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Endophyte-mediated mechanisms of drought and salinity tolerance in rice: physiological, molecular, and field perspectives

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ABSTRACT

Rice (*Oryza sativa* L.) is highly susceptible to drought and salinity, two major abiotic stresses that severely constrain global productivity under climate change. Endophytic microorganisms have emerged as promising biological tools for enhancing stress tolerance; however, their mechanisms and field applicability in rice remain insufficiently integrated. This review synthesizes current advances in rice–endophyte interactions with a specific focus on mechanistic and functional outcomes. Evidence from bacterial and fungal endophytes, including *Bacillus*, *Pseudomonas*, *Enterobacter*, and *Trichoderma* spp., demonstrates improved drought and salinity tolerance through measurable traits such as enhanced root architecture, increased water-use efficiency, maintenance of Na^+/K^+ homeostasis, and improved biomass and yield stability. These effects are mediated via key pathways including ACC deaminase activity (ethylene regulation), modulation of antioxidant systems (SOD, CAT, APX), osmolyte accumulation, and hormonal crosstalk involving abscisic acid (ABA), indole-3-acetic acid (IAA), and gibberellins. Under salinity, endophytes contribute to ion homeostasis through regulation of transporters such as HKT1;5, while under drought they enhance hydraulic conductivity via aquaporin regulation through plasma membrane intrinsic proteins (PIPs) and tonoplast intrinsic proteins (TIPs). Despite promising results under controlled conditions, inconsistencies in field performance remain a major limitation due to genotype dependence, environmental variability, and challenges in colonization and inoculum stability. This review integrates molecular, physiological, and applied perspectives and proposes a framework for linking rice genotype, endophyte function, and environmental conditions to improve reproducibility and field-scale application. These insights provide a foundation for developing climate-resilient rice systems through targeted microbial inoculants.

1. Introduction

Rice (*Oryza sativa* L.) is a major staple crop that supplies more than half of the global population's caloric intake (Ganie et al., 2022; Ngalimat et al., 2021). However, rice productivity is increasingly threatened by climate change–driven abiotic stresses, particularly drought and salinity, which are among the most severe constraints across major rice-growing regions (Hussain et al., 2020; Pickson et al., 2021; Dar et al., 2021; Saud et al., 2022). Projected changes in rainfall patterns, rising temperatures, and sea-level rise are expected to further intensify these stresses, leading to substantial yield instability if effective mitigation strategies are not implemented (Dar et al., 2021; Sarma et al., 2023; Panda et al., 2021). Conventional approaches, including irrigation management, soil amendments, and the breeding of stress-tolerant cultivars, have achieved only limited success. For instance, irrigation management is often labor-intensive and difficult to optimize under unpredictable water availability, while soil amendments typically exhibit slow and site-specific impacts on soil health and crop performance. Similarly, breeding for stress tolerance is a lengthy process with slow genetic gains, and improved cultivars frequently show

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genotype-specific responses and inconsistent performance under variable environmental conditions (Panda et al., 2021; Yang et al., 2019; Upadhyaya and Panda, 2019).

In recent years, plant-associated microbiomes have emerged as important determinants of plant stress resilience (Shaffique et al., 2023; Poudel et al., 2021; Liu et al., 2020). Among these, endophytes—microorganisms that colonize internal plant tissues without causing disease—have gained attention due to their stable association with host plants and their ability to influence plant physiological and molecular processes (Yang et al., 2019; Upadhyaya and Panda, 2019; Shaffique et al., 2023; Poudel et al., 2021; Liu et al., 2020; Rana et al., 2019; Yadav, 2020; Lee et al., 2004; Das and Varma, 2009; Verma et al., 2021). In rice, several bacterial and fungal endophytes, including *Bacillus*, *Pseudomonas*, *Enterobacter*, and *Trichoderma* species, have been shown in experimental studies to enhance tolerance to drought and salinity. For example, inoculation with *Bacillus* and *Pseudomonas* strains has been reported to improve root architecture, biomass accumulation, and water-use efficiency under water-deficit conditions, while *Trichoderma* spp. have been associated with improved ion homeostasis and reduced Na^{+} accumulation under salinity stress. These effects are supported by primary studies demonstrating measurable improvements in plant growth and physiological traits under controlled and field conditions (Shaffique et al., 2023; Poudel et al., 2021; Liu et al., 2020; Rana et al., 2019; Yadav, 2020; Lee et al., 2004; Das and Varma, 2009; Verma et al., 2021).

These beneficial effects are mediated through multiple interconnected mechanisms. For instance, ACC deaminase (ACCD; EC 3.5.99.7)–producing endophytes reduce stress-induced ethylene levels, thereby promoting root elongation and improving plant growth under osmotic stress conditions (Morsy et al., 2020; Ullah et al., 2019; Pandey et al., 2019). Endophytes can also modulate phytohormone signaling pathways involving abscisic acid (ABA), indole-3-acetic acid (IAA), and gibberellins (GA). For example, several *Bacillus* and *Pseudomonas* strains have been reported to alter endogenous IAA levels and enhance root system architecture, while other endophytes influence ABA-mediated stomatal regulation and stress-responsive gene expression under drought conditions (Wahab et al., 2022; Khan et al., 2023; Ma et al., 2020a). Under salinity stress, endophytes contribute to Na^{+} exclusion and maintenance of Na^{+}/K^{+} homeostasis through modulation of ion transport systems such as HKT1; 5 (Bundó et al., 2022; Rodríguez-Navarro and Rubio, 2006; Ali et al., 2021; Shahid et al., 2020; Yildiz et al., 2020; Bouzouina et al., 2021). In contrast, under drought stress, they enhance water uptake and transport by influencing root architecture and regulating aquaporin expression (PIPs/TIPs), thereby improving plant water status and hydraulic conductivity (Ranjan et al., 2022; Kim et al., 2020). These findings suggest that endophytes function as integrative regulators linking molecular mechanisms with whole-plant physiological responses in rice.

Despite these advances, current knowledge remains fragmented and lacks systematic integration. While several studies have successfully linked specific endophyte strains to defined plant traits and underlying molecular pathways, a substantial proportion of the literature still focuses on isolated physiological or biochemical responses without comprehensive integration across scales. In addition, most findings are derived from controlled environments, whereas evidence from field conditions remains comparatively limited. This gap restricts understanding of how endophyte-mediated effects vary across rice genotypes, soil types, and diverse environmental conditions. Furthermore, the interaction between intrinsic rice stress tolerance mechanisms and endophyte-mediated responses remains insufficiently explored, limiting the development of a coherent framework for practical application.

Therefore, there is a critical need to integrate the "genotype × endophyte × environment" concept into rice stress biology to improve reproducibility and field applicability. This review aims to provide a focused synthesis of endophyte-mediated mechanisms underlying drought and salinity tolerance in rice, including key processes such as nutrient acquisition, phytohormone modulation, osmolyte accumulation, and ion homeostasis, with an emphasis on mechanistic clarity, functional outcomes, and experimental validation. It further highlights recent advances in omics-based approaches and microbiome engineering, and identifies key limitations and research priorities necessary to translate laboratory findings into sustainable, field-level solutions for climate-resilient rice production.

2. Abiotic stresses in rice

Rice (*Oryza sativa* L.) is a major staple crop; however, its productivity is increasingly threatened by climate-driven abiotic stresses, particularly drought and salinity, which are widely recognized as major constraints in rice-growing regions (Ganie et al., 2022; Ngalimat et al., 2021; Hussain et al., 2020). These stresses have been reported to cause substantial yield losses—often ranging from 20 to 50% under severe drought and up to 50% or more under high salinity—depending on growth stage and severity. They reduce yield and grain quality by disrupting plant water balance, impairing photosynthesis, and causing ionic toxicity and nutrient imbalance.

Drought stress limits water availability, leading to reduced turgor, impaired photosynthesis, and increased oxidative stress, while salinity imposes both osmotic stress and ionic toxicity through excessive Na^{+} accumulation and nutrient imbalance (Abbas and Mayo, 2021a; Liu et al., 2019; Jia et al., 2019; Rashid et al., 2023; Hussain et al., 2019). Rice is particularly sensitive to these stresses, largely due to its relatively shallow root system, which restricts access to deeper soil moisture, and its limited capacity for salt exclusion compared to more tolerant cereal crops (Fahad et al., 2019; Aguilar-Rivera et al., 2019; Watts et al., 2023). Under these conditions, maintaining Na^{+}/K^{+} balance and efficient water uptake becomes essential for stress tolerance.

Although other stresses, such as temperature extremes and heavy metal contamination, also affect rice productivity, their roles are secondary compared to drought and salinity-driven yield loss (Dar et al., 2021; Hussain et al., 2019; Fahad et al., 2019; Aguilar-Rivera et al., 2019). Consequently, current research increasingly focuses on biological strategies, particularly endophytic microorganisms, which enhance stress tolerance by improving water and nutrient uptake, regulating ion transport, and strengthening antioxidant defense systems (Shaffique et al., 2023; Verma et al., 2021; Watts et al., 2023).

2.1. Drought and salinity stress

Drought and salinity impose overlapping but distinct physiological constraints on rice. Drought primarily affects plant water status, leading to reduced cell turgor, which in turn limits leaf expansion, suppresses photosynthetic activity, and constrains root–shoot growth, as consistently reported in physiological studies (Poudel et al., 2021; Wahab et al., 2022; Yang et al., 2021). In contrast, salinity introduces both osmotic stress and ionic toxicity, resulting in excessive Na^{+} accumulation, disruption of enzyme activity, and membrane instability (Shahid et al., 2020; Liu et al., 2019; Jia et al., 2019; Rashid et al., 2023).

Under drought stress, adaptive responses such as improved root architecture, increased root depth, and enhanced water transport capacity play a critical role in maintaining plant function by facilitating access to deeper soil moisture and sustaining plant water status, as demonstrated in physiological studies (Das and Varma, 2009; Ranjan et al., 2022; Kim et al., 2020). Under salinity stress, the ability to regulate Na^{+} exclusion and maintain a low Na^{+}/K^{+} ratio is essential for protecting metabolic processes and preserving photosynthetic function (Bundó et al., 2022; Rodríguez-Navarro and Rubio, 2006; Ali et al., 2021; Bouzouina et al., 2021). These stress-specific traits represent key targets for endophyte-mediated improvement in rice.

2.2. ROS and stress responses

Abiotic stresses such as drought and salinity disrupt cellular homeostasis and promote the excessive production of reactive oxygen species (ROS), including superoxide radicals ($O_2^{\bullet -}$), hydrogen peroxide (H_2O_2), hydroxyl radicals (•OH), and singlet oxygen ($^1O_2$). These ROS are primarily generated in chloroplasts, mitochondria, peroxisomes, and the plasma membrane during stress-induced disturbances in photosynthetic and respiratory electron transport (Sachdev et al., 2021; Hasanuzzaman et al., 2020; Al Mahmud et al., 2019). Excessive ROS accumulation causes oxidative damage to lipids, proteins, nucleic acids, and cellular membranes, ultimately impairing plant growth and productivity if not effectively controlled (Sachdev et al., 2021; Hasanuzzaman et al., 2020; Al Mahmud et al., 2019).

To maintain cellular redox homeostasis, plants activate both enzymatic and non-enzymatic antioxidant defense systems. The enzymatic antioxidant network includes superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX), which sequentially detoxify ROS and limit oxidative damage. Non-enzymatic antioxidants, including ascorbate, glutathione, carotenoids, and phenolic compounds, further contribute to ROS scavenging and cellular protection under stress conditions (Hasanuzzaman et al., 2020; Al Mahmud et al., 2019; Kumari et al., 2020; Gill and Tuteja, 2010).

Recent studies demonstrate that endophytic microorganisms contribute to ROS homeostasis by enhancing antioxidant defense capacity and reducing oxidative damage in host plants. Endophytes have been reported to increase the activities of antioxidant enzymes such as SOD, CAT, and APX, decrease lipid peroxidation, and improve membrane stability under drought and salinity stress. In addition, endophyte-mediated modulation of phytohormone signaling and osmotic adjustment further contributes to maintaining cellular redox balance and enhancing stress tolerance in rice (Gupta et al., 2023; Sun et al., 2020).

2.3. Impact of stress on plants

Abiotic stresses such as drought and salinity adversely affect rice growth by disrupting key physiological, biochemical, and metabolic processes. Water deficit and excessive salt accumulation reduce photosynthetic efficiency, impair respiration, restrict nutrient and water uptake, and disturb cellular ion homeostasis, ultimately leading to reduced biomass production and grain yield (Wahab et al., 2022; Wu et al., 2022). These stresses also induce excessive accumulation of reactive oxygen species (ROS), resulting in oxidative damage to lipids, proteins, and nucleic acids despite the activation of antioxidant defense systems (Sachdev et al., 2021; Hasanuzzaman et al., 2020; Al Mahmud et al., 2019; Kumari et al., 2020; Gill and Tuteja, 2010). Furthermore, drought and salinity alter hormonal balance, promote stomatal closure, reduce leaf expansion, and modify root architecture, thereby limiting carbon assimilation and overall plant productivity (Wahab et al., 2022; Yang et al., 2021; Wu et al., 2022).

In addition to these direct effects on plant physiology, abiotic stress also influences plant–microbe interactions by modifying root exudation patterns and the composition of root-associated microbial communities (Liu et al., 2020). Beneficial endophytes can partially alleviate these adverse effects by improving nutrient acquisition, modulating phytohormone signaling, enhancing antioxidant defense systems, promoting osmolyte accumulation, and maintaining cellular homeostasis under stress conditions (Verma et al., 2021; Watts et al., 2023; Ma et al., 2020b). The major mechanisms underlying endophyte-mediated drought and salinity tolerance in rice are summarized in Fig. 1. Representative endophytic microorganisms, their mechanisms of action, and their effects on drought and salinity tolerance in rice and related cereals are summarized in Table 1. These beneficial plant–endophyte interactions provide the basis for the mechanistic pathways discussed in the following sections.

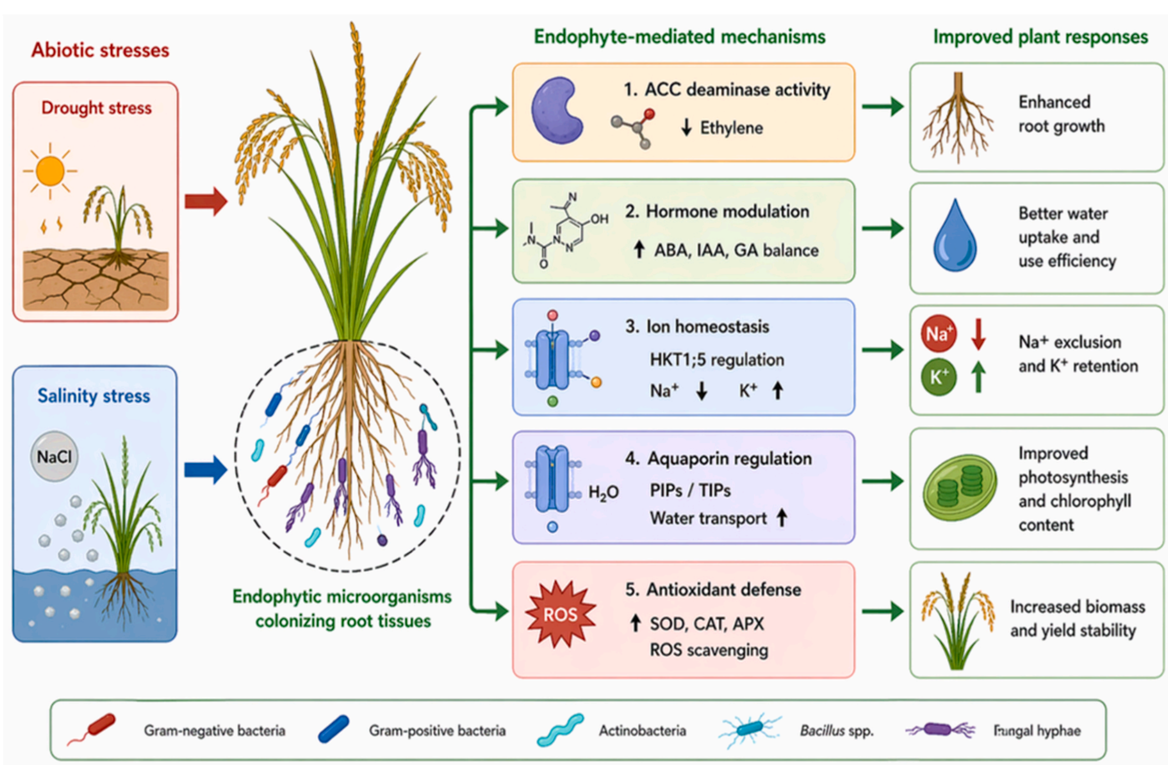

Fig. 1. Endophyte-mediated mechanisms enhancing drought and salinity tolerance in rice.

Table 1
Endophytic microorganisms enhancing drought and salinity tolerance in rice and closely related cereals.

Stress Type	Endophyte	Host Plant	Key Mechanism	Observed Effect	Reference
Salinity	*Bacillus subtilis*	*Oryza sativa*	ACCD activity; antioxidant enhancement	Reduced Na^+ toxicity, improved growth and chlorophyll content	(Sagar et al., 2020; Jaemsaeng et al., 2018)
Salinity	*Pseudomonas* spp.	*Oryza sativa*	Regulation of Na^+/K^+ homeostasis; ion transport modulation	Improved ion balance and biomass under salt stress	(Chakrovarty et al., 2026; Shilev, 2020)
Salinity	*Enterobacter* spp.	*Oryza sativa*	ACCD activity; osmolyte production	Enhanced seedling vigor and stress tolerance	(Sagar et al., 2020; Jaemsaeng et al., 2018; Chakrovarty et al., 2026; Shilev, 2020; Kumawat et al., 2023)
Drought	*Bacillus cereus*	*Oryza sativa* (or cereals)	Osmolyte accumulation; antioxidant activity	Improved water status and membrane stability	Roy Choudhury et al. (2023)
Drought	*Pseudomonas* spp.	*Oryza sativa* (or cereals)	IAA production; root growth promotion	Enhanced root development and drought tolerance	Ullah et al. (2019)
Drought	*Gluconacetobacter diazotrophicus*	Cereals	IAA and proline production	Improved osmotic adjustment and growth under drought	Dubey et al. (2021)
Drought	Fungal endophytes (*Paraphoma*, *Cladosporium*)	Cereals	Root architecture modification	Increased water uptake and drought resilience	Nong et al. (2023)
Salinity	Endophytic consortia	*Oryza sativa*	Antioxidant enzyme activation (SOD, CAT, APX)	Reduced oxidative damage and improved physiological performance	(Gupta et al., 2023; Sun et al., 2020)

2.4. Endophytes and their role in rice stress adaptation

Endophytes are microorganisms that colonize internal plant tissues, typically without causing disease symptoms in their host, and are widely distributed in the roots, stems, and leaves of rice plants (Li et al., 2019; Jha et al., 2019). In rice, these microorganisms establish close associations with host tissues, enabling direct modulation of physiological and molecular processes involved in stress adaptation.

Endophytic microbes contribute to drought and salinity tolerance by enhancing key plant functions, including nutrient acquisition, root system development, and stress signaling pathways. For example, endophytes such as *Bacillus* and *Pseudomonas* species produce bioactive compounds including indole-3-acetic acid (IAA), siderophores, and phosphate-solubilizing enzymes, which enhance nutrient availability and stimulate root growth under stress conditions (Jha et al., 2019; Kumari et al., 2023). These microbial activities have been associated with measurable improvements in plant traits, including increased biomass accumulation, root length, and water-use efficiency under drought and salinity stress.

Under drought and salinity stress, endophytes regulate plant responses through multiple mechanisms, including modulation of phytohormones, activation of antioxidant defense systems, and enhancement of osmotic adjustment. In rice, inoculation with beneficial endophytes such as *Bacillus*, *Pseudomonas*, and *Trichoderma* species has been associated with increased chlorophyll content, improved photosynthetic performance, reduced lipid peroxidation, and enhanced tolerance to osmotic stress, as demonstrated in controlled and field-based studies (Verma et al., 2021; Morsy et al., 2020).

Collectively, these findings highlight the role of endophytes as key regulators linking microbial activity with plant physiological responses, providing a foundation for developing sustainable strategies to improve rice resilience under drought and salinity stress.

2.5. Endophyte-driven mechanisms for enhancing plant growth and stress tolerance in rice

Endophytic microorganisms play a key role in enhancing rice growth and stress tolerance by modulating physiological, biochemical, and molecular processes (Verma et al., 2021; Watts et al., 2023). In rice, inoculation with endophytes such as *Bacillus*, *Pseudomonas*, *Enterobacter*, and *Trichoderma* species has been shown to improve measurable traits, including root system architecture, biomass accumulation, nutrient uptake efficiency, and water-use efficiency under both optimal and stress conditions, as demonstrated in multiple experimental studies (Verma et al., 2021; Watts et al., 2023).

One major mechanism involves improved nutrient acquisition, whereby endophytes enhance the availability and uptake of essential elements such as nitrogen, phosphorus, and potassium through processes including biological nitrogen fixation, phosphate solubilization, and siderophore-mediated iron acquisition, thereby promoting plant growth and metabolic activity (Watts et al., 2023). In addition, endophytes regulate phytohormone signaling by producing or modulating hormones such as indole-3-acetic acid (IAA), abscisic acid (ABA), and gibberellins (GA), which influence root development, stomatal conductance, and stress adaptation (Wahab et al., 2022; Khan et al., 2023; Ma et al., 2020a).

Endophytes also contribute to stress tolerance through ACCD activity, which lowers stress-induced ethylene levels and thereby promotes root elongation and plant growth under drought and salinity conditions, as demonstrated in studies involving endophytic bacteria such as *Bacillus* and *Pseudomonas* spp. (Morsy et al., 2020; Ullah et al., 2019; Pandey et al., 2019; Kamran et al., 2022a). Furthermore, endophyte-mediated osmolyte accumulation (e.g., proline and soluble sugars) supports osmotic adjustment, helping to maintain cellular turgor under water deficit.

Another critical mechanism involves the regulation of oxidative stress. Endophytes enhance antioxidant defense systems in rice by increasing the activity of key enzymes such as superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX), thereby reducing reactive oxygen species (ROS) accumulation and limiting cellular damage under stress conditions, as demonstrated in studies involving endophytic bacteria such as *Bacillus* and *Pseudomonas* spp. (Gupta et al., 2023; Sun et al., 2020; Singh et al., 2023). This improved redox balance contributes to enhanced photosynthetic efficiency and overall plant performance.

In addition to abiotic stress tolerance, endophytes can contribute to plant health by suppressing pathogens through the production of antimicrobial compounds and the induction of plant defense responses, as reported in studies on endophytic bacteria and fungi such as *Bacillus*, *Pseudomonas*, and *Trichoderma* spp. (Gul et al., 2025; del C et al., 2020; Shahid et al., 2023). However, in the context of rice drought and salinity tolerance, their primary role lies in coordinating growth regulation, ion homeostasis, water balance, and oxidative stress mitigation.

Collectively, these mechanisms demonstrate that endophytes act as integrative regulators linking molecular pathways with whole-plant physiological responses in rice, making them promising tools for improving crop resilience under environmental stress.

3. Molecular mechanisms underlying endophyte-mediated stress tolerance in rice

Endophyte-mediated stress tolerance in rice is governed by several interconnected molecular mechanisms. Among the most extensively studied are ACCD-mediated ethylene regulation, HKT1; 5-mediated ion homeostasis, and aquaporin-mediated water transport, which collectively contribute to improved adaptation to drought and salinity stress (Verma et al., 2021; Ma et al., 2020a; Watts et al., 2023; Kamran et al., 2022a). The following subsections summarize these key molecular mechanisms and their roles in enhancing stress tolerance in rice. These molecular mechanisms operate in a coordinated manner rather than independently, collectively enhancing rice adaptation to drought and salinity stress through complementary physiological and biochemical pathways.

3.1. ACC deaminase-mediated ethylene regulation

ACCD produced by several bacterial and fungal endophytes catalyzes the conversion of 1-aminocyclopropane-1-carboxylate (ACC), the immediate precursor of ethylene, into α-ketobutyrate and ammonia, thereby lowering stress-induced ethylene levels in plants (del C et al., 2020; Shahid et al., 2023; Glick, 2014). Under drought and salinity stress, excessive ethylene accumulation inhibits root growth and accelerates senescence; accordingly, ACCD-producing endophytes have been shown to support plant growth under osmotic stress conditions, particularly through the promotion of root elongation and stress adaptation.

In rice, inoculation with ACCD-producing endophytes such as Enterobacter spp. And Bacillus spp. Has been shown to enhance seedling vigor, root elongation, and biomass accumulation under salinity and drought conditions in pot-based and controlled environment studies (Jaemsaeng et al., 2018; Kumawat et al., 2023). These improvements have been associated with reduced ethylene levels, increased chlorophyll content, and enhanced nutrient uptake efficiency, as reported in experimental studies (Jaemsaeng et al., 2018; Kumawat et al., 2023). Mechanistically, reduced ACC availability alleviates ethylene-mediated inhibition of auxin transport, thereby promoting lateral root formation and root system expansion (Kumawat et al., 2023; Fadiji et al., 2022).

In addition to growth regulation, ACCD activity is linked to improved oxidative stress tolerance. In rice, inoculation with ACCD-producing endophytes has been reported to increase the activities of antioxidant enzymes, including superoxide dismutase (SOD) and catalase (CAT), while reducing malondialdehyde (MDA) levels, indicating lower lipid peroxidation and enhanced cellular stability under stress conditions (Sagar et al., 2020; Gupta et al., 2021, 2022). These combined effects contribute to improved plant survival and physiological performance under both drought and salinity stress.

Despite its well-established role, the effectiveness of ACCD-mediated stress mitigation varies among endophyte strains and environmental conditions. Differences in enzyme activity, colonization efficiency, and host genotype compatibility can influence outcomes. Therefore, standardized evaluation of ACCD activity—typically involving enzyme assays and plant growth response measurements—along with validation under pot, microplot, and multilocation field conditions, is widely recommended to ensure reproducibility and practical applicability of ACCD-based bioinoculants in rice systems (Shahid et al., 2023; Gupta et al., 2021, 2022; Reshma and Dileep, 2024).

3.2. HKT1; 5-mediated ion homeostasis under salinity

Na^+ exclusion from photosynthetically active tissues is a central mechanism of salinity tolerance in rice. The high-affinity potassium transporter OsHKT1; 5, predominantly expressed in xylem parenchyma cells of the root stele, retrieves Na^+ from the xylem sap, thereby limiting its translocation to shoots and maintaining a low Na^+/K^+ ratio essential for ion homeostasis and metabolic stability under salinity stress (Rasheed et al., 2022; Sackey et al., 2025). Genetic and physiological studies, including analyses of contrasting rice genotypes and allele-specific variation, have demonstrated that favorable *OsHKT1;5* alleles significantly reduce Na^+ accumulation in leaves, thereby protecting photosynthetic tissues and improving growth performance under saline conditions (Ren et al., 2022; Kobayashi et al., 2017).

In rice, inoculation with beneficial endophytes, including Pseudomonas spp. And Bacillus spp., has been shown to enhance salinity tolerance by reducing Na^+ accumulation and improving Na^+/K^+ balance in pot-based and controlled environment studies (Chakrovarty et al., 2026; Shilev, 2020). These effects have been associated with improved membrane stability, increased chlorophyll content, and enhanced biomass accumulation under salt stress, as reported in experimental studies (Chakrovarty et al., 2026; Shilev, 2020). Mechanistically, endophytes may complement HKT1; 5-mediated ion regulation by reducing Na^+ bypass flow and promoting the development of root apoplastic barriers, such as suberization, which restrict excessive Na^+ entry into the vascular system (Chakrovarty et al., 2026).

In addition, endophytes modulate phytohormone signaling pathways, particularly abscisic acid (ABA) and cytokinins, which are known to regulate the expression and activity of ion transporters, including members of the HKT family, thereby contributing to improved ion homeostasis under salinity stress (Chakrovarty et al., 2026). Enhanced K^+ uptake and the accumulation of osmoprotectants further support cellular ion balance and help maintain membrane integrity under saline conditions (Shilev, 2020). The proposed mechanisms underlying endophyte-enhanced HKT1; 5-mediated ion homeostasis and Na^+ exclusion in rice under salinity stress are summarized in Fig. 2.

Despite these promising findings, the effectiveness of endophyte-mediated ion regulation varies depending on microbial strain, rice genotype, and environmental conditions, as demonstrated by differential responses observed across endophyte–host combinations and growth environments in several studies (Shilev, 2020; Sackey et al., 2025; Kobayashi et al., 2017). For example, certain endophytic strains show enhanced performance only in specific rice genotypes or under defined salinity levels, highlighting the context-dependent nature of these interactions. Therefore, integrating stress-tolerant OsHKT1; 5 alleles with functionally characterized endophytic inoculants represents a genotype-aware strategy for improving rice performance in saline soils. Future studies should focus on multi-omics validation, ionomic profiling, and multi-location field trials to ensure reproducibility and scalability of these approaches (Shilev, 2020; Sackey et al., 2025; Kobayashi et al., 2017).

3.3. Aquaporin-mediated water transport under drought and salinity

Aquaporins (AQPs), including PIPs and TIPs, are widely recognized as key regulators of water transport in rice roots, contributing to the control of radial and axial hydraulic conductivity under drought and salinity stress (Bai et al., 2021; Ding et al., 2019). Their activity is regulated by factors such as phosphorylation status, cytosolic PH, and redox conditions, enabling dynamic adjustment of membrane water permeability in response to environmental stress signals (Maurel et al., 2015; Verdoucq et al., 2014).

In rice, inoculation with beneficial endophytes has been shown to improve plant water status by enhancing aquaporin-mediated hydraulic conductivity in pot-based and controlled environment studies (Kamran et al., 2022b; Gao et al., 2022; Kuang et al., 2025). These effects are reflected in measurable traits such as increased relative water content, improved leaf water potential, and sustained photosynthetic activity under drought and salinity stress. Mechanistically, these responses may be linked to endophyte-induced modulation of abscisic acid (ABA) signaling, which is known to regulate aquaporin expression and activity at both transcriptional and post-translational levels, although direct evidence for this pathway in rice–endophyte interactions remains limited (Kamran et al., 2022b; Gao et al., 2022).

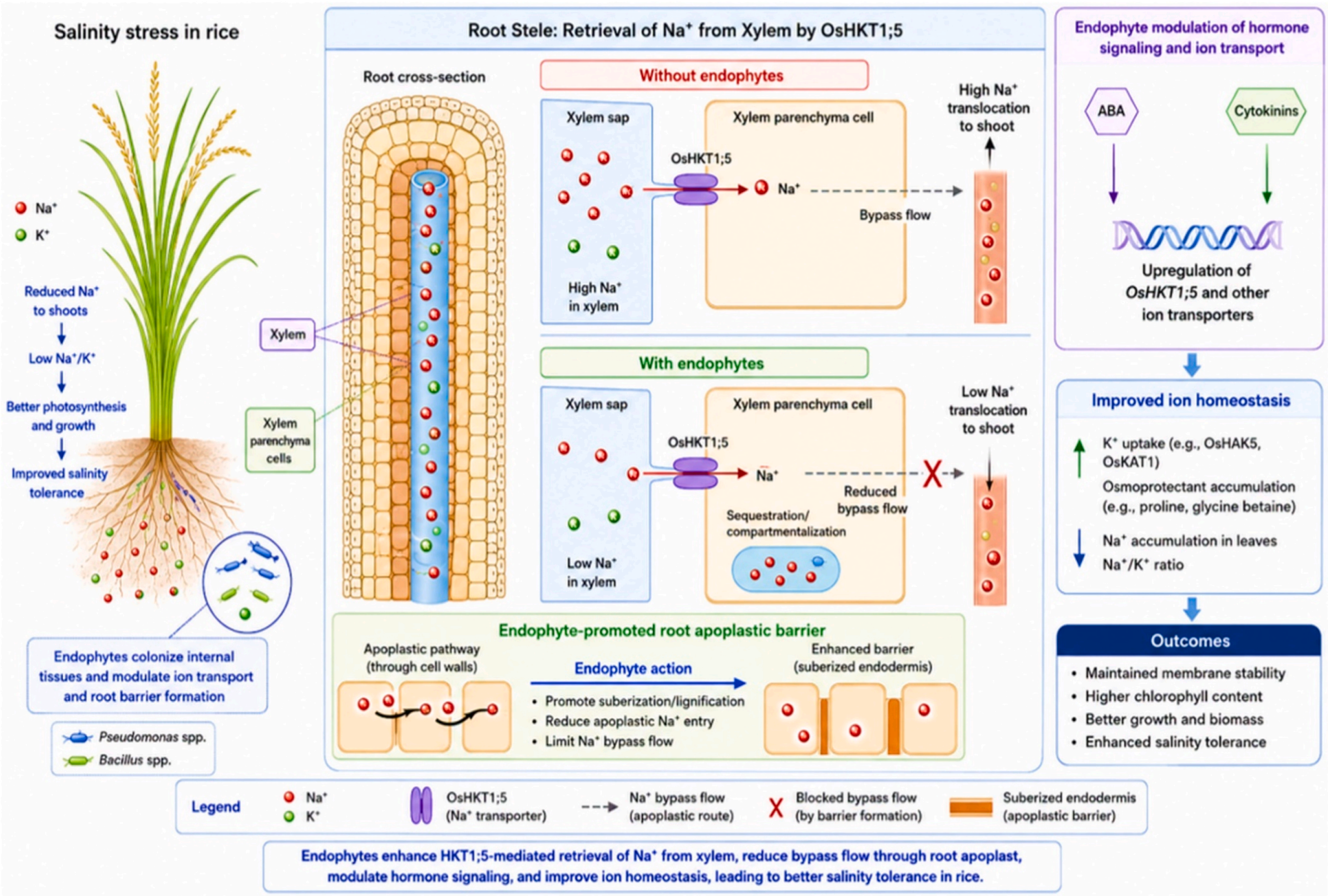

Fig. 2. Proposed mechanism of endophyte-enhanced HKT1; 5-mediated ion homeostasis and Na^+ exclusion in rice under salinity stress.

Endophytes may also contribute to maintaining aquaporin functionality under stress by reducing reactive oxygen species (ROS) accumulation and lipid peroxidation, thereby limiting oxidative damage to membrane proteins and helping to preserve water transport efficiency, as suggested by studies on endophyte-mediated oxidative stress mitigation (Gao et al., 2022). In addition, endophyte-mediated osmotic adjustment supports stable cellular water balance, further contributing to improved hydraulic performance.

Genotype-dependent variation in aquaporin expression has been linked to differences in drought avoidance and salinity tolerance in rice. Notably, endophyte inoculation has been associated with the upregulation of specific aquaporin genes, including *OsPIP1;3* and *OsPIP2* isoforms, which in some studies correlate with improved root hydraulic conductivity, enhanced water uptake, and increased plant survival under severe stress conditions (Ding et al., 2019; Kuang et al., 2025). However, the relationship between aquaporin gene expression and plant hydraulic performance is complex and context-dependent, varying with genotype, stress intensity, and environmental conditions, and is not consistently observed across all systems.

Despite these promising findings, the effectiveness of aquaporin-mediated responses depends on interactions among endophyte strain, host genotype, and environmental conditions. Therefore, integrated approaches combining physiological analyses (e.g., gas exchange, relative water content, ion profiling), genomic and transcriptomic characterization (e.g., gene expression analysis of aquaporins and stress-responsive genes), and hydraulic measurements (e.g., root hydraulic conductivity and aquaporin activity assays), together with multi-environment validation trials, are required to identify robust endophyte–rice combinations for improving water-use efficiency and stress resilience under field conditions. The integration of endophyte-mediated responses involved in drought and salinity tolerance, including ACCD-mediated ethylene regulation, HKT1; 5-mediated ion homeostasis, aquaporin-mediated water transport, phytohormone signaling, and ROS regulation, is summarized in Fig. 3.

4. Limitations and challenges in field application of endophytes

Despite promising results under controlled conditions, the performance of endophyte-based approaches in field environments remains inconsistent due to multiple interacting factors (Kamran et al., 2022a; Ren et al., 2022; Jayakumar et al., 2020). One major limitation is competition with native soil microbiota, where indigenous microbial communities can outcompete introduced endophytes for ecological niches and resources, thereby suppressing their establishment and persistence and leading to reduced colonization efficiency (Kamran et al., 2022a; Ren et al., 2022).

In addition, host genotype plays a critical role in determining the success of endophyte inoculation, as the same microbial strain may produce variable effects across different rice cultivars. For example, certain endophytic strains have been reported to enhance growth and stress tolerance in salt-tolerant cultivars but show limited or inconsistent effects in sensitive genotypes, reflecting differences in host–microbe compatibility and signaling interactions (Ma et al., 2020a; Jayakumar et al., 2020). Environmental heterogeneity further complicates these interactions; factors such as soil physicochemical properties (Ph, salinity, and nutrient availability), temperature fluctuations, and irrigation regimes significantly influence both microbial activity and plant response (Dar et al., 2021; Sarma et al., 2023; Panda et al., 2021).

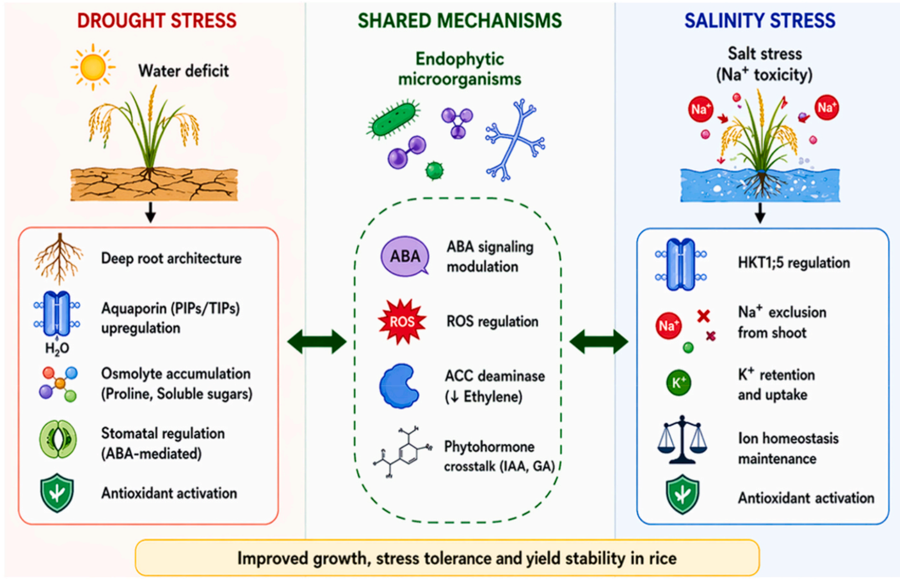

Fig. 3. Integrated model of endophyte-mediated mechanisms enhancing drought and salinity tolerance in rice.

Practical challenges related to inoculum application also contribute to inconsistent outcomes. Variations in inoculum dose, timing, formulation, and shelf-life can affect microbial viability and effectiveness (Watts et al., 2023; Ma et al., 2020b; Ren et al., 2022). Moreover, stress conditions in the field are highly dynamic and fluctuate over time, in contrast to the constant stress levels typically imposed in laboratory or pot-based studies. For example, intermittent drought cycles, fluctuations in soil salinity due to irrigation or rainfall, and temperature variability can alter microbial survival, colonization efficiency, and the consistency of plant responses, thereby limiting the transferability of results from controlled environments to field conditions (Abbas and Mayo, 2021b).

Another critical issue is the lack of standardized experimental protocols. Many studies do not consistently report essential parameters such as endophyte identity, inoculum viability, colonization efficiency, and environmental conditions, making reproducibility difficult (Morsy et al., 2020; Ren et al., 2022; Jayakumar et al., 2020). Furthermore, the majority of current research is based on controlled experiments, with limited validation under multi-location and multi-season field conditions (Abbas and Mayo, 2021b).

Addressing these limitations requires the development of standardized methodologies, integration of genotype-specific endophyte selection, and extensive field validation to ensure the reliability and scalability of endophyte-based strategies for improving rice tolerance to drought and salinity (Morsy et al., 2020; Abbas and Mayo, 2021b; Ren et al., 2022). The major factors limiting the field performance of endophyte-based strategies in rice are summarized in Fig. 4.

5. Integration of endophyte-mediated responses under drought and salinity

Drought and salinity impose both overlapping and distinct physiological constraints on rice, requiring coordinated adaptive responses at

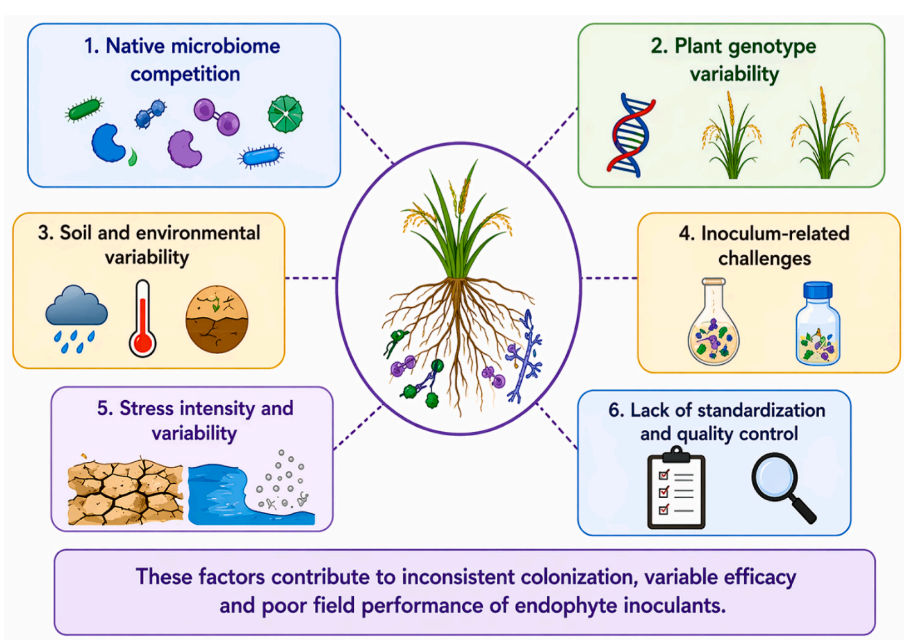

Fig. 4. Factors limiting field performance of endophyte-based strategies in rice.

molecular, cellular, and whole-plant levels. Both stresses initially induce osmotic imbalance, leading to reduced cellular turgor, inhibition of leaf expansion, and activation of common signaling pathways, including abscisic acid (ABA) accumulation, reactive oxygen species (ROS) signaling, and antioxidant defense mechanisms (Long et al., 2023; Chen et al., 2021; Asif et al., 2023). These shared responses provide key targets for endophyte-mediated regulation, particularly through modulation of hormone balance, enhancement of antioxidant systems, and improvement of water-use efficiency.

Despite these similarities, drought and salinity differ fundamentally in their downstream effects. Salinity stress introduces ionic toxicity, primarily through excessive Na^+ accumulation, which disrupts cellular ion homeostasis and damages photosynthetic tissues. In this context, mechanisms such as HKT1; 5-mediated Na^+ retrieval, maintenance of Na^+/K^+ balance, and reinforcement of root apoplastic barriers are critical for tolerance (Liu et al., 2023; Platten et al., 2013; Mansour, 2023). Endophytes contribute to these processes by enhancing ion regulation, improving membrane stability, and supporting K^+ uptake.

In contrast, drought stress primarily affects plant water relations, requiring efficient water acquisition and transport. Adaptive responses include enhanced root system architecture, increased root depth, and regulation of aquaporins (PIPs and TIPs) to maintain hydraulic conductivity under limited water availability (Andreo-Jimenez et al., 2023; Younas et al., 2025). Endophytes facilitate these processes by promoting root growth, modulating aquaporin expression, and improving osmotic adjustment.

Importantly, both stresses involve interconnected signaling networks, including ABA–ROS–Ca^{2+} pathways, where endophytes act as integrative modulators. By simultaneously influencing hormonal balance, redox homeostasis, and physiological processes, endophytes enhance plant resilience under combined or fluctuating stress conditions. However, the effectiveness of these interactions depends on the compatibility among rice genotype, endophyte strain, and environmental conditions. Therefore, targeted selection of endophytes based on specific plant traits and stress scenarios is essential for improving field-level performance.

6. Omics-based insights into Rice–Endophyte interactions

Advances in integrated omics technologies, including genomics, transcriptomics, metabolomics, and microbiome profiling, have significantly enhanced understanding of stress tolerance mechanisms in rice (Andreo-Jimenez et al., 2023; Younas et al., 2025). These approaches enable the identification of key regulatory genes, metabolic pathways, and microbial functions associated with drought and salinity adaptation.

Genome-wide association studies (GWAS) and transcriptomic analyses have identified several stress-responsive genes involved in ion homeostasis, hormone signaling, osmotic regulation, and antioxidant defense. For example, genes such as *OsHKT1;5*, *OsDRO1*, and *OsP5CS1* play critical roles in salinity tolerance, root system architecture, and osmoprotectant synthesis, respectively (Younas et al., 2025; Usman et al., 2023; Samreen et al., 2021). These traits are directly relevant to endophyte-mediated stress responses. Key rice genes associated with drought and salinity tolerance and their relevance to endophyte-mediated responses are summarized in Table 2.

Importantly, recent studies highlight the integration of plant and microbial omics, enabling characterization of endophytic communities and their functional traits. Metagenomic and microbiome analyses reveal that endophytes contribute to stress tolerance through mechanisms such as phytohormone production, ion regulation, and redox modulation. These findings support the development of targeted microbial inoculants based on functional traits identified through omics approaches. Overall, integrating plant genomics with microbiome data provides a powerful framework for understanding genotype–endophyte interactions and improving stress resilience in rice under field conditions.

7. Future perspectives and research directions

Future research should focus on integrating endophyte-based approaches with advanced genomic and microbiome engineering strategies to enhance stress tolerance in rice. These include genome-guided selection and editing of beneficial endophytes (e.g., CRISPR/Cas-based modification of stress-related traits), metagenomic and transcriptomic profiling to identify functionally important microbial communities, and the design of synthetic microbial consortia with complementary traits such as ACCD activity, phytohormone production, and nutrient solubilization. Such precision microbiome engineering approaches offer promising opportunities to develop endophyte-based solutions tailored to specific rice genotypes and environmental conditions.

In addition, the discovery and characterization of novel endophytes from diverse ecological niches may reveal unique mechanisms for improving plant resilience. However, a major priority is the validation of these approaches under field conditions. Multi-location and multi-season trials are essential to evaluate the stability, reproducibility, and scalability of endophyte-mediated stress tolerance. Combining omics-based insights with physiological and agronomic analyses will further improve understanding of host–microbe interactions and support the development of robust, climate-resilient rice production systems.

Future studies should also consider biosafety and ecological aspects when developing endophyte-based technologies for agricultural applications. Particular attention should be given to evaluating potential effects on native microbial communities, environmental sustainability, and regulatory compliance under diverse field conditions. Comprehensive ecological risk assessment, long-term environmental monitoring, and appropriate regulatory evaluation will be important to ensure the

Table 2
Key genes associated with drought and salinity tolerance in rice relevant to endophyte-mediated responses.

Stress Type	Gene Symbol	Gene Function	Role in Stress Tolerance	Relevance to Endophyte Interaction	Reference
Drought	OsDRO1	Root architecture regulator	Promotes deeper rooting	Enhances water uptake through endophyte-induced root growth	Samreen et al. (2021)
Drought	OsASR5	ABA-responsive protein	Regulates stress signaling	Linked to endophyte-mediated ABA modulation	Samreen et al. (2021)
Drought	OsDST	Transcription factor	Controls stomatal behavior and ROS homeostasis	Supports endophyte-regulated ROS homeostasis	Samreen et al. (2021)
Osmotic	OsP5CS1	Proline biosynthesis enzyme	Promotes osmoprotectant accumulation	Endophytes enhance osmolyte production	Samreen et al. (2021)
Salinity	OsHKT1; 5	Na^+ transporter	Mediates Na^+ exclusion and Na^+/K^+ homeostasis	Target of endophyte-mediated ion regulation	(Ren et al., 2022; Kobayashi et al., 2017)
Salinity	OsHAK5	K^+ transporter	Maintains K^+ uptake	Endophytes improve K^+ retention	Samreen et al. (2021)
Salinity	OsKAT1	K^+ channel protein	Regulates ion homeostasis	Supports membrane stability under stress	Samreen et al. (2021)
Salinity	OsBADH1	Osmoprotectant enzyme	Glycine betaine synthesis	Linked to microbial-mediated osmotic protection	Samreen et al. (2021)

safe and sustainable implementation of endophyte-based strategies in rice production (Trabelsi and Mhamdi, 2013; Kumari et al., 2022; Díaz-Rodríguez et al., 2025).

8. Conclusion

Endophytic microorganisms represent a promising and sustainable approach for enhancing drought and salinity tolerance in rice. Through coordinated regulation of key mechanisms, including ACCD activity, ion homeostasis via HKT1; 5, aquaporin-mediated water transport, phytohormone signaling, and antioxidant defense systems, endophytes improve plant growth, physiological stability, and stress resilience. Despite these advances, variability in field performance remains a major challenge due to complex interactions among microbial strains, host genotypes, and environmental conditions. Addressing these limitations requires standardized methodologies, genotype-specific endophyte selection, and extensive field validation. Advances in omics technologies and microbiome engineering provide new opportunities to develop efficient and scalable endophyte-based solutions. Integrating these approaches with climate-smart breeding strategies will be essential for translating mechanistic insights into practical applications, ultimately contributing to sustainable and resilient rice production under changing environmental conditions.

CRediT authorship contribution statement

Mostafa Mohammed Atiyah: Writing – Original Draft, Visualization, Methodology, Investigation. **Wijdan Saad Aziz**: Resources, Formal analysis, Data Curation. **Mostafa Qahtan Al-Smail:** Resources, Data analysis. **Gian Marco Ludovici:** Formal analysis, Investigation, Resources, Software, Validation. **Andrea Malizia:** Formal analysis, Investigation, Resources, Software, Validation. **Sijo Asokan:** Software, Resources, Investigation. **Hussain Alwan Mana:** Formal analysis, Data Curation. **Smitha Vijayan:** Review & Editing, Supervision, Methodology, Conceptualization, Validation, and Project Administration.

Consent for publication

The final version of the manuscript was read and approved by all authors.

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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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Data availability

Data will be made available on request.

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