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REVIEW

Microbe-Mediated Abiotic Stress Tolerance in Rice (*Oryza sativa* L.) as a Strategy for Climate Change Adaptation

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ABSTRACT: Rice (*Oryza sativa* L.) is central to global food security, yet its production systems remain highly vulnerable to environmental pressures. Climate change is increasing the frequency and severity of abiotic stresses, including drought, salinity, extreme temperatures, flooding, and heavy metal toxicity, which significantly reduce global rice productivity. Conventional strategies, including breeding and genetic engineering, have improved stress tolerance; however, their effectiveness is often constrained by long development timelines, complex genetic regulation, and limited performance under multiple concurrent stresses. In this context, plant-associated microorganisms have emerged as a sustainable and promising approach to enhancing rice plant resilience. This review synthesizes current knowledge on beneficial microbes such as plant growth promoting rhizobacteria (PGPR), arbuscular mycorrhizal fungi (AMF), endophytes, and cyanobacteria and their roles in mediating abiotic stress tolerance in rice. These microorganisms enhance plant performance through diverse mechanisms, including modulation of phytohormone balance, improved nutrient acquisition, maintenance of ion homeostasis, activation of antioxidant defense systems, and induction of systemic tolerance. Furthermore, microbial interactions influence gene expression, signaling pathways, and epigenetic regulation, thereby strengthening plant adaptive responses to environmental stress. This review also highlights microbe-mediated mitigation of specific stresses and discusses key challenges, particularly inconsistent field performance and the complexity of plant microbiome interactions. Emerging approaches such as omics technologies, synthetic microbiome engineering, and artificial intelligence assisted microbial design offer new opportunities to improve the reliability and scalability of microbe-based strategies for climate resilient rice production.

KEYWORDS: Abiotic stress tolerance; climate change adaptation; microbiome engineering; PGPR; plant–microbe interactions; rice

1 Introduction

Rice (*Oryza sativa* L.) is one of the most important staple crops supporting global food security, particularly in Asia [1,2]. Beyond its role as a major source of calories for billions of people, rice cultivation sustains rural livelihoods, contributes significantly to the agricultural sector, and supports employment in many developing countries [3]. Because rice is cultivated across diverse agroecosystems, its production is highly sensitive to environmental fluctuations and climate-related stresses that directly affect yield

stability and food availability [4,5]. At the same time, global warming has emerged as one of the most critical environmental challenges facing human societies and ecosystems. Rising global temperatures and associated climatic shifts are already influencing ecological balance, food systems, and socioeconomic development worldwide [6–8]. Agricultural systems are particularly vulnerable to these changes because crop productivity is strongly dependent on environmental factors such as temperature, precipitation patterns, and atmospheric conditions [9–12]. Variability in these climatic drivers can disrupt crop phenology, increase the frequency of extreme weather events, and alter the distribution of pests and diseases, ultimately reducing crop productivity and quality [13]. Consequently, ensuring stable rice production under changing climatic conditions has become a major priority for global food security.

Rice is highly sensitive to climatic fluctuations, particularly under abiotic stress conditions [14–16]. For instance, elevated temperatures during the flowering stage can induce spikelet sterility and reduce grain formation, leading to substantial yield losses [17,18]. In addition, irregular precipitation patterns associated with climate change increase the occurrence of both drought and flooding in major rice-growing regions [19]. Long-term climate projections further suggest that each 1°C rise in global temperature may reduce rice yields by approximately 10% due to increased respiration rates and shortened grain-filling periods [20–22]. These projections highlight the urgent need to develop climate-resilient rice production systems capable of maintaining productivity under increasing environmental variability.

Abiotic stresses including drought, salinity, extreme temperature, and flooding represent major constraints to rice growth and productivity [14,23,24]. Drought stress affects approximately 23 million hectares of rainfed rice annually and disrupts key physiological processes such as photosynthesis, stomatal regulation, and carbohydrate metabolism, ultimately leading to severe yield losses [25,26]. Salinity stress, often intensified by sea-level rise and excessive irrigation, causes ionic toxicity and osmotic imbalance as elevated sodium (Na^+) concentrations interfere with potassium (K^+) uptake, which is necessary for essential enzymatic functions [25,27]. These physiological disruptions collectively compromise plant growth, development, and yield formation in rice.

Extreme temperature impairs rice metabolism and development [28]. Heat stress adversely affects panicle development and pollination, whereas low temperatures delay germination and inhibit early seedling growth [29]. Flooding and submergence reduce oxygen diffusion in the soil, forcing rice roots to rely on anaerobic respiration, which significantly limits energy production [30]. In addition, heavy metal contamination resulting from industrial and agricultural activities introduces another layer of abiotic stress, inducing oxidative damage and inhibiting nutrient uptake in rice plants [31,32]. Together, these abiotic stresses represent major barriers to sustainable rice production under rapidly changing environmental conditions.

Conventional strategies for improving stress tolerance in rice have largely relied on traditional breeding approaches [33,34]. While these programs have successfully produced several improved cultivars, they are inherently time-consuming because they require multiple generations of selection and are often constrained by complex genetic inheritance patterns and genotype–environment interactions [35,36]. Advances in molecular breeding and marker-assisted selection have accelerated crop improvement; however, identifying and stably integrating traits associated with abiotic stress tolerance remains challenging due to the polygenic nature of stress responses [37,38]. Genetic engineering provides a more targeted approach by enabling the introduction of stress-responsive genes and the manipulation of metabolic pathways involved in tolerance mechanisms [39]. Nevertheless, the deployment of genetically modified crops is frequently limited by regulatory constraints, biosafety concerns, and public acceptance challenges in many countries [40]. Moreover, most transgenic strategies focus on tolerance to individual stress factors, whereas crops in natural environments typically experience multiple, interacting stresses simultaneously [41–43]. These

limitations highlight the need for complementary and sustainable approaches to enhance crop resilience under complex field conditions.

In this context, plant-associated microorganisms have emerged as promising biological resources for improving crop tolerance to abiotic stress [44–46]. Beneficial microbes including plant growth–promoting rhizobacteria (PGPR), endophytes, arbuscular mycorrhizal fungi (AMF), and cyanobacteria can enhance plant performance through multiple mechanisms [47,48]. These include improving nutrient availability, producing phytohormones, lowering stress-induced ethylene levels via 1-aminocyclopropane-1-carboxylate (ACC) deaminase activity, and strengthening antioxidant defense systems [49,50]. Microbial-based strategies are generally cost-effective, environmentally sustainable, and compatible with diverse rice genotypes, offering significant advantages over conventional breeding and transgenic approaches [51–53].

Despite the growing body of literature on plant-associated microbes and their role in abiotic stress tolerance, many existing reviews primarily focus on individual microbial groups or specific mechanisms without providing an integrated perspective across multiple levels of plant–microbe interactions [51,54,55]. In addition, limited attention has been given to the comparative effectiveness of different microbial strategies under varying environmental conditions and to the persistent gap between laboratory findings and field-level performance [56,57]. Therefore, a more integrative and critically evaluative synthesis is needed to better understand the complex interactions underlying microbe-mediated stress tolerance in rice.

In this context, the present review proposes an integrative framework linking microbial diversity, functional mechanisms, and stress-specific plant responses within a unified conceptual perspective. Rather than treating microbial taxa and mechanisms in isolation, this review synthesizes physiological, biochemical, molecular, and ecological processes to provide a more holistic understanding of stress adaptation in rice. Furthermore, the review critically evaluates field-level applicability and discusses emerging approaches, including omics technologies, synthetic microbiomes, and artificial intelligence-assisted microbial design, to support the development of climate-resilient rice production systems.

This review aims to synthesize current knowledge on the role of plant-associated microbes in enhancing abiotic stress tolerance in rice. Specifically, it examines the structure and function of the rice microbiome, key beneficial microbial groups involved in stress mitigation, and the underlying mechanisms governing plant–microbe interactions. In addition, the review discusses microbial responses to specific abiotic stresses and highlights emerging research directions, including the integration of omics technologies, synthetic microbiome design, and gene-editing approaches to develop climate-resilient rice production systems.

2 Overview of Plant-Microbe Interactions in Rice

2.1 The Rice Microbiome: Rhizosphere, Endosphere, and Phyllosphere Communities

Rice plants harbor a complex and dynamic microbiome distributed across three primary ecological niches: the rhizosphere, endosphere, and phyllosphere [58,59]. The rhizosphere microbiome, which develops in the narrow zone of soil influenced by root exudates, contains diverse bacterial and fungal populations that play essential roles in nutrient cycling, organic matter decomposition, and plant growth promotion [60,61]. Root exudates including sugars, amino acids, and secondary metabolites serve as chemical signals and energy sources that selectively recruit beneficial microorganisms from the surrounding soil [62]. In contrast, the endosphere microbiome comprises microorganisms that colonize internal plant tissues without causing disease [63]. These endophytic microbes can directly influence plant metabolism, enhance tolerance to environmental stress, and modulate host gene expression through complex biochemical interactions [64,65]. The phyllosphere, which encompasses the aerial surfaces of the plant, also supports diverse microbial communities adapted to fluctuating environmental conditions such as temperature variability, ultraviolet

radiation, and limited water availability [66]. Certain phyllosphere-associated bacteria contribute to plant health by producing bioactive compounds and inducing systemic stress tolerance [67]. Collectively, these microbial assemblages form an integrated plant–microbe system, often described as a holobiont, that contributes to plant adaptation and resilience under stressful environmental conditions [68].

Beyond their spatial distribution, rice-associated microbial communities interact dynamically with each other and with the host plant, forming interconnected networks that regulate plant health and stress responses [59]. Communication among microbial populations across plant compartments can occur through metabolite exchange, signaling molecules, and plant-mediated systemic responses [68]. For instance, root-associated beneficial microbes may influence aboveground microbial communities by activating systemic signaling pathways that modify the composition of the leaf microbiome [69]. Beneficial rhizobacteria are known to induce systemic resistance and reshape phyllosphere microbial assemblages, thereby enhancing plant tolerance to both biotic and abiotic stresses, including drought and salinity [55]. These cross-compartment interactions emphasize that the rice microbiome functions as an integrated ecological system rather than independent microbial niches [70].

2.2 Types of Beneficial Microbes

Beneficial microorganisms associated with rice plants play critical roles in enhancing plant growth, nutrient acquisition, and tolerance to environmental stresses [64,71,72]. These microbes colonize different plant-associated habitats including the rhizosphere, endosphere, and phyllosphere where they establish complex interactions with plant tissues and influence multiple physiological processes [73]. Through these interactions, microbial communities contribute to nutrient cycling, phytohormone production, and improved plant resilience against abiotic stresses [72,74]. Consequently, plant-associated microbes are increasingly recognized as sustainable biological resources for improving crop productivity while reducing reliance on chemical fertilizers and other agricultural inputs [75].

Fungi represent an important component of the beneficial microbiome associated with rice plants, particularly through symbiotic interactions with plant roots [76]. AMF form mutualistic associations with plant roots that enhance nutrient uptake, especially phosphorus, by extending hyphal networks into the surrounding soil beyond the root depletion zone [77]. These symbiotic fungi also contribute to improved drought tolerance by increasing water uptake capacity and enhancing root system efficiency [78,79]. In addition, fungal endophytes can produce diverse secondary metabolites that promote plant growth and enhance tolerance to environmental stresses such as salinity, temperature extremes, and oxidative stress [80].

Bacteria also constitute a major group of beneficial microbes associated with rice plants, particularly those categorized as PGPR [49,61]. These bacteria enhance plant growth through multiple mechanisms, including phytohormone production, nutrient solubilization, and biological nitrogen fixation in the rhizosphere [61]. Some PGPR strains produce ACC deaminase, an enzyme that lowers stress-induced ethylene levels in plants and thereby improves tolerance to abiotic stresses such as drought and salinity [50,81]. In addition, many rhizobacteria synthesize siderophores that facilitate iron acquisition and suppress competing microorganisms in the soil [82].

A summary of the major functional roles of beneficial bacteria and fungi associated with rice plants is presented in Table 1. These microorganisms contribute to plant growth and stress tolerance through complementary mechanisms, highlighting their potential for sustainable crop management and climate-resilient agricultural systems.

Table 1: Functional roles of beneficial bacteria and fungi associated with rice plants.

Microbial Species	Stress Types	Mechanisms	Observed Effects	References
Bacillus subtilis	Salinity stress	Antioxidant enzyme activation, ion homeostasis regulation, osmotic adjustment	Improved chlorophyll content, reduced oxidative damage, enhanced salt tolerance in rice	[83]
B. aryabhattai	Salinity stress	Regulation of antioxidant defense and photosynthetic parameters	Enhanced Reactive oxygen species (ROS) detoxification and photosynthetic efficiency under salt stress	[83]
B. amyloliquefaciens SN13	Salinity stress	Modulation of stress-responsive gene expression and osmolyte accumulation	Increased biomass, proline accumulation, and salt tolerance in rice	[84]
Pseudomonas fluorescens	Drought stress	ACC deaminase activity and phytohormone production	Improved stress adaptation and plant growth under drought conditions	[85]
Lysinibacillus fusiformis	Salinity stress	Regulation of antioxidant system and stress-responsive genes	Increased chlorophyll content and stress tolerance in rice	[86]
Brevibacterium pityocampae	Salinity stress	Modulation of endogenous hormones and antioxidant activity	Enhanced growth and physiological stability under salt stress	[86]

2.3 Mechanisms of Interaction between Rice and Beneficial Microbes

Interactions between rice plants and beneficial microorganisms involve complex biochemical signaling processes that regulate plant growth, development, and adaptation to environmental conditions [87,88]. When beneficial microbes colonize the rhizosphere or internal plant tissues, they communicate with host cells through chemical signals that trigger various physiological responses [89]. These microbial signals can influence plant hormonal balance, particularly pathways involving auxin, cytokinin, abscisic acid (ABA), and ethylene, which play central roles in regulating plant growth and stress responses [81,90]. In rice cultivation systems, microbial colonization has been reported to stimulate root development and improve nutrient acquisition efficiency, thereby enhancing overall plant vigor and productivity [91].

Beyond nutrient exchange and antioxidant regulation, another important mechanism of plant–microbe interaction is the induction of systemic responses that prepare plants to cope with future stress [65,92,93]. Beneficial microorganisms can trigger a physiological phenomenon known as microbial priming, in which plants develop an enhanced capacity to respond rapidly and efficiently to subsequent environmental stresses [94–97]. This priming effect strengthens plant defense readiness without imposing substantial metabolic costs, allowing plants to maintain growth while increasing stress tolerance [79]. Overall, these interaction mechanisms demonstrate how beneficial microorganisms function as key biological partners that enhance rice resilience and support sustainable crop production under changing environmental conditions.

3 Microbial Mechanisms for Enhancing Abiotic Stress Tolerance in Rice

3.1 Physiological and Biochemical Modulation

Beneficial microorganisms enhance the physiological performance of rice plants under abiotic stress by modulating plant growth processes and metabolic activities [74]. One of the most prominent effects

of plant-associated microbes is the improvement of root system architecture, including increased root length, branching, and surface area [52,98]. These changes enable plants to explore a larger soil volume for water and nutrients under adverse environmental conditions [89]. PGPR, such as *Azospirillum* and *Bacillus*, stimulate root development through the production of phytohormones, particularly indole-3-acetic acid (IAA), which regulates cell elongation and root differentiation [99–102]. In addition, symbiotic fungi such as AMF enhance nutrient acquisition by extending hyphal networks beyond the root depletion zone, thereby increasing the uptake of essential nutrients including phosphorus and micronutrients under nutrient-limited conditions [77].

Beneficial microbes also contribute to plant stress adaptation by modulating hormonal balance within plant tissues [76]. Microbial production of plant hormones including auxins, gibberellins, cytokinins, and ABA can influence plant growth patterns, stomatal regulation, and water-use efficiency during drought and salinity stress [61]. These hormonal adjustments enable plants to maintain physiological stability and sustain growth under unfavorable environmental conditions [103]. Furthermore, microbial interactions can stimulate the accumulation of osmoprotectants such as proline, glycine betaine, and soluble sugars, which protect cellular proteins and membranes from osmotic damage during water deficit or salinity stress [39].

Another important physiological mechanism involves the enhancement of antioxidant defense systems [92,104]. Abiotic stresses often cause excessive accumulation of ROS, which can damage cellular structures, lipids, proteins, and nucleic acids [105]. Beneficial microbes can increase the activity of antioxidant enzymes such as superoxide dismutase, catalase, and peroxidase, thereby reducing oxidative damage and maintaining cellular homeostasis [106]. Through these physiological and biochemical modifications, plant-associated microbes significantly enhance the capacity of rice plants to maintain growth and metabolic stability under abiotic stress conditions.

3.2 Molecular and Genetic Regulation

Beyond physiological modulation, beneficial microbes enhance plant stress tolerance at the molecular and genetic levels by regulating the expression of stress-responsive genes and signaling pathways [79]. Microbial colonization of plant roots can activate complex signaling networks that regulate gene expression and coordinate adaptive responses to environmental stress [107]. These signaling pathways frequently involve interactions with plant hormone signaling systems, calcium-mediated signaling, and mitogen-activated protein kinase (MAPK) cascades that transmit stress signals from the site of microbial perception to the plant nucleus [108]. As a result, plants undergo transcriptional reprogramming that supports metabolic adjustments and improves tolerance to adverse environmental conditions.

Beneficial microbes can also influence the activity of key transcription factors involved in plant stress responses [109]. Transcription factor families such as DREB (Dehydration Responsive Element Binding), NAC, and WRKY play central roles in regulating gene networks associated with drought, salinity, and temperature stress [110]. Microbial interactions may stimulate the expression of these transcription factors, thereby activating downstream protective genes involved in osmotic regulation, antioxidant defense, and cellular protection mechanisms [111]. Through such transcriptional regulation, plant-associated microbes contribute to improved physiological stability and enhanced stress resilience in rice plants.

In addition to transcriptional regulation, recent studies suggest that beneficial microbes may influence plant adaptation through epigenetic mechanisms [112,113]. Microbial associations can induce modifications in DNA methylation patterns and histone structures that alter gene expression without changing the underlying DNA sequence [114]. These epigenetic adjustments may contribute to the development of stress memory, enabling plants to respond more efficiently to recurring environmental stress events [115]. Such

molecular and epigenetic regulation highlights the long-term influence of microbial associations on plant adaptation to environmental stress.

Several rice-specific stress-responsive genes have been reported to participate in microbe-mediated abiotic stress tolerance pathways. Beneficial microorganisms can regulate transcription factors such as *OsDREB*, *OsWRKY*, and *OsNAC*, which are associated with drought and salinity stress responses [116,117]. In saline environments, microbial inoculation has also been associated with the regulation of ion transporter genes, including *OsHKT1;5* and *OsSOS1*, which contribute to sodium exclusion and ion homeostasis in rice plants [25]. These molecular responses collectively enhance osmotic adjustment, antioxidant defense, stress signaling pathways, and overall plant adaptation under adverse environmental conditions [55].

3.3 Microbe-Derived Metabolites and Enzymes

Microbial metabolites and enzymes represent another important mechanism by which beneficial microorganisms enhance plant tolerance to abiotic stress [118]. Many plant-associated microbes produce siderophores specialized molecules that bind and mobilize iron thereby increasing its availability to plants in iron-limited soils [81]. Through improving iron acquisition, siderophores help maintain essential metabolic processes and reduce oxidative stress associated with nutrient imbalance in the rhizosphere.

Another key microbial enzyme involved in stress mitigation is ACC deaminase. This enzyme degrades the ethylene precursor ACC, thereby reducing ethylene accumulation in plant tissues under stress conditions [50]. Elevated ethylene levels typically inhibit root elongation and overall plant growth during stress [119]. Consequently, the activity of ACC deaminase allows plants to maintain root growth and nutrient uptake even under severe environmental conditions [120]. Plants inoculated with ACC-deaminase-producing bacteria frequently exhibit improved growth under drought, salinity, and heavy metal stress [121].

Beneficial microbes also produce extracellular polymers and signaling compounds that influence plant stress tolerance [122]. Exopolysaccharides secreted by certain rhizobacteria improve soil aggregation, enhance soil moisture retention, and mitigate sodium toxicity in saline soils [123]. Additionally, microbial volatile organic compounds (VOCs) such as acetoin and 2,3-butanediol act as signaling molecules that stimulate plant growth and activate stress-response pathways [124]. Together, these microbial metabolites create a protective biochemical environment that supports plant growth and enhances resilience to environmental stress.

3.4 Induced Systemic Tolerance (IST)

Induced systemic tolerance (IST) is a plant-wide adaptive response triggered by beneficial microorganisms that enhances the ability of plants to withstand subsequent abiotic stress conditions [125]. During microbial colonization, plants undergo physiological and molecular adjustments that prime their stress-response systems, enabling faster and more effective reactions when environmental stress occurs [126]. This priming process often involves the accumulation of signaling molecules, activation of antioxidant systems, and pre-conditioning of stress-responsive genes [127].

A key feature of IST is that it enhances plant stress tolerance without imposing substantial metabolic costs on plant growth [128]. Primed plants maintain a heightened readiness of protective pathways, allowing rapid activation of defense mechanisms when stress conditions arise [129]. Consequently, plants exhibiting IST often show improved tolerance to drought, salinity, temperature extremes, and oxidative stress compared with non-primed plants [130].

IST is conceptually related to other systemic plant defense responses, including induced systemic resistance (ISR) and systemic acquired resistance (SAR), which primarily function in protection against

pathogens [93]. In contrast, IST focuses on enhancing tolerance to abiotic stresses that frequently limit crop productivity [107]. Given the increasing frequency and intensity of climate-related stresses in agricultural systems, the ability of beneficial microbes to induce systemic tolerance represents a promising strategy for improving the resilience of rice cultivation.

3.5 Comparative and Critical Analysis

While diverse microbial groups contribute to abiotic stress tolerance in rice, their effectiveness varies significantly depending on environmental conditions, plant genotype, and interactions with native soil microbiota [52,55]. PGPR, for instance, often exhibit rapid responses through phytohormone modulation, ACC deaminase activity, and osmolyte regulation, making them particularly effective under short-term stress conditions such as early-stage drought [50,131]. In contrast, AMF generally provide more stable and long-term benefits by enhancing water uptake, improving nutrient acquisition, and maintaining soil structure, especially in nutrient-deficient or saline soils [132].

However, comparative observations indicate that microbial performance is not always consistent across environments because introduced inoculants frequently compete with indigenous microbial communities under field conditions [56]. In addition, AMF colonization efficiency and functional performance are strongly influenced by soil physicochemical properties and host compatibility, which may limit their effectiveness in certain agroecosystems [133].

Furthermore, synergistic effects between microbial groups frequently reported under controlled conditions are often inconsistent in field environments, reflecting the complexity of plant–microbe–environment interactions [134]. These inconsistencies highlight the importance of adopting a context-dependent approach to microbial application rather than relying solely on single-strain inoculants [135–137].

Recent studies suggest that functionally complementary microbial consortia may provide more stable and reliable performance across diverse environmental conditions [138,139]. Therefore, future studies should prioritize comparative evaluation under realistic agricultural conditions and integrate ecological, physiological, and molecular perspectives to better understand the determinants of microbial effectiveness in rice agroecosystems.

4 Comparative Effectiveness under Different Abiotic Stresses

4.1 Drought Stress

Drought is one of the most severe environmental constraints limiting rice growth and productivity [79]. Water deficit reduces photosynthetic activity, restricts nutrient transport, and disrupts cellular metabolism [140]. Under prolonged drought conditions, plants exhibit reduced stomatal conductance, oxidative stress, and metabolic imbalance that ultimately lead to significant yield losses [140]. Beneficial microorganisms can mitigate these adverse effects by improving root architecture, enhancing osmotic adjustment, and stimulating antioxidant defense systems [79,140]. PGPR stimulate the development of longer and more branched root systems, enabling plants to explore deeper soil layers for water and nutrients [111]. In addition, microbial inoculation often increases the accumulation of osmoprotectants such as proline and soluble sugars, which stabilize cellular structures and maintain turgor pressure during water deficit [141]. These physiological and biochemical adjustments allow rice plants to sustain growth even under limited water availability.

Several microbial species have been identified as key contributors to drought tolerance in rice. *A. brasilense* is widely recognized for its ability to produce IAA, which stimulates root elongation and increases root surface area for water absorption [102]. Similarly, *B. subtilis* enhances drought tolerance by producing extracellular polymers that improve soil water retention around the root zone [142]. Endophytic bacteria

such as *Enterobacter cloacae* also contribute to drought resilience by promoting proline accumulation and activating antioxidant enzymes in plant tissues [29]. In addition to bacteria, AMF such as *Rhizophagus irregularis* extend hyphal networks into surrounding soil, effectively increasing the plant's absorptive surface area and improving water-use efficiency during drought stress [78].

4.2 Salinity Stress

Salinity stress represents a major abiotic constraint affecting rice cultivation, particularly in coastal and irrigated agricultural systems [143]. High concentrations of sodium ions disrupt cellular ion homeostasis, inhibit enzyme activity, and induce osmotic stress that restricts plant growth and productivity [143]. Beneficial microorganisms can alleviate salinity stress through multiple mechanisms, including maintaining ion balance, enhancing osmolyte production, and activating antioxidant defense pathways [143]. Microbial inoculation can increase the expression of plant transporters responsible for maintaining Na^+/K^+ balance in plant tissues, which is essential for sustaining cellular metabolism under saline conditions [144]. Furthermore, microbes may produce compatible solutes such as trehalose and glycine betaine that stabilize proteins and cellular membranes during osmotic stress [123].

Various salt-tolerant microbes have been reported to enhance salinity tolerance in rice. *P. fluorescens* improves plant tolerance by producing exopolysaccharides that bind sodium ions in the rhizosphere, thereby reducing their uptake by plant roots [145]. Likewise, *B. amyloliquefaciens* can regulate plant ion transport and increase potassium accumulation, helping maintain ionic balance under salt stress [146]. Endophytic bacteria such as *Halomonas* spp. also contribute to salt tolerance by synthesizing osmoprotective compounds and stimulating antioxidant enzyme systems [147]. In addition, arbuscular mycorrhizal fungi such as *Funneliformis mosseae* improve phosphorus uptake and membrane stability, thereby supporting plant growth under saline conditions [148]. Collectively, these microbial interactions help maintain ionic homeostasis and physiological stability in rice plants exposed to saline environments.

4.3 Temperature Stress

Extreme temperature, including both heat and cold stress, can severely disrupt rice growth by affecting enzyme activity, membrane stability, and reproductive development [18]. Heat stress often leads to protein denaturation and oxidative damage, whereas cold stress interferes with membrane fluidity and metabolic processes [18]. Beneficial microorganisms can mitigate these effects by activating stress-responsive signaling pathways and strengthening antioxidant defense systems [149]. Microbial interactions may stimulate the production of heat shock proteins and protective metabolites that help plants maintain cellular homeostasis under temperature stress [46]. Additionally, microbial metabolites can regulate hormonal signaling pathways that facilitate plant acclimation to fluctuating temperature [150].

Several microbial species have been identified as contributors to temperature stress tolerance [151]. *B. cereus* has been reported to enhance heat tolerance in rice by increasing antioxidant enzyme activity and stabilizing cellular membranes under elevated temperatures [152]. Similarly, *P. putida* produces volatile organic compounds that activate systemic stress responses and protect plants from heat-induced oxidative damage [153]. In cold environments, fungal endophytes such as *T. harzianum* promote the expression of cold-responsive genes and stimulate the accumulation of protective metabolites within plant tissues [154]. Another example is the endophytic fungus *Piriformospora indica*, which enhances cold tolerance by regulating antioxidant pathways and improving nutrient uptake efficiency [155,156].

4.4 Flooding and Submergence Stress

Flooding and submergence frequently occur in rice-growing regions, particularly in lowland paddy ecosystems [157]. These conditions drastically reduce oxygen availability in the soil, forcing plants to rely on anaerobic metabolism that limits energy production and root growth [158]. Prolonged flooding can also result in the accumulation of toxic compounds such as reduced iron and sulfide in the rhizosphere [159]. Beneficial microbes present in flooded soils can help alleviate these stresses by facilitating nutrient cycling, improving redox balance, and supporting plant metabolic adaptation [159]. Microbial communities also contribute to nitrogen fixation and organic matter decomposition, which help maintain soil fertility under anaerobic conditions [72,160].

Several microbial groups play important roles in supporting rice growth under submerged conditions [29]. Cyanobacteria such as *Anabaena* and *Nostoc* are capable of fixing atmospheric nitrogen and supplying bioavailable nitrogen to rice plants in flooded environments [161]. Nitrogen-fixing bacteria including *Azotobacter* and *Azospirillum* also contribute to nutrient availability and stimulate root growth even under low-oxygen conditions [49]. Some rhizobacteria, such as *Enterobacter* spp., produce ACC deaminase that reduces ethylene accumulation in plant tissues, thereby preventing the inhibition of root growth under hypoxic stress [162]. Additionally, certain anaerobic bacteria assist in maintaining soil redox balance, reducing the accumulation of toxic compounds that could otherwise damage plant roots during prolonged flooding.

4.5 Heavy Metal and Oxidative Stress

Heavy metal contamination in agricultural soils poses a significant threat to rice production and food safety [163]. Toxic metals such as cadmium (Cd), arsenic (As), and lead (Pb) can accumulate in plant tissues, disrupt enzymatic processes, and induce severe oxidative stress [163]. Beneficial microorganisms can reduce heavy metal toxicity through several mechanisms, including immobilizing metals in the rhizosphere, enhancing antioxidant defenses, and modifying plant metal uptake pathways [163]. Many microbes produce metal-chelating compounds that bind toxic ions and prevent their entry into plant tissues [164]. In addition, microbial inoculation often enhances the activity of antioxidant enzymes that detoxify reactive oxygen species generated during metal stress [165].

Several microbial species have demonstrated strong potential for mitigating heavy metal toxicity in rice systems [166,167]. *B. megaterium* has been reported to reduce cadmium accumulation in rice by producing extracellular polymers that immobilize metal ions in the soil [168]. Similarly, *P. aeruginosa* produces siderophores that bind heavy metals and decrease their bioavailability to plants [169]. Fungal species such as *Aspergillus niger* can adsorb heavy metals on their cell surfaces, thereby reducing metal uptake by plant roots [170]. Another beneficial fungus, *Trichoderma asperellum*, enhances antioxidant enzyme activity and improves plant tolerance to metal-induced oxidative stress [71,171]. Through these mechanisms, microbial partners play a crucial role in protecting rice plants from heavy metal toxicity and maintaining productivity in contaminated soils.

5 Field-Level Challenges and Ecological Constraints

Although plant-associated microorganisms offer promising strategies for enhancing abiotic stress resilience in rice, several scientific and practical challenges must be addressed before microbial technologies can be widely integrated into climate-smart agricultural systems [172]. One of the primary challenges is the inconsistency between laboratory results and field performance, which often limits the large-scale adoption of microbial bioinoculants [173,174]. Microbial efficacy observed under controlled conditions may not always translate into similar outcomes under natural field environments due to environmental variability

and the complexity of soil ecosystems [175]. Another major challenge is the intricate nature of microbial interactions within natural soil microbiomes [176]. Introduced microbial inoculants frequently compete with indigenous microorganisms, struggle to establish stable populations, or lose functional efficiency under fluctuating environmental conditions [55].

The complexity of these interactions is illustrated in Fig. 1, which summarizes the major compartments of the rice microbiome and highlights the multiple signaling and functional relationships between plants and beneficial microorganisms [177]. These interactions include nutrient exchange, hormone regulation, stress signaling, and activation of plant defense pathways that collectively enhance plant adaptation to environmental stresses [178].

In addition, the development and commercialization of microbial technologies require comprehensive regulatory frameworks, standardized quality control systems, and scalable production methods to ensure product stability and reliability [54,179]. Addressing these challenges will require integrated research efforts combining microbiology, plant science, agronomy, ecology, and computational biology [180]. Future strategies are expected to incorporate advanced omics technologies, genome editing tools, ecological engineering, and artificial intelligence to design next-generation microbial consortia tailored for diverse rice-growing environments [181]. Such multidisciplinary approaches will be essential for unlocking the full potential of plant-associated microbes as tools for improving climate resilience and sustainable rice production [172].

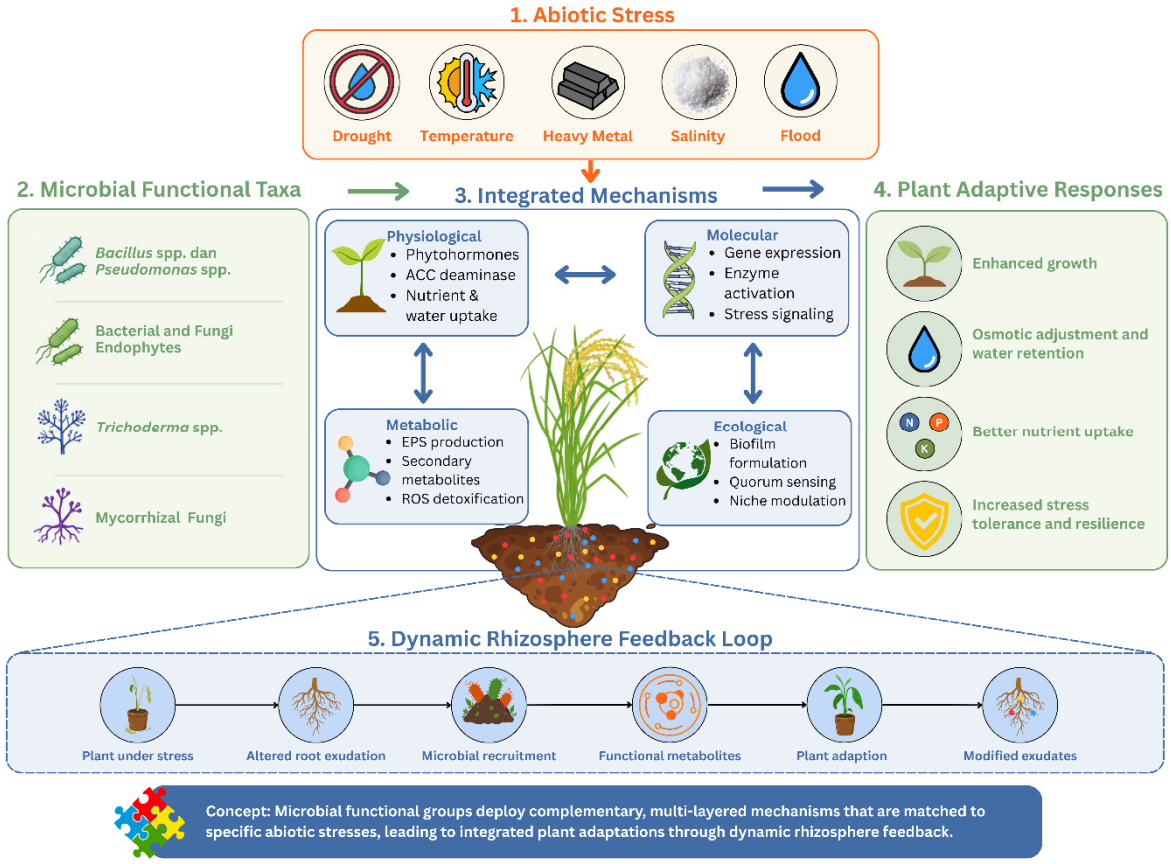

Figure 1: Overview of plant–microbe interactions in rice and their role in abiotic stress tolerance (Adapted from Muhammad et al. [182], the journal does not require permission to use the materials).

5.1 Challenges in Translating Laboratory Success to Field Performance

One of the most persistent challenges in microbe-based agricultural technologies is the considerable gap between laboratory findings and field performance [174]. Under controlled laboratory or greenhouse conditions, microbial inoculants often demonstrate strong plant growth–promoting and stress-mitigating effects due to stable temperature regimes, adequate nutrient availability, and the absence of competing microbial populations [55]. However, natural field environments present a far more complex and dynamic system characterized by soil heterogeneity, fluctuating temperature and moisture conditions, nutrient variability, pathogen pressure, and intense competition from native microbial communities [183].

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Although many microbial inoculants demonstrate promising results under laboratory and greenhouse conditions, their performance often becomes less predictable when applied under field environments [54,56]. Environmental heterogeneity, including variations in soil physicochemical properties, climatic conditions, agricultural management practices, and interactions with indigenous microbial communities, can substantially influence microbial establishment and functionality [55,103]. As a result, translating experimental success into consistent field performance remains one of the major challenges in the development of microbial-based technologies for sustainable rice production [61,83].

5.2 Comparative Effectiveness of Different Microbial Groups

Different groups of beneficial microorganisms contribute to abiotic stress tolerance through distinct yet complementary mechanisms [54,55]. PGPR enhance plant performance through phytohormone production, ACC deaminase activity, nutrient solubilization, and modulation of plant stress-responsive pathways [52,55]. AMF improve nutrient acquisition, water-use efficiency, and soil aggregation, thereby enhancing plant resilience under adverse environmental conditions [185]. Endophytic microorganisms colonize internal plant tissues and regulate physiological and molecular processes associated with stress adaptation [186,187]. Cyanobacteria contribute to biological nitrogen fixation and long-term improvements in soil fertility, which can indirectly strengthen crop tolerance to environmental stressors [188,189].

Despite their demonstrated benefits, no single microbial group consistently outperforms others across all abiotic stress conditions and agroecosystems [190,191]. The efficacy of microbial inoculants is highly dependent on environmental conditions, host genotype, soil characteristics, and stress intensity [192]. For example, PGPR often provide rapid physiological benefits through phytohormone production and ACC deaminase activity, but their effectiveness may decline under field conditions due to limited persistence and competition with indigenous microbial communities [56]. In contrast, AMF generally exhibit greater stability in improving nutrient and water acquisition, although their performance can be constrained by soil properties and host compatibility [63]. Similarly, endophytes can directly modulate stress-responsive pathways within plant tissues, yet the mechanisms underlying their long-term establishment and functional stability remain insufficiently understood [193].

Although numerous studies have reported positive effects of microbial inoculants on rice tolerance to abiotic stress, considerable variability persists among experimental systems and environmental

settings [194,195]. Benefits observed under controlled greenhouse conditions are often reduced under field conditions because of environmental fluctuations, soil heterogeneity, and interactions with native microbial populations [196,197]. Furthermore, microbial strains that are highly effective against a specific stress factor may exhibit limited performance under different stress scenarios, highlighting the context-dependent nature of microbial-mediated stress tolerance [198]. These limitations underscore the need to better understand ecological compatibility, microbial persistence, and functional stability under realistic agricultural conditions.

Collectively, current evidence suggests that microbial-mediated stress tolerance is governed by complex interactions among plant genotype, microbial traits, and environmental factors. Consequently, the development of functionally complementary microbial consortia may offer greater resilience, stability, and adaptability than single-strain inoculants under field conditions [199–201]. Future research should therefore focus on mechanistic investigations, long-term field validation, and the optimization of multi-species inoculants to improve the reliability, scalability, and practical application of microbial-based technologies for sustainable rice production.

5.3 Ecological and Technical Constraints in Field Application

One of the major limitations in the application of beneficial microbes for rice production is the inconsistency between laboratory efficacy and field-level performance [56]. Under field conditions, introduced microbial inoculants must compete with indigenous microbial communities that are already well adapted to local environmental, often limiting microbial establishment and persistence in the rhizosphere [103].

Environmental variability, including differences in soil type, pH, temperature, moisture availability, and agricultural management practices, can also influence microbial survival, colonization efficiency, and functional activity [52]. In addition, the effectiveness of microbial inoculants is strongly influenced by formulation quality and delivery methods because poor carrier materials, limited shelf life, and inadequate application techniques may reduce microbial viability before reaching the target plant environment [202].

Host genotype dependency further complicates microbial application, as different rice cultivars may exhibit variable compatibility with specific microbial strains, leading to inconsistent physiological responses under stress conditions [55]. Moreover, microbial interactions that appear synergistic under controlled greenhouse conditions may become unstable in open-field ecosystems due to fluctuating environmental pressures and complex ecological interactions [133].

These challenges indicate that successful field application of beneficial microorganisms requires not only effective microbial strains but also a deeper understanding of ecological adaptability, formulation technology, and host–microbe compatibility under realistic agricultural environments. Therefore, future research should prioritize long-term multi-location field trials and the development of robust microbial consortia capable of maintaining functional stability across diverse agroecosystems [20,139].

5.4 Microbiome-Host Genotype Interactions and Commercialization Challenges

Microbiome–host genotype interactions represent another important challenge in microbial-based rice agriculture because different rice cultivars may respond differently to the same microbial inoculants [203,204]. Variations in root exudate composition, root architecture, nutrient acquisition strategies, and plant immune signaling pathways can influence microbial colonization and functionality [205,206]. Consequently, microbial strains that improve stress tolerance in one rice genotype may not necessarily produce similar benefits in other cultivars [207].

In addition to genotype dependency, biosafety assessment and regulatory approval remain important considerations for the large-scale deployment of microbial products [208,209]. Introduced microorganisms may alter indigenous microbial communities or interact with non-target organisms, necessitating long-term ecological evaluations before commercialization [210,211]. Furthermore, formulation stability, production costs, storage requirements, and quality control challenges continue to constrain commercial development and adoption [212]. Addressing these limitations will require genotype-specific microbial selection, standardized biosafety frameworks, and improved formulation technologies to enhance the reliability and scalability of microbial-based solutions for sustainable rice production systems.

5.5 Future Directions

Future advances in microbe-assisted rice stress management are expected to rely on emerging technologies that optimize microbial communities and enhance their functional performance [212]. One promising approach is the development of synthetic microbiomes, in which carefully selected microbial strains are combined to form stable and synergistic consortia capable of providing multiple beneficial functions simultaneously [213–215]. Unlike single-strain inoculants, synthetic microbial communities can perform complementary roles such as nutrient mobilization, hormone regulation, stress signal modulation, and detoxification of harmful compounds [216]. This functional diversity may improve the stability and consistency of microbial performance under field conditions [217]. Recent progress in microbiome engineering has further demonstrated that rationally assembled microbial consortia can be designed based on functional traits rather than taxonomic identity, enabling more predictable plant growth–promoting outcomes and improved stress resilience in rice systems [218–221]. Another transformative approach involves the application of CRISPR-based genome editing technologies to engineer microbial strains with enhanced beneficial traits [222]. Genome editing can enable precise modifications that improve stress-related metabolite production, colonization efficiency, or compatibility with specific rice cultivars [200]. Such engineered microbes may provide more targeted and efficient plant growth–promoting functions under stressful conditions [223]. In addition to microbial engineering, CRISPR technologies have increasingly been explored to manipulate plant–microbe interactions through targeted modification of signaling pathways, root exudate composition, and microbial recognition mechanisms that influence rhizosphere assembly and stress adaptation [224–227]. These approaches may improve the establishment and persistence of beneficial microbial communities under fluctuating environmental conditions while enhancing rice tolerance to drought, salinity, flooding, and temperature stress [215,221,228].

Artificial intelligence (AI) and machine learning technologies are also emerging as powerful tools for microbial discovery and optimization [229]. By analyzing large omics datasets and environmental variables, AI algorithms can predict microbial functional traits, identify promising microbial candidates, and design optimized microbial consortia for specific soil types or climatic conditions [171]. When integrated with ecological engineering and climate modeling approaches, these technologies may enable the development of next-generation microbial solutions capable of sustaining rice productivity under increasingly challenging environmental conditions [230–232]. Nevertheless, despite promising laboratory and greenhouse results, large-scale field application of microbial inoculants often faces substantial ecological and environmental constraints, including microbial competition with native microbiota, inconsistent colonization efficiency, environmental variability, soil physicochemical heterogeneity, and limited persistence under field conditions [51,56]. These limitations contribute to inconsistent inoculation performance across locations and seasons, highlighting the need for long-term field validation and region-specific microbial formulation strategies [233,234]. Furthermore, emerging evidence suggests that microbiome-mediated epigenetic regu-

lation may play an important role in enhancing plant stress memory and adaptive responses through DNA methylation, histone modification, and small RNA-mediated pathways [235–238]. Understanding these microbiome-driven epigenetic mechanisms could provide new opportunities for developing durable and climate-resilient rice production systems in the future.

6 Conclusion

Beneficial microorganisms play important roles in enhancing rice tolerance to abiotic stresses through diverse physiological, biochemical, and molecular mechanisms. PGPR, AMF, endophytes, and other beneficial microbial groups contribute to stress adaptation by regulating phytohormone balance, nutrient acquisition, antioxidant defense systems, osmotic adjustment, and stress-responsive gene expression.

Recent advances in microbiome research, multi-omics technologies, and microbiome engineering have significantly improved our understanding of plant–microbe interactions and their potential applications in climate-resilient rice production systems. However, despite promising laboratory and greenhouse results, the large-scale agricultural application of microbial inoculants remains constrained by inconsistent field performance, ecological variability, host genotype dependency, formulation instability, and regulatory challenges.

Future research should therefore prioritize long-term field validation, development of functionally stable microbial consortia, integration of multi-omics approaches, and genotype-specific microbial application strategies under diverse agroecosystems. In addition, greater attention should be directed toward biosafety assessment, formulation technology, and ecological sustainability to improve the reliability and commercialization potential of microbial-based agricultural products. Overall, integrating beneficial microorganisms into sustainable rice cultivation systems represents a promising strategy to improve crop resilience, reduce dependence on chemical inputs, and support global food security under increasingly challenging climate conditions.

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