Na^+) and chloride (Cl^-) ions creates osmotic stress and ion toxicity, limiting water absorption and the availability of essential nutrients required for normal growth and development. Consequently, plant biomass, yield, and overall productivity are significantly reduced under saline conditions (Rameeh et al., 2012). Comparative evaluations have shown that salinity markedly reduces shoot and root biomass, chlorophyll content, protein concentration, and the uptake of essential nutrients such as nitrogen (N), phosphorus (P), and potassium (K), while increasing the accumulation of free amino acids as part of the osmotic adjustment process. However, tolerant genotypes maintain relatively better physiological performance than susceptible ones owing to their superior ability to regulate ion homeostasis and metabolic processes. These findings emphasize the importance of identifying resilient genotypes for cultivation and breeding in salt-affected environments (Zahoor et al., 2011).

Plant adaptation to salinity involves multiple physiological and biochemical mechanisms that collectively enhance stress tolerance. These include maintenance of a favorable K^+/Na^+ ratio, regulation of plant growth, selective uptake of essential ions, compartmentalization or exclusion of toxic Na^+ ions, and efficient ion transport systems. The coordinated operation of these mechanisms enables plants to minimize ionic toxicity and sustain normal physiological functions under saline conditions (Ali, 2011). Salinity also causes profound physiological disturbances that directly impair plant growth and productivity. Elevated concentrations of Na^+ and Cl^- reduce chlorophyll content, stomatal conductance, transpiration rate, and photosynthetic efficiency while simultaneously decreasing the uptake of essential mineral nutrients such as potassium (K), calcium (Ca), and magnesium (Mg). These physiological disruptions reduce carbon assimilation and metabolic activity, ultimately limiting plant growth and yield under saline conditions (Azuma et al., 2010).

Research gaps in salinity biology

Despite significant advances in understanding the physiological, biochemical, molecular, and ecological mechanisms of plant responses to salinity, major knowledge gaps remain. Salinity tolerance is a complex trait governed by interactions among genetic, epigenetic, physiological, biochemical, microbial, and environmental factors. Although numerous genes, signaling pathways, metabolites, and beneficial microorganisms associated with salinity adaptation have been identified, translating these discoveries into stable improvements in crop performance under field conditions remains challenging. Future research should prioritize integrated, multidisciplinary approaches to enhance crop resilience in saline and climate-affected environments (Negrão et al., 2017; Isayenkov & Maathuis, 2019). Most salinity studies rely on controlled laboratory or greenhouse conditions, which do not adequately represent the complexity of agricultural environments. In the field, plants experience fluctuating salinity, heterogeneous soil properties, microbial

interactions, nutrient limitations, and combined stresses such as drought, heat, flooding, and pathogen attacks. Consequently, promising technologies often show limited effectiveness under practical conditions. Long-term, multi-location field experiments are therefore essential to evaluate crop responses and validate salinity management strategies under realistic environmental conditions. Another major gap concerns the complex regulatory networks governing salinity tolerance. Although quantitative trait loci (QTLs), regulatory genes, transcription factors, and epigenetic mechanisms have been identified, research has largely focused on individual genes or signaling pathways rather than their coordinated interactions. Integrating genomics, transcriptomics, proteomics, metabolomics, ionomics, and phenomics could identify key regulatory hubs and support breeding strategies that improve multiple stress-response mechanisms simultaneously. Despite advances in multi-omics technologies, integrating these datasets remains challenging. Independent analyses of transcripts, proteins, metabolites, and ions limit the understanding of their relationships with physiological traits. Combining multi-omics approaches with advanced bioinformatics, network biology, and computational modeling could clarify the regulatory mechanisms underlying salinity tolerance and identify biomarkers for rapid screening of resilient genotypes. Furthermore, emerging techniques, including single-cell and spatial transcriptomics, spatial metabolomics, and single-cell proteomics, offer opportunities to investigate tissue-specific responses and cellular heterogeneity, thereby revealing regulatory mechanisms overlooked by conventional bulk analyses.

Table 1 Digital phenotyping and imaging technologies for assessing plant responses to salinity stress

Technology/approach	Major measurements	Salinity-related applications	Major advantages	References
Digital phenotyping platforms	Growth, plant architecture, leaf morphology, canopy development, biomass, root architecture, and physiological traits	Continuous monitoring and high-throughput screening of plant responses and salinity tolerance	Non-destructive, automated, high-throughput, and suitable for whole-life-cycle monitoring	Furbank & Tester (2011); He et al. (2024a)
RGB imaging	Plant size, leaf area, canopy structure, color, morphology, and growth dynamics	Assessment of growth inhibition, leaf development, and morphological changes caused by salinity	Simple, rapid, relatively low-cost, and suitable for automated image analysis	Araus et al. (2022)
Thermal infrared imaging	Leaf/canopy temperature and temperature distribution	Detection of changes in stomatal conductance, transpiration, plant water status, and stress severity	Rapid, non-contact detection of physiological responses	Zhang et al. (2023)
Chlorophyll fluorescence imaging	Fv/Fm, PSII efficiency, electron transport, and photochemical performance	Early detection of salinity-induced impairment of photosynthetic machinery	Sensitive indicator of photosynthetic stress before visible symptoms	Zhang et al. (2023)
Hyperspectral imaging (HSI)	Spectral reflectance across visible, NIR, and SWIR regions	Detection of changes in pigments, water status, osmotic adjustment, membrane integrity, nutrient status, and photosynthetic activity	Non-destructive, highly sensitive, and capable of detecting stress before visible symptoms	Mishra et al. (2017)
LiDAR and 3D imaging	Plant height, canopy architecture, structural traits, and biomass-related characteristics	Quantification of structural changes and growth responses under salinity	Provides three-dimensional structural information	Araus et al. (2022)
UAV-based imaging and field sensors	Canopy-level spectral, thermal, morphological, and spatial information	Large-scale field screening of genotypes and spatial assessment of salinity responses	Rapid field assessment over large areas and diverse environments	Araus et al. (2022)
Artificial intelligence and machine learning	Image-derived patterns, spectral signatures, stress severity, and predicted physiological traits	Automated classification of salinity stress, prediction of tolerance, and identification of superior genotypes	High analytical capacity, rapid processing, and improved prediction accuracy	Singh et al. (2018); He et al. (2024a)
Integrated digital phenotyping	Imaging, environmental, genomic, and multi-omics datasets	Prediction of salinity tolerance and identification of superior breeding materials	Combines multiple data sources for comprehensive and predictive phenotyping	Araus et al. (2022); He et al. (2024a)

Conclusion

This review highlights recent advances in salinity biology and their progress toward field application. First, salinity tolerance depends on the coordinated regulation of ion transport (Na^+ exclusion, xylem retrieval, vacuolar sequestration, and K^+ retention), osmotic adjustment, ROS homeostasis, and hormonal signaling, fine-tuned by epigenetic mechanisms and non-coding RNAs. Ion transporters such as HKT1;5 are well-validated targets, associated with a major QTL in rice and yield improvements in wheat. Second, multi-omics and genetic mapping have facilitated candidate gene identification, but field validation remains limited. Third, CRISPR/Cas editing of negative regulators, including OsRR22 in rice and SlHyPRP1 in tomato, demonstrates the potential for precise improvements in salinity tolerance, although effects on yield, trade-offs, and regulatory acceptance require further investigation. Editing antioxidant and osmolyte pathways and multiplex genome editing also warrant further validation. Fourth, salt-adapted plant growth-promoting rhizobacteria (PGPR), arbuscular mycorrhizal fungi (AMF), synthetic microbial communities (SynComs), and improved organic matter and nutrient management can enhance plant performance and soil health, although field outcomes remain variable. Digital phenotyping and machine learning offer rapid, non-destructive screening, but their application across heterogeneous field environments requires standardization. Climate change further intensifies salinity risks through increased evaporative demand, altered rainfall, sea-level rise, and secondary salinization, while reducing the reliability of leaching-based management. Therefore, no single technology can ensure sustainable salinity tolerance. Durable improvements require combining salt-tolerant genotypes with integrated soil, water, nutrient, organic matter, and microbial management. Translating molecular discoveries into agricultural benefits through genome editing or marker-assisted selection, followed by multi-location, multi-season field validation with complementary microbial and agronomic strategies will be essential for developing locally adapted cultivars and sustaining crop production on saline soils.

Recommendations

Future research should integrate multi-omics approaches, including genomics, transcriptomics, proteomics, metabolomics, ionomics, and phenomics, to elucidate the molecular networks governing salinity tolerance. CRISPR/Cas genome editing, particularly precision and multiplex editing should be advanced to modify genes involved in ion transport, osmotic regulation, and antioxidant defense. Greater emphasis is needed on epigenetic regulation and non-coding RNAs, including DNA methylation, histone modifications, microRNAs, and long non-coding RNAs, to clarify stress memory and transgenerational adaptation. Climate-resilient crop varieties should be developed by integrating genome editing, genomic selection, marker-assisted breeding, speed breeding, and artificial intelligence-assisted approaches. Root microbiome engineering and beneficial microbial consortia should also be promoted as sustainable strategies to improve plant growth, salinity tolerance, and soil health, supported by metagenomics, ecological network analysis, and systems biology to better understand plant–microbe–soil interactions. Investment in digital phenotyping technologies, including hyperspectral imaging, unmanned aerial vehicles (UAVs), and remote sensing should be increased for rapid, non-destructive assessment of salinity stress, while artificial intelligence, machine learning, and big-data analytics should integrate genomic, phenotypic, environmental, and management data to accelerate crop improvement. Integrated climate-smart soil and water management practices, including efficient irrigation, improved drainage, conservation agriculture, organic amendments, biochar application, and precision nutrient management, should be implemented to minimize secondary salinization. Priority should be given to multi-location, multi-season field trials to validate salt-tolerant genotypes, genome-edited lines, and microbial inoculants, with particular attention to yield stability and potential trade-offs under saline and non-saline conditions. Breeding programs should combine marker-assisted or genomic selection for complex tolerance traits with genome editing of validated major-effect genes, supported by image-based phenotyping calibrated against field performance. Finally, salinity management strategies should be adapted to local soil conditions, irrigation-water quality, and climate, with regular soil salinity monitoring and long-term evaluation of organic and microbial amendments to ensure sustainable improvements in soil health and crop productivity.

Acknowledgement: The authors sincerely acknowledge their respective institutions for providing academic support, research facilities, and a collaborative research environment. The authors also thank their colleagues and mentors for their valuable suggestions, constructive feedback, and support during the preparation of this review article.

Authors' contribution statement: A.: Conceptualization, literature collection, investigation, writing original draft, and manuscript preparation. I.M. and S.A.: Literature review and critical analysis. S.Z. and A.G.: Literature collection, scientific interpretation and discussion. S.A.J.: Visualization and critical review. All authors read and approved the final manuscript.

Funding: This study did not receive any grant or funding from individuals or organizations.

Availability of data and materials: All data generated or analyzed during this study are included in this published article.

Declarations

i. Ethics approval and consent to participate: Not applicable.

ii. Competing interests: The authors declare no conflict of interest.

Publisher's note: All claims shared in this article are entirely those of the authors and do not reflect the positions of their affiliated institutions, AgriBio e-Spectrum (the publisher), editors, or reviewers. Any mention or assessment of a product, as well as any claims made by its manufacturer, are not endorsed or guaranteed by the publisher.

References

Abbasi, G. H., Akhtar, J., Haq, M. A., Ali, S., Chen, Z. H., & Malik, W. (2014). Exogenous potassium differentially mitigates salt stress in tolerant and sensitive maize hybrids. *Pakistan Journal of Botany, 46*(1), 135–146.

Abdallah, M. M., Suo, C., Cui, Y., Ullah, R. H., Nhung, H. H., Li, L., & Liu, C. (2025). Arbuscular mycorrhizal fungi as integrative modulators of plant tolerance to drought, salinity, and heavy metal stress: Mechanistic insights and future directions. *Journal of Genetic Engineering and Biotechnology, 24*(1), 100636. doi:10.1016/j.jgeb.2025.100636

Abebe, A. M., Kim, Y., Kim, J., Kim, S. L., & Baek, J. (2023). Image-based high-throughput phenotyping in horticultural crops. *Plants, 12*(10), 2061. doi:10.3390/plants12102061

Achard, P., Cheng, H., De Grauwe, L., Decat, J., Schoutteten, H., Moritz, T., … Harberd, N. P. (2006). Integration of plant responses to environmentally activated phytohormonal signals. *Science*, *311*(5757), 91–94. https://doi.org/10.1126/science.1118642

Ahmed, K., Saqib, M., Akhtar, J., & Ahmad, R. (2012). Evaluation and characterization of genetic variation in maize (Zea mays L.) for salinity tolerance. *Pakistan Journal of Agricultural Sciences, 49*(4), 521–526.

Akram, M., Ashraf, M. Y., Ahmad, R., Waraich, E. A., Iqbal, J., & Mohsan, M. (2010). Screening for salt tolerance in maize (Zea mays L.) hybrids at an early seedling stage. *Pakistan Journal of Botany, 42*(1), 141–154.

Alam, K. M., Rashid, M. H., Bose, S., Fakir, O. A., Islam, M., Hossain, A. K. M. Z., & Hossain, A. (2018). Effects of salinity on seedling growth of four maize (Zea mays L.) cultivars under hydroponics. *Journal of Agricultural Studies, 6*(1), 56–69.

Ali, B., Imran, A., Iftikhar, H., Khan, Z., Saeed, F., Hussain, Z., Waheed, A., Abdel Latef, A. A. H., & Imin, N. (2026). Classical phytohormones and peptide plant hormones in abiotic stress tolerance: Crosstalk, physiological integration, and crop improvement. *Plants, 15*(10), 1538. https://doi.org/10.3390/plants15101538

Ali, F. Z. M. (2011). *The determinants of salinity tolerance in maize (Zea mays L.)* (Doctoral dissertation, University of Groningen).

Ali, M., Afzal, S., Parveen, A., Kamran, M., Javed, M. R., Abbasi, G. H., ... Ali, S. (2020). Silicon mediated improvement in the growth and ion homeostasis by decreasing Na^+ uptake in maize (Zea mays L.) cultivars exposed to salinity stress. *Plant Physiology and Biochemistry, 158*, 113–122.

Ali, S., & Goh, H.-H. (2026). Multi-omics integration for abiotic stress acclimation in tropical and underutilized plants. *Phyton-International Journal of Experimental Botany, 95*(6). doi:10.32604/phyton.2026.084657

Ali, S., Tyagi, A., & Bae, H. (2021). Ionomic approaches for discovery of novel stress-resilient genes in plants. International Journal of Molecular Sciences, 22(13), 7182. doi:10.3390/ijms22137182

Alrajeh, S., Khan, M. N., Putra, A. I., Al-ugaili, D. N., Alobaidi, K. H., Al Dossary, O., Al-Obaidi, J. R., Jamaludin, A. A., Allawi, M. Y., Al-Taie, B. S., Abdul Rahman, N., & Rahmad, N. (2024). Mapping proteomic response to salinity stress tolerance in oil crops: Towards enhanced plant resilience. *Journal of Genetic Engineering and Biotechnology, 22*(4), 100432. https://doi.org/10.1016/j.jgeb.2024.100432

Al-Tamimi, N., Brien, C., Oakey, H., Berger, B., Saade, S., Ho, Y. S., … Negrão, S. (2016). Salinity tolerance loci revealed in rice using high-throughput non-invasive phenotyping. *Nature Communications*, *7*, 13342. https://doi.org/10.1038/ncomms13342

Altpeter, F., Springer, N. M., Bartley, L. E., Blechl, A. E., Brutnell, T. P., Citovsky, V., … Stewart, C. N. (2016). Advancing crop transformation in the era of genome editing. *The Plant Cell*, *28*(7), 1510–1520.

Amato, R., & Del Buono, D. (2021). Use of a biostimulant to mitigate salt stress in maize plants. *Agronomy, 11*(9), 1755.

Ameen, M., Mahmood, A., Sahkoor, A., Zia, M. A., & Ullah, M. S. (2024). The role of endophytes to combat abiotic stress in plants. *Plant Stress, 12*, 100435. doi:10.1016/j.stress.2024.100435

Amouyal, A., Reichmann, O., & Litaor, M. I. (2026). Modeling salinity and sodicity risks under long-term irrigation with medium salinity water: Kinneret catchment as a case study. *Agricultural Water Management, 326*, 110245. doi:10.1016/j.agwat.2026.110245

Anee, T. I., Sewelam, N. A., Bautista, N. S., Hirayama, T., & Suzuki, N. (2025). Roles of ROS and NO in plant responses to individual and combined salt stress and waterlogging. *Antioxidants, 14*(12), 1455. https://doi.org/10.3390/antiox14121455

Araus, J. L., & Cairns, J. E. (2014). Field high-throughput phenotyping: The new crop breeding frontier. *Trends in Plant Science*, *19*(1), 52–61. https://doi.org/10.1016/j.tplants.2013.09.008

Araus, J. L., Kefauver, S. C., Vergara-Díaz, O., Gracia-Romero, A., Rezzouk, F. Z., Segarra, J., Buchaillot, M. L., Chang-Espino, M., Vatter, T., Sanchez-Bragado, R., Fernandez-Gallego, J. A., Serret, M. D., & Bort, J. (2022). Crop phenotyping in a context of global change: What to measure and how to do it. *Journal of Integrative Plant Biology, 64*(2), 592–618. https://doi.org/10.1111/jipb.13191

Assaha, D. V. M., 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. doi:10.3389/fphys.2017.00509

Awlia, M., Nigro, A., Fajkus, J., Schmoeckel, S. M., Negrão, S., Santelia, D., … Panzarová, K. (2016). High-throughput non-destructive phenotyping of traits that contribute to salinity tolerance in Arabidopsis thaliana. *Frontiers in Plant Science*, *7*, 1414. https://doi.org/10.3389/fpls.2016.01414

Azuma, R., Ito, N., Nakayama, N., Suwa, R., Nguyen, N. T., Larrinaga-Mayoral, J. A., Esaka, M., Fujiyama, H., & Saneoka, H. (2010). Fruits are more sensitive to salinity than leaves and stems in pepper plants (Capsicum annuum L.). *Scientia Horticulturae, 125*(2), 171–178.

Backer, R., Rokem, J. S., Ilangumaran, G., Lamont, J., Praslickova, D., Ricci, E., Subramanian, S., & Smith, D. L. (2018). Plant growth-promoting rhizobacteria: Context, mechanisms of action, and roadmap to commercialization of biostimulants for sustainable agriculture. *Frontiers in Plant Science, 9*, 1473. https://doi.org/10.3389/fpls.2018.01473

Banerjee, S., Schlaeppi, K., & van der Heijden, M. G. A. (2018). Keystone taxa as drivers of microbiome structure and functioning. *Nature Reviews Microbiology, 16*(9), 567–576. https://doi.org/10.1038/s41579-018-0024-1

Batool, A., Zhang, K., Abbas, F., Akhtar, A., & Mao, J. (2026). A comparative evaluation of soil amendments in mitigating soil salinization and modifying geochemical processes in arid land. *Agronomy, 16*(2), 222. doi:10.3390/agronomy16020222

Bayat, H., Alirezaie, M., & Neamati, H. (2012). Impact of exogenous salicylic acid on growth and ornamental characteristics of calendula (*Calendula officinalis* L.) under salinity stress. *Journal of Stress Physiology & Biochemistry, 8*(4), 258–267.

Bibi, H., Abubakr, M., Iqbal, J., Abbasi, B. A., Anas, M., & Zahra, S. A. (2024). Epigenetic regulation of stress responses in plants. In *Molecular biology of plant stress responses* (pp. 78–96). CABI. https://doi.org/10.1079/9781800628823.0005

Billah, M., Latif, M. A., Hossain, N., & Uddin, M. S. (2017). Evaluation and selection of salt tolerant hybrid maize under hydroponics culture. *Research on Crops, 18*(3), 481–489.

Canellas, L. P., Olivares, F. L., Aguiar, N. O., Jones, D. L., Nebbioso, A., Mazzei, P., & Piccolo, A. (2015). Humic and fulvic acids as biostimulants in horticulture. *Scientia Horticulturae*, *196*, 15–27. https://doi.org/10.1016/j.scienta.2015.09.013

Cao, Y., Zhou, X., Song, H., Zhang, M., & Jiang, C. (2023). Advances in deciphering salt tolerance mechanism in maize. *The Crop Journal, 11*(2), 1001–1010.

Carrera, F. P., Noceda, C., Maridueña-Zavala, M. G., & Cevallos-Cevallos, J. M. (2021). Metabolomics, a powerful tool for understanding plant abiotic stress. *Agronomy*, *11*(5), 824. https://doi.org/10.3390/agronomy11050824

Chakraborty, K., Basak, N., Bhaduri, D., Ray, S., Vijayan, J., Chattopadhyay, K., & Sarkar, R. K. (2018). Ionic basis of salt tolerance in plants: Nutrient homeostasis and oxidative stress tolerance. In *Plant nutrients and abiotic stress tolerance* (pp. 325–362). doi:10.1007/978-981-10-9044-8_14

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, D., Smagghe, G., Su, J., Ma, S., Liu, R., Zhang, W., Zhang, Z., Zhang, R., Wang, F., Zhong, F., & Muhae-Ud-Din, G. (2026). Microbial allies for salinity resilience: Mechanisms, innovations, and holobiont strategies for sustainable crop production. *Plant Stress, 22*, 101446. doi:10.1016/j.stress.2026.101446

Chen, L., Liu, Y., Wu, G., Njeri, K. V., Shen, Q., Zhang, N., & Zhang, R. (2016). Induced maize salt tolerance by rhizosphere inoculation of Bacillus amyloliquefaciens SQR9. *Physiologia Plantarum, 157*(4), 490–502.

Cheng, Z., Park, E., & Glick, B. R. (2007). 1-Aminocyclopropane-1-carboxylate deaminase from Pseudomonas putida UW4 facilitates the growth of canola in the presence of salt. *Canadian Journal of Microbiology*, *53*(7), 912–918.

Chu, S., Wang, Y., Yan, X., Zhang, T., Yang, M., & Wang, J. (2026). The role of miRNA in woody plants' response to salt stress. *Plant Stress, 20*, 101331. https://doi.org/10.1016/j.stress.2026.101331

Collard, B. C. Y., & Mackill, D. J. (2008). Marker-assisted selection: An approach for precision plant breeding in the twenty-first century. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *363*(1491), 557–572.

Compant, S., Samad, A., Faist, H., & Sessitsch, A. (2024). Strategies for combating plant salinity stress: The potential of plant growth-promoting microorganisms. *Frontiers in Plant Science, 15*, 1406913. https://doi.org/10.3389/fpls.2024.1406913

Corpas, F. J., Taboada, J., & Palma, J. M. (2026). Integration of NO and H_2S signaling in higher plants. *Plant Communications, 7*(3), 101664. https://doi.org/10.1016/j.xplc.2025.101664

Corwin, D. L. (2021). Climate change impacts on soil salinity in agricultural areas. *European Journal of Soil Science*, *72*(2), 842–862. https://doi.org/10.1111/ejss.13010

Cui, D., Wu, D., Liu, J., Li, D., Xu, C., Li, S., et al. (2015). Proteomic analysis of seedling roots of two maize inbred lines that differ significantly in the salt stress response. *PLoS ONE, 10*(2), e0116697.

Dakal, T. C., Dagariya, S., Goswami, B., Rathore, R., Rankawat, R., Bhargavi, H. A., Rana, A., Srivastava, S., & Gadi, B. R. (2025). Integrative multi-omics approaches for crop abiotic stress tolerance. *Discover Plants, 2*, 361. doi:10.1007/s44372-025-00431-w

Das, P., Agarwala, N., Gill, S. S., & Varshney, R. K. (2023). Emerging role of plant long non-coding RNAs (lncRNAs) in salinity stress response. *Plant Stress, 9*, 100265. https://doi.org/10.1016/j.stress.2023.100265

Devi, R., & Rana, A. (2026, September). Digital phenotyping: The new eyes of plant breeders. *Agriculture & Food: E-Newsletter, 8*(9), 68–70.

dos Reis, R. A., Seabra, A. B., Aragão, C. B., Halfeld, M., Nunes, R. S., Rodriguez, R., Benavides-Mendoza, A., Rubilar, O., & Tortella, G. R. (2026). Nitric oxide and hydrogen sulfide crosstalk in plants: Redox regulation, stress adaptation, and emerging applications. *International Journal of Molecular Sciences, 27*(11), 4962. https://doi.org/10.3390/ijms27114962

Egamberdieva, D., Wirth, S., Bellingrath-Kimura, S. D., Mishra, J., & Arora, N. K. (2019). Salt-tolerant plant growth promoting rhizobacteria for enhancing crop productivity of saline soils. *Frontiers in Microbiology*, *10*, 2791. https://doi.org/10.3389/fmicb.2019.02791

Fang, W., Raza, A., Zhu, Q., Wang, Q., Ren, Q., Liu, M., Wang, S., & Hassan, M. A. (2026). Regulatory networks and molecular mechanisms underlying salt stress

tolerance in rice. *Frontiers in Plant Science, 17*, 1757448. https://doi.org/10.3389/fpls.2026.1757448

Farooq, M., Hussain, M., Wakeel, A., & Siddique, K. H. M. (2015). Salt stress in maize: Effects, resistance mechanisms, and management. *Agronomy for Sustainable Development, 35*(2), 461–481.

Ferreira, L. J., Azevedo, V., Maroco, J., Oliveira, M. M., & Santos, A. P. (2015). Salt tolerant and sensitive rice varieties display differential methylome flexibility under salt stress. *PLoS ONE*, *10*(5), e0124060. https://doi.org/10.1371/journal.pone.0124060

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

Food and Agriculture Organization of the United Nations. (2024). *Global status of salt-affected soils: Main report*. Rome, Italy: Food and Agriculture Organization of the United Nations. https://doi.org/10.4060/cd3044en

Fu, S., Wang, L., Li, C., Zhao, Y., Zhang, N., Yan, L., Li, C. M., & Niu, Y. (2024). Integrated transcriptomic, proteomic, and metabolomic analyses revealed molecular mechanism for salt resistance in soybean (*Glycine max* L.) seedlings. *International Journal of Molecular Sciences, 25*(24), 13559. https://doi.org/10.3390/ijms252413559

Furbank, R. T., & Tester, M. (2011). Phenomics—Technologies to relieve the phenotyping bottleneck. *Trends in Plant Science, 16*(12), 635–644. https://doi.org/10.1016/j.tplants.2011.09.005

Gao, P., Bai, X., Yang, L., Lv, D., Pan, X., Li, Y., … Zhu, Y. (2011). osa-MIR393: A salinity- and alkaline stress-related microRNA gene. *Molecular Biology Reports*, *38*(1), 237–242.

Gao, Y., Lu, Y., Wu, M., Liang, E., Li, Y., Zhang, D., et al. (2016). Ability to remove Na^+ and retain K^+ correlates with salt tolerance in two maize inbred lines seedlings. *Frontiers in Plant Science, 7*, 1716.

Gill, S. S., & Tuteja, N. (2010). Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. *Plant Physiology and Biochemistry*, *48*(12), 909–930. https://doi.org/10.1016/j.plaphy.2010.08.016

Glick, B. R. (2012). Plant growth-promoting bacteria: Mechanisms and applications. *Scientifica*, *2012*, Article 963401. https://doi.org/10.6064/2012/963401

Golldack, D., Li, C., Mohan, H., & Probst, N. (2014). Tolerance to drought and salt stress in plants: unraveling the signaling networks. *Frontiers in Plant Science, 5*, 151.

Gupta, B., & Huang, B. (2014). Mechanism of salinity tolerance in plants: Physiological, biochemical, and molecular characterization. *International Journal of Genomics, 2014*, 701596. doi:10.1155/2014/701596

Habtemariam, A. A. (2026). Modulation of root exudate–microbe interactions for sustainable rhizosphere function and soil health. In V. D. Rajput (Ed.), *Engineering of the rhizosphere: An emerging approach for sustainability*. IntechOpen. doi:10.5772/intechopen.1017823

Haider, S., Singh, A. P., Panthi, B., Sindhu, S. R., Safa, N. T., Malik, S., & Rahimi, M. (2026). Advances in CRISPR/Cas9 genome editing for crop improvement and global food security. Current Plant Biology, 46, Article 100593. https://doi.org/10.1016/j.cpb.2026.100593

Han, D., Zhang, D., Han, D., Ren, H., Wang, Z., Zhu, Z., Sun, H., Wang, L., Qu, Z., Lu, W., & Yuan, M. (2023). Effects of salt stress on soil enzyme activities and rhizosphere microbial structure in salt-tolerant and salt-sensitive soybean. *Scientific Reports, 13*, 17057. https://doi.org/10.1038/s41598-023-44266-5

Hassani, A., Azapagic, A., & Shokri, N. (2021). Global predictions of primary soil salinization under changing climate in the 21st century. *Nature Communications*, *12*, 6663. https://doi.org/10.1038/s41467-021-26907-3

He, K., Zhang, Q., Ai, Z., Xu, N., Qiao, Y., Tian, C., Leng, P., Cheng, H., Chen, G., & Li, F. (2024b). Characteristics and influence factors of soil water and salt movement in the Yellow River irrigation district. *Agronomy, 14*(1), 92. doi:10.3390/agronomy14010092

He, S., Li, X., Chen, M., Xu, X., Tang, F., Gong, T., Xu, M., Yang, W., & Liu, W. (2024a). Crop HTP technologies: Applications and prospects. *Agriculture, 14*(5), 723. https://doi.org/10.3390/agriculture14050723

Hussain, S. S., Rasheed, M., Saleem, M. H., Ahmed, Z. I., Hafeez, A., Jilani, G., et al. (2023). Salt tolerance in maize with melatonin priming to achieve sustainability in yield in salt affected soils. *Pakistan Journal of Botany, 55*(1), 19–35.

Intergovernmental Panel on Climate Change. (2023). *Climate change 2023: Synthesis report*. Geneva, Switzerland: Intergovernmental Panel on Climate Change. https://doi.org/10.59327/IPCC/AR6-9789291691647

Isayenkov, S. V., & Maathuis, F. J. M. (2019). Plant salinity stress: Many unanswered questions remain. *Frontiers in Plant Science*, *10*, 80. https://doi.org/10.3389/fpls.2019.00080

Islam, W., Waheed, A., Naveed, H., & Zeng, F. (2022). MicroRNAs mediated plant responses to salt stress. *International Journal of Molecular Sciences, 23*(18), 10432. https://doi.org/10.3390/ijms231810432

Jacoby, R., Peukert, M., Succurro, A., Koprivova, A., & Kopriva, S. (2017). The role of soil microorganisms in plant mineral nutrition—Current knowledge and future directions. *Frontiers in Plant Science, 8*, 1617. https://doi.org/10.3389/fpls.2017.01617

Jana, G. A., Glick, B. R., & Yaish, M. W. (2022). Salt tolerance in plants: Using OMICS to assess the impact of plant growth-promoting bacteria (PGPB). In *Mitigation of plant abiotic stress by microorganisms: Applicability and future directions* (pp. 299–320). Elsevier. https://doi.org/10.1016/B978-0-323-90568-8.00014-6

Kaminsky, L. M., Trexler, R. V., Malik, R. J., Hockett, K. L., & Bell, T. H. (2019). The inherent conflicts in developing soil microbial inoculants. *Trends in Biotechnology*, *37*(2), 140–151.

Kaniganti, S., Saini, H., Chaitanya, A. K., Hegde, N., Shah, P., Magar, N. D., Rijal, R., Kaushik, J. J., Nanda, D., Sachan, S., Kumar, A., Bhoite, R., & Jamedar, H. R. (2026). CRISPR/Cas genome editing and its applications in cereal crop improvement. *Plant-Environment Interactions, 7*(2), e70133. https://doi.org/10.1002/pei3.70133

Kaur, R., Paul, N., Raja, V., Awasthi, N. S., Sidhu, H. K., & Hakeem, K. R. (2026). Multi-omics biomarkers of plant

abiotic-stress resilience: Discovery, validation, integration, and translational applications. *Phyton-International Journal of Experimental Botany.* doi:10.32604/phyton.2026.088865

Kaya, C., Akram, N. A., Ashraf, M., & Sonmez, O. (2018). Exogenous application of humic acid mitigates salinity stress in maize (Zea mays L.) plants by improving some key physico-biochemical attributes. *Cereal Research Communications, 46*(1), 67–78.

Kesawat, M. S., Satheesh, N., Kherawat, B. S., Kumar, A., Kim, H.-U., Chung, S.-M., & Kumar, M. (2023). Regulation of reactive oxygen species during salt stress in plants and their crosstalk with other signaling molecules—Current perspectives and future directions. *Plants, 12*(4), 864. doi:10.3390/plants12040864

Kumar, M. K., Prusty, M. R., Pandey, M. K., Singh, P. K., Bohra, A., Guo, B., & Varshney, R. K. (2023). Application of CRISPR/Cas9-mediated gene editing for abiotic stress management in crop plants. *Frontiers in Plant Science, 14*, 1157678. https://doi.org/10.3389/fpls.2023.1157678

Kumar, N., Haldar, S., & Saikia, R. (2023). Root exudation as a strategy for plants to deal with salt stress: An updated review. *Environmental and Experimental Botany, 216*, 105518. doi:10.1016/j.envexpbot.2023.105518

Lämke, J., & Bäurle, I. (2017). Epigenetic and chromatin-based mechanisms in environmental stress adaptation and stress memory in plants. *Genome Biology, 18*, Article 124. https://doi.org/10.1186/s13059-017-1263-6

Lee, U., Chang, S., Putra, G. A., Kim, H., & Kim, D. H. (2018). An automated, high-throughput plant phenotyping system using machine learning-based plant segmentation and image analysis. *PLoS ONE, 13*(4), e0196615. doi:10.1371/journal.pone.0196615

Lehmann, J., Bossio, D. A., Kögel-Knabner, I., & Rillig, M. C. (2020). The concept and future prospects of soil health. *Nature Reviews Earth & Environment, 1*(10), 544–553. https://doi.org/10.1038/s43017-020-0080-8

Lei, M., Liu, Y., Zhou, J., Qi, Z., & Jia, R. (2026). Salinity effects on water surface and phreatic evaporation in arid regions: Evidence from controlled experiments. *Journal of Hydrology: Regional Studies, 66*, 103752. doi:10.1016/j.ejrh.2026.103752

Lekshmy, S. A. J., & Achari, V. S. (2026). Climate change impact on groundwater and soil geochemistry—Emerging challenges: A review. *Applied Water Science, 16*, 160. doi:10.1007/s13201-026-02827-9

Lesk, C., Anderson, W., Rigden, A., Coast, O., Jägermeyr, J., McDermid, S., Davis, K. F., & Konar, M. (2022). Compound heat and moisture extreme impacts on global crop yields under climate change. *Nature Reviews Earth & Environment, 3*, 872–889. https://doi.org/10.1038/s43017-022-00368-8

Li, J., Zhu, Q., Jiao, F., Yan, Z., Zhang, H., Zhang, Y., et al. (2023). Research progress on the mechanism of salt tolerance in maize: A classic field that needs new efforts. *Plants, 12*(12), 2356.

Liu, Y., Hu, Y., Wei, C., Zeng, W., Huang, J., & Ao, C. (2024). Synergistic regulation of irrigation and drainage based on crop salt tolerance and leaching threshold. *Agricultural Water Management, 292*, 108679. https://doi.org/10.1016/j.agwat.2024.108679

Liu, Y., Shi, A., Chen, Y., Xu, Z., Liu, Y., Yao, Y., Wang, Y., & Jia, B. (2025). Beneficial microorganisms: Regulating growth and defense for plant welfare. *Plant Biotechnology Journal, 23*(3), 986–998. https://doi.org/10.1111/pbi.14554

Luo, M., Zhao, Y., Zhang, R., Xing, J., Duan, M., Li, J., et al. (2017). Mapping of a major QTL for salt tolerance of mature field-grown maize plants based on SNP markers. *BMC Plant Biology, 17*(1), 140.

Luo, Y., Yu, H., Yu, J., Liu, F., Wang, Q., & Liu, J. (2026). The perspective functions of organic acids to restore salt-affected soils and plant stress resistance. *Plant Stress, 20*, 101321. doi:10.1016/j.stress.2026.101321

Machado, R. M. A., & Serralheiro, R. P. (2017). Soil salinity: Effect on vegetable crop growth. Management practices to prevent and mitigate soil salinization. *Horticulturae*, *3*(2), 30. https://doi.org/10.3390/horticulturae3020030

Maciel-Rodríguez, M., Moreno-Valencia, F. D., & Plascencia-Espinosa, M. (2025). The role of plant growth-promoting bacteria in soil restoration: A strategy to promote agricultural sustainability. *Microorganisms, 13*(8), 1799. doi:10.3390/microorganisms13081799

Masuda, M. S., Azad, M. A. K., Hasanuzzaman, M., & Arifuzzaman, M. (2021). Evaluation of salt tolerance in maize (Zea mays L.) at seedling stage through morphological characters and salt tolerance index. *Plant Physiology Reports, 26*(3), 541–554.

Mazhar, S., Pellegrini, E., Contin, M., Bravo, C., & De Nobili, M. (2022). Impacts of salinization caused by sea level rise on the biological processes of coastal soils: A review. *Frontiers in Environmental Science, 10*, 909415. https://doi.org/10.3389/fenvs.2022.909415

Miller, G., Suzuki, N., Ciftci-Yilmaz, S., & Mittler, R. (2010). Reactive oxygen species homeostasis and signalling during drought and salinity stresses. *Plant, Cell & Environment*, *33*(4), 453–467. https://doi.org/10.1111/j.1365-3040.2009.02041.x

Mishra, A., Bhardwaj, A., Bhatt, U., & Soni, V. (2026). Reactive oxygen species as integrators of stress signalling and developmental regulation in plants. *Discover Plants, 3*, 320. https://doi.org/10.1007/s44372-026-00800-z

Mishra, P., Asaari, M. S. M., Herrero-Langreo, A., Lohumi, S., Diezma, B., & Scheunders, P. (2017). Close range hyperspectral imaging of plants: A review. *Biosystems Engineering, 164*, 49–67. https://doi.org/10.1016/j.biosystemseng.2017.09.009

Mohamed, H. I., Khan, A., & Basit, A. (2024). CRISPR-Cas9 system mediated genome editing technology: An ultimate tool to enhance abiotic stress in crop plants. *Journal of Soil Science and Plant Nutrition, 24*, 1799–1822. https://doi.org/10.1007/s42729-024-01778-x

Munns, R. (2002). Comparative physiology of salt and water stress. *Plant, Cell & Environment*, *25*(2), 239–250. https://doi.org/10.1046/j.0016-8025.2001.00808.x

Munns, R. (2005). Genes and salt tolerance: Bringing them together. *New Phytologist*, *167*(3), 645–663. https://doi.org/10.1111/j.1469-8137.2005.01487.x

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

Munns, R., James, R. A., Xu, B., Athman, A., Conn, S. J., Jordans, C., … Gilliham, M. (2012). Wheat grain yield on saline soils is improved by an ancestral Na^+ transporter gene. *Nature Biotechnology*, *30*(4), 360–364.

Mutlu-Durak, H., Arikan, Y., & Kutman, B. Y. (2023). Willow (Salix babylonica) extracts can act as biostimulants for enhancing salinity tolerance of maize grown in soilless culture. *Plants, 12*(4), 856.

Nai, J., Ma, T., Liu, Y., & Zhou, Y. (2023). Identification of small RNAs associated with salt stress in chrysanthemums through high-throughput sequencing and bioinformatics analysis. *Genes, 14*(3), 561. https://doi.org/10.3390/genes14030561

Negrão, S., Schmöckel, S. M., & Tester, M. (2017). Evaluating physiological responses of plants to salinity stress. *Annals of Botany*, *119*(1), 1–11. https://doi.org/10.1093/aob/mcw191

Nicholls, R. J., Hoozemans, F. M. J., & Marchand, M. (2021). Increasing flood risk and wetland loss due to sea-level rise: Global impacts and adaptation challenges. *Nature Climate Change, 11*, 595–601.

Nie, W., He, Q., Guo, H., Zhang, W., Ma, L., Li, J., & Wen, D. (2024). Arbuscular mycorrhizal fungi: Boosting crop resilience to environmental stresses. *Microorganisms, 12*(12), 2448. https://doi.org/10.3390/microorganisms12122448

Omari, M. K., Lee, J., Faqeerzada, M. A., Joshi, R., Park, E., & Cho, B.-K. (2020). Digital image-based plant phenotyping: A review. *Korean Journal of Agricultural Science, 47*, 119–130.

Ondrasek, G., Rathod, S., Manohara, K. K., et al. (2022). Salt stress in plants and mitigation approaches. *Plants, 11*(6), 717.

Osei-Wusu, M. O., Adjei, R. R., Appiah, K. S., Ankamah-Yeboah, T., & Adusei-Fosu, K. (2025). Advanced breeding strategies for combating rice salinity stress in Ghana: A critical review and future perspective. *Scientific African, 29*, e02784. https://doi.org/10.1016/j.sciaf.2025.e02784

Qadir, M., Oster, J. D., Schubert, S., Noble, A. D., & Sahrawat, K. L. (2007). Phytoremediation of sodic and saline-sodic soils. *Advances in Agronomy, 96*, 197–247. https://doi.org/10.1016/S0065-2113(07)96006-X

Qadir, M., Tubeileh, A., Akhtar, J., Larbi, A., Minhas, P. S., & Khan, M. A. (2008). Productivity enhancement of salt-affected environments through crop diversification. *Land Degradation & Development, 19*(4), 429–453. https://doi.org/10.1002/ldr.853

Qin, T., Zhao, H., Cui, P., Albesher, N., & Xiong, L. (2017). A nucleus-localized long non-coding RNA enhances drought and salt stress tolerance. *Plant Physiology*, *175*(3), 1321–1336.

Qiu, C. W., Zhang, S., Gao, Z. F., Chen, Z. H., Wu, F., & colleagues. (2026). First *Tetraploa* genome and multi-omics analysis reveal key plant–microbe–soil interactions for salt tolerance and yield improvement of wheat. *Plant Biotechnology Journal*. https://doi.org/10.1111/pbi.70663

Rai, K. K. (2022). Integrating speed breeding with artificial intelligence for developing climate-smart crops. *Molecular Biology Reports, 49*(12), 11385–11402. https://doi.org/10.1007/s11033-022-07769-4

Rameeh, V., Cherati, A., & Abbaszadeh, F. (2012). Relationship between seed yield and shoot ions at vegetative and reproductive stages of rapeseed genotypes under saline environment. *International Journal of Plant Research, 2*(3), 61–64.

Ramya, B., & Vishnumolakala, S. S. S. (2025). Soil salinity management in irrigated zones: Challenges and solutions. *Agriculture & Food: E-Newsletter, 7*(7), 216–218.

Rasool, S., Hameed, A., Azooz, M. M., Rehman, M., Siddiqi, T. O., & Ahmad, P. (2013). Salt stress: Causes, types and responses of plants. In P. Ahmad, M. M. Azooz, & M. N. V. Prasad (Eds.), Ecophysiology and responses of plants under salt stress (pp. 1–24). New York, NY: Springer.

Raza, A., Salehi, H., Rahman, M. A., Zahid, Z., Madadkar Haghjou, M., Najafi-Kakavand, S., ... Zhuang, W. (2022). Plant hormones and neurotransmitter interactions mediate antioxidant defenses under induced oxidative stress in plants. *Frontiers in Plant Science, 13*, 961872. https://doi.org/10.3389/fpls.2022.961872

Ren, J., Ye, J., Yin, L., Li, G., Deng, X., & Wang, S. (2020). Exogenous melatonin improves salt tolerance by mitigating osmotic, ion, and oxidative stresses in maize seedlings. *Agronomy, 10*(5), 663.

Roy, S. J., Negrão, S., & Tester, M. (2014). Salt resistant crop plants. *Current Opinion in Biotechnology*, *26*, 115–124.

Roychowdhury, R., Das, S. P., Gupta, A., Parihar, P., Chandrasekhar, K., Sarker, U., Kumar, A., Ramrao, D. P., & Sudhakar, C. (2023). Multi-omics pipeline and omics-integration approach to decipher plant's abiotic stress tolerance responses. *Genes, 14*(6), 1281. doi:10.3390/genes14061281

Ryu, H., & Cho, Y.-G. (2015). Plant hormones in salt stress tolerance. *Journal of Plant Biology*, *58*(3), 147–155.

Saddiqe, Z., Javeria, S., Khalid, H., & Farooq, A. (2016). Effect of salt stress on growth and antioxidant enzymes in two cultivars of maize (Zea mays L.). *Pakistan Journal of Botany, 48*(4), 1361–1370.

Salt, D. E., Baxter, I., & Lahner, B. (2008). Ionomics and the study of the plant ionome. *Annual Review of Plant Biology, 59*, 709–733. https://doi.org/10.1146/annurev.arplant.59.032607.092942

Samanta, I., Ghosh, K., Saikia, R., Savita, Jha Maity, P., & Chowdhary, G. (2025). Arbuscular mycorrhizal fungi—a natural tool to impart abiotic stress tolerance in plants. *Plant Signaling & Behavior, 20*(1), 2525843. doi:10.1080/15592324.2025.2525843

Sarić, R., Nguyen, V. D., Burge, T., Berkowitz, O., Trtílek, M., Whelan, J., Lewsey, M. G., & Čustović, E. (2022). Applications of hyperspectral imaging in plant phenotyping. *Trends in Plant Science, 27*(3), 301–315. doi:10.1016/j.tplants.2021.12.003

Seleiman, M. F., Ahmad, A., & Alshahrani, T. S. (2023). Integrative effects of zinc nanoparticle and PGRs to mitigate salt stress in maize. *Agronomy, 13*(6), 1655.

Sen, S., Prakash, A., Van Staden, J., & Kumar, V. (2024). Epigenetic control of plant regeneration: Unraveling the role of histone methylation. *Plant Cell Reports*. Advance online publication.

Seyfferth, C., Renema, J., Wendrich, J. R., Eekhout, T., Seurinck, R., Vandamme, N., … De Rybel, B. (2021). Advances and opportunities in single-cell transcriptomics for plant research. *Annual Review of Plant Biology*, *72*, 847–866.

Shilpa, Thakur, R., & Prasad, P. (2024). *Epigenetic regulation of abiotic stress responses in plants*. *Biochimica et Biophysica Acta (BBA) - Gene Regulatory Mechanisms*. Advance online publication. https://doi.org/10.1016/j.bbagen.2024.130661

Shrivastava, P., & Kumar, R. (2015). Soil salinity: A serious environmental issue and plant growth promoting bacteria as one of the tools for its alleviation. *Saudi Journal of Biological Sciences, 22*(2), 123–131.

Shu, H., Jiang, Y., Ma, Q., Yu, Q., & Wang, Q. (2026). Research progress on saline soil improvement: Mechanisms, influencing factors, and technologies. *Journal of Cold Regions Engineering, 41*(1). https://doi.org/10.1061/JCRGEI.CRENG-1278

Singh, A. K., Ganapathysubramanian, B., Sarkar, S., & Singh, A. (2018). Deep learning for plant stress phenotyping: Trends and future perspectives. *Trends in Plant Science, 23*(10), 883–898. https://doi.org/10.1016/j.tplants.2018.07.004

Singh, A., Mazahar, S., Chapadgaonkar, S. S., Giri, P., & Shourie, A. (2023). Phyto-microbiome to mitigate abiotic stress in crop plants. *Frontiers in Microbiology, 14*, 1210890. https://doi.org/10.3389/fmicb.2023.1210890

Srivastava, Y., Saini, N., Nishu, Yadav, S., Tripathi, S., Kumar, A., Yadav, N., Saini, M., & Sangwan, N. S. (2026). Responses and adaptations of plants to abiotic stress: Transcriptional regulation of secondary metabolic pathways, metabolomics, and nanobiological approaches. *Frontiers in Genetics, 17*, Article 1762633. https://doi.org/10.3389/fgene.2026.1762633

Su, Q., Kambale, R. D., Tzeng, J.-H., Amy, G. L., Ladner, D. A., & Karthikeyan, R. (2025). The growing trend of saltwater intrusion and its impact on coastal agriculture: Challenges and opportunities. *Science of the Total Environment, 966*, 178701. https://doi.org/10.1016/j.scitotenv.2025.178701

Sun, X., Wu, F., Ma, Z., Liang, G., Chen, S., Hu, X., Fan, S., & Zhao, Y. (2026). Systematic synthesis of CRISPR/Cas applications for enhancing salt tolerance in crops: A decade of progress and challenges. *BMC Plant Biology, 26*, Article 506. https://doi.org/10.1186/s12870-026-08295-2

Takagi, H., Tamiru, M., Abe, A., Yoshida, K., Uemura, A., Yaegashi, H., … Terauchi, R. (2015). MutMap accelerates breeding of a salt-tolerant rice cultivar. *Nature Biotechnology*, *33*(4), 445–449. https://doi.org/10.1038/nbt.3188

Tang, H., Niu, L., Wei, J., Chen, X., & Chen, Y. (2019). Phosphorus limitation improved salt tolerance in maize through tissue mass density increase, osmolytes accumulation, and Na^+ uptake inhibition. *Frontiers in Plant Science, 10*, 856.

Tardieu, F., Cabrera-Bosquet, L., Pridmore, T., & Bennett, M. (2017). Plant phenomics, from sensors to knowledge. *Current Biology*, *27*(15), R770–R783.

Tarolli, P., Luo, J., Park, E., Barcaccia, G., & Masin, R. (2024). Soil salinization in agriculture: Mitigation and adaptation strategies combining nature-based solutions and bioengineering. *iScience, 27*(2), 108830. doi:10.1016/j.isci.2024.108830

Tran, M. T., Doan, D. T. H., Kim, J., Song, Y. J., Sung, Y. W., Das, S., … Kim, J.-Y. (2021). CRISPR/Cas9-based precise excision of SlHyPRP1 domain(s) to obtain salt stress-tolerant tomato. *Plant Cell Reports*, *40*(6), 999–1011.

Trevisan, S., Manoli, A., & Quaggiotti, S. (2019). A novel biostimulant, belonging to protein hydrolysates, mitigates abiotic stress effects on maize seedlings grown in hydroponics. *Agronomy, 9*(1), 28.

Trivedi, P., Leach, J. E., Tringe, S. G., Sa, T., & Singh, B. K. (2020). Plant–microbiome interactions: From community assembly to plant health. *Nature Reviews Microbiology, 18*(11), 607–621. https://doi.org/10.1038/s41579-020-0412-1

van Zelm, E., Zhang, Y., & Testerink, C. (2020). Salt tolerance mechanisms of plants. *Annual Review of Plant Biology*, *71*, 403–433. https://doi.org/10.1146/annurev-arplant-050718-100005

Vives-Peris, V., de Ollas, C., Gómez-Cadenas, A., & Pérez-Clemente, R. M. (2020). Root exudates: From plant to rhizosphere and beyond. *Plant Cell Reports*, *39*(1), 3–17.

Wahab, A., Muhammad, M., Munir, A., Abdi, G., Zaman, W., Ayaz, A., Khizar, C., & Reddy, S. P. P. (2023). Role of arbuscular mycorrhizal fungi in regulating growth, enhancing productivity, and potentially influencing ecosystems under abiotic and biotic stresses. *Plants, 12*(17), 3102. doi:10.3390/plants12173102

Waheed, A., Zhuo, L., Wang, M., Hailiang, X., Tong, Z., Wang, C., & Aili, A. (2024). Integrative mechanisms of plant salt tolerance: Biological pathways, phytohormonal regulation, and technological innovations. *Plant Stress, 14*, 100652. https://doi.org/10.1016/j.stress.2024.100652

Walia, H., Wilson, C., Zeng, L., Ismail, A. M., Condamine, P., & Close, T. J. (2005). Comparative transcriptional profiling of two contrasting rice genotypes under salinity stress during the vegetative growth stage. *Plant Physiology*, *139*(2), 822–835.

Wang, W., Rong, Y., Su, H., Xu, H., Zhang, C., Wang, C., & Huo, Z. (2026). Soil salinity-constrained evolution of cropping structure under climate change and water-saving strategies in an arid irrigation district. *Agricultural Water Management, 329*, 110391. doi:10.1016/j.agwat.2026.110391

Yang, Z., Dong, T., Dai, X., Wei, Y., Fang, Y., Zhang, L., Zhu, M., Nawaz, G., Cao, Q., & Xu, T. (2022). Comparative analysis of salt responsive microRNAs in two sweetpotato *[Ipomoea batatas* (L.) Lam.] cultivars with different salt stress resistance. *Frontiers in Plant Science, 13*, 879819. https://doi.org/10.3389/fpls.2022.879819

Yu, Z., Duan, X., Luo, L., Dai, S., Ding, Z., & Xia, G. (2020). How plant hormones mediate salt stress responses. *Trends in Plant Science*, *25*(11), 1117–1130.

Yuan, J., Cao, H., Qin, W., Yang, S., Zhang, D., Zhu, L., Song, H., & Zhang, Q. (2025). Genomic and modern biotechnological strategies for enhancing salt tolerance in crops. *New Crops, 2*, 100057. https://doi.org/10.1016/j.ncrops.2024.100057

Yuan, J., Cao, H., Qin, W., Yang, S., Zhang, D., Zhu, L., Song, H., & Zhang, Q. (2025). Genomic and modern biotechnological strategies for enhancing salt tolerance in crops. *New Crops, 2*, 100057. doi:10.1016/j.ncrops.2024.100057

Yung, W.-S., Li, M.-W., Sze, C.-C., Wang, Q., & Lam, H.-M. (2021). Histone modifications and chromatin remodelling in plants in response to salt stress. *Physiologia Plantarum, 173*(4), 1495–1513. https://doi.org/10.1111/ppl.13467

Yusuf, A., Li, M., Zhang, S.-Y., Odedishemi-Ajibade, F., Luo, R.-F., Wu, Y.-X., Zhang, T.-T., Ugya, A. Y., Zhang, Y., & Duan, S. (2025). Harnessing plant–microbe interactions: Strategies for enhancing resilience and nutrient acquisition for sustainable agriculture. Frontiers in Plant Science, 16, 1503730. doi:10.3389/fpls.2025.1503730

Zahoor, M., Khaliq, R., Zafar, Z. U., & Athar, H. R. (2011). Degree of salt tolerance in some newly developed maize (*Zea mays* L.) varieties. *Iranian Journal of Plant Physiology, 1*(4), 223–232.

Zhang, A., Liu, Y., Wang, F., Li, T., Chen, Z., Kong, D., … Luo, L. (2019). Enhanced rice salinity tolerance via CRISPR/Cas9-targeted mutagenesis of the OsRR22 gene. *Molecular Breeding*, *39*(3), 47.

Zhang, D., Zhang, D., Zhang, Y., Li, G., Sun, D., Zhou, B., & Li, J. (2024a). Insights into the epigenetic basis of plant salt tolerance. *International Journal of Molecular Sciences, 25*(21), 11780. https://doi.org/10.3390/ijms252111780

Zhang, H., Kim, M.-S., Sun, Y., Dowd, S. E., Shi, H., & Paré, P. W. (2008). Soil bacteria confer plant salt tolerance by tissue-specific regulation of the sodium transporter HKT1. *Molecular Plant-Microbe Interactions*, *21*(6), 737–744.

Zhang, Y., Gu, S., Du, J., Huang, G., Shi, J., Lu, X., Wang, J., Yang, W., Guo, X., & Zhao, C. (2024b). Plant microphenotype: From innovative imaging to computational analysis. *Plant Biotechnology Journal, 22*(4), 802–818. https://doi.org/10.1111/pbi.14244

Zhang, Y., Liu, G. M., Wang, Z. F., Zhang, A. M., & Yang, Y. L. (2023). Exogenous calcium-alleviating effect on sodium salt-induced phytotoxicity associated with changes in photosynthetic characteristics of wheat seedlings. *Photosynthetica, 62*(1), 16–26. https://doi.org/10.32615/ps.2023.039

Zhao, B., Ge, L., Liang, R., Li, W., Ruan, K., Lin, H., … Jin, Y. (2009). Members of miR-169 family are induced by high salinity and transiently inhibit the NF-YA transcription factors. *BMC Molecular Biology*, *10*, 29. https://doi.org/10.1186/1471-2199-10-29

Zhao, C., Zhang, H., Song, C., Zhu, J.-K., & Shabala, S. (2020). Mechanisms of plant responses and adaptation to soil salinity. *The Innovation*, *1*(1), 100017. https://doi.org/10.1016/j.xinn.2020.100017

Zhao, Q., Xin, M., Ai, P., & Ma, Y. (2025). Effects of continuous saline water irrigation on soil salinization characteristics and dryland jujube tree. *Agronomy, 15*(8), 1898. https://doi.org/10.3390/agronomy15081898

Zhu, C., Ding, Y., & Liu, H. (2011). MiR398 and plant stress responses. *Physiologia Plantarum*, *143*(1), 1–9.

Zhu, F., Sun, Y., Jadhav, S. S., Cheng, Y., Alseekh, S., & Fernie, A. R. (2023). The plant metabolic changes and the physiological and signaling functions in the responses to abiotic stress. In *Plant abiotic stress tolerance: Methods and protocols* (pp. 129–150). Humana Press. https://doi.org/10.1007/978-1-0716-3044-0_7

Zhu, Y., & Gong, H. (2014). Beneficial effects of silicon on salt and drought tolerance in plants. *Agronomy for Sustainable Development*, *34*(2), 455–472.

Zia, A., Munsif, F., Jamal, A., Mihoub, A., Saeed, M. F., Fawad, M., Ahmad, I., & Ali, A. (2022). Morpho-physiological attributes of different maize (*Zea mays* L.) genotypes under varying salt stress conditions. *Gesunde Pflanzen, 74*(5), 619–633.

Copyright: © 2026 by the author(s). This open access article is distributed under a Creative Commons Attribution License (CC BY 4.0), https://creativecommons.org/licenses/by/4.0/