



Salinity and sodicity tolerance in rice: Physiological, morpho-anatomical, molecular and hormonal mechanisms with special reference to traditional landraces

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Abstract

Soil salinity and sodicity are critical abiotic stresses that severely affect global rice production by causing osmotic stress, ionic toxicity, oxidative damage and nutrient imbalance, collectively impairing plant growth and yield. This review highlights the physiological, morpho-anatomical, molecular and hormonal mechanisms underlying salt tolerance, with particular emphasis on traditional landraces as reservoirs of adaptive genetic diversity. Tolerant mechanisms include osmotic adjustment via compatible osmolytes, antioxidant defence systems, ion homeostasis through salt overly sensitive (SOS), Na⁺/H⁺ exchanger (NHX) and high-affinity K⁺ transporter (HKT), root apoplastic barriers by lignin and suberin deposition and aerenchyma-mediated sodium (Na) sequestration. The contributions of stress-responsive genes, transcription factors and quantitative trait loci (QTLs), with particular emphasis on the Saltol QTL, in governing salt tolerance are comprehensively discussed. The role of key hormonal regulators, including abscisic acid (ABA), auxin, gibberellins (GA), cytokinins (CK), ethylene, melatonin, jasmonic acid (JA) and salicylic acid in mediating stress adaptation is also elaborated. Additionally, the efficacy of exogenous ameliorants such as silicon, biochar and microbial biostimulants in alleviating salt-induced damage is evaluated. The remarkable adaptive potential of traditional landraces and wild rice species is highlighted as a crucial genetic resource for breeding stress-resilient cultivars, offering a comprehensive framework for advancing salt tolerance research and ensuring food security in increasingly salt-affected agricultural environments.

Keywords: mitigation; rice landraces; salt stress; tolerant mechanisms

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1. Introduction

Rice is a staple food crop that serves as the primary food source for more than 50 % of the world's population and therefore plays a central role in global food security (1, 2). Rice can be grown in a wide range of environmental conditions, from tropical and subtropical to temperate zones (2). However, crop production is affected by diverse biotic and abiotic stresses. Among the abiotic stresses, soil salinity and sodicity have emerged as major constraints to rice production, limiting soil fertility and crop growth (3). Saline soils are defined by an electrical conductivity greater than 4 dS m⁻¹, an exchangeable sodium (Na) percentage less than 15 and a pH less than 8.5. In contrast, sodic soils have an electrical conductivity less than 4 dS m⁻¹, an exchangeable sodium percentage greater than 15 and a pH between 8.5 and 10 (4). Salinity is caused by the accumulation of sodium chloride (NaCl), whereas sodium carbonate (Na₂CO₃)

and sodium bicarbonate (NaHCO₃) are responsible for sodicity (Fig. 1) (5, 6).

Salt stress is a major threat to agricultural productivity, as it adversely affects plant growth and development by inducing osmotic stress, ion toxicity and oxidative stress, thereby disrupting physiological and biochemical processes (7). Although salt stress affects all stages of the rice crop, the seedling stage and the reproductive stage are the most sensitive stages (8). Regions of saline soil are expected to increase because of limited rainfall, high surface evaporation, weathering of rocks and inefficient farming practices (9). Additionally, coastal areas are becoming salinity-prone due to seawater incursion and rising sea levels (10). On the other hand, the increasing world population necessitates an increase in rice production to meet higher demand and to ensure food security (11). To address this challenge, developing rice varieties with improved salt tolerance is essential to minimise the detrimental effects of salinity and sodicity on rice yield (12). Screening and

development of salt-tolerant varieties will reduce the effect of salt stress on rice productivity and safeguard food security (13). This article focuses on understanding the physiological, biochemical and morphological mechanisms underlying salt (salinity and sodicity) tolerance in rice, with special reference to traditional rice landraces as reservoirs of adaptive genetic diversity, to facilitate the identification and development of resilient genotypes capable of sustaining productivity under saline and sodic conditions.

2. Materials and Methods

Information sources and search strategy

A systematic literature search was conducted to compile relevant studies on salinity and sodicity tolerance in rice. The search was performed between November 2025 and January 2026 using major scientific databases, including Scopus (<https://www.scopus.com/>), Web of Science, PubMed (<https://pubmed.ncbi.nlm.nih.gov/>) and Google Scholar (<http://scholar.google.com>), to ensure comprehensive coverage of available literature. Various combinations of keywords and Boolean operators related to salt stress, salinity, sodicity, rice and tolerance were used to retrieve relevant research articles. The complete keyword combinations and search strings used for the literature search are provided in Table 1.

Inclusion and exclusion criteria

Studies were selected based on predefined criteria to ensure relevance and scientific quality. Only peer-

reviewed journal articles focusing on rice (*Oryza sativa* L.) under salinity and/or sodicity stress were included, particularly those addressing physiological, biochemical, molecular, anatomical and hormonal mechanisms such as sodium (Na^+)/potassium (K^+) homeostasis, ion transport, osmotic adjustment, antioxidant defence and gene regulation. Studies on crops other than rice, articles not directly related to salinity or sodicity stress, non-peer-reviewed sources, duplicate records and studies lacking defined salinity or sodicity stress conditions, appropriate controls or measurable responses related to key tolerance mechanisms, including ion homeostasis, osmotic adjustment, antioxidant activity, photosynthetic stability, root adaptation, molecular and hormonal regulation or full-text availability were excluded.

Relevancy, duplicates and quality assessment

The PRISMA flow diagram was used to represent the study selection process (Fig. 2). Initially, relevant publications on salinity and sodicity tolerance in rice were identified from databases such as Scopus, Web of Science and Google Scholar. During the screening phase, duplicates and non-relevant studies were removed, retaining articles focused on physiological, biochemical, morpho-anatomical, molecular and hormonal mechanisms of salt stress. Full-text articles were further assessed based on title, abstract and keyword relevance. Finally, only original research studies addressing salt tolerance mechanisms and mitigation strategies in rice were included after eligibility assessment, ensuring the quality and relevance of the selected literature.

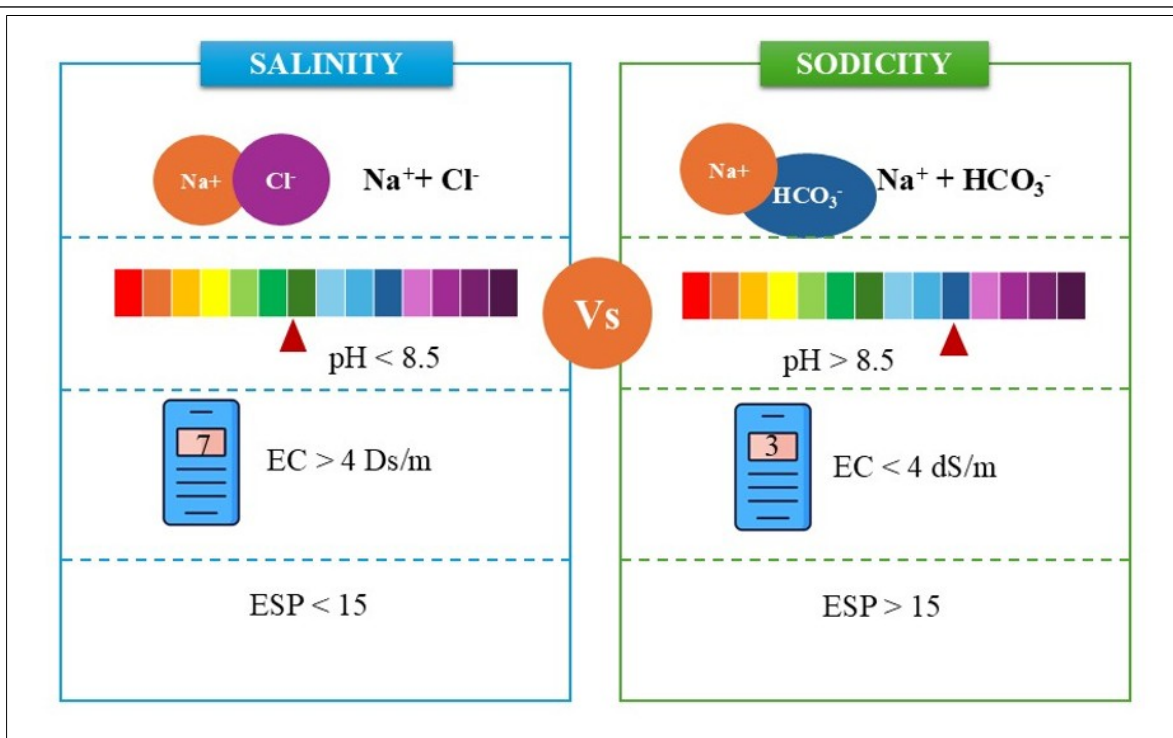
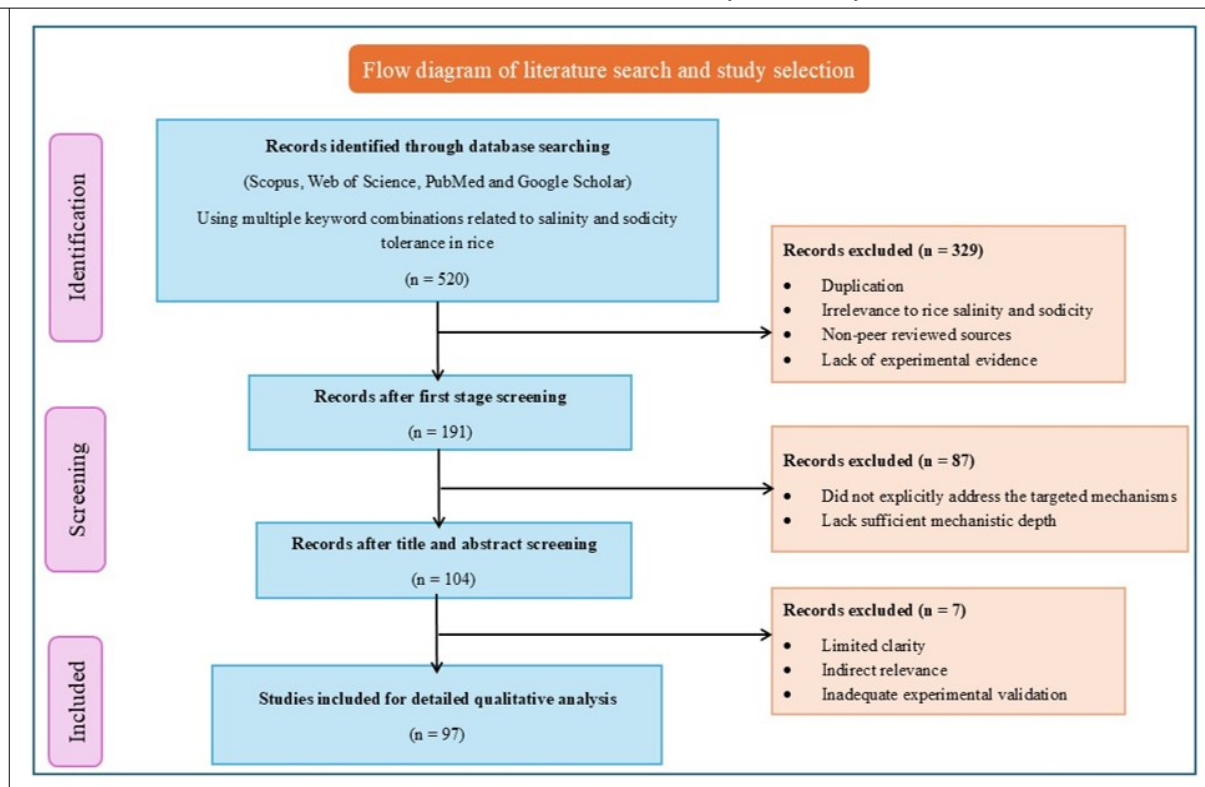


Fig. 1. Characteristics of saline and sodic soils with their dominant ions.

Table 1. Keywords used as search strings in Scopus, Web of Science, PubMed and Google Scholar

Sl. No	Search strings
1	"Rice" and "Salinity stress" and "Crop productivity"
2	"Rice" and "Sodicity stress" and "Physiological responses"
3	"Oryza sativa" and "Salt stress" and "Molecular mechanisms"
4	"Rice" and "Na ⁺ /K ⁺ homeostasis" and "Ion transporters"
5	"Rice" and "SOS pathway" and "Salt stress"
6	"Rice" and "Reactive oxygen species" and "Antioxidant defense"
7	"Gene regulation" and "Salt stress"
8	"Rice" and "Phytohormones" and "Salinity stress"
9	"Rice" and "Root anatomical adaptations" and "Salinity tolerance"
10	"Traditional landraces" and "saltinity and sodicity tolerance"

**Fig. 2.** The PRISMA flow diagram representing the number of studies taken for systemic review.

3. Results and Discussion

Publication analysis from search strings

A systematic literature search was conducted using multiple keyword combinations related to salinity and sodicity tolerance in rice across major databases, including Scopus, Web of Science, PubMed and Google Scholar, as described in the methodology. The search strategy covered multiple dimensions of salt stress biology, including physiological, biochemical, morpho-anatomical, molecular and hormonal mechanisms, along with specific terms such as ion homeostasis, salt overly sensitive (SOS) signalling, antioxidant defence, gene regulation, phytohormones and traditional landraces. The initial search yielded a total of 520 publications (n = 520). During the first stage of screening, 329 records were

excluded (n = 329) due to duplication, irrelevance to rice salinity and sodicity, non-peer-reviewed sources and lack of experimental evidence, leaving 191 studies (n = 191) for further evaluation. In the second stage, title and abstract screening resulted in the exclusion of 87 articles (n = 87) that did not explicitly address the targeted mechanisms or lacked sufficient mechanistic depth, with 104 studies (n = 104) progressing to full-text assessment. Subsequently, full-text evaluation led to the exclusion of an additional 7 studies (n = 7) due to limited clarity, indirect relevance or inadequate experimental validation. Finally, 97 studies (n = 97) were included for detailed qualitative synthesis, as they satisfied all inclusion criteria and contributed directly to understanding the physiological, molecular and adaptive mechanisms governing salinity and sodicity tolerance in rice.

Effect of salinity and sodicity

Salinity is one of the important factors affecting the growth of rice plants, as it drastically changes the morphology and physiology (14). Salt stress negatively impacts the growth and yield of rice, but the severity of damage varies with the stage of the crop, salt concentration, duration of stress and the variety's tolerance. It also differs among genotypes (13). Salt stress manifests its effect progressively, starting from osmotic stress, followed by ionic toxicity and nutrient imbalance, which ultimately affect plant morphology and lower the reproductive success (Fig. 3) (15). The visual symptoms under salt stress include leaf chlorosis, leaf rolling and senescence, which eventually reduce the yield by affecting photosynthetic activity (16).

Osmotic stress

The reduction in water uptake under salt stress is due to the accumulation of salts, which lowers the osmotic potential near the root zone (17). Osmotic stress caused by excess solutes in the rhizosphere reduces water uptake by the plant, affecting cell expansion and turgidity (18). Osmotic stress also disrupts nutrient uptake, limits photosynthesis and enzyme activity because water is a critical medium for metabolic reactions. Especially under sodicity, the increased Na^+ level in the soil degrades the soil structure and permeability, further complicating the water uptake (19). Excess accumulation of Na^+ in leaves causes osmotic stress affecting several metabolic processes, leading to acceleration of leaf senescence and resulting in a significant reduction of biomass (20). When rice plants are exposed to high salinity, they produce an excess of reactive oxygen species (ROS) such as superoxide

(O_2^-), hydrogen peroxide (H_2O_2) and hydroxyl radicals ($\text{OH}^\cdot$). Although ROS are normal byproducts of cellular metabolism, their levels rise sharply under salt stress. This overproduction of ROS surpasses the plant's antioxidant defences and leads to oxidative stress. These highly reactive molecules attack cellular components such as membrane lipids, which weakens membrane integrity and increases ion leakage. Proteins suffer structural changes and enzyme inactivation, disrupting the majority of the biochemical processes. It also damages the nucleic acids (DNA/RNA), leading to genetic instability and impaired cellular functions (21). This disruption also impairs key physiological processes like photosynthesis and respiration, ultimately reducing plant growth, biomass and grain yield under saline conditions.

Ion toxicity

The harmful effects of salinity are mainly due to increased accumulation of Na^+ ions inside the plant, which impairs the ionic homeostasis. Ionic homeostasis is important as it controls various physiological functions such as osmoregulation, development of chloroplasts, stomatal conductance, maintaining pH, phloem translocation and membrane stability (22). Ionic imbalance is due to elevated uptake of toxic ions such as Na^+ and Cl^- . Increased Na^+ concentration will ultimately limit the K^+ uptake, affects the ion homeostasis, causing nutrient imbalance. Under salt stress, there would be competition in the uptake of Na^+ and K^+ as both are monovalent cations. This ultimately results in an increased Na^+/K^+ ratio in the plant tissues. Further, there will be leakage of K^+ ions from the plant due to depolarisation of the plasma membrane by increased Na^+ accumulation (23).

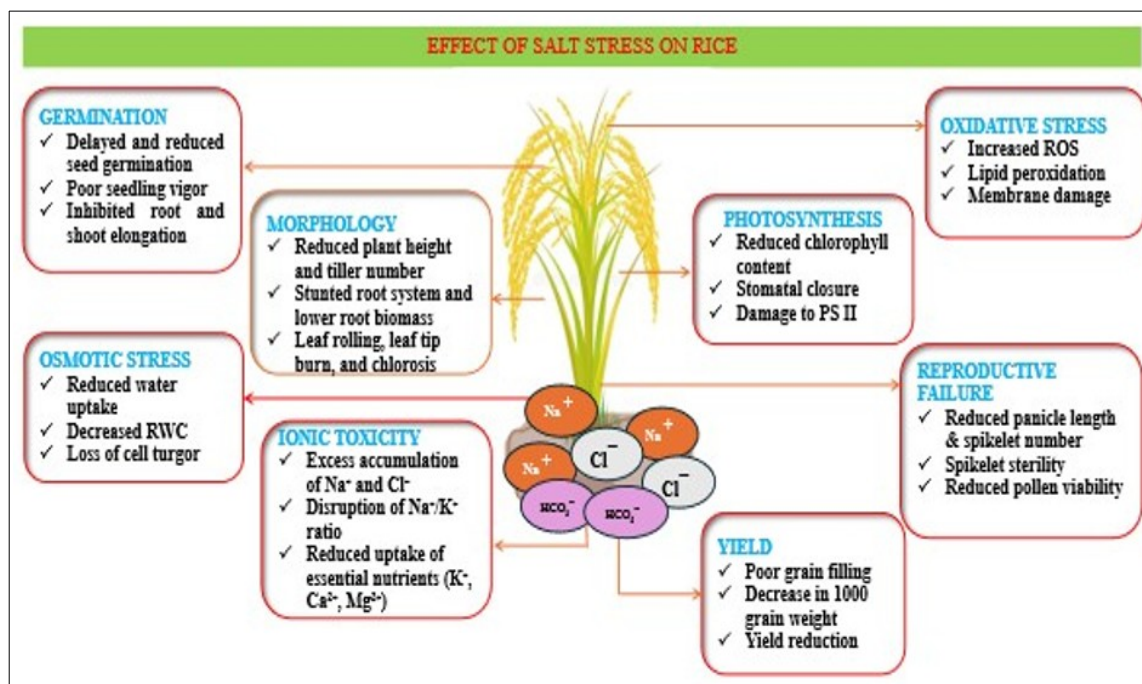


Fig. 3. Effects on the seedling, morphological, biochemical and yield parameters of rice under salt stress.

Effect on germination, seedling and growth parameters

High salt concentration increases the osmotic pressure of the solution, hindering the uptake of water during germination. Salt stress disrupts the plasma membrane, leading to increased permeability of the membrane; as a result, germination is reduced (13). Saline conditions hinder the cell cycle, resulting in reduced growth of the plant's plumule and radicle. Salt stress during the entire seedling phase significantly decreases the germination index and vigour of seedlings (24). Salinity decreases the growth of the shoot and root significantly in the rice cultivars. It also causes a reduction in plant height and the number of tillers per hill (7). It was also evident from the experiments that there is a significant reduction in shoot and root biomass under stress in comparison with the control (25). The major reason for growth inhibition under salt stress is due to the quick build-up of Na^+ concentration that interferes with several metabolic processes that normally facilitate growth and development (26).

Effect on gas exchange parameters and chlorophyll content

Photosynthesis plays a major role in converting the solar energy into chemical energy to be utilised by the plants, which is drastically reduced under salt stress (27). Salt stress severely impairs the chloroplast structure, which intensifies degradation of chlorophyll pigment, resulting in decreased absorption of light and photosynthetic efficiency (28). It also causes a considerable reduction in chlorophyll synthesis. Salt stress inhibits photosynthesis to a considerable extent, which ultimately limits the resources for cell division to take place (14). Salinity and sodicity create osmotic and ionic stress, resulting in partial or complete stomatal closure to limit water loss. This stomatal limitation impairs stomatal conductance, transpiration rate and restricts internal CO_2 diffusion. Thus, the reduced internal CO_2 concentration causes a pronounced reduction in photosynthetic rate (27). Additionally, photosynthesis is also reduced by stress as it disrupts the enzyme activity (29), restricting the electron flow (30), stimulating the ROS production (31) and impairing chloroplasts (32). Salt-affected plants constrain the area of the photosynthetic carbon pool and create a scenario in which the plant becomes vulnerable to quenching excess light (33).

Effect on biochemical parameters: Proline, malondialdehyde and relative water content

A considerable reduction in intracellular proline with increasing salt concentration has been reported in rice, potentially due to reduced biosynthesis and enhanced catabolism of proline (7). Reduced P5CS (Δ^1 -pyrroline-5-carboxylate synthetase) activity and enhanced proline dehydrogenase (PDH) activity may contribute to decreased endogenous proline accumulation under severe stress conditions. Proline accumulation is not universal and may vary with genotype, tissue developmental stage and stress

intensity or duration. Proline metabolism may differ between tolerant and susceptible genotypes, with tolerant genotypes potentially maintaining a better balance between synthesis and degradation to support osmotic adjustment and cellular protection, whereas susceptible genotypes may exhibit insufficient accumulation or enhanced depletion under stress (34). Under salinity and sodicity, plants experience oxidative stress due to excess ROS. These ROS attack membrane lipids in a process called lipid peroxidation. During this process, malondialdehyde (MDA) is formed as a by-product and higher MDA levels serve as an indicator of cellular damage. When the redox system (balance between antioxidants and ROS) becomes disturbed, the plant's cell membranes become damaged, affecting normal growth and function (18). In saline soils, the accumulation of salt reduces the soil water potential, limiting the plant's ability to absorb water from the soil. This will lead to a decline in leaf relative water content (RWC), despite sufficient moisture being present in the soil (35).

Effect on nutrient transport and mobilisation - nutrient dynamics

Elevated Na^+ can inhibit K^+ uptake and disrupt K^+ homeostasis, which are essential for plant growth and development (24). The concentration and solubility of nutrients are altered by salinity. Under salt stress, there will be a reduction in the solubility of iron (Fe^{3+}), which results in chlorosis. There is also a considerable decline in the uptake of zinc (Zn^{2+}) (25). Under sodic conditions, the alkaline pH has a strong influence on the solubility and uptake of nutrients by the rice roots. Higher pH causes precipitation of phosphorus in the form of calcium phosphates, limiting the solubility and hence the availability of phosphorus to the rice roots. Alkalinity also leads to chemical infertility, a case in which nutrients are present but physiologically unavailable (3). Excess accumulation of Na^+ disturbs the $\text{Na}^+/\text{Ca}^{2+}$ balance, limiting calcium uptake and leading to nutrient deficiency in plants. It further reduces the movement and availability of essential nutrients such as nitrate, sulphate, calcium (Ca), magnesium (Mg), silica (Si), boron (B) and particularly K^+ , whose absorption is suppressed by Na. Further, higher salt concentration also leads to cadmium toxicity in rice (15). As K is vital for enzyme function, cell turgor maintenance, photosynthesis and carbohydrate transport, its decline negatively affects plant growth and metabolism. It also leads to reduced uptake of N, which significantly impairs the normal growth and development (36).

Effect on yield and grain quality

Salt stress (salinity and sodicity) results in a considerable reduction in the number of spikelets per panicle. There was a reduction in floret fertility with increasing sodicity. A significant decrease in thousand-seed weight is also observed under salt stress (37). Genotypic factors such as ecotype, genotype and tolerance type were shown to significantly influence



yield and its components under salinity stress (38). The yield loss of salt-sensitive cultivars is significantly higher because they have a simultaneous negative effect on all the yield components. It was also reported that there is a reduction in milling quality and increased chalkiness of susceptible varieties under saline conditions. It is evident from several studies that the amylopectin content and protein content increase and starch content decreases under salt stress. This will eventually reduce the cooking and eating quality of rice grains (39).

Molecular mechanism of salt tolerance in rice

Rice responds to salt stress through numerous coordinated mechanisms. Rice maintains ion homeostasis under salt stress by regulating key ion transporters, including OsHKT1;1, OsHKT1;5, OsSOS1 and OsNHX1-OSNHX5, which mediate Na^+ exclusion, redistribution and vacuolar sequestration, together with K^+ transporters such as OsHAK21 to maintain Na^+/K^+ balance. It also maintains the osmotic balance by facilitating the accumulation of compatible osmolytes like proline and glycine betaine. Further, rice plants enhance antioxidant defence through increased activity of antioxidant enzymes along with non-enzymatic antioxidants (40). The interplay of these mechanisms allows rice to perceive, respond and adapt to saline environments, ensuring survival and functional integrity

under stress. Understanding these integrated responses provides a comprehensive framework for studying the physiological and molecular basis of salt tolerance in rice (Fig. 4).

Osmotic adjustment

To counter the effects of osmotic stress, rice plants accumulate several osmolytes. These osmolytes play a key role in maintaining osmotic balance and protecting the cell organelles from harmful effects of salt stress (40). This osmotic adjustment maintains an osmotic equilibrium inside the vacuole. These are soluble and low molecular weight osmolytes facilitating intracellular osmotic adjustment and ROS scavenging. They also play a crucial role in stabilising the membrane structure without affecting the plant metabolism (41). Cellular osmotic adjustment facilitates the cells to maintain internal salt concentrations, thus regulating the water uptake under stress conditions, resulting in reduced water loss (25). Tolerant genotypes usually exhibit higher osmotic potential than susceptible genotypes. It is due to the accumulation of compatible osmolytes like proline, total sugar and K^+ ion content (40). The tolerant capacity of the plant to survive under saline conditions depends on the degree of osmotic adjustment. In rice, trehalose and other carbohydrates play a greater role than proline and other osmoprotectants (36).

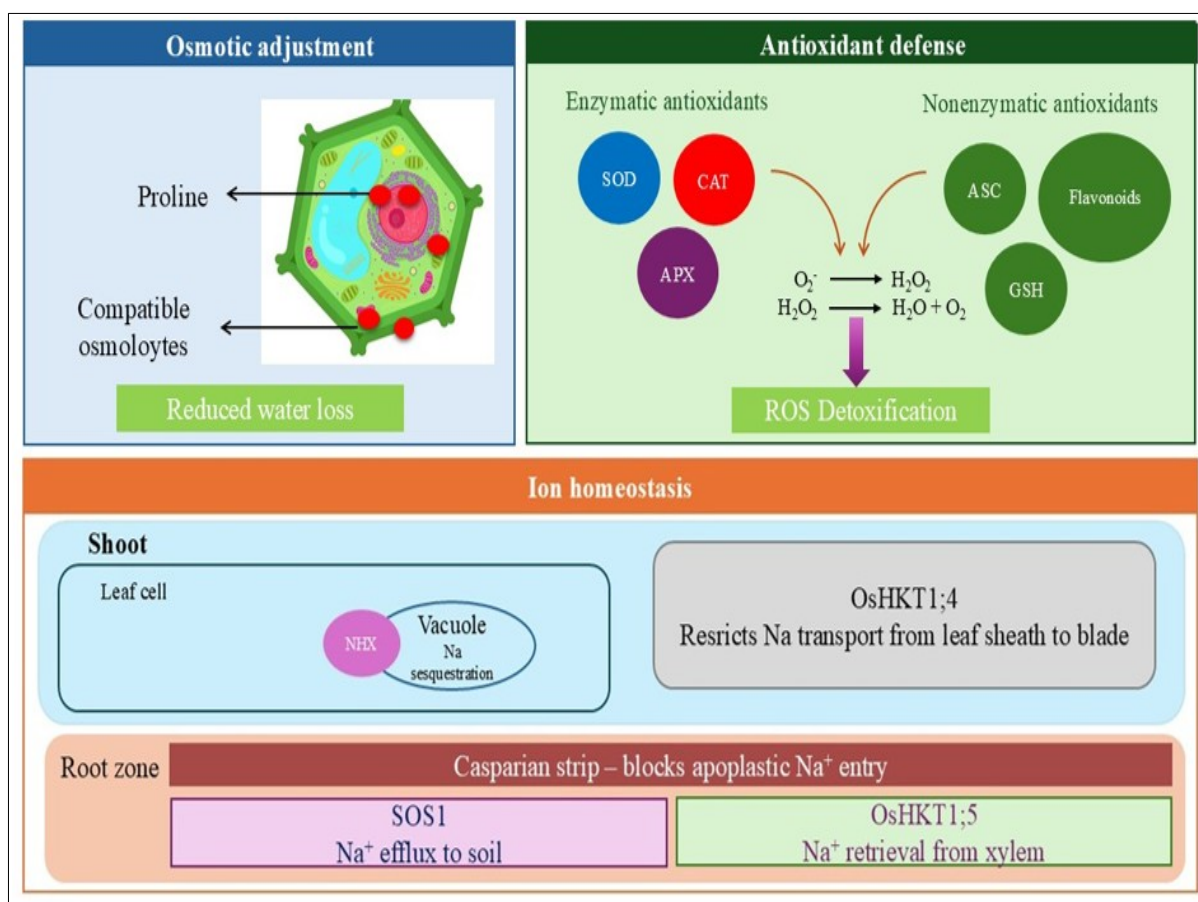


Fig. 4. Physiological and molecular mechanisms of salt tolerance in rice.

Antioxidant defence

Plants overcome the effect of ROS generated as a result of oxidative stress by employing a two-stage system of defence to maintain redox homeostasis. One is through enzymatic antioxidants like superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), glutathione peroxidase (GPX) and by non-enzymatic antioxidants such as ascorbate (ASC), glutathione (GSH), tocopherols, phenolics and flavonoids (42). The most common ROS produced under salt stress include H_2O_2 , singlet oxygen, hydroxyl radicals and superoxide. These harmful molecules are mostly neutralised by antioxidant enzymes, starting with SOD, which enables the conversion of superoxide radicals into oxygen and H_2O_2 . The resulting H_2O_2 is further detoxified by peroxidase (POX) and CAT, helping protect plant cells from oxidative damage (43).

Ion homeostasis

Plants evolved several ion exclusion and sequestration mechanisms to counter the detrimental effects driven by salt stress and to eliminate the buildup of toxicity (44). The magnitude of salt tolerance of tolerant genotypes is highly associated with the root system architecture, as they have the potential to elongate roots for nutrient uptake even in saline conditions (20). Several researchers reported that the selectivity of root to Na-K, along with the restriction of Na^+ transport to leaves, plays a key role in determining the tolerance (40). Salt Overly Sensitive 1 (SOS1), a membrane Na^+/H^+ exchanger, is crucial for facilitating salt tolerance in rice. It is involved in the efflux of Na^+ from the root and in xylem loading of Na^+ . SOS1 is also important for K^+ retention as it has a positive correlation with salt tolerance and maintains a low Na^+/K^+ ratio (24). Members of the Na/proton antiporter (NHX) family are involved in maintaining Na^+ homeostasis in plants and play a key role in imparting salinity tolerance. These antiporters ensure salt tolerance by sequestering Na^+ , thereby reducing the accumulation of toxic ions inside the cytoplasm. Mutations studied confirmed that the loss-of-function mutants of SOS1 have shown increased sensitivity under saline and alkaline conditions (45). In rice, HKT transporters contribute to salt tolerance by regulating Na^+ distribution within the plant. OsHKT 1; 5 limits Na^+ in shoots by retrieving it from the xylem, while OsHKT1; 4 prevents its movement from leaf sheath to blade under stress. Thus, HKT family transporters contribute to salt tolerance particularly during the reproductive stage (18).

However, the relative contribution of salt-tolerance mechanisms varies with plant developmental stage. During the seedling stage, ion homeostasis, particularly Na^+ exclusion and maintenance of ionic balance, is critical for minimising ion toxicity and sustaining early growth (24). During the vegetative stage, tolerance increasingly depends on the coordinated action of ionic homeostasis, osmotic adjustment and antioxidant defence to maintain cellular

integrity and physiological activity under prolonged salt stress (25). During the reproductive stage, sustained ion homeostasis and tissue tolerance become particularly important for protecting reproductive development and maintaining yield under salinity and sodicity (45). Thus, salt tolerance is a developmentally dynamic trait and mechanisms conferring seedling-stage tolerance may not necessarily ensure reproductive-stage tolerance or yield stability.

Quantitative trait loci governing salinity and sodicity tolerance in rice

Salt tolerance in rice is a complex quantitative trait controlled by multiple interacting genes that cooperatively regulate ion balance, stress responses and growth under stress environments. Quantitative trait loci (QTLs) are regions of the genome that comprise the genes controlling these quantitative traits (46). Among these, the Saltol QTL on chromosome 1 associated with the Pokkali-derived salt-tolerance region (47, 48), remains one of the most extensively characterised loci for seedling-stage salinity tolerance, particularly through its association with Na^+ exclusion and maintenance of shoot Na^+/K^+ homeostasis. Recent genome-wide analysis in an indica multi-parent advanced generation inter-cross (MAGIC) population detected the SKC1 gene within the Saltol region, confirming its continued relevance to salt tolerance. However, Saltol should not be considered the single or universal determinant of tolerance, as the study identified multiple additional loci associated with salinity tolerance on chromosomes 1, 5, 11 and 12 and distinct loci associated with sodicity tolerance on chromosomes 4, 6 and 11, highlighting the polygenic nature of salt tolerance (8). Development of QTLs related to the reproductive stage is crucial for alleviating the yield losses. QTLs of the reproductive stage are more important for survivability and yield than the seedling stage. Previous studies have reported nearly 18 QTLs identified by RIL populations that have significant yield advantages under saline and sodic conditions (49). Thus, multiple salt-tolerant varieties can be developed by integrating these QTLs into high-yielding salt-sensitive cultivars.

Genes involved in regulation of tolerance in rice

Salt stress is becoming a major abiotic stress threatening rice cultivation and reducing its productivity across the globe. It was calculated that around 20 % of the world's land is affected by salinity and is predicted to reach around 50 % by 2050 (50). Though the rice plant has evolved several molecular mechanisms to cope with salt stress, there are numerous genes and key transcription factors involved in the regulation of salt tolerance. OsPP2C8, a protein phosphatase 2C involved in abscisic acid (ABA)-dependent stress signalling, contributes to seedling-stage salt tolerance by regulating downstream ABA-responsive stress responses. Its salt-induced expression and sequence variation in the highly tolerant rice landrace Changnmaogu suggest a role in enhancing cellular



stress adaptation, which may help maintain photosynthetic machinery including PS II, under salinity and sodicity (51). Another gene, BIG RICE GRAIN1 (BIRG1), encodes a detoxification efflux carrier belonging to the DTX/MATE transporter family that regulates grain size and salt tolerance in rice by maintaining cellular Cl^- homeostasis (52).

OsMPK4, a mitogen-activated protein kinase, contributes to salt tolerance in rice by regulating the stability of Ideal Plant Architecture 1 (IPA1/SPL14), a transcription factor governing tillering, panicle branching and plant architecture. OsMPK4-mediated phosphorylation of IPA1 promotes its degradation, redirecting the plant's response from growth to stress response, ultimately enhancing tolerance (53). Transcriptome analysis revealed the upregulation of the OsWRKY54 transcription factor under salt stress. This gene regulates Na^+ and K^+ homeostasis in rice. Loss-of-function mutants of OsWRKY54 showed an imbalance in Na^+/K^+ homeostasis, representing the role of this gene in enhancing salt tolerance (54).

Root apoplastic barrier

Roots are the primary plant organs that encounter salt stress, responsible for structural and anatomical modifications that help restrict excessive Na movement into the root xylem. Under stress conditions, plants undergo modifications such as variations in root diameter, thickening of cortical tissues and vascular reorganisation (55). Water and dissolved substances move from the outer to the inner parts of the root through three main pathways: the symplastic, apoplastic and transcellular routes (56). Under salt stress, the symplastic pathway becomes less efficient, so the apoplastic pathway becomes the primary route for Na entry due to its high concentration in the soil. In such conditions, a well-lignified endodermis plays a crucial role by forming a strong barrier that restricts excessive Na^+ entry into the plant (55).

Plant roots have the capacity to modify their root system architecture, root growth and morphology to overcome the deleterious effects of salt stress. The plant cell wall is composed of lignin and polysaccharides. Lignin contributes to mechanical strength and its deficiency leads to dwarfism, xylem collapse and increased sensitivity to stress. Casparian strips and suberin lamellae are the root transport barriers in the root apoplast, which restrict the entry of toxic Na and chloride ions into the rice shoot (56). Salt stress causes the casparian strips to develop near the root tips to block the entry of Na^+ and ensure improved survival under stress (57). Exposure to high salinity conditions modifies root cell wall structure by reducing cellulose levels, interfering with pectin cross-linking and increasing lignin deposition. These structural adjustments reduce the permeability of the cell wall, restrict Na^+ movement into the stele and thereby enhance the salt tolerance (58).

Lignin deposition at the sites of casparian strips in response to salt stress is governed by OsDIR55, a dirigent (DIR) family protein acting as a positive regulator of root lignification (59). The casparian strip must remain as a continuous band in the endodermis for proper regulation of water and ion movement. If the strip is broken or poorly formed, it loses its ability to control nutrient uptake effectively, leading to an imbalance in ion distribution within the plant (60). The accumulation of phenolic and lipophilic biopolymers in the primary cell wall makes the endodermis hydrophobic, establishing an effective apoplastic barrier against water and ion movement. Activation of the CIF1/2–SGN3–SGN1 (SCHENGEN) signalling pathway triggers lignin deposition on the endodermal cell wall, forming a continuous 'U'-shaped lignified structure (Fig. 5) that restricts Na^+ influx into the stele and thereby contributes to salt tolerance (55).

Additionally, several abiotic stresses, including salinity, will induce the suberin lamellae (Fig. 6), another major component of the root diffusion barrier (61). Enhanced suberisation is often triggered by a deficit in lignin deposition. This compensation helps maintain the root diffusion barrier, facilitating effective control of water and solute movement despite structural damage (62).

Aerenchyma gas space formation

Salt-tolerant rice genotypes also exhibit tolerance through the formation of aerenchyma gas spaces (AGS). Its development occurs through ROS-mediated programmed cell death in root cortical tissues, which creates intercellular spaces that restrict Na^+ movement through the xylem and limit K^+ loss (63). Under stress conditions, these air spaces sequester Na^+ ions, restricting their entry into the shoot. The cortical cells actively exclude Na^+ ions into the air spaces, preventing their entry into the vascular system, thus minimising damage (64). At the molecular level, respiratory burst oxidase homologs (RBOHs/NOXs), especially OsNOX5, OsNOX9 and OsRbohA, promote ROS production and aerenchyma formation, supporting K^+ homeostasis and salt tolerance. This anatomical adaptation lowers the metabolic cost of root maintenance and enhances plant survival under saline conditions (63).

Root system architecture under salt stress

Root image analysis is a rapid and easy method to evaluate the root architecture under different salt stress (56). Root image analysis enables precise, quantitative assessment of root system architecture, including root length, surface area and branching patterns, which are critical for water and nutrient uptake. The WINRHIZO software quantitatively measures root architectural traits like total root length, root surface area and average root diameter (65). During stress conditions, tolerant and sensitive rice genotypes exhibited different morphological responses. Tolerant genotypes initially showed a decrease in root growth, surface area and tip number but recovered later, reflecting effective adaptation under stress (66).



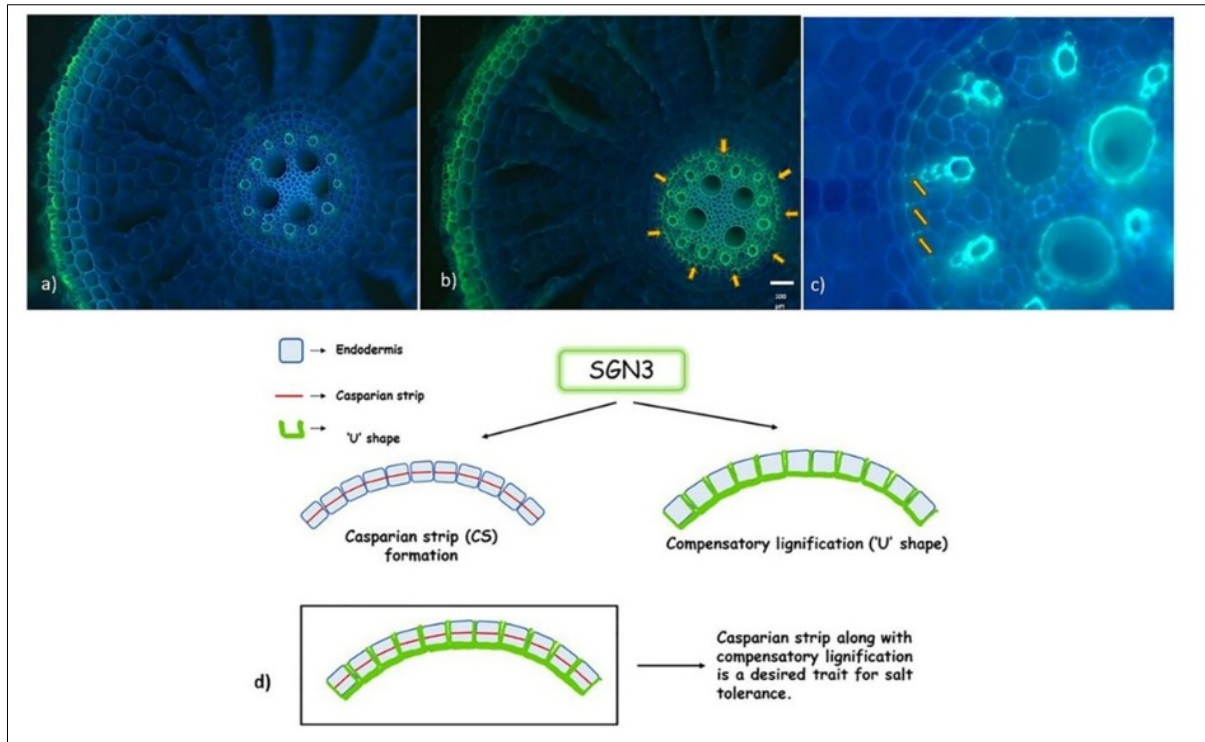


Fig. 5. Casparian strip formation and salt stress induced lignification in rice roots.

(a) Fluorescent microscopic images showing casparian strip formation and lignification in roots of salt sensitive cultivar CO 52, (b) salt tolerant landrace Mundan with 'U' shaped lignification (represented by arrows), (c) Formation of dot-like casparian strips during early stages of root differentiation in the salt tolerant landrace Mundan, (d) Schematic representation of lignification patterns showing Casparian strip (CS) formation and compensatory 'U'-shaped lignification along the endodermal walls, which together enhance the apoplastic barrier and contribute to salt tolerance (55).

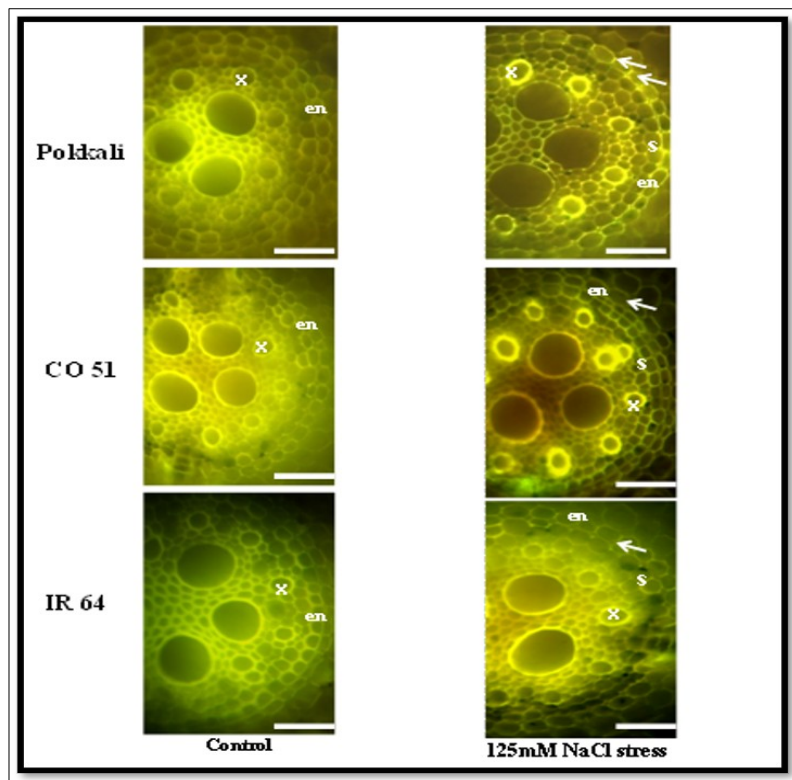


Fig. 6. Development of casparian bands and suberin lamella in endodermis (indicated by arrows) of three rice genotypes under salt stress observed by fluorescent staining of root cross sections.

en: endodermis; s: suberin lamella; x: xylem (56).

Hormonal regulation of salt tolerance

Salt stress significantly influences plant hormonal balance and the coordinated interaction of phytohormones is essential for stress perception, signal transduction and adaptive responses. Salt stress induces ABA accumulation in rice, activating the PYL/RCAR-PP2C-SnRK2 signalling pathway, which regulates stomatal closure, ion homeostasis and ROS detoxification (67). Absciscic acid-mediated stomatal regulation and ion transport facilitate water conservation, Na^+ sequestration and Na^+/K^+ homeostasis, with vacuolar Na^+/H^+ antiporters limiting cytosolic Na^+ toxicity. Absciscic acid also enhances antioxidant defence and the ascorbate-glutathione cycle, promoting ROS scavenging and limiting oxidative damage. Furthermore, ABA interacts with ROS and other hormonal pathways, particularly jasmonate, to coordinate ion transport and antioxidant defence. This hormonal interaction integrates ion compartmentalisation, ROS detoxification and stress-responsive growth, thereby increasing salt tolerance (68).

Indole-3-acetic acid (IAA) contributes to rice salinity and sodicity tolerance by regulating auxin homeostasis, polar transport and signalling, thereby influencing cell division, elongation, lateral-root initiation and overall root-system architecture. Salt-induced changes in IAA distribution can alter the TIR1/AFB-Aux/IAA-ARF signalling pathway, leading to changes in auxin-responsive gene expression and root-system plasticity that may improve water and nutrient acquisition under stress. The effect of IAA therefore depends on its spatial and temporal distribution rather than simply its absolute concentration. Indole-3-acetic acid also interacts with hormones like ABA, cytokinins and brassinosteroids to coordinate root development and stress responses. IAA-mediated hormonal interactions contribute to the coordination of root development and stress adaptation in rice (69).

Reduced gibberellin (GA) accumulation, mediated by GA catabolic genes *OsGA2ox5* and *OsCYP71D8L*, enhances salt tolerance in rice by restricting excessive plant growth and redirecting resources towards stress adaptation. Reduced GA levels promote growth restraint through GA-responsive growth pathways, thereby limiting energy expenditure during stress. GA-mediated growth regulation is closely associated with ABA-GA cross-talk, in which increased ABA signalling promotes stress responses while reduced GA availability favours growth inhibition, allowing plants to balance growth with stress survival. Consequently, the ABA-GA balance links hormonal signalling with growth regulation, contributing to salt tolerance (67).

Cytokinins (CKs) regulate plant growth, development and stress responses, with their homeostasis contributing to salinity and sodicity tolerance. Salt stress alters CK distribution between roots and shoots, thereby influencing root-shoot growth and stress responses. In rice, RST31 regulates salt

tolerance through the CK pathway, highlighting the role of CK signalling in stress adaptation (70). Cytokinin-mediated responses may also contribute to root structural modifications associated with diffusion barrier formation, which restricts uncontrolled ion and solute movement towards the stele and supports ion homeostasis (59). Cytokinin signalling further interacts with other hormones, particularly ABA and auxin, to coordinate root development and stress tolerance. Cytokinin-mediated salt tolerance integrates hormonal signalling, root barrier function and ion homeostasis to coordinate growth and stress responses (70).

Under salinity and sodicity, increased ethylene biosynthesis activates the ETR/ERS-CTR1-EIN2-EIN3/EIL-ERF pathway, leading to expression of stress-responsive genes. In rice, *OsEIN3/EIL* proteins respond to salt stress, ABA and jasmonic acid (JA), indicating an important node of ethylene-ABA-JA interaction. Ethylene also interacts with auxin, coordinating root development and adaptive root growth under salt stress, while interactions with ABA and JA integrate hormonal signalling with ROS metabolism and stress tolerance. Downstream ethylene signalling coordinates ROS homeostasis, ion transport, osmotic adjustment and root development, while its interactions with ABA, JA and auxin collectively contribute to salinity and sodicity tolerance (71).

Melatonin enhances rice salt tolerance by acting as a ROS scavenger and antioxidant regulator, reducing H_2O_2 and MDA through upregulation of *OsAPX1*, cytosolic APX, CAT, GPOD, Mn-SOD and Cu/Zn-SOD, while improving Na^+/K^+ homeostasis, proline accumulation and relative water content. Melatonin also preserves chlorophyll, photosynthetic activity and root-shoot growth under stress. Its association with ABA-responsive genes such as *OsABI3* and *OsLEA* indicates interaction with ABA-mediated stress signalling, integrating antioxidant defence, osmotic adjustment and hormonal responses (14).

Jasmonic acid enhances salt tolerance by upregulating SOD, POD, CAT and APX, reducing membrane damage and protecting cellular membranes. Jasmonic acid promotes GSH, chlorophyll and carotenoid accumulation and interacts with ABA and SA to coordinate ROS detoxification, osmotic adjustment, membrane protection and photosynthetic stability, thereby enhancing salt tolerance (72). Exogenous SA enhances rice salt tolerance by improving ion homeostasis, antioxidant defence and GA-ABA hormonal balance. It promotes Na^+ exclusion and reduces the Na^+/K^+ ratio through *OsHKT* and *OsSOS1* pathways, while increasing SOD, POD and CAT activities to control ROS and membrane damage (73).

Mitigation of salinity and sodicity

Soil salinity poses a significant threat to global rice (*O.sativa*) production by inducing osmotic stress, ion imbalance and oxidative damage, which collectively impair plant growth, physiology and yield (74). To



sustain rice productivity under saline conditions, research has increasingly focused on strategies that enhance stress resilience beyond inherent tolerance mechanisms. Among these, the exogenous application of plant hormones, biostimulants and beneficial microbial consortia has emerged as a promising and environmentally friendly suite of approaches for mitigating salt-induced damage in rice (68). Microbial biostimulants, particularly halophilic microbial consortia comprising *Staphylococcus arlettae* and *Paraburkholderia fungorum*, can enhance rice resilience under sodic conditions through their salt-tolerance and plant growth-promoting properties, including Na⁺ stress mitigation, exopolysaccharide and antioxidant production and improved nutrient availability (75).

Biochar has also been identified to ameliorate the effects of saline-sodic stress in plants. Biochar enhances yield under stress conditions by maintaining ionic balance and by regulating enzyme activities. Biochar, considered as one of the potent sources of Ca²⁺ and Mg²⁺, enables the exclusion of Na⁺ from the exchange sites, thus contributing to ion homeostasis. It

also upregulates the activities of sucrose synthase, ADGP pyrophosphorylase, starch synthase and starch branching enzyme in the rice grains grown under saline-sodic soils. Furthermore, biochar has emerged as a soil amendment with the potential for the reclamation of salt-affected soils (6). Silicon is recognised as a beneficial component that promotes healthy plant growth and development. External silicon application in the root zone can mitigate the negative effects of salinity. Silicon accumulation in rice develops a protective physical barrier through the formation of a thick layer of silicified cells underneath the cuticular layer of leaf blades, thus reducing the Na accumulation. Stress conditions induce the generation of ROS, which will cause membrane damage. Silicon controls or reduces excessive ROS generation under stress conditions, resulting in reduced electrolyte leakage and MDA content, ensuring membrane stability and salt tolerance (76). Together, these interventions represent a multilayered mitigation strategy that operates at physiological, biochemical and molecular levels, offering sustainable avenues to enhance rice resilience in salt-affected environments (Table 2).

Table 2. Role of exogenously applied hormones, chemicals, nutrients and soil-based amendments in alleviating salt stress

Type of stress	Ameliorant	Physiological responses	Reference
Salinity	Salicylic acid	Enhanced antioxidant activity	(74)
	Silicon (Si)	Reduced Na accumulation, lipid peroxidation, enhanced antioxidant activity	(76)
	Methyl jasmonic acid (MeJA)	Modulated fatty acid profiles, Metabolic reprogramming	(77)
	Absciscic acid (ABA)	Improved photosynthesis, pollen viability, grain yield, reduced spikelet sterility	(78)
	Brassinosteroids (BRs)	Enhanced photosynthetic efficiency, grain development and reduced spikelet sterility	(78)
	Auxin (IAA)	Improved grain filling and starch accumulation under salt stress	(79)
	Cytokinin (CK)	Delayed senescence, maintains photosynthesis and improved carbohydrate partitioning	(79)
Sodicity	Potassium nitrate, Salicylic acid, Thio-urea	Increased photosynthesis, physiological traits, Na/K balance and yield	(80)
	Daincha	Reduced exchangeable sodium percentage (ESP), improved soil organic matter and nutrient availability	(81)
	Anti-oxidant microbial consortia (AOMC)	Increased proline and chlorophyll content, enhanced osmotic adjustment	(81)
Saline- sodic stress	Zinc (Zn ²⁺)	Regulated chlorophyll fluorescence and carbohydrate metabolism, improved seedling vigour	(82)

Traditional rice varieties as source of tolerance

Salt tolerance (ST) is a complex quantitative trait governed by multiple genes and shaped by a wide range of molecular and biological processes (83). It is inferred that the identification of tolerance from modern cultivars has reached a steady state. This might be due to the long-term domestication of these varieties (84). Domesticated varieties have a narrow genetic base for salinity tolerance (85). There is one more reason that stands as a bottleneck for using modern cultivars as a source of tolerance because it might cause linkage drag of detrimental characteristics like photosensitivity, reduced standability and inferior yield performance (86). Traditional rice genotypes act as a reservoir of beneficial alleles providing tolerance against major biotic and abiotic stresses across the globe (Table 3). This will facilitate modern rice cultivars in acquiring adaptation to climate change and gaining resistance to counteract various stresses (87). Landraces have the adaptive ability to thrive in local environments, attributed to metabolic components specific to the landraces (88). Traditional varieties possess broad genetic diversity with vital quantitative and qualitative traits, making them a rich source of valuable genes for crop improvement (Table 4) (89). Wild rice species exhibit superior salinity tolerance compared to cultivated rice, employing diverse adaptive mechanisms including salt gland secretion, enhanced ion homeostasis, osmolyte accumulation, ROS scavenging and osmotic adjustment. Collectively, wild rice species represent valuable genetic resources for enhancing salinity tolerance in cultivated rice (90).

Research gaps, emerging mechanisms and future directions

Despite extensive research on salt tolerance in rice, several gaps persist in translating well-established mechanisms into field-level applications. Key adaptive responses such as ion homeostasis, osmotic adjustment and antioxidant defences are widely recognised, where Na^+ exclusion and sequestration mediated by transporters such as SOS1, NHX and HKT maintain ionic balance and reduce toxicity (50). Osmolyte accumulation supports cellular osmotic equilibrium and membrane stability (41) and ROS detoxification is achieved through enzymatic antioxidant systems (48). Additionally, hormonal regulation involving ABA, auxin, CK and ethylene plays a crucial role in coordinating stress perception, signalling and adaptation (78). Nevertheless, much of this mechanistic understanding has been generated under controlled hydroponic or growth-chamber conditions, which may not fully represent the complex and heterogeneous conditions encountered in the field. Variations in soil salinity and sodicity, soil nutrient availability, temperature and the occurrence of multiple stresses can modify the effectiveness of individual tolerance mechanisms, resulting in differences between controlled-environment responses and field performance. Beyond this translational limitation, the integration of the above-mentioned mechanisms within higher-order regulatory networks remains poorly understood. In particular, miRNA-mediated regulation, which potentially links ion transport, ROS detoxification, transcriptional control and hormonal signalling, is still insufficiently characterised. Although miRNAs are proposed as key post-transcriptional regulators coordinating gene expression, ion homeostasis and stress signalling under salinity, their mechanistic integration and application in crop improvement remain largely unexplored (97).

Table 3. Phenotypic and physiological responses of rice genotypes and landraces to salinity stress

Genotypes	Region	Stress level	Observed responses	References
Traditional landraces vs high yielding varieties	India	0–250 mM NaCl	Landraces outperformed high-yielding varieties (HYVs) in biomass, chlorophyll retention and stress tolerance	(11)
Rice landraces	India	6–12 dS m ⁻¹	Traditional landraces showed higher shoot and root length and lower salt injury score	(20)
76 germplasm accessions	India	6 and 12 dS m ⁻¹	FL478 and MTU1290 maintained low Na^+/K^+ ratio and higher seedling biomass	(24)
79 landraces and 18 varieties	Vietnam	8 dS m ⁻¹	Tolerant genotypes showed reduced Na^+ accumulation in shoot	(91)
8 Landraces	Thailand	75–100 mM NaCl	Tolerant landraces maintained high photosynthesis and antioxidant activity	(92)

Table 4. Quantitative comparison of salt-tolerance indices, Saltol-QTL allele combinations and salt-responsive gene expression in rice landraces

	Landrace		Indices studied			Key findings	Reference
	Pokkali	Salt Susceptibility index	Salt tolerance index	Salt response index			
Salt tolerance index		4.35	0.96	1.20		Stable yield under stress conditions	(93)
	Komol Bhog	Indices studied				Superior salinity tolerance with minimal growth reduction and better biomass retention	(94)
		Shoot Length stress index (%)	Root Length stress index (%)	Shoot dry weight stress index (%)	Root dry weight stress index (%)		
Saltol-QTL allele combinations	Pokkali	76.47	73.68	71.74	68.09		
		QTL	Chromosomal location	Associated gene	Trait controlled	Contribution to salt tolerance	
		Saltol	Chromosome 1	<i>OsHKT1;5</i>	Shoot Na ⁺ /K ⁺ ratio	Improved ionic homeostasis and seedling stage salinity tolerance	
		qSNC1	Chromosome 1	<i>OsHKT1;5</i>	Shoot Na ⁺ concentration	Removes Na ⁺ from xylem sap and restricts Na ⁺ transport to shoots	(95)
		qSKC1	Chromosome 1	<i>OsHKT1;5</i>	Shoot K ⁺ concentration	Maintains K ⁺ homeostasis during salt stress	
		qRKC1	Chromosome 1	<i>OsHKT1;5</i>	Root K ⁺ concentration	Enhances K ⁺ uptake and retention in roots	
		qRNK1	Chromosome 1	<i>OsHKT1;5</i>	Root Na ⁺ /K ⁺ ratio	Regulates Na ⁺ exclusion from roots	
Key transporter Gene Expression	Pokkali	Gene	Increase in gene expression	Site of induction	Physiological significance	Key findings	
		<i>OsHKT1;5</i>	2-fold increase	Roots	Enhanced Na ⁺ retrieval from xylem and reduced Na ⁺ transport to shoots	Increased gene expression restricted Na ⁺ transport to shoots, improved cellular ion compartmentalisation and sustained better physiological balance under stress	(96)
		Myo-inositol oxygenase (Os06g36560)	4.8-fold increase	Roots	Osmotic adjustment and salinity-responsive metabolic regulation		

Future research should adopt an integrative multi-omics framework to elucidate miRNA-centred regulatory networks and their interactions with physiological and biochemical traits under field conditions. Functional validation of key miRNAs and their targets using genome editing and transgenic approaches is essential for establishing their roles in salt tolerance, particularly genes involved in ion homeostasis such as *OsHKT1;5*, *OsSOS1* and *OsNHX1*. Genomic selection integrating genome-wide markers with multi-environment phenotypic data can accelerate the identification and deployment of polygenic salt-tolerance alleles. The incorporation of speed breeding with marker-assisted and genomic selection can further reduce generation time and accelerate the development of improved rice varieties. Similarly, high-throughput phenomics,

including root-system analysis and multispectral imaging, can support rapid screening of large breeding populations. Potential alleles from tolerant traditional landraces can be introduced into elite varieties through advanced backcrossing, together with marker-assisted and genomic selection, while reducing undesirable genetic linkages. Overall, combining multi-omics, genome editing, genomic selection, speed breeding, phenomics and advanced backcrossing can help bridge the gap between laboratory findings and field performance and provide a more effective pathway for developing rice cultivars with durable salinity and sodicity tolerance.

4. Conclusion

Salinity and sodicity tolerance in rice are regulated by coordinated physiological, anatomical and molecular mechanisms that maintain ion homeostasis, osmotic balance and cellular protection under stress. Traditional landraces should be prioritised as donor parents in breeding programmes as they possess efficient sodium (Na^+) exclusion, potassium (K^+) retention, antioxidant defence and adaptive root traits. Key transporter and regulatory genes including *SOS1*, *NHX1*, *HKT1;5*, *OsAKT2*, *OsWRKY54*, *OsDIR55* and *OsPP2C8* represent potential targets in genome editing for improving salt tolerance through coordinated ion regulation and root barrier development. While *Saltol* remains an important seedling-stage quantitative trait locus (QTL), future breeding strategies should focus on stacking *Saltol* with reproductive-stage QTLs, root architectural traits, apoplastic barrier genes and stress-responsive regulatory loci, which will be essential for achieving tolerance throughout the plant's life cycle and stabilising grain yield under saline and sodic conditions. Integrating landrace diversity, multi-omics and genome editing approaches will contribute significantly to developing climate-resilient rice cultivars.

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Authors' contributions

All authors contributed to the conception and design of the study. The study of the work, material preparation, literature collection and manuscript preparation were performed by JJJ. VR contributed to the technical guidance, review and supervision of the work. VR, DV, LA and SR assisted in manuscript preparation and organisation of the review content. VR and DV contributed to the review and editing of the manuscript. All authors have read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest

Authors do not have any conflict of interests to declare.

Ethical issues

None

References

1. Farooq M, Jang YH, Kim EG, Park JR, Eom GH, Zhao DD, et al. Evaluation of amino acid profiles of rice genotypes under different salt stress conditions. *Plants*. 2023;12(6):1315. <http://doi.org/10.3390/plants12061315>
2. Zhang C. The role of rice in global food security: Strategies for sustainable production. *J Rice Res*. 2024;12:411.
3. Liu B, Huang L, Jiang X, Liu Y, Huang G, Yang C, et al. Quantitative evaluation and mechanism analysis of soil chemical factors affecting rice yield in saline-sodic paddy fields. *Sci Total Environ*. 2024;929:172584. <http://doi.org/10.1016/j.scitotenv.2024.172584>
4. Richard LA. Diagnosis and improvement of saline and alkaline soils. USDA Handbook No. 60. 1954.
5. Gregorio GB, Senadhira D, Mendoza RD. Screening rice for salinity tolerance. *IRRI Discussion Paper Ser*. 1997;22(1):30.
6. Che W, Li X, Piao J, Zhang Y, Miao S, Wang H, et al. Biochar improves yield by reducing saline-alkaline stress, enhancing filling rate of rice in soda saline-alkaline paddy fields. *Plants*. 2024;13:2237. <http://doi.org/10.3390/plants13162237>
7. Bhowmik U, Kibria MG, Rhaman MS, Murata Y, Hoque MA. Screening of rice genotypes for salt tolerance by physiological and biochemical characters. *Plant Sci Today*. 2021;8(3):467–72. <http://doi.org/10.14719/pst.2021.8.3.1098>
8. Krishnamurthy SL, Sharma PC, Dewan D, Lokeshkumar BM, Rathor S, Warraich AS, et al. Genome-wide association study of MAGIC population reveals a novel QTL for salinity and sodicity tolerance in rice. *Physiol Mol Biol Plants*. 2022;28(4):819–35. <http://doi.org/10.1007/s12298-022-01174-8>
9. Shrivastava P, Kumar R. Soil salinity: A serious environmental issue and plant growth-promoting bacteria as one of the tools for its alleviation. *Saudi J Biol Sci*. 2014;22(2):123. <http://doi.org/10.1016/j.sjbs.2014.12.001>
10. Ashokkumar K, Kowsalya M, Vivekanandhan S, Jothika J, Sivakumar P. Assessment of traditional and modern rice varieties for salt tolerance at early growth stages. *J Curr Opin Crop Sci*. 2023;4(2):50–5. <http://doi.org/10.62773/jcocs.v4i2.195>
11. Mervat M, Elsherif AI, Abdelfatah Sobhy Gharieb, Gharieb AS. Improving salt tolerance rice (*Oryza sativa* L.) variety by conventional and molecular breeding to enhance productivity. *Menoufia J Plant Prod*. 2025;10(3):43–55. <http://doi.org/10.21608/mjppf.2025.357144.1068>
12. Molla KA. Molecular switch to regulate salt tolerance in rice. *Plant Cell*. 2023;35:3396–7. <http://doi.org/10.1093/plcell/koad178>
13. Zhang R, Hussain S, Wang Y, Liu Y, Li Q, Chen Y, et al. Comprehensive evaluation of salt tolerance in rice (*Oryza sativa* L.) germplasm at the germination stage. *Agronomy*. 2021;11:1569. <http://doi.org/10.3390/agronomy11081569>
14. Ubaidillah M, Farooq M, Kim KM. Enhancing salt tolerance in rice genotypes through exogenous melatonin application by modulating growth patterns and antistress agents. *Sci Rep*. 2024;14(1):25217. <http://doi.org/10.1038/s41598-024-77161-8>
15. Hussain S, Zhang JH, Zhong C, Bohr JA. Effects of salt stress on rice growth, development characteristics and the regulating ways: A review. *J Integr Agric*. 2017;16(11):2357–74. [http://doi.org/10.1016/S2095-3119\(16\)61608-8](http://doi.org/10.1016/S2095-3119(16)61608-8)
16. Solis CA, Yong MT, Zhou M, Venkataraman G, Shabala L, Holford P, et al. Evolutionary significance of *NHX* family and *NHX1* in salinity stress adaptation in the genus *Oryza*. *Int J Mol Sci*. 2022;23(4):2092. <http://doi.org/10.3390/ijms23042092>
17. Abbasi H, Jamil M, Haq A, Ali S, Ahmad R, Malik Z, et al. Salt stress manifestation on plants, mechanism of salt tolerance and potassium role in alleviating it: A review. *Zemdirb Agric*.



- 2016;103(2):229–38. <http://doi.org/10.13080/z-a.2016.103.030>
18. El Mahi H, Pérez-Hormaeche J, De Luca A, Villalta I, Espartero J, Gámez-Arjona F, et al. A critical role of sodium flux via the plasma membrane Na⁺/H⁺ exchanger SOS1 in the salt tolerance of rice. *Plant Physiol.* 2019;180(2):1046–65. <http://doi.org/10.1104/pp.19.00324>
 19. Sree SS, Al-Zharani M, Nasr FA, Alneghery LM, Ajith Kumar TT, Sureshkumar BT, et al. Innovative bio-amelioration strategies for sustainable reclamation of salt-affected agroecosystems: A review. *Plant Soil.* 2025;1–48. <http://doi.org/10.1007/s11104-025-07749-0>
 20. Hepziba SJ, Anisha PR, Aashika N, Aathilakshmi S, Kavitha PA, Arumugachamy S. Screening for salinity tolerance in rice landraces through morphological and molecular markers. *Plant Sci Today.* 2025;12:8540. <http://doi.org/10.14719/pst.8540>
 21. Shaban AS, Abouzeid R, Wu Q, Subudhi PK. Lignin-containing cellulose nanofiber–selenium nanoparticle hybrid enhances tolerance to salt stress in rice genotypes. *Sci Rep.* 2025;15(1):14173. <http://doi.org/10.1038/s41598-025-98906-z>
 22. Assaha DVM, Ueda A, Saneoka H, Al-Yahyai R, Yaish MW. The role of Na⁺ and K⁺ transporters in salt stress adaptation in glycophytes. *Front Physiol.* 2017;8:509. <http://doi.org/10.3389/fphys.2017.00509>
 23. Chen T, Niu Y, Yang C, Liang Y, Xu J. Screening of rice (*Oryza sativa* L.) genotypes for salinity tolerance and dissecting determinants of tolerance mechanism. *Plants.* 2024;13(7):1036. <http://doi.org/10.3390/plants13071036>
 24. Pranaya J, Roja V, Venkata Ramana Rao P, Girija Rani M, Ramesh D. Evaluation of germplasm for seedling stage salinity tolerance in rice (*Oryza sativa* L.). *Int J Plant Soil Sci.* 2024;36:73–81. <http://doi.org/10.9734/ijpss/2024/v36i54503>
 25. Kumar V, Srivastava AK, Sharma D, Pandey SP, Pandey M, Dudwadkar A, et al. Antioxidant defense and ionic homeostasis govern stage-specific response of salinity stress in contrasting rice varieties. *Plants.* 2024;13(6):778. <http://doi.org/10.3390/plants13060778>
 26. Gerona MEB, Deocampo MP, Egdane JA, Ismail AM, Dionisio-Sese ML. Physiological responses of contrasting rice genotypes to salt stress at reproductive stage. *Rice Sci.* 2019;26(4):207–19. <http://doi.org/10.1016/j.rsci.2019.05.001>
 27. Huo J, Yu M, Feng N, Zheng D, Zhang R, Xue Y, et al. Integrated transcriptome and metabolome analysis of salinity tolerance in response to foliar application of choline chloride in rice (*Oryza sativa* L.). *Front Plant Sci.* 2024;15:1440663. <http://doi.org/10.3389/fpls.2024.1440663>
 28. Yan F, Zhang J, Li W, Ding Y, Zhong Q, Xu X, et al. Exogenous melatonin alleviates salt stress by improving leaf photosynthesis in rice seedlings. *Plant Physiol Biochem.* 2021;163:367–75. <http://doi.org/10.1016/j.plaphy.2021.03.058>
 29. Wang Y, Tan C, Li Y, Meng F, Du Y, Zhang S, et al. 5-ALA, DTA-6 and nitrogen mitigate NaCl stress by promoting photosynthesis and carbon metabolism in rice seedlings. *Metabolites.* 2024;14:142. <http://doi.org/10.3390/metabo14030142>
 30. Challabathula D, Analin B, Mohanan A, Bakka K. Differential modulation of photosynthesis, ROS and antioxidant enzyme activities in stress-sensitive and tolerant rice cultivars during salinity and drought upon restriction of COX and AOX pathways of mitochondrial oxidative electron transport. *J Plant Physiol.* 2022;268:153583. <http://doi.org/10.1016/j.jiplph.2021.153583>
 31. Ling F, Su Q, Jiang H, Cui J, He X, Wu Z, et al. Effects of strigolactone on photosynthetic and physiological characteristics in salt-stressed rice seedlings. *Sci Rep.* 2020;10:6183. <http://doi.org/10.1038/s41598-020-63352-6>
 32. Yoo YH, Hong WJ, Jung KH. A systematic view exploring the role of chloroplasts in plant abiotic stress responses. *BioMed Res Int.* 2019;2019:6534745. <http://doi.org/10.1155/2019/6534745>
 33. Zuo G, Zhang R, Feng N, Zheng D. Photosynthetic responses to salt stress in two rice (*Oryza sativa* L.) varieties. *Agronomy.* 2024;14:2134. <http://doi.org/10.3390/agronomy14092134>
 34. El Moukhtari A, Cabassa-Hourton C, Farissi M, Savouré A. How does proline treatment promote salt stress tolerance during crop plant development? *Front Plant Sci.* 2020;11:1127. <http://doi.org/10.3389/fpls.2020.01127>
 35. Aninbon C, Ruttanaprasert R, Pinta W, Rodnuch N, Boonsom M, Thabthimtho T, et al. Impact of salinity stress during reproductive stage on physiological responses and yield of landrace rice genotypes. *BMC Plant Biol.* 2026;26:08355-7.
 36. Rodríguez Coca LI, García González MT, Gil Unday Z, Jiménez Hernández J, Rodríguez Jáuregui MM, Fernández Cancio Y. Effects of sodium salinity on rice (*Oryza sativa* L.) cultivation: A review. *Sustainability.* 2023;15(3):1804. <http://doi.org/10.3390/su15031804>
 37. Tian Q, Shen L, Luan J, Zhou Z, Guo D, Shen Y, et al. Rice shaker potassium channel OsAKT2 positively regulates salt tolerance and grain yield by mediating K⁺ redistribution. *Plant Cell Environ.* 2021;44(9):2951–65. <http://doi.org/10.1111/pce.14101>
 38. Zheng C, Liu C, Liu L, Tan Y, Sheng X, Yu D, et al. Effect of salinity stress on rice yield and grain quality: A meta-analysis. *Eur J Agron.* 2023;144:126765. <http://doi.org/10.1016/j.eja.2023.126765>
 39. Li Z, Zhou T, Zhu K, Wang W, Zhang W, Zhang H, et al. Effects of salt stress on grain yield and quality parameters in rice cultivars with differing salt tolerance. *Plants.* 2023;12(18):3243. <http://doi.org/10.3390/plants12183243>
 40. Li Q, Zhu P, Yu X, Xu J, Liu G. Physiological and molecular mechanisms of rice tolerance to salt and drought stress: Advances and future directions. *Int J Mol Sci.* 2024;25(17):9404. <http://doi.org/10.3390/ijms25179404>
 41. Sharma A, Shahzad B, Kumar V, Kohli SK, Sidhu GPS, Bali AS, et al. Phytohormones regulate accumulation of osmolytes under abiotic stress. *Biomolecules.* 2019;9(7):285. <http://doi.org/10.3390/biom9070285>
 42. Sofy AR, Dawoud RA, Sofy MR, Mohamed HI, Hmed AA, El-Dougoudg NK. Improving regulation of enzymatic and non-enzymatic antioxidants and stress-related gene stimulation in Cucumber mosaic cucumovirus-infected cucumber plants treated with glycine betaine, chitosan and combination. *Molecules.* 2020;25(10):2341. <http://doi.org/10.3390/molecules25102341>
 43. Qamer Z, Chaudhary MT, Du X, Hinze L, Azhar MT. Review of oxidative stress and antioxidative defense mechanisms in *Gossypium hirsutum* L. in response to extreme abiotic conditions. *J Cotton Res.* 2021;4(1):9. <http://doi.org/10.1186/s42397-021-00086-4>
 44. Amin I, Rasool S, Mir MA, Wani W, Masoodi KZ, Ahmad P. Ion homeostasis for salinity tolerance in plants: A molecular approach. *Physiol Plant.* 2021;171:578–94. <http://doi.org/10.1111/ppl.13185>
 45. Munns R, James RA, Gilliam M, Flowers TJ, Colmer TD. Tissue tolerance: An essential but elusive trait for salt-tolerant crops. *Funct Plant Biol.* 2016;43(12):1103–13. <http://doi.org/10.1071/FP16187>
 46. Beerelli K, Balakrishnan D, Addanki KR, Surapaneni M, Yadavalli VR, Neelamraju S. Mapping of QTLs for yield traits using F2:3:4 populations derived from two alien introgression lines reveals qTGW8.1 as a consistent QTL for grain weight from *Oryza nivara*. *Front Plant Sci.* 2022;13:790221. <http://doi.org/10.3389/fpls.2022.790221>

47. Lutambi KK, Henry A, De Ocampo M, Chebotarov D, Pedersen O, Nchimbi Msolla S, et al. Genotypic screening for salinity tolerance of rice genotypes from Eastern and Southern Africa at seedling stage. *J Plant Interact.* 2024;19(1):2349623. <http://doi.org/10.1080/17429145.2024.2349623>
48. Geetha S, Vasuki A, Jagadeesh Selvam P, Saraswathi R, Krishnamurthy SL, Dhasarathan M, et al. Development of sodicity tolerant rice varieties through marker-assisted backcross breeding. *Electron J Plant Breed.* 2017;8(4):1013–31. <http://doi.org/10.5958/0975-928X.2017.00151.X>
49. Sugasi YD, Srivastava A, Badri J, Pandey M, Parmar B, Singh AK, et al. Mapping quantitative trait loci (QTLs) for reproductive stage salinity tolerance in rice. *Crops.* 2024;4(4):684–700. <http://doi.org/10.3390/crops4040047>
50. Zhang H, Yu F, Xie P, Sun S, Qiao X, Tang S, et al. A Gγ protein regulates alkaline sensitivity in crops. *Science.* 2023;379(6638). <http://doi.org/10.1126/science.ade8416>
51. Sun BR, Fu CY, Fan ZL, Chen Y, Chen WF, Zhang J, et al. Genomic and transcriptomic analysis reveal molecular basis of salinity tolerance in a novel strong salt-tolerant rice landrace Changmaogu. *Rice.* 2019;12:99. <http://doi.org/10.1186/s12284-019-0360-4>
52. Ren Z, Bai F, Xu J, Wang L, Wang X, Zhang Q, et al. A chloride efflux transporter, BIG RICE GRAIN 1, is involved in mediating grain size and salt tolerance in rice. *J Integr Plant Biol.* 2021;63(12):2150–63. <http://doi.org/10.1111/jipb.13178>
53. Jia M, Luo N, Meng X, Song X, Jing Y, Kou L, et al. OsMPK4 promotes phosphorylation and degradation of IPA1 in response to salt stress to confer salt tolerance in rice. *J Genet Genomics.* 2022;49(8):766–75. <http://doi.org/10.1016/j.jgg.2022.03.010>
54. Huang J, Liu F, Chao D, Xin B, Liu K, Cao S, et al. The WRKY transcription factor OsWRKY54 is involved in salt tolerance in rice. *Int J Mol Sci.* 2022;23(19):11999. <http://doi.org/10.3390/ijms231911999>
55. Swetha R, Sridhanya VM, Varanasiappan S, Kumar KK, Kokiladevi E, Ravichandran V, et al. Root apoplastic barrier mechanism: An adaptive strategy to protect against salt stress. *Mol Biol Rep.* 2025;52(1):56. <http://doi.org/10.1007/s11033-024-10171-x>
56. Lakshmi S. Study on anatomical and physiological basis of salt tolerance in rice genotypes (*Oryza sativa* L.). M.Sc. Thesis. Tamil Nadu Agricultural University, Coimbatore, India; 2020.
57. Xue B, Duan W, Gong L, Zhu D, Li X, Li X, et al. The OsDIR55 gene increases salt tolerance by altering the root diffusion barrier. *Plant J.* 2024;118(5):1550–68. <http://doi.org/10.1111/tjp.16696>
58. Byrt CS, Munns R, Burton RA, Gilliam M, Wege S. Root cell wall solutions for crop plants in saline soils. *Plant Sci.* 2018;269:47–55. <http://doi.org/10.1016/j.plantsci.2017.12.012>
59. Gao YQ, Huang JQ, Reyt G, Song T, Love A, Tiemessen D, et al. A dirigent protein complex directs lignin polymerization and assembly of the root diffusion barrier. *Science.* 2023;382(6669):464–71. <http://doi.org/10.1126/science.adi5032>
60. Pfister A, Barberon M, Alassimone J, Kalmbach L, Lee Y, Vermeer JE, et al. A receptor-like kinase mutant with absent endodermal diffusion barrier displays selective nutrient homeostasis defects. *eLife.* 2014;3. <http://doi.org/10.7554/eLife.03115>
61. Barberon M, Vermeer JEM, De Bellis D, Wang P, Naseer S, Andersen TG, et al. Adaptation of root function by nutrient-induced plasticity of endodermal differentiation. *Cell.* 2016;164(3):447–59. <http://doi.org/10.1016/j.cell.2015.12.021>
62. Wang Z, Zhang B, Chen Z, Wu M, Chao D, Wei Q, et al. Three OsMYB36 members redundantly regulate Casparian strip formation at the root endodermis. *Plant Cell.* 2022;34(8):2948–68. <http://doi.org/10.1093/plcell/koac140>
63. Mondal S, Panda B, Nayak JK, Pradhan C, Chattopadhyay K, Chakraborty K. The role of aerenchymatous gas spaces in root sodium ion management under salt stress: Do they matter in rice? *Ann Bot.* 2025;136(5–6):1279–94. <http://doi.org/10.1093/aob/mcaf134>
64. Paul A, Mondal S, Chakraborty K. The role of aerenchyma in Na⁺ management: Do they matter for withstanding salt stress? *J Plant Growth Regul.* 2025;44(8):4538–40. <http://doi.org/10.1007/s00344-025-11704-9>
65. Shafeeqa T, Ravichandran V, Senthil A, Arul L, Radhamani S. Assessment of seedling traits of rice landraces under different saline conditions. *J Appl Nat Sci.* 2022;14(4). <http://doi.org/10.31018/jans.v14i4.3887>
66. Ijaz B, Sudiro C, Jabir R, Lo Schiavo F, Hyder MZ, Yasmin T. Adaptive behaviour of roots under salt stress correlates with morpho-physiological changes and salinity tolerance in rice. *Int J Agric Biol.* 2019. <http://doi.org/10.17957/ijab/15.0943>
67. Liu C, Mao B, Yuan D, Chu C, Duan M. Salt tolerance in rice: Physiological responses and molecular mechanisms. *Crop J.* 2022;10(1):13–25. <http://doi.org/10.1016/j.cj.2021.02.010>
68. Jiang S, Lan Z, Zhang Y, Kang X, Zhao L, Wu X, et al. Mechanisms by which exogenous substances enhance plant salt tolerance through the modulation of ion membrane transport and reactive oxygen species metabolism. *Antioxidants.* 2024;13(9):1050. <http://doi.org/10.3390/antiox13091050>
69. Guo L, Yu H, Zhang C, Kharbach M. The role of phytohormones in alleviating salt stress in rice. *Phyton.* 2024;93(12). <http://doi.org/10.32604/phyton.2024.058622>
70. He L, Chen T, Zhao C, Zhao L, Zhao Q, Yao S, et al. RST31 controls salt tolerance in rice (*Oryza sativa*) by regulating the cytokinin pathway. *Plant Physiol Biochem.* 2024;216:109075. <http://doi.org/10.1016/j.plaphy.2024.109075>
71. Zhang X, Sun J, Dong CH. Molecular regulations of ethylene signalling in plant salt stress responses. *Plant Stress.* 2024;14:100583. <http://doi.org/10.1016/j.stress.2024.100583>
72. Qiu ZB, Guo JL, Zhu AJ, Zhang L, Zhang MM. Exogenous jasmonic acid enhances tolerance of wheat seedlings to salt stress. *Ecotoxicol Environ Saf.* 2014;202–8. <http://doi.org/10.1016/j.ecoenv.2014.03.014>
73. Liu Z, Ma C, Hou L, Wu X, Wang D, Zhang L, et al. Exogenous SA affects rice seed germination under salt stress by regulating Na⁺/K⁺ balance and endogenous GAs and ABA homeostasis. *Int J Mol Sci.* 2022;23(6):3293. <http://doi.org/10.3390/ijms23063293>
74. Wu Y, Duan Y, Luo X, Li M, Gao H, Zhu W, et al. Molecular regulation of antioxidant defense and metabolic reprogramming in Xiaozhan rice genotypes: Differential roles of salicylic acid and melatonin under salt stress. *Curr Issues Mol Biol.* 2025;47(6):432. <http://doi.org/10.3390/cimb47060432>
75. Fathima F, Suma R, Asha NN, Ananthakumar MA, Keshavaiah KV. Exploiting biostimulants and micronutrients for optimal rice yield in sodic soil: A strategic approach to salt stress resilience. *Plant Arch.* 2024;24(1):768–74. <http://doi.org/10.51470/PLANTARCHIVES.2024.v24.no.1.105>
76. Kim YH, Khan AL, Waqas M, Shim JK, Kim DH, Lee KY, et al. Silicon application to rice root zone influenced the phytohormonal and antioxidant responses under salinity stress. *J Plant Growth Regul.* 2014;33(2):137–49. <http://doi.org/10.1007/s00344-013-9356-2>
77. Zainordin ZFM, San Cha T, Ahmad A. Foliar sprays of methyl jasmonic acid shift the endogenous fatty acid levels to support rice plant growth in saline soil. *Plant Stress.* 2023;10:100221. <http://doi.org/10.1016/j.stress.2023.100221>

78. Hussain S, Nanda S, Ashraf M, Siddiqui AR, Masood S, Khaskheli MA, et al. Interplay impact of exogenous application of abscisic acid (ABA) and brassinosteroids (BRs) in rice growth, physiology and resistance under sodium chloride stress. *Life*. 2023;13(2):498. <http://doi.org/10.3390/life13020498>
79. Ghorbani Javid M, Sorooshzadeh A, Modarres Sanavy SAM, Allahdadi I, Moradi F. Effects of the exogenous application of auxin and cytokinin on carbohydrate accumulation in grains of rice under salt stress. *Plant Growth Regul.* 2011;65(2):305–13. <http://doi.org/10.1007/s10725-011-9602-1>
80. Singh A, Bali A, Kumar A, Yadav RK, Minhas PS. Foliar spraying of potassium nitrate, salicylic acid and thiourea: Effects on growth, physiological processes and yield of sodicity-stressed paddy (*Oryza sativa* L.) with alkali water irrigation. *J Plant Growth Regul.* 2022;41(5):1989–98. <http://doi.org/10.1007/s00344-022-10575-8>
81. Janaki P, Alagesan A, Ejilane J, Nithila S, Balasubramaniam P, Santhy P. Effect of soil and crop management practices on sodicity stress alleviation and rice productivity under water-scarce condition. *J Appl Nat Sci.* 2021;13(4). <http://doi.org/10.31018/jans.v13i4.2930>
82. Dang K, Mu J, Tian H, Gao D, Zhou H, Guo L, et al. Zinc regulation of chlorophyll fluorescence and carbohydrate metabolism in saline-sodic stressed rice seedlings. *BMC Plant Biol.* 2024;24(1):464. <http://doi.org/10.1186/s12870-024-05170-w>
83. Deinlein U, Stephan AB, Horie T, Luo W, Xu G, Schroeder JI. Plant salt tolerance mechanisms. *Trends Plant Sci.* 2014;19(6):371–9. <http://doi.org/10.1016/j.tplants.2014.02.001>
84. Solis CA, Yong MT, Venkataraman G, Milham P, Zhou M, Shabala L, et al. Sodium sequestration confers salinity tolerance in an ancestral wild rice. *Physiol Plant.* 2021;172(3):1594–608. <http://doi.org/10.1111/ppl.13352>
85. Solis CA, Yong MT, Vinarao R, Jena K, Holford P, Shabala L, et al. Back to the wild: On a quest for donors toward salinity tolerant rice. *Front Plant Sci.* 2020;11:323. <http://doi.org/10.3389/fpls.2020.00323>
86. Leung H, Raghavan C, Zhou B, Oliva R, Choi IR, Lacorte V, et al. Allele mining and enhanced genetic recombination for rice breeding. *Rice.* 2015;8(1):34. <http://doi.org/10.1186/s12284-015-0069-y>
87. Subramanian V, Dhandayuthapani UN, Kandasamy S, Sivaprakasam JV, Balasubramaniam P, Shanmugam MK, et al. Unravelling the metabolomic diversity of pigmented and non-pigmented traditional rice from Tamil Nadu, India. *BMC Plant Biol.* 2024;24(1):402. <http://doi.org/10.1186/s12870-024-05123-3>
88. Fukuoka S, Suu TD, Ebana K, Trinh LN, Nagamine T, Okuno K. Diversity in phenotypic profiles in landrace populations of Vietnamese rice: A case study of agronomic characters for conserving crop genetic diversity on farm. *Genet Resour Crop Evol.* 2006;53(4):753–61. <http://doi.org/10.1007/s10722-004-4635-1>
89. Raja K, Sivaranjani K. Variations in morphological traits of traditional rice varieties in major rice growing regions of Tamil Nadu: Morphological traits in traditional rice varieties. *Indian J Tradit Know.* 2025;24(4):349–60. <http://doi.org/10.56042/ijtk.v24i4.8322>
90. Padmavathi G, Bangale U, Rao KN, Balakrishnan D, Arun MN, Singh RK, et al. Progress and prospects in harnessing wild relatives for genetic enhancement of salt tolerance in rice. *Front Plant Sci.* 2024;14:1253726. <http://doi.org/10.3389/fpls.2023.1253726>
91. Nguyen TT, Dwiyantri MS, Sakaguchi S, Koide Y, Le DV, Watanabe T, et al. Identification of a Saltol-independent salinity tolerance polymorphism in rice Mekong delta landraces and characterization of a promising line, Doc Phung. *Rice.* 2022;15(1):65. <http://doi.org/10.1186/s12284-022-00613-0>
92. Nounjan N, Sanitchon J, Pamuta D, Theerakulpisut P. Differential physiological responses to salt stress in rice landraces in Thailand. *Not Bot Horti Agrobo.* 2024;52(3):13778. <http://doi.org/10.15835/nbha52313778>
93. Senguttuvel P, Raju NS, Padmavathi G, Sundaram RM, Madhav S, Hariprasad AS, et al. Identification and quantification of salinity tolerance through salt stress indices and variability studies in rice (*Oryza sativa* L.). *SABRAO J Breed Genet.* 2016;48(2):172–9.
94. Tahjib-Ul-Arif M, Sayed MA, Islam MM, Siddiqui MN, Begum SN, Hossain MA. Screening of rice landraces (*Oryza sativa* L.) for seedling stage salinity tolerance using morpho-physiological and molecular markers. *Acta Physiol Plant.* 2018;40(4):70. <http://doi.org/10.1007/s11738-018-2650-5>
95. Thomson MJ, de Ocampo M, Egdane J, Rahman MA, Sajise AG, Adorada DL, et al. Characterizing the Saltol quantitative trait locus for salinity tolerance in rice. *Rice.* 2010;3(2):148–60. <http://doi.org/10.1007/s12284-010-9053-8>
96. Cotsaftis O, Plett D, Johnson AAT, Walia H, Wilson C, Ismail AM, et al. Root-specific transcript profiling of contrasting rice genotypes in response to salinity stress. *Mol Plant.* 2011;4(1):25–41. <http://doi.org/10.1093/mp/ssq056>
97. Islam W, Waheed A, Naveed H, Zeng F. MicroRNAs mediated plant responses to salt stress. *Cells.* 2022;11(18):2806. <http://doi.org/10.3390/cells11182806>

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