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Salt stress in rice: Morpho-physiological effects, nitrogen dynamics and integrated management strategies for yield improvement in saline soils

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ABSTRACT

Soil salinization, intensified by global climate change and unsustainable agricultural practices, has become a critical factor limiting agricultural productivity. There is a pressing need for globally applicable and scalable salinity mitigation strategies in rice cultivation. This review systematically clarifies the interactions between salt stress and soil physicochemical properties and rice root architecture, nutrient uptake, and growth dynamics. In addition, it critically evaluates innovative agronomic strategies for yield enhancement in saline conditions, including organic fertilization, deep tillage, biochar amendment, exogenous growth hormone application, inoculation with halotolerant plant growth-promoting bacteria, nanomaterial utilization, and integration of calcium-based soil amendments. Salt stress elevates soil exchangeable sodium content, reducing soil porosity and water and nutrient retention capacities. These reductions in turn decrease soil fertility, microbial activity, and nitrogen supply to rice. Concurrently, osmotic, ionic, and oxidative stresses induced by salinity hinder root development and vigor, disrupt nutrient absorption/transport, and perturb nitrogen allocation between roots and shoots, collectively constraining rice growth and reducing yield. These emphasize the necessity for identifying the drivers and severity of soil salinization and developing targeted salinity mitigation or cultivation strategies tailored to local soil texture, climatic conditions, and resource availability, thereby enhancing agricultural productivity in salt-affected regions and contributing to the Sustainable Development Goal 2 (SDG2: zero hunger) of achieving zero hunger globally.

Key Words: exogenous plant hormone, deep tillage, halotolerant plant growth-promoting bacteria, nanomaterial, organic fertilization, root architecture, salinity mitigation, soil salinization

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INTRODUCTION

Rice (*Oryza sativa* L.), a cornerstone of global food security, sustains more than half of the world's population (Li Y S *et al*., 2025). Current rice cultivation spans 162 million hectares, yielding 756 million tons of rice annually (Khan *et al*., 2023). However, rice production needs to be increased by approximately 70%–110% to meet the projected demand for rice in 2050 (Tilman *et al*., 2011). This challenge is particularly pressing in regions with rapid population growth, such as Asia, Africa, and the Americas, where rice consumption and production are the most concentrated (Kumari *et al*., 2022; Samal *et al*., 2022). To ensure a stable food supply and agricultural sustainability, efforts must focus on both expanding cultivation areas and enhancing productivity per unit land (Choudhary *et al*., 2017). However, with current grain yield per unit area approaching its maximum potential, achieving further gains in productivity is increasingly challenging. Therefore, reclaiming and utilizing underused land resources, particularly salinized soils, to expand rice cultivation has become a crucial strategy for addressing food security.

Salinized soil is defined as soil with an electrical conductivity (EC) $\geqslant 4$ dS m^{-1} (40 mmol L^{-1} sodium chloride) in the root zone at 25 °C (Jamil *et al*., 2011). High salinity impairs crop growth and drastically reduces yields. Globally, salinized soils affect approximately one-quarter to one-third of agricultural productivity (Li *et al*., 2025b). Specifically, these soils affect 1 billion hectares of total land, including $> 20\%$ of irrigated farmlands across 118 countries (Negacz *et al*., 2022). On an annual basis, global soil salinization proceeds at a rate equivalent to a loss of 3 hectares of land per minute (Khan *et al*., 2023), driven by global climate change (*e.g*., increased evapotranspiration and saltwater intrusion due to rising sea levels) and improper agricultural practices such as inefficient irrigation

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and excessive fertilization (Etesami and Beattie, 2018; Liu *et al.*, 2023). Harnessing salinized soils as viable agricultural resources to expand rice cultivation is a crucial approach to mitigating global production shortages (Hayat *et al.*, 2020).

Nitrogen (N) is a key macronutrient for plant growth, development, and productivity. It serves as a building block for proteins, nucleotides, chlorophyll, and cellular structures, consequently regulating primary production in agricultural systems (Teo *et al.*, 2022). It is widely recognized as a major limiting factor for plant growth in natural and agricultural ecosystems. Salt stress typically inhibits plant N uptake (Abouelsaad *et al.*, 2016). Rice primarily absorbs N as nitrate (NO_3^-) and ammonium (NH_4^+) through root epidermal and cortical cell membranes (Dai *et al.*, 2015). These molecules are converted into organic compounds (*e.g.*, glutamine and glutamate) through the sequential actions of nitrate reductase (NR), nitrite reductase (NiR), and the glutamine synthetase (GS)/glutamate synthase (GOGAT) cycle. These compounds are essential for the synthesis of other nitrogenous metabolites and macromolecules (Zhao *et al.*, 2025). Under salt stress, this process is disrupted: N uptake is reduced and NO_3^--assimilating enzyme activity declines, limiting nutrient acquisition (Ashraf *et al.*, 2018). In addition, excessive accumulation of reactive oxygen species (ROS) under salt stress damages cell structure and membrane proteins, hinders root development, and reduces water and nutrient absorption, leading to decreased aboveground biomass (Cheng *et al.*, 2024). These effects collectively reduce rice yield and N utilization efficiency (NUE) under salt stress (Guo *et al.*, 2021).

To meet the increasing global food demand, exploiting salinized land for crop cultivation and using abundant brackish water resources have become critical priorities (Li *et al.*, 2023). Understanding the effects of soil salinization on rice growth, development, and N absorption is crucial for optimizing rice cultivation on salinized soils. This review aimed to discuss the effects of salt stress on the nutrient absorption, growth, development, yield, and quality of rice and to explore strategies for optimizing rice cultivation and management techniques on salinized soils, improving plant growth conditions, and increasing NUE in rice. It provides theoretical guidance for utilizing saline soils for rice cultivation and expanding rice production to ensure global food security.

CHARACTERISTICS OF SALINIZED SOILS

As a type of degraded agricultural land, salinized soils are characterized by diminished fertility and productivity, posing a serious threat to global crop yields and food security (Fadiji *et al.*, 2023). Existing classification systems categorize salt-affected soils into three primary types based on EC, sodium (Na) adsorption ratio, and exchangeable sodium percentage (ESP): saline, saline-sodic, and sodic (Poulopoulos and Inglezakis, 2016). A core constraint of these soils is their high concentration of soluble salts, particularly Na^+, which form compounds such as sodium chloride, sodium carbonate, and sodium sulfate (Choudhary and Kharche, 2018). These Na^+-dominated salts trigger cascading physicochemical deterioration, such as expansion and dispersion of clay minerals, which block soil pores, reduce porosity, and impair hydraulic properties such as water permeability and gas exchange (Liu B S *et al.*, 2024). This structural damage decreases soil organic matter content and depletes both macronutrients and micronutrients. Furthermore, high salinity-induced osmotic stress limits the water and nutrient uptake of roots. These changes collectively reduce agricultural productivity in salt-affected areas (Elayaraja and Sathiyamurthi, 2020; Qi *et al.*, 2025).

Soil microbial communities, key indicators of soil health, are severely disrupted by salinity. Salinity-induced osmotic and ionic stresses reduce microbial biomass, enzyme activities, and N mineralization (Fu *et al.*, 2024). Under high salinization, microbial abundance and species diversity decline (Hui *et al.*, 2022), accompanied by reduced microbial biomass carbon content, microbial biomass N content, and basal respiration (Liu L *et al.*, 2024). In addition, the activities of key enzymes such as dehydrogenase, phosphatase, and urease are inhibited due to salt-induced protein denaturation (Bonea *et al.*, 2021; Wei *et al.*, 2021), impairing nutrient cycling, particularly N availability, as nitrification is suppressed by salinity (Gondek *et al.*, 2020). Altogether, ionic toxicity induced by a high ESP and osmotic imbalance resulting from high salinity disrupts the structural homeostasis of salinized soils, diminishing soil fertility and microbial activity and consequently impairing the capacity of the soil to supply N to crops (Sun *et al.*, 2021).

ROOT STRUCTURE CHANGES UNDER SALT STRESS

As the primary sensor of soil salinity, the root system plays an important role in water and nutrient uptake for plant growth (Song *et al.*, 2023). Owing to their direct contact with soil, roots are more susceptible to ionic toxicity than other organs (Farooq *et al.*, 2024). Notably, rice roots exhibit adaptive traits such as organic acid exudation and selective ion uptake, which enhance soil aggregation and water retention. Therefore, rice cultivation is a promising strategy for the phytoremediation of saline soils (Zhang *et al.*, 2025).

High Na^+ accumulation in soil reduces water potential, leading to osmotic stress when the osmotic pressure of root cells decreases below that of the soil (Chen Y L *et al.*, 2021). This phenomenon impairs water uptake, induces cellular dehydration, and inhibits root cell division and elongation, reducing apical meristem size, cortex/mesocarp diameters, root hair length/density, and overall root architecture such as root diameter, surface area, volume, primary root length, and lateral root density (Rachmawati *et al.*, 2021; Zhao *et al.*, 2025). Elevated intracellular Na^+ concentrations disrupt ion homeostasis by interfering with plasma membrane transporters such as potassium (K) channels, reducing K uptake, which is a crucial nutrient for enzymatic reactions and metabolite synthesis (Ponce *et al.*, 2021). In addition, Na^+ accumulation triggers ROS overproduction, causing oxidative damage to proteins, DNA, lipids, and chloroplasts and destroying cell membranes and organelles (Saleem *et al.*, 2025). Malondialdehyde (MDA) accumulation further impairs root cell membrane integrity, ion/water channel activity, and lipid fluidity, reducing root vigor, nutrient uptake, and N translocation between roots and shoots and consequently decreasing yield (Torabian *et al.*, 2018; Sultan *et al.*, 2025).

Transcriptomic studies have shown that transcriptional changes in rice root genes under salt stress are mainly related to protein kinase and calcium (Ca)-binding proteins, plant hormone signaling and metabolism, transcriptional regulation, metabolic pathways, antioxidant activity, and ion transport (Song *et al.*, 2023). Abscisic acid (ABA) signaling and metabolic pathways are involved in the response and tolerance to salt stress. The ABA biosynthetic gene *OsNCED4* and the ABA-regulated transcription factors OsbZIP66 and OsbZIP23 are significantly upregulated under salt stress. High-affinity K transporter (HKT) genes (*e.g.*, *OsHKT1;5* and *OsHKT2;1*) regulate Na^+/K^+ homeostasis, with OsMYBc enhancing salt tolerance by activating these genes (Wang *et al.*, 2015; Qin and Huang, 2020). Ethylene signaling also plays a role in this process. OsEIL1/2 inhibits salt tolerance by upregulating *OsHKT2;1*, whereas salt-induced suppression of OsDOF15 (a negative regulator of ethylene biosynthesis) increases ethylene concentration, promoting ABA, indole-3-acetic acid (IAA), jasmonic acid (JA), and gibberellin biosynthesis, Na^+ uptake, and ROS accumulation and consequently inhibiting plant growth (Qin *et al.*, 2019). Furthermore, salt stress downregulates NH_4^+ assimilation genes (*e.g.*, *OsGS1.2*, *OsGS2*, *OsNR1*, and *OsFd-GOGAT*) and alters NO_3^- distribution through upregulation of *NRT1.8/NPF7.2* and downregulation of *NRT1.5/NPF7.3*, thereby restricting NO_3^- transport to shoots and reducing NUE (Wang *et al.*, 2012; Zhang *et al.*, 2014). These factors collectively impair root function and decrease rice yield under saline conditions by affecting root structure, ion balance, oxidation status, and gene regulation.

EFFECTS OF SALT STRESS ON RICE GROWTH, DEVELOPMENT AND NUTRIENT UPTAKE

Rice productivity is governed by complex interactions between edaphic conditions, nutrient availability, and biotic-abiotic factors (Gouda *et al.*, 2018), with soil salinity emerging as a principal yield-limiting abiotic factor. The effects of salinity vary with intensity: mild to moderate salinity ($2 \text{ dS m}^{-1} < \text{EC} < 4 \text{ dS m}^{-1}$) causes yield reductions of 20%–30%, intermediate salinity ($4 \text{ dS m}^{-1} < \text{EC} < 8 \text{ dS m}^{-1}$) causes an approximately 50% reduction in yield, and severe salinity ($\text{EC} > 8 \text{ dS m}^{-1}$) typically results in plant death (Thitisaksakul *et al.*, 2015; Li *et al.*, 2023).

In rice, salt stress mainly leads to osmotic stress and ionic toxicity (Sackey *et al.*, 2025). Osmotic stress arises when salt accumulation in the root zone elevates the osmolality of soil above that of root cells, reducing soil water potential and inhibiting water uptake. Rice responds by accumulating compatible osmolytes (*e.g.*, proline, betaine, and late embryogenesis abundant proteins) to maintain cellular osmotic balance; however, the response efficacy diminishes under severe salt stress (Yang and Guo, 2018; Yan *et al.*, 2020). Concurrently, stomatal closure to minimize transpiration reduces the intercellular carbon dioxide (CO_2) concentration, impairing photosynthesis (Zhao *et al.*, 2020; Li Y S *et al.*, 2025). Ionic toxicity, driven by excessive Na^+ accumulation, disrupts enzyme activity, protein synthesis, and redox homeostasis, leading to ROS buildup (Shultana *et al.*, 2021). Furthermore, Na^+ accumulation in rice leads to yellowing, necrosis, and premature senescence, limiting photosynthate production, inducing spikelet sterility, and consequently suppressing yield formation (Song *et al.*, 2022; Li R Y *et al.*, 2025). Osmotic stress-induced stomatal closure restricts CO_2 uptake, whereas thylakoid dysfunction hinders electron transport and adenosine triphosphate (ATP) synthesis, suppressing nicotinamide adenine dinucleotide phosphate oxidation (Etesami and Glick, 2020; Sackey *et al.*, 2025). An excessive reduction in photosystem I electron carriers triggers the Mehler reaction, generating ROS that peroxidize membrane lipids, degrade the chloroplast structure, and reduce chlorophyll levels (Sarkar *et al.*, 2018a). In addition, salinity inhibits the uptake of N (essential for chlorophyll) and magnesium (Mg), further impairing photosynthetic pigment synthesis and light absorption (Gonzalez-Villagra *et al.*, 2021). These changes eventually suppress photosynthate transport and crop yield (Kamran *et al.*, 2020).

Nitrogen is required for chlorophyll production and photosynthesis in the plant body and serves as an important component of various enzymes involved in catalyzing and regulating plant growth processes (Alam *et al.*, 2023). Nitrogen uptake and metabolism are severely disrupted under salinity. High salt concentrations damage root membranes, whereas the antagonism between chloride ions (Cl^-) and NO_3^- inhibits NO_3^- uptake, significantly limiting N accumulation (Liu *et al.*, 2022; Tzortzakis *et al.*, 2022). Intracellular Na^+ accumulation suppresses the activities of N-assimilating enzymes, such as NR, NiR, GS, and GOGAT, suppressing amino acid synthesis (Zhao *et al.*, 2025).

Salt stress impacts rice growth across all stages. Germination rate, radicle length, and seedling biomass decline under salinity (Hakim *et al*., 2010). At the vegetative stage, salt stress stunts plant height, suppresses tillering, and limits biomass, reducing carbohydrate reserve required for grain filling (Li *et al*., 2023). As shown in Fig. 1, tiller number and rice biomass decrease significantly with an increase in soil salt concentration. At the reproductive stage, salt stress reduces spikelet number (Fig. 2), pollen viability, and fertility, reducing yield (Garg *et al*., 2025; Li Y S *et al*., 2025). In addition, a decrease in the content of straight-chain starch and an increase in the chalky white percentage, chalkiness, and protein content of rice grains degrade rice quality (Cui *et al*., 2024).

Altogether, salt stress reduces N uptake/assimilation, impairs photosynthesis, and disrupts nutrient transport from vegetative to reproductive organs, eventually decreasing rice yield in salinized soils (Li *et al*., 2025a). The adverse effects of salt stress on rice growth and development are presented in Fig. 3. Addressing these effects is crucial for sustaining rice productivity and quality in salt-affected areas.

MEASURES FOR INCREASING RICE PRODUCTIVITY ON SALINIZED SOILS

Management and remediation of salinized soils are essential for enhancing ecosystem stability and resource utilization efficiency (Wang *et al*., 2023). Common management strategies for enhancing the salt tolerance of rice include organic fertilization, deep tillage, biochar application, and halotolerant plant growth-promoting bacteria (HT-PGPB) inoculation (Fig. 4). Numerous studies have been conducted on salt stress management strategies and their effects on plant growth in salinized soils (Table I).

Organic fertilization

Salt stress inhibits soil nitrification processes and promotes N loss pathways such as denitrification, ammonia volatilization, and leaching, leading to low fertilizer utilization efficiency and resource waste (Ghosh *et al*., 2017; Wang *et al*., 2018). Climate change exacerbates these challenges. Consequently, the application of organic fertilizers has become a key strategy for addressing salinization and climate-induced soil degradation. It effectively increases soil organic matter, total N, organic carbon, and available phosphorus (P) contents to maintain soil fertility under salt stress (An *et al*., 2022). In addition, it improves the water retention capacity of soil by promoting aggregation, thereby reducing salt accumulation driven by evaporation (Ni *et al*., 2023; Peng *et al*., 2023). Studies have indicated that returning straw to fields as a common organic input can reduce soil bulk density, increase soil porosity, promote deep root development, and enhance water/nutrient absorption capacity, which is crucial for resisting the dual stresses of drought and salinization under global warming (Xu *et al*., 2018). In addition, the improved soil structure reduces erosion risks during extreme rainfall events and mitigates secondary salinization (Jin *et al*., 2020). The specific microbial communities enriched in compost can also enhance the tolerance of crops to high soil EC, thereby attenuating the inhibitory effects of salinity on growth (Hafez *et al*., 2021).


Fig. 2 Photo showing the obvious degradation of rice spikelets under salt stress (source: photographed by the author).

However, excessive application of organic fertilizers, such as manure and compost, can introduce excessive soluble salts (Gondek *et al*., 2020), increasing soil EC and exacerbating salinization. High N inputs can stimulate denitrification, leading to the release of nitrous oxide, a potent greenhouse gas, and amplifying climate feedback (Ghosh *et al*., 2017). In addition, P and N leaching resulting from excessive application of organic fertilizers can contaminate water bodies, triggering eutrophication (Cid *et al*., 2021). An imbalanced nutrient supply can disrupt soil pH and microbial community structure, reducing the effectiveness of salinization mitigation (Castiglione *et al*., 2021). Therefore, optimizing organic fertilizer management based on soil

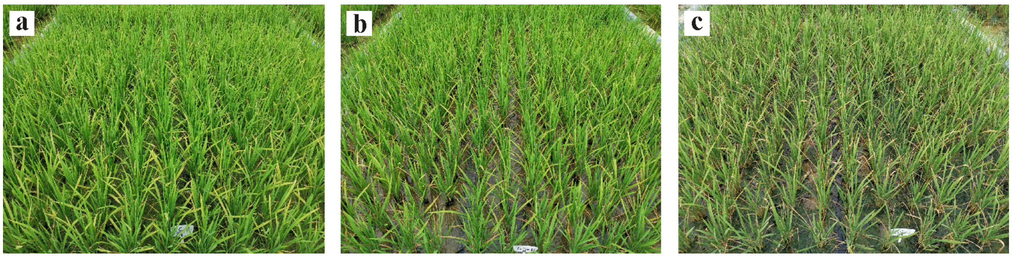

Fig. 1 Photos showing marked decreases in rice tiller number and biomass with soil salt concentration increasing from 0 g kg^{-1} (a) to 3 g kg^{-1} (b) and then to 6 g kg^{-1} (c) (source: photographed by the author).

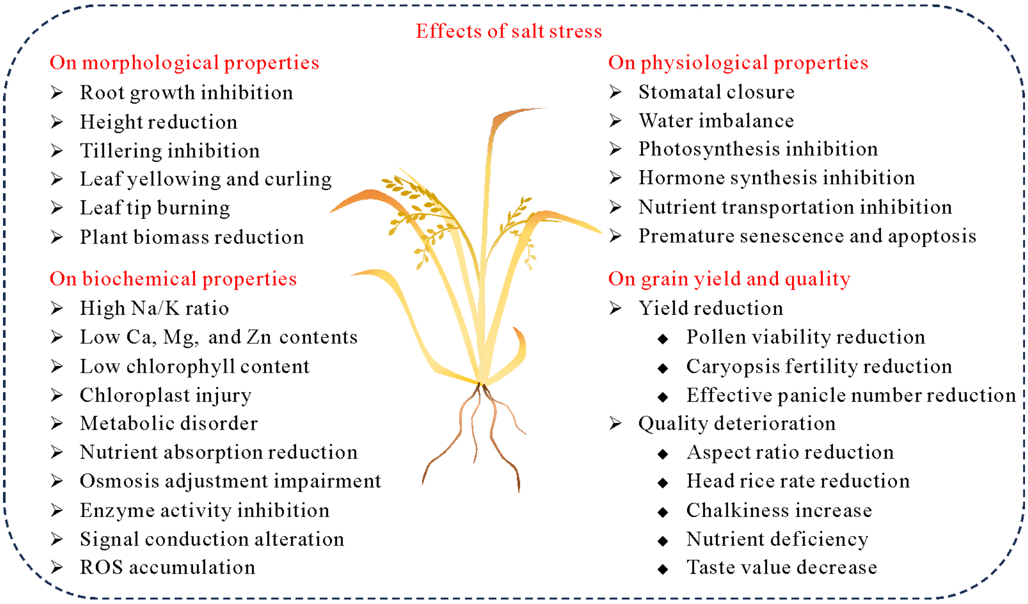

Fig. 3 Schematic diagram showing the adverse effects of salt stress on rice growth and development. ROS = reactive oxygen species.

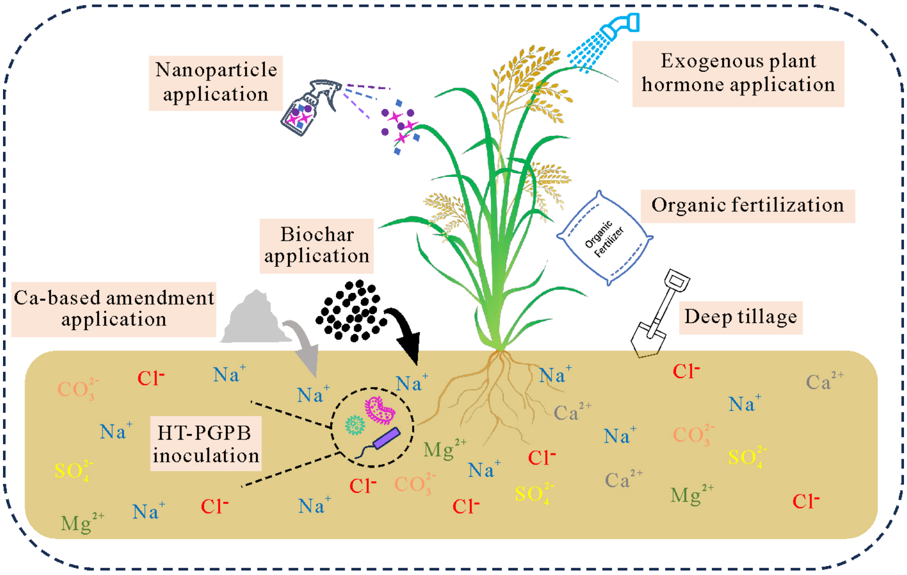

Fig. 4 Schematic diagram showing some management strategies for enhancing the salt tolerance of rice. HT-PGPB = halotolerant plant growth-promoting bacteria.

salinization levels, crop requirements, and regional climate patterns is crucial for balancing the benefits of improved soil fertility, structure, and microbial activity with the risks of salt accumulation and greenhouse gas emissions. This optimization may offer a sustainable strategy for mitigating climate-induced salinization while ensuring high rice yields.

Deep tillage

Tillage is a crucial agricultural practice for reclaiming salinized lands. Different tillage methods exert varying impacts on soil bulk density and moisture dynamics (Liu *et al*., 2015). This relevance is amplified in the context of climate change, which exacerbates soil salinization through intensified evapotranspiration (amplifying salt accumulation in arid regions) and saltwater intrusion (threatening coastal farmlands through sea level increase) (Liu *et al*., 2023; Li Y S *et al*., 2025). Deep tillage, particularly deep vertical rotary tillage, can effectively loosen deep soil layers without disrupting soil structure, thereby reducing soil bulk density and permeability resistance, and improving porosity, hydraulic conductivity, and water infiltration (Feng *et al*., 2024). These changes significantly increase deep soil moisture content, reduce surface salinity, and promote the leaching of surface-accumulated salts (owing to reduced rainfall in arid regions or intensified coastal storm surges) into deeper layers. In addition, deep plowing enhances the

TABLE I

Salt stress management strategies and their effects on plant growth on salinized soils

Management strategy[a]	Effects[b]	Reference
Compost application	Increased uptake of nutrients (N, P, K, Fe, Mn, and Zn), straw biomass, and grain and 1 000-grain weights of rice	Zaki, 2016
Ca-based amendment (CaSiO$_3$) application	Increased rice root length, root fresh/dry weight, and root anatomical traits (epidermis thickness, cortex thickness, stele diameter, root diameter, and endodermic wall thickness), enhanced root cell wall metaplasia and lignification, decreased salt ion influx	Rachmawati *et al*., 2021
Nanoparticle (nano-ZnSO$_4$) application	Improved nutrient balance, increased plant height, panicle length, grain weight, yield, and grain macronutrient and protein contents in rice	Ahmed *et al*., 2023
Biochar application	Improved rice root structure integrity, root activity, and root length, enhanced chloroplast function, increased seedling emergence rate, plant height, and biomass	Zhang *et al*., 2019
	Decreased Na content and Na/K ratio in rice leaves, stems, sheaths, and panicles, increased K content, plant height, chlorophyll content, panicle number, spikelets per panicle, 1 000-grain weight, seed-setting rate, yield, biomass, and harvest index, improved leaf water status	Ran *et al*., 2020
	Decreased rice Na accumulation, chalkiness, chalkiness ratio, amylose content, and protein content, increased dry matter accumulation, yield, panicle number, spikelets per panicle, seed-setting rate, brown rice, milled rice, head rice percentage, and grain length/width ratio	Jin *et al*., 2018
EPH application		
GA	Increased expression of monogalactosyldiacylglycerol synthase, catalytic synthesis of monogalactosyldiacylglycerol, chlorophyll content, and rice biomass, improved chloroplast lipid composition, photosystem stability, and membrane stability	Liu *et al*., 2018
SA	Increased rice seed germination rate, root length, shoot length, plant height, yield, panicle number, spikelets per panicle, 1 000-grain weight, and contents of K, endogenous SA, carbohydrate, and protein, decreased Na and Cl contents and antioxidant enzyme activities	Jini and Joseph, 2017
BR	Increased rice biomass, activities of SOD, POD, CAT, and APX, photosynthetic system function, contents of K, Ca, ASA, GSH, soluble protein, proline, IAA, SA and zeatin, decreased ROS accumulation and contents of MDA, Na, and ABA	Mu *et al*., 2022b
SL	Decreased rice MDA content, increased plant height, root length, POD and SOD activities, and leaf photosynthetic parameters, including $\mathrm{P_n}$, $\mathrm{T_r}$, $\mathrm{g_s}$, and intercellular CO$_2$ concentration	Ling *et al*., 2020
MT	Decreased rice seedling relative electrolyte leakage, increased fresh/dry weight, NOS and NR activities, polyamine content, root ATP content, arginine utilization, H$^+$-ATPase activity in root plasma membrane and tonoplast, Na$^+$ efflux, and K$^+$ inflow (K$^+$/Na$^+$ balance maintained)	Yan *et al*., 2020
	Decreased ROS burst, upregulated expression of the HKT gene *OsHAK*, enhanced K retention, improved salt tolerance, increased photosynthesis, antioxidant capacity, and yield	Chen T X *et al*., 2021
HT-PGPB inoculation		
Trichoderma koningiopsis, *Trichoderma asperellum*	Increased rice root length, shoot length, biomass, tillering number, spikelets per panicle, 1 000-grain weight, and flag leaf length	Anshu *et al*., 2022
Pseudomonas multiresinivorans, *Microbacterium esteraromaticum*, *Bacillus subtilis*	Increased rice root length, volume, and fresh/dry weight, shoot fresh/dry weight, and plant height	Bhambure *et al*., 2018
Bacillus pumilus	Decreased rice seedling Na and Cl contents, increased aboveground biomass, contents of chlorophyll, K, Ca, and Mg, and activities of SOD, POD, and CAT	Khan *et al*., 2016
Burkholderia sp. MTCC 12259	Decreased SOD and CAT activities and proline content, increased germination rate, root/shoot fresh/dry weight, root/shoot length, amylase and protease activities, and contents of auxin, chlorophyll, total soluble sugar, and total protein in rice	Sarkar *et al*., 2018b
AMF (*Claroideoglomus etunicatum*) inoculation	Decreased actual quantum efficiency of PSII photochemistry, NPQ quantum yield, increased $\mathrm{P_n}$, $\mathrm{T_r}$, $\mathrm{g_s}$, total Rubisco activity, and aboveground biomass	Porcel *et al*., 2015
HT-EF (*Aspergillus terreus*) inoculation	Decreased Na, Cl, H$_2$O$_2$, and MDA contents, increased shoot length, fresh/dry weight, $\mathrm{F_v/F_m}$ ratio, contents of leaf relative water, total chlorophyll, proline, GA, and K in rice and maize	Siddiqui *et al*., 2022

[a] EPH = exogenous plant hormone; GA = gibberellic acid; SA = salicylic acid; BR = brassinolide; SL = strigolactone; MT = melatonin; HT-PGPB = halotolerant plant growth-promoting bacteria; AMF = arbuscular mycorrhizal fungi; HT-EF = halotolerant endophytic fungi.

[b] SOD = superoxide dismutase; POD = peroxidase; CAT = catalase; APX = ascorbate peroxidase; ASA = ascorbic acid; GSH = glutathione; IAA = indole-3-acetic acid; ROS = reactive oxygen species; MDA = malondialdehyde; ABA = abscisic acid; $\mathrm{P_n}$ = net photosynthetic rate; $\mathrm{g_s}$ = stomatal conductance; $\mathrm{T_r}$ = transpiration rate; NOS = nitric oxide synthase; NR = nitrate reductase; ATP = adenosine triphosphate; H$^+$-ATPase = hydrogen ion-translocating adenosine triphosphatase; HKT = high-affinity K transporter; PSII = photosystem II; NPQ = non-photochemical quenching; $\mathrm{F_v/F_m}$ ratio = variable fluorescence/maximum fluorescence ratio, indicating the maximum quantum yield of PSII photochemistry.

adaptability of soil microbial communities to moisture and salinity fluctuations by regulating them (*e.g.*, by enriching salt-tolerant microorganisms) (Yao *et al*., 2023). This process promotes organic matter decomposition and nutrient cycling, enhancing soil resilience against climate disturbances such as irregular precipitation, high temperatures, and strong evaporation. Therefore, moderate deep tillage reduces root-zone salinity by enhancing leaching, alleviating immediate salt stress. It also enhances soil resilience against climate-induced compaction and supports microbial functional stability. By regulating water and salt dynamics in the root zone, deep tillage not only helps improve crop yield in the current season but also establishes long-term soil resilience to address the growing threat of climate-driven salinization.

Biochar application

Biochar is a carbon-rich porous material derived from the pyrolysis of biomass under anaerobic or oxygen-limited conditions at relatively low temperatures (< 700 °C). It has low bulk density, high specific surface area, and strong adsorption capacity (Xiang *et al.*, 2021). Its application exhibits distinct regional relevance, primarily shaped by the availability of biomass feedstocks and the scalability of production. In developing nations, where agricultural wastes (*e.g.*, rice straw and sugarcane bagasse) are abundant but underutilized, biochar production can be decentralized using low-tech pyrolysis systems, producing a cost-effective soil amendment for small-scale farms (Akhtar *et al.*, 2015; Jin *et al.*, 2018). Application of biochar to soil offers numerous benefits, including enhanced carbon sequestration, improved soil nutrient retention (Yuan *et al.*, 2011), reduced greenhouse gas emissions, modified soil microbial community diversity, and increased plant growth (Xie *et al.*, 2015; Alkharabsheh *et al.*, 2021). Notably, biochar holds great potential as an ecological remediation agent for coastal salinized soils, particularly in resource-limited regions requiring low-input salinity mitigation (Fei *et al.*, 2019; Sun J H *et al.*, 2020). It exerts long-term effects on salinized soils. Its addition improves soil pore structure by promoting uniform pore distribution and increasing pore space variability, thereby decreasing soil bulk density, reducing compaction, and increasing water-holding capacity and effective water content (Sun *et al.*, 2021). In addition, the porous structure and high specific surface area of biochar enable strong adsorption of Na^+, decreasing its concentration in soil (Akhtar *et al.*, 2015). This decrease significantly reduces Na^+ accumulation in plants and maintains an optimal K^+/Na^+ ratio (Zheng *et al.*, 2018). Enhanced K^+ availability improves leaf water status and photosynthetic rates, alleviating both ionic toxicity and osmotic stress induced by soil salinity (Rao *et al.*, 2013; Chakraborty *et al.*, 2016). Furthermore, biochar application decreases the concentrations of superoxide anions and hydrogen peroxide (H_2O_2), thereby mitigating oxidative stress (Farhangi-Abriz and Torabian, 2017) and enhancing root growth and nutrient translocation capacity under salt stress in rice. Moreover, nutrient release from biochar increases the levels of available nutrients such as N, P, K, and Ca in salinized soils (Biederman and Harpole, 2013; Gao *et al.*, 2019), improving soil nutrient availability and enhancing rice productivity under salt stress (Zhang *et al.*, 2019).

Exogenous plant hormone application

Phytohormones are key signaling molecules that coordinate the adaptive responses of plants to various abiotic stresses, including salinity, by regulating growth and stress tolerance pathways (Qin and Huang, 2020; Sackey *et al.*, 2025). Recent studies have highlighted their roles in modulating ion homeostasis, redox balance, and photosynthetic efficiency under salt stress, providing promising avenues for crop improvement.

Exogenous gibberellic acid (GA) application enhances salt tolerance in rice by orchestrating numerous physiological adjustments. It increases the accumulation of osmolytes (*e.g.*, proline, soluble sugars, and proteins) and essential inorganic nutrients (*e.g.*, K, Mg, and Ca) and the contents of chlorophyll and phenolic compounds to mitigate oxidative damage. Mechanistically, GA_3 upregulates genes encoding monolactosyl diacylglycerol synthase and phospholipid metabolism-related enzymes, promoting lipid biosynthesis and stabilizing the chloroplast membrane structure under salinity (Liu *et al.*, 2023). These changes collectively reduce membrane permeability, alleviate ionic toxicity, and enhance plant growth under salt stress (Wang *et al.*, 2020).

Salicylic acid (SA) is a key factor regulating salt tolerance in rice. Exogenous SA application can enhance the absorption of nutrients such as Ca^{2+}, PO_4^{3-}, and K while reducing the accumulation of Na^+ and Cl^-, thereby maintaining ionic balance (Ahmad *et al.*, 2022). In addition, SA enhances the activities of antioxidant enzymes such as superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT), reducing ROS levels and improving photosynthetic efficiency (Ahanger *et al.*, 2020; Yang *et al.*, 2023). Application of 1 mmol L^{-1} SA can increase germination rate, root and stem lengths, plant height, number of grains per spike, number of saturated grains per spike, 1 000-grain weight, number of spikes per plant, yield, and carbohydrate and protein contents in rice (Jini and Joseph, 2017).

As a plant steroid hormone, brassinolide (BR) modulates salt stress responses through integrated physiological and molecular pathways (Nolan *et al.*, 2020). Exogenous 24-epibrassinolide application maintains endogenous hormonal balance by increasing IAA, zeatin, and SA levels while downregulating ABA level, thereby promoting plant growth under salinity (Tanveer *et al.*, 2018). Brassinolide enhances antioxidant capacity by increasing the activities of SOD, ascorbate peroxidase, and CAT and the expression of related genes, reducing MDA accumulation. In addition, BR protects photosynthetic machinery by regulating stomatal dynamics, pigment content, and light energy utilization, ensuring efficient carbon assimilation under salt stress (Mu *et al.*, 2022a; Wu *et al.*, 2025).

Application of strigolactones (SLs) can enhance the growth of rice seedlings and increase POD and SOD activities and intercellular CO_2 concentration under salt stress, significantly decreasing MDA level and alleviating salt stress-induced damage. In addition, SLs have positive effects on the photosynthetic parameters of rice seedlings, such as the net photosynthetic rate, transpiration rate, stomatal conductance, and intercellular CO_2 concentration, which are correlated with SL concentration (Ling *et al*., 2020).

Application of JA can improve rice growth under salt stress. Studies have shown that JA can increase leaf water potential, photosynthetic rate, the maximum quantum yield efficiency of photosystem II, and the contents of K, Ca, and Mg while reducing Na accumulation in rice plants (Kang *et al*., 2005). In addition, it increases the activities of antioxidant enzymes under salt stress, effectively protecting rice seedlings against salt stress-induced damage in early growth stages (Sheteiwy *et al*., 2021).

Melatonin, a ubiquitous and multifunctional plant signaling molecule, has been shown to improve salt tolerance in rice by upregulating K^+ transport genes, regulating K^+ homeostasis, and scavenging hydroxyl radicals (Liu *et al*., 2020). It also enhances root architecture and reduces electrolyte leakage under high salinity, thereby improving photosynthetic capacity (Yan *et al*., 2020; Altaf *et al*., 2021). The simultaneous application of melatonin and Ca can reduce MDA and H_2O_2 levels, increase proline and chlorophyll contents, and promote dry matter accumulation by enhancing K and Ca uptake (Ebrahimi *et al*., 2023; Vafadar and Ehsanzadeh, 2023).

In addition, several non-enzymatic antioxidants, such as glutathione and ascorbic acid, play a crucial role in maintaining ROS homeostasis under salt stress. Exogenous application of glutathione and ascorbic acid reduces ROS accumulation, enhances antioxidant enzyme activity, and improves salt tolerance by modulating redox signaling pathways (Chen *et al*., 2023; Cao *et al*., 2024).

HT-PGPB inoculation

Rhizosphere microorganisms form intricate symbiotic networks with plants, wherein microbial consortia, rather than a single species, drive plant adaptation to adverse environments through synergistic interactions. As functional microorganisms with strong growth-promoting and salt-tolerance-enhancing traits, HT-PGPB thrive under high osmotic stress and abnormal salt concentrations (Porcel *et al*., 2015). The inoculation of HT-PGPB can enhance plant salt tolerance through coordinated mechanisms, such as accumulating osmolytes (*e.g*., proline, glutamate, and soluble sugars) to maintain root water conductivity, inhibiting Na uptake, activating host stress responses to scavenge ROS, and improving water and essential nutrient uptake under salt stress (Siddiqui *et al*., 2022; Álvarez *et al*., 2023). The efficacy of HT-PGPB is amplified when they interact with other microbial taxa, such as arbuscular mycorrhizal fungi (AMF) and cyanobacteria, collectively modulating soil properties and plant responses to salinity. For instance, N-fixing HT-PGPB (*e.g*., *Azospirillum brasilense*) and cyanobacteria (*e.g*., *Anabaena oryzae*) can synergistically alleviate N limitation. Cyanobacteria fix atmospheric dinitrogen and release ammonia, whereas HT-PGPB convert the released ammonia into plant-available forms through nitrification, increasing the total N content of soil by 15%–25% under salinity. Furthermore, microbial consortia can strengthen soil physical structure through coordinated production of exopolysaccharides and organic acids (Sun L *et al*., 2020). Exopolysaccharides bind to Na^+ to reduce root Na^+ uptake, whereas organic acids decrease soil pH, increasing Ca^{2+} and Mg^{2+} to displace exchangeable Na^+ from soil colloids (Anshu *et al*., 2022; Saranya *et al*., 2022). In addition, synergistic interactions between AMF and *Trichoderma harzianum* under salt stress induce the synthesis of specific secondary metabolites (*e.g*., oxaloacetic acid, Δ^1-piperidine-6-carboxylic acid, and cadaverine), further promoting plant growth (Eftekhari *et al*., 2025).

Owing to their low cost, ease of propagation from local isolates, and compatibility with traditional practices, HT-PGPB are particularly suitable for developing regions. By synergistically improving soil structure, nutrient cycling, and plant stress tolerance, HT-PGPB inoculation represents a sustainable strategy for revitalizing salt-affected soils, from coastal rice paddies to inland saline fields, and enhancing crop productivity (Mahmud *et al*., 2023; Abbas *et al*., 2024).

Nanoparticle (NP) application

In sustainable agricultural development, nanotechnology is considered the fifth revolutionary technology (Ioannou *et al*., 2020), with its ability to improve crop yields under environmental stress receiving significant attention (Khan *et al*., 2025). Nanoparticles exhibit high affinity for and are readily absorbed by plant roots and buds, thereby enhancing the efficacy of micronutrients in fertilizers (Kolenčík *et al*., 2020; Tanveer *et al*., 2023). As a crucial plant growth factor, zinc (Zn) activates the synthesis of proteins, sugars, carbohydrates, and amylases. This process enhances photosynthetic activity, glucose production, and carbohydrate biosynthesis, eventually promoting seed filling in cereal crops (Faran *et al*., 2019). Under low availability of N, P, and K, Zn applied as NPs outperforms conventional Zn formulations in increasing crop chlorophyll content and photosynthetic rate, thereby improving growth, development, and yield (Dimkpa *et al*., 2017; Adil *et al*., 2022). Specifically, Zn sulfate NPs can enhance soil Na adsorption and pH regulation, maintain nutrient balance, and increase the bioavailability of K and P in saline soils (Ahmed *et al*., 2023). In addition, foliar application of Zn oxide (ZnO) NPs effectively improves nutrient use efficiency and yield components in rice, leading to increased grain production (Fakharzadeh *et al.*, 2020; Itroutwar *et al.*, 2020).

Nanotriggering, a new technology involving the use of NPs to enhance seed germination and initial growth, has been used to improve rice seed germination and seedling vigor under salt stress (Mu *et al.*, 2024). For instance, nanosilver priming can significantly enhance germination rates and seedling vigor by increasing α-amylase activity and aquaporin gene expression during rice seed germination (Mahakham *et al.*, 2017). Studies have shown that the combined application of plant growth-promoting rhizobacteria (*e.g.*, *Pseudomonas koreensis* and *Bacillus coagulans*) and silicon NPs can enhance the antioxidant capacity of salt-stressed rice and mitigate salt-induced damage (Alharbi *et al.*, 2022). Similarly, the combined application of microorganisms and magnesium oxide NPs increases intracellular osmolyte levels, reduces plant Na accumulation, and enhances photosynthetic pigments, growth, and yield in salt-stressed sweet potatoes (El-Mageed *et al.*, 2022).

To maintain the health, functionality, and sustainability of both natural and agricultural ecosystems, the application of NPs for alleviating salt stress must strictly adhere to product guidelines, application protocols, and safety measures to ensure efficacy and environmental safety. Nanomaterials, such as ZnO NPs and nanosilver, are more feasible in technologically advanced regions, where high-cost synthesis and environmental risk assessment frameworks can be readily implemented. Owing to high production costs and limited technical capacity, nanomaterials are less accessible in developing nations, where low-cost alternatives such as organic fertilizers or microbial inoculants are prioritized (Fakharzadeh *et al.*, 2020; Ahmed *et al.*, 2023).

Ca-based soil amendment application

Calcium-based soil conditioners, which contain bioavailable Ca as their core functional component, play an important role in mitigating soil salinization, particularly in rice-growing regions characterized by a high ESP (Fan *et al.*, 2025). Common types include lime (calcium carbonate or calcium oxide) and gypsum (calcium sulfate dihydrate), each with distinct mechanisms (Xu *et al.*, 2023). Lime acts primarily in moderately alkaline-sodic soils (pH 8.5–10) by gradually releasing Ca^{2+} through dissolution, which displaces the adsorbed Na^{+} from clay colloids and reduces ESP. This process mitigates clay dispersion, promotes aggregation, and buffers extreme pH, thereby enhancing the activities of microbes (*e.g.*, nitrifying bacteria) and increasing the bioavailability of P and micronutrients such as iron and Zn (Wu *et al.*, 2021). The low cost and widespread availability of lime make it a preferred choice in resource-limited regions. Gypsum exhibits high solubility, enabling rapid Ca^{2+} release to displace Na^{+} in soil, which is an advantage in poorly drained rice paddies where lime dissolution is limited by anaerobic conditions. By supplying both Ca^{2+} and sulfate ions, gypsum enhances soil aggregate stability and hydraulic conductivity, facilitating Na^{+} leaching from the root zone (Zhang *et al.*, 2021; Qadir *et al.*, 2022). Notably, the combination of Ca-based amendments with other strategies can amplify their efficacy. For instance, combining gypsum with biochar enhances Ca^{2+} retention in sandy soils, whereas its co-application with organic fertilizers stimulates microbial activity and nutrient cycling, collectively reducing oxidative stress, increasing antioxidant enzyme activity, and improving salt tolerance in rice (Hamoud *et al.*, 2024).

Scientific decision-making for diverse saline land types

Rice cultivation spans highly diverse agroecological zones, where salinity characteristics are shaped by distinct geomorphic and climatic drivers (Li *et al.*, 2023). The differences in the origin of soil salinity necessitate context-specific management strategies, as soil type, climate, and water availability collectively determine their efficacy. In coastal saline regions (*e.g.*, the Mekong Delta and coastal regions of Bangladesh), soils are predominantly classified as sandy loam with high permeability but low water-holding capacity. In humid climates, monsoon rainfall interacts with tidal inundation to introduce Na^{+} and Cl^{-} as primary salts with EC of 8–20 dS m^{-1}. Given these regional characteristics, strategies prioritizing rapid salt adsorption and enhanced water retention are more effective. High-porosity biochar can mitigate root-zone ionic toxicity by adsorbing Na^{+} (Sun *et al.*, 2021), and HT-PGPB consortia (*e.g.*, AMF and cyanobacteria) can strengthen N cycling and secrete exopolysaccharides. Combining these treatments with organic fertilizers can optimize soil structure, improving soil aggregate stability (Álvarez *et al.*, 2023). Inland saline-alkali regions (*e.g.*, Northwest China and arid regions of India) are characterized by the presence of clay with low permeability, arid/semi-arid climates (annual rainfall < 400 mm), and scarce freshwater. Salinity arises from parent material weathering and evaporation-driven salt accumulation, resulting in a high ESP and strong alkalinity (pH 8.5–10). Therefore, agronomic measures in these regions should focus on optimizing soil structure and ion exchange. Deep tillage (60–100 cm) breaks compacted soil layers, increasing water infiltration (Feng *et al.*, 2024). Calcium-based soil conditioners (*e.g.*, gypsum and lime) displace Na^{+} with Ca^{2+}, reducing ESP and modulating pH to enhance P and Zn availability (Wu *et al.*, 2021). In addition, inoculating local drought- and salt-tolerant microbes (*e.g.*, *Bacillus subtilis*) can enhance root penetration depth and synergistically alleviate salt stress in rice (Fadiji *et al.*, 2023). Regional economic and technological capacities further refine strategy selection. In technologically advanced regions, nanomaterials can be integrated with exogenous hormones to enhance antioxidant activity. However, in resource-limited regions, low-cost combinations such as straw return and Ca-based amendments are prioritized. Altogether, salinity mitigation strategies should be tailored to soil texture, climate, and resource availability to ensure efficient and sustainable rice production across diverse salt-affected regions.

CONCLUSIONS AND FUTURE OUTLOOK

Soil salinization severely threatens global agriculture by altering soil properties and nutrient availability. Enhancing rice production on salinized soils is essential for promoting sustainable agriculture and global food security. Given the adverse effects of saline soils on crop growth, we comprehensively reviewed effective strategies for improving salt tolerance in rice, including organic fertilization, deep tillage, and application of biochar, exogenous growth hormones, HT-PGPB, nanomaterials, and Ca-based soil amendments. Targeted, evidence-based implementation of these measures, tailored to local conditions, holds promise in mitigating salt stress, facilitating soil restoration, and enhancing crop productivity. Given the significant regional variations in the drivers and severity of salinization, future studies should focus on quantifying region-specific damage severity, identifying dominant stressors, and developing targeted salinity mitigation or crop cultivation strategies. Notably, agricultural intervention measures require rigorous cost-benefit assessments to balance yield increases with economic feasibility. In addition, combining technological advancements with existing agricultural practices may promote sustainable improvements in the salt tolerance and yield of rice.

DECLARATION OF COMPETING INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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CONTRIBUTION OF AUTHORS

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