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Review

Harnessing microbial interactions with rice: Strategies for abiotic stress alleviation in the face of environmental challenges and climate change

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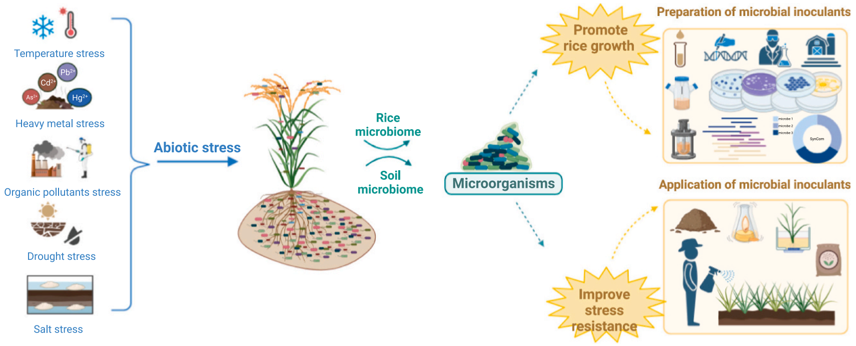
HIGHLIGHTS

- A comprehensive panoramic view of rice responses to various abiotic stress factors.
- Deep exploration of soil and rice microbes confronting environmental challenges.
- Unveiling the intricate interactions and mechanisms between rice and microbes.
- Customized microbial inoculants leading sustainable advancements in rice agriculture.
- Future perspective on the symbiosis of rice and microbes in innovative agriculture.

GRAPHICAL ABSTRACT



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ABSTRACT

Rice, which feeds more than half of the world's population, confronts significant challenges due to environmental and climatic changes. Abiotic stressors such as extreme temperatures, drought, heavy metals, organic pollutants, and salinity disrupt its cellular balance, impair photosynthetic efficiency, and degrade grain quality. Beneficial microorganisms from rice and soil microbiomes have emerged as crucial in enhancing rice's tolerance to these stresses. This review delves into the multifaceted impacts of these abiotic stressors on rice growth, exploring the origins of the interacting microorganisms and the intricate dynamics between rice-associated and soil

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Abbreviations: ROS, reactive oxygen species; ABA, abscisic acid; GA, gibberellin; Pb, lead; As, arsenic; Cd, cadmium; Hg, mercury; Tl, thallium; Cr, chromium; SynComs, synthetic microbial communities; NGS, next-generation sequencing; IAA, indole-3-acetic acid; SOD, superoxide dismutase; CAT, catalase; PGPR, plant growth-promoting rhizobacteria; EPS, exopolysaccharides; ACC, 1-aminocyclopropane-1-carboxylic acid; SA, salicylic acid; JA, jasmonic acid; P, phosphorus; N, nitrogen.

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Microbial inoculants
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microbiomes. We highlight their synergistic roles in mitigating rice's abiotic stresses and outline rice's strategies for recruiting these microorganisms under various environmental conditions, including the development of techniques to maximize their benefits. Through an in-depth analysis, we shed light on the multifarious mechanisms through which microorganisms fortify rice resilience, such as modulation of antioxidant enzymes, enhanced nutrient uptake, plant hormone adjustments, exopolysaccharide secretion, and strategic gene expression regulation, emphasizing the objective of leveraging microorganisms to boost rice's stress tolerance. The review also recognizes the growing prominence of microbial inoculants in modern rice cultivation for their eco-friendliness and sustainability. We discuss ongoing efforts to optimize these inoculants, providing insights into the rigorous processes involved in their formulation and strategic deployment. In conclusion, this review emphasizes the importance of microbial interventions in bolstering rice agriculture and ensuring its resilience in the face of rising environmental challenges.

1. Introduction

Rice (*Oryza sativa* L.) feeds over half of the world's population and is vital for global food security (Xu et al., 2022). However, with the intensifying impacts of climate change and environmental challenges, rice is facing a variety of abiotic stresses. Factors like extreme temperatures, drought, pollution, and salinity, which have become significant obstacles to its yield and quality (Patel and Mishra, 2019). These stresses disrupt critical growth stages and physiological processes in rice (Jiang et al., 2020; Pandey et al., 2017).

While traditional mitigation strategies are available, they are often inefficient, costly, and environmentally harmful (Gribaldi et al., 2017; Iqbal et al., 2020), making the pursuit of sustainable alternatives essential (Chaudhary et al., 2022; Phour and Sindhu, 2022). Current research has increasingly focused on the rice microbiome, especially microorganisms present in its roots, leaves, and growth environment (Banerjee and van der Heijden, 2023; Chouhan et al., 2021; Lakshmanan et al., 2014; Wang et al., 2016). These microbes not only offer eco-friendly solutions but also provide new strategies for enhancing rice's resilience to abiotic stresses.

Indeed, several studies have analyzed rice's responses to individual abiotic stressors or delved deep into specific microbial interactions. Yet, a coherent integration combining the full spectrum of stressors, the scope of microbial interactions, and emphasizing the complex mechanisms of these relationships is notably absent.

In this review, we present a cohesive analysis of the myriad ways abiotic stresses affect rice, from temperature extremes to pollutants, offering a comprehensive and detailed perspective. Furthermore, we reveal the intricate origins of microbes interacting with rice, exploring the interactions of the rice-soil microbiome and complex strategies of microbial acquisition. We investigate how symbiotic microbes bolster rice against environmental challenges, outlining the physiological mechanisms and the potential for microbial inoculants in sustainable rice cultivation.

We hope this review serves as a valuable reference for researchers and practitioners in rice cultivation, assisting them in identifying effective strategies in the face of climate change and other environmental challenges, thereby promoting the sustainability and resilience of rice cultivation.

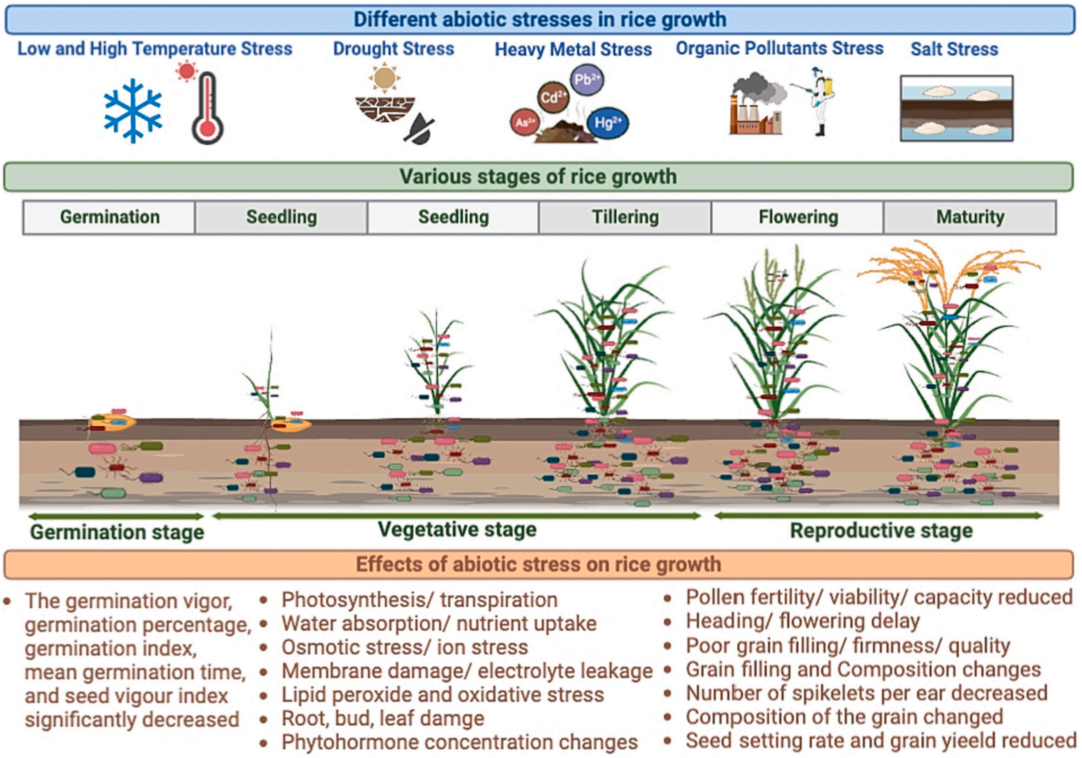


Fig. 1. Abiotic stressors and their impact on rice development. Throughout the rice growth stages, rice experiences multiple abiotic stressors including variations in temperature, drought, exposure to heavy metals, organic pollutants, and salinity. These stressors can manifest individually or concomitantly at any rice growth stage. Depending on the growth stage—be it germination, vegetative, or reproductive—these stressors distinctly impact rice's physiological, biochemical, and metabolic processes. Created with BioRender.com.

2. Effects of abiotic stress on rice growth

Rice faces a multitude of abiotic stresses due to environmental and climatic shifts, including temperature extremes, drought, heavy metal pollution, organic contaminants, and salinity. Studies indicate that rice is often simultaneously affected by several of these stressors, compounding their impact across all growth stages from germination to reproduction (Fig. 1).

During germination, rice seeds initiation is slowed. The vegetative stage experiences changes in key functions like photosynthesis, chlorophyll production, transpiration, hormone regulation, and nutrient absorption. At the reproductive stage, disruptions in pollen development and grain formation occur, which affects the overall quality of the rice. Properly addressing these stresses during pivotal growth stages can help reduce their negative effects.

Moreover, different rice cultivars exhibit inherent genetic and physiological variations, influencing their sensitivities and adaptability under abiotic stress. Some may show greater tolerance to extreme temperatures, while others are better adapted to drought or salinity (Almeida et al., 2016). These distinctions offer strategic insights for agricultural practices and provide a multifaceted framework to study the impacts of abiotic stressors on rice (Fernandes et al., 2022).

To elucidate the intricate effects of these abiotic stressors on rice, and to foster improved mitigation strategies against them, we will delve into a detailed examination of individual and combined abiotic stress impacts on rice.

2.1. Effects of temperature stress on rice growth

Rice's growth and yield are profoundly influenced by environmental temperatures. Low temperature stress during the seedling stage induces metabolic and physiological changes, affecting chlorophyll synthesis, accumulation of reactive oxygen species (ROS) and malondialdehyde. This stress alters levels of endogenous hormones like abscisic acid (ABA) and gibberellin (GA) (Hsu and Hsu, 2019; Jia et al., 2019). As rice reaches the reproductive stage, colder temperatures can induce pollen sterility, delay heading, and directly contribute to yield reductions. Specifically, cold stress during the reproductive phase significantly impacts pollen production in anthers.

On the flip side, rising global temperatures pose another set of challenges for rice. Excessive heat affects important rice organs and reduces chlorophyll function and the efficiency of photosynthesis (Shrestha et al., 2022). Especially during the reproductive and grain-filling stages, high temperatures can reduce pollen vitality and seeds setting, leading to marked yield losses (Arshad et al., 2017; Tu et al., 2022; Hu et al., 2021).

2.2. Effects of drought stress on Rice growth

Drought stress is a growing concern for rice farming due to climate change. It leads to soil degradation and challenges rice production. Rice, as a crop heavily reliant on a consistent water supply, is more susceptible to yield losses under drought conditions than many other crops (Palanog et al., 2014). Lack of water impairs crucial processes such as photosynthesis, energy production, and lipid metabolism, particularly affecting grain quality and yield during the reproductive phase (Hameed et al., 2014; Hussain et al., 2022; Yang et al., 2019). Drought induces oxidative stress, leading to electrolyte leakage and potential cellular damage, which further hinders rice growth (Pang et al., 2020; Kamoshita et al., 2008).

Genotypic variations in rice significantly influence its drought response. For instance, different Indica rice genotypes show varied proteomic responses under drought conditions, highlighting the diversity in drought sensitivity among rice varieties (Hamzelou et al., 2020). Moreover, drought stress alters the root-associated microbiomes of rice, changing the microbial community composition and the physical structure of the roots, including length, density, and arrangement (Luo et al., 2021; Santos-Medellín et al., 2017).

2.3. Effects of heavy metal stress on rice growth

Rice cultivation is at risk from soil and irrigation water contamination by heavy metals, notably lead (Pb), arsenic (As), cadmium (Cd), mercury (Hg), thallium (Tl), chromium (Cr). These metals are absorbed by rice plants from the soil and accumulate in the grains, increasing their concentration in the food chain and posing health risks (Khanna et al., 2022a; Chiao et al., 2020; Rizwan et al., 2016; Haider et al., 2023). The absorption of heavy metals disrupts rice's physiological and reproductive functions, leading to challenges like reduced germination, developmental delays, and symptoms such as leaf chlorosis (Zulfiqar et al., 2022).

These metals further constrain growth, impacting morphological attributes and suppressing physiological processes like photosynthesis (Rizwan et al., 2016; Zulfiqar et al., 2022). On the cellular level, they inflict oxidative stress and can cause genetic disruptions (Khanna et al., 2022a). During grain development, these metals interfere with rice metabolism, potentially reducing yield and degrading grain quality (Tian et al., 2019).

2.4. Effects of organic pollutants stress on rice growth

Organic pollutants, like polycyclic aromatic hydrocarbons, benzene-related compounds, and small plastics, are long-lasting and toxic. (Wang et al., 2022a). These pollutants affect many ecosystems, including soil and water, and rice plants can absorb them through roots and transpiration. (Fu et al., 2022; Zhang et al., 2021). Absorbing these pollutants has negative effects on both rice growth and human health, as they remain in plant tissues and reduce rice quality.

The presence of these pollutants in rice plants can obstruct water flow, hinder nutrient uptake, and disrupt the conversion of sunlight into energy. They can impair critical systems in rice such as photosynthesis, antioxidant enzymes, and sugar metabolism, resulting in altered germination rates, root growth, plant height, and other developmental indicators (Wang et al., 2022b). Furthermore, organic pollutants disrupt essential biological pathways, including RNA metabolism and protein synthesis in rice, leading to reduced production of amino acids and nucleic acids, ultimately affecting rice yield and quality (Wang et al., 2022b; Wu et al., 2020).

2.5. Effects of salt stress on Rice growth

Salt stress significantly impacts rice, a crop notably sensitive to salinity, leading to reduced growth rates and grain yields (Razzaq et al., 2020). The seedling and reproductive stages are particularly susceptible. Exposure to salt stress in young rice plants can damage roots, shoots, and leaves due to excessive sodium (Na^+) accumulation, negatively affecting cellular functions (Hoang et al., 2016). Additionally, salt stress triggers the production of ROS, causing oxidative damage and impairing normal cell activities (Negrão et al., 2011). Notably, a study highlighted differential responses of the antioxidative defense system to prolonged salinity stress between salt-tolerant and salt-sensitive Indica rice seedlings, underscoring inherent variances in coping mechanisms among rice varieties (Mishra et al., 2013).

Salt stress also inhibits photosynthesis, disrupts hormonal balances, and can lead to premature plant senescence. In reproductive stages, salt stress affects flowering, seeds setting, and grain yield, primarily via hampered pollen activity (Razzaq et al., 2020). Moreover, salt stress negatively influences yield attributes, interferes with grain-filling processes, and alters grain composition, particularly impacting carbohydrate and protein contents.

2.6. *Effects of combined abiotic stresses on rice growth*

Rice encounters amplified challenges when simultaneously exposed to multiple abiotic stressors. These stressors interact in complex ways, often producing combined or opposing effects rather than simply additive ones. For example, concurrent salinity and drought conditions, or the mix of high temperatures with heavy metal pollution, significantly hinder rice growth by presenting unique physiological stresses (Kota et al., 2023). Rice growing in soils contaminated with both heavy metals and organic pollutants undergoes intensified defense mechanisms. Furthermore, the combination of heat and drought stress accelerates leaf aging and disrupts grain formation, resulting in decreased yields (Farhat et al., 2021).

The presence of multiple stresses intensifies ROS production, causing significant cellular damage (Sánchez-Bermúdez et al., 2022). This complexity in stress responses arises from interactions among various stress signaling pathways, resulting in diverse gene activations. Additionally, combined stresses modify the rice root microbiome, with certain bacterial taxa becoming more dominant, potentially aiding in stress mitigation. Understanding the intricate effects of combined stresses is vital for advancing studies on rice-microbiome interactions, with the goal of enhancing rice's resilience to abiotic stresses and supporting sustainable agriculture in the face of increasing environmental challenges.

3. Exploring microorganisms interacting with rice: sources, synergies, dynamics, and acquisition

Using microorganisms to reduce the impact of abiotic stress on rice growth and reproduction is becoming a popular method for green and sustainable farming. These microorganisms originate mainly from two sources: the rice microbiome and the soil microbiome (Fig. 2). Understanding the intricate dynamics between the rice and soil microbiomes is crucial, as it allows us to explore their functional characteristics and harness them to enhance rice growth and stress resilience. In certain environmental conditions, the strategic recruitment and augmentation of these beneficial microorganisms can also significantly improve rice's growth environment. Employing advanced research techniques and methods is essential to unravel these complex interactions.

3.1. *Rice microbiome: rice microbiome: unveiling the intricate microbial network within rice*

The rice microbiome, consisting of diverse microorganisms within and on rice tissues, plays a vital role in rice health and productivity. These microorganisms, residing in parts such as roots, stems, leaves, and seeds, contribute to biological control against pathogens, promote plant growth, and enhance stress tolerance. Rice plants actively recruit these beneficial microorganisms from various sources, including the surrounding soil and plant tissues, to maintain a balanced and functional microbial ecosystem (Jana et al., 2022).

Rice roots, in direct contact with the soil, develop a unique and diverse microbiome, capitalizing on the soil's rich microbial resources. This root microbiome, including the endosphere (root interior), the rhizoplane (roots surface), and the rhizosphere (soil close to the root surface), is selectively formed by recruiting specific soil microbes (Li et al., 2023; Edwards et al., 2015). Its composition is influenced by a range of factors such as plant adaptation, genetic makeup, growth stage, and external environmental conditions including soil type, location, cultivation methods, and management practices (Bai et al., 2022; Xun et al., 2021).

Rice stems also house various microorganisms, including abundant endophytes within the stalks, an essential vegetative tissue. The

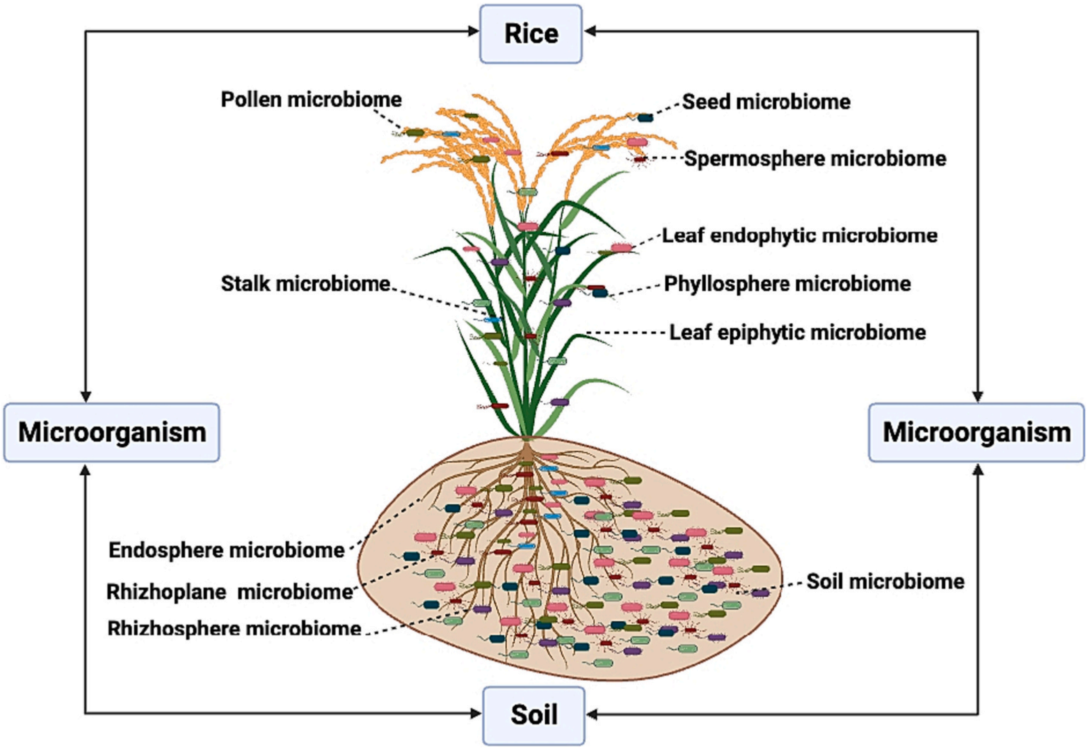


Fig. 2. Origins of microorganisms interacting with rice. Rice interacts with microorganisms originating from both its intrinsic microbiome and the external soil microbiome. The intrinsic rice microbiome comprises microbial entities located in varied rice tissues including pollen, seeds, stalks, leaves, and roots. Intricate distinctions can be noted within a single tissue's microbial composition. For instance, root-associated microorganisms can be categorized into the endosphere (inside the root), the rhizoplane (root surface), and the rhizosphere (proximal soil region). Similarly, leaf microbes can be segmented into endophytic, phyllosphere, and epiphytic microbiomes. Created with BioRender.com.

microorganisms in stems are interconnected with those in seeds, roots, and leaves (Cui et al., 2019). During plant development, specific bacterial and fungal taxa are transmitted, enriching the rice-microbe interactions and fostering a beneficial microbial environment for growth (Wang et al., 2016). Some microorganisms may enter plant tissues through stomata or wounds, or by secreting enzymes that attack plant cell walls, then becoming rice endophytes (Roman-Reyna et al., 2020).

Rice seeds are pivotal sources of endophytic bacteria, playing a crucial role throughout the rice plant's lifecycle. Seeds house diverse bacterial communities that are vertically transmitted and preserved across generations, adapting to environmental changes, and protecting plants from generation to generation (Guo et al., 2021; Zhang et al., 2022; Kaga et al., 2009). During growth, rice plants can absorb environmental microbes, such as those from soil, allowing specific bacterial species to colonize within the grains. These microbes act as natural biofertilizers and protectors, enhancing the plant's lifecycle.

3.2. *Soil microbiome: the dynamic microbial ecosystem interacting with rice*

The soil microbiome is a cornerstone of agricultural productivity, influencing environmental factors like pH, salinity, nutrient cycling, and fertility (Ali et al., 2022; Bahram et al., 2018; Edwards et al., 2019). It comprises diverse microorganisms essential for biochemical reactions in the soil (Banerjee and van der Heijden, 2023; Dubey et al., 2020). Factors such as crop acclimatization, water management, pH value, electrical conductivity, salt content, temperature, vegetation cover, farming methods, soil management, host type, microbial interactions, and abiotic stress shape the soil microbiome. The soil microbiome greatly influences the health of both plants and animals in land ecosystems. It also shapes the rice rhizosphere microbiome, which is crucial for the well-being of the plant (Fierer, 2017; Maron et al., 2011; Das et al., 2022). It assists rice in pest and disease defense, nutrient acquisition, and abiotic stress tolerance (Adomako et al., 2022; Bakker et al., 2018).

3.3. *Interaction between rice microbiome and soil microbiome*

In agricultural ecosystems, interactions between the rice and soil microbiomes significantly influence plant health and stress responses. Rice roots release organic compounds, such as sugars and acids, that selectively induce specific soil microbes, thereby influencing the composition and functions of the soil microbial community (Uphoff and Thies, 2023). The soil microbiome, in turn, offers a reservoir of microbial diversity, with certain microbes responding to rice-derived signals and interacting with the plant, possibly becoming part of the rice microbiome (Fernández-Baca et al., 2021).

Despite the abundance of soil microbes, rice selectively recruits specific microbial types, using its defense system as a “gatekeeper” to control the attachment and colonization of external microorganisms on its roots. This selectivity is influenced by the rice genotype, which not only provides a physical host for microbes but also acts as a signal to shape the diversity and functionality of root communities (Semchenko et al., 2022; Singh et al., 2022). Soil microorganisms may colonize various rice tissues, including seeds, potentially being vertically transmitted, thus contributing to a form of “soil inheritance”. Abiotic stressors can affect the composition and formation of the microbiome, with plant-soil interactions and soil memory playing roles in enhancing rice's abiotic stress tolerance (Kong et al., 2019).

3.4. *Recruitment of rice and soil microbial communities under normal and stress-induced conditions*

The interplay between rice and soil microbiome is highly responsive to environmental shifts. These microbial communities adapt dynamically to both regular and stress-induced conditions, supporting not only their survival but also optimizing rice growth and resilience. Under regular growth conditions, rice can establish symbiotic relationships with certain beneficial microbes, promoting nutrient uptake and overall health. However, when faced with stressors such as drought or high salinity, rice releases specific root exudates to attract microbes that can alleviate these stresses (Rizaludin et al., 2021).

Similarly, the soil microbiome shifts in response to varying environmental stressors. In areas with heavy metal contamination or salinity, certain resilient microbial populations may become dominant (Abdul Rahman et al., 2021; Yu et al., 2021). These microbes can not only alter the soil environment but also interact positively with rice plants, further enhancing their resistance to various abiotic stresses. This tight interplay between rice and soil microbes becomes especially crucial under stress conditions, as their combined microbial communities collaborate to bolster the rice's resilience, ensuring its healthy growth.

In conclusion, understanding this natural recruitment process between rice and soil microbes is essential. Researchers can develop specific “Synthetic Microbial Communities” (SynComs) by emulating natural microbial symbioses and leveraging their collective benefits. These are engineered assemblies of microbes, designed to optimize plant health and adaptability, tailored to various environmental conditions (de Souza et al., 2020).

3.5. *Strategies for acquiring microbes interacting with rice: a comparison of traditional cultivation methods and modern next-generation sequencing (NGS) techniques*

Effective identification and acquisition of microbes interacting with rice is crucial for understanding their roles, particularly under abiotic stress. Traditional cultivation methods and modern Next-Generation Sequencing (NGS) techniques both play pivotal roles in this field.

Traditionally, microbial identification relied on cultivation on specific media. For instance, Damo et al. (2022) isolated phosphate solubilizing bacteria from rice paddy soils using such methods. These techniques excel in providing live microbial samples for functional studies and validating interactions, and they offer insights into individual microbial behaviors with rice. However, they may overlook rare but functionally important microbes that require unique growth conditions.

Conversely, NGS techniques offer a comprehensive overview of microbial communities by analyzing DNA directly from samples. Cheng et al. (2023) utilized metagenomics and machine learning to identify the root-associated microbiomes of different rice cultivars. Similarly, Zhang et al. (2019) used 16S rRNA gene profiling to differentiate root microbiota between indica and japonica rice, linking them with the *NRT1.1B* nitrate transporter. However, NGS has its own challenges, particularly in data interpretation and anaerobic resolution.

NGS can reveal a wealth of information about non-culturable microbes, but understanding their direct interactions with rice, especially under stress conditions, often necessitates further analysis. Metagenomic and metatranscriptomic approaches can uncover potential functions of these microbes. A combined approach, integrating both cultivation-dependent and -independent methods, can offer a more comprehensive understanding of the microbial role in stress mitigation. Therefore, depending on research objectives and available resources, it is crucial to fully utilize these two key approaches for discovering and acquiring microorganisms associated with rice.

4. Microbial intervention in enhancing rice's tolerance against abiotic stresses: exploring the key mechanisms

Microorganisms, nature's tiny helpers, play a key role in boosting rice's ability to withstand abiotic stresses. In the realm of modern agronomy, leveraging these multifaceted microorganisms marks a significant step towards sustainable agriculture, particularly as the global focus shifts towards eco-friendly practices. Understanding how these microorganisms assist rice in countering abiotic challenges is increasingly important.

Various microorganisms, each with their distinct traits, play a vital role in helping rice combat the negative impacts of abiotic stresses. In the face of diverse and unpredictable environmental challenges, the strategic selection and application of these microorganisms not only enhance rice's resistance but also potentially increase its yield (Table 1).

Through a systematic exploration of the mechanisms by which microorganisms augment resistance to varied abiotic stresses, we underscore the transformative potential of microbial interventions (Fig. 3). This study highlights a promising path forward, balancing the goals of sustainability and future food security.

4.1. Microbial strategies for augmenting rice's extreme temperatures tolerance: nutrient synthesis, hormonal modulation, and antioxidant activation

The augmentation of rice's temperature tolerance through microbial interactions is gaining significant attention in the field of agronomy. Drawing from the rhizosphere soil of rice fields, rhizobacteria present a potential tool for tolerance enhancement. A study by de Souza et al. (2021) highlights this, identifying key prokaryotic communities in cold-affected rice fields that enhance cold tolerance without compromising yield.

A deeper dive into the underlying dynamics reveals several intertwined mechanisms. One of them is the synthesis and absorption of nutrients and compounds in rice promoted by microorganisms. These microorganisms not only enhance the production and availability of essential compounds like indole-3-acetic acid (IAA) but also exhibit a propensity for inorganic phosphate solubilization. Another critical mechanism is the modulation of plant hormones. The endophytic fungus *Paecilomyces fowleri* LWL1, as noted by Waqas et al. (2015), produces phytohormones that support rice growth and provide heat stress protection. Additionally, *Bacillus amylobacter* SN13, as explored by Tiwari et al. (2017), acts as a regulator of plant hormones and stress-responsive genes. Lastly, the regulation of antioxidant enzymes, such as superoxide dismutase (SOD) and Catalase (CAT), is crucial in mitigating temperature stresses, as evidenced by the work of Kakar et al. (2016).

In conclusion, the combined effects of microbial nutrient production, hormone adjustment, and antioxidant control highlight a hopeful direction in improving rice's resistance to temperature changes.

4.2. Microbial mechanisms enhancing drought tolerance in rice: leveraging defensive compounds, exopolysaccharide, and gene regulation

Drought significantly alters the microbial community around rice roots, favoring those adapted to arid conditions (Tiwari et al., 2017). These microorganisms bolster rice's defense against drought by enhancing growth, aiding stress management, and minimizing crop loss from unfavorable weather (Ali and Khan, 2021; Santos-Medellín et al., 2017; Ullah et al., 2019; Vurukonda et al., 2016).

Various strategies employed by microorganisms include the release of drought-defensive compounds, production of exopolysaccharides, enhancement of antioxidant capabilities, improvement in growth and root characteristics, and support of drought-avoidance mechanisms. They also influence plant hormone balance, nutrient absorption, and osmolyte accumulation (Ahmad et al., 2022; Naseem et al., 2018). Stress-responsive gene modulation and bolstered antioxidant responses, both enzymatic and non-enzymatic, further contribute to drought-stress alleviation (Gowtham et al., 2022; Singh et al., 2020).

Studies like that of (Gusain et al., 2015) showed how plant growth-promoting rhizobacteria (PGPR) reduced oxidative damage in drought-stressed rice, thereby enhancing growth and antioxidant defense. Sun et al. (2020) found that exopolysaccharides (EPS) from *Pantoea alhagi* NX-11 fortified drought tolerance in rice seedlings. Rice harbors endophytic bacteria, releasing drought-tolerance compounds like ABA, IAA, 1-Aminocyclopropane-1-carboxylic acid (ACC) deaminase and volatile compounds, furthering drought tolerance (Barnawal et al., 2019; Kaushal, 2019). Qin et al. (2019) highlighted endophytic fungi with significant antioxidant activity, reducing drought-induced damage in rice. Similarly, Singh et al. (2020) pinpointed the enhanced *PAL* gene expression due to microbial inoculants, leading to a surge in plant antioxidants under drought. Sarapat et al. (2020) leveraged endophytes like SUTN9–2 to elevate ACC deaminase activity in rice, enhancing its drought tolerance and overall yield.

In summary, the multifaceted interactions between rice and microorganisms present a robust defense against the detrimental effects of drought. From making drought-fighting compounds to adjusting genes, microorganisms play a big part in helping rice thrive in dry conditions.

4.3. Microbial facilitation of heavy metal tolerance in rice: hormonal, nutritional, genetic interventions, metal absorption enhancement, and bioavailability modification

Harnessing microorganisms to bolster rice's heavy metal tolerance offers a pivotal strategy to diminish heavy metal accumulation, ensuring safer rice production and effective bioremediation of cadmium-contaminated rice (Pramanik et al., 2018). These microbial interactions bolster heavy metal tolerance in rice through various mechanisms, including enhancing antioxidant defenses, modulating endogenous hormones, amplifying stress-related genes, assisting nutrient assimilation, and modifying heavy metal absorption and bioavailability.

Microorganisms resilient to high concentrations of heavy metals play a crucial role in rice's tolerance (Ghosh et al., 2018). They adsorb heavy metals, either via extracellular polysaccharides or by internal accumulation, effectively shielding the rice plant (Mitra et al., 2018b; Wei et al., 2023). Beyond absorption, these microbes optimize rice growth under metal stress and influence hormonal regulation involving ABA, salicylic acid (SA), jasmonic acid (JA), and others. The uptake of essential nutrients like phosphorus (P), nitrogen (N), and siderophores is enhanced, bolstering rice's defenses against heavy metal (Mitra et al., 2018a; Mukherjee et al., 2022; Shahzad et al., 2019). ACC deaminase activity in some microbes moderates ethylene stress hormone effects under heavy metal conditions (Ghosh et al., 2018; Treesubsuntorn et al., 2018). These beneficial microbes also demonstrate antioxidant enzyme activity, protecting rice from oxidative stress caused by heavy metals (Xie et al., 2019). Additionally, microbial inoculation reshapes the expression landscape of genes linked with heavy metal stress in rice, leading to reduced metal uptake (Jan et al., 2019).

In conclusion, the complex interaction between rice and microorganisms leads to enhanced resistance against heavy metals. Through diverse mechanisms, these microorganisms not only diminish heavy metal toxicity but also curtail the accumulation of cadmium in rice (Fig. 4), resulting in safer and healthier rice production.

4.4. Microbial mechanisms bolstering rice's tolerance to organic pollutants: plant vitality enhancement, pollutant biodegradation, and activity mitigation

The use of microorganisms as bioremediation agents in rice fields contaminated with organic pollutants is recognized for its efficacy, cost-effectiveness, and environmental friendliness (He et al., 2020; Singha et al., 2018). The symbiotic relationship between rice and specific microorganisms offers mutual benefits: rice provides a habitat and nutrients, while microorganisms reduce the adverse effects of organic pollutants, thereby enhancing rice's stress tolerance and growth (Afzal et al., 2014).

Beyond their primary plant growth-promoting roles, which include IAA production, phosphate solubilization, atmospheric nitrogen fixation, and siderophore release, the pivotal mechanism lies in their capacity to degrade organic pollutants. This biotransformation reduces the

Table 1
The microorganisms enhance tolerance of rice under different stress conditions.

Abiotic stress	Mechanisms	Strains	Soil/plant/tissue	Reference
Temperature stress	Having the plant growth promoting (PGP) traits, such as production of auxins, siderophores, ACC deaminase activity, mobilization of soil nutrients.	*Kosakonia* sp. CIR2 and *Staphylococcus* sp. CSR1T2	Rhizospheric Soil of rice	(de Souza et al., 2021)
Temperature stress	Having activities of antioxidant enzymes (SOD and CAT). Producing high amounts of IAA and siderophores, the capability to form biofilms and solubilize inorganic phosphate.	*Bacillus amyloliquefaciens* Bk7 and *Brevibacillus laterosporus* B4	Rhizospheric Soil of rice	(Kakar et al., 2016)
Temperature stress	Having lower endogenous level of stress-signaling compounds such as ABA and JA.	*Paecilomyces formosus* LWL1	Roots of cucumber	(Waqas et al., 2015)
Temperature stress	Having membrane integrity and osmolyte accumulation, gene expression in rice to regulate plant responses to phytohormones.	*Bacillus amyloliquefaciens* NBRI-SN13 (SN13)	Alkaline soil of Banthara	(Tiwari et al., 2017)
Drought stress	Genes of key metabolic pathways including SOD, ascorbate peroxidase (APX), Peroxidase (POD) and CAT etc. were over-expressed.	*Pseudomonas fluorescens* (Pf) and *Trichoderma asperellum* (Th)	Rhizospheric soil of rice	(Singh et al., 2020)
Drought stress	Improving plant growth and activated antioxidant defense systems, improving stability of membranes in plant cells.	*Pseudomonas fluorescence* P2*, Pseudomonas jessenii* R62*, Pseudomonas synxantha* R81*, Bacillus cereus* BSB 38 (14B)*, Arthrobacter nitroguajacolicus* YB3 *and YB5*	Rhizobacterial strains	(Gusain et al., 2015)
Drought stress	EPS from *P. alhagi* NX-1 made malondialdehyde content reduced while total chlorophyll, proline, and soluble sugar content, prominent enhanced. The antioxidant enzymes, CAT, POD, and SOD, were also significantly increased	*Pantoea alhagi* NX-11	Rhizosphere soil of sea rice	(Sun et al., 2020)
Drought stress	Maintain the membrane integrity and regulate the antioxidant activity under oxidative stress.	*Aspergillus fumigatus* SG-17	Tissues of *M. laxiflora* pre- and post- flooding	(Qin et al., 2019)
Drought stress	Having ACC deaminase-producing ability.	*Bradyrhizobium* strain SUTN9–2	*Aeschynomene americana*	(Sarapat et al., 2020)
Heavy metal stress	Exhibiting N fixation, IAA production, P solubilization, ACC deaminase activity and reducing oxidative stress, stress ethylene.	*Enterobacter aerogenes* MCC 3092	Rhizospheric soil of cultivated rice (*Oryza sativa* L.)	(Pramanik et al., 2018)
Heavy metal stress	Having high heavy metal stress tolerance, high removal, and bioaccumulation, exhibited IAA and siderophore production, P-solubilization and ACC deaminase activity.	*Bacillus aryabhattai* MCC3374	The rhizospheric (rice) soil	(Ghosh et al., 2018)
Heavy metal stress	Bioaccumulating cadmium intracellularly and reducing oxidative stress and stress ethylene under Cd exposure.	*Enterobacter* sp. S2	Rhizospheric soil	(Mitra et al., 2018b)
Heavy metal stress	Promotes plant growth (ACC deaminase, IAA, P-solubilization, N-fixation), high Cd removal, intracellular accumulation, reduces oxidative stress.	*Klebsiella michiganensis* MCC3089	Heavy metal contaminated rhizospheric soil	(Mitra et al., 2018a)
Heavy metal stress	Showing Cd tolerance, Cd-bioaccumulation efficiencies, and displayed ACC deaminase activity, P-solubilization, produced IAA, GA, siderophore.	*Colletotrichum* sp. ALE15 and ALE18	Leaf endophyte of *Eupatorium triplinerve*	(Mukherjee et al., 2022)
Heavy metal stress	ABA and JA were significantly reduced in RWL-1-inoculated seedlings.	*Bacillus amyloliquefaciens* RWL-1	Endophytic strain isolated from rice seeds	(Shahzad et al., 2019)
Heavy metal stress	Presenting the ability to solubilize phosphate, produce IAA, and control ethylene levels by ACC deaminase activity.	*Bacillus subtilis, Bacillus cereus*, and commercial effective microorganism	Paddy soil contaminated with Cd	(Treesubsuntorn et al., 2018)
Heavy metal stress	High Cd tolerance and removal, bioactivator synthesis, reducing Cd-induced lipid peroxidation, enhancing antioxidant enzymes.	*Aspergillus aculeatus*	Cd-polluted soil	(Xie et al., 2019)
Heavy metal stress	Regulating the heavy metal stress-responsive genes, ABA, and SA	*Enterobacter ludwigii* SAK5 and *Exiguobacterium indicum* SA22	Endophytic bacteria were isolated from various plants (*Artemisia princeps, Chenopodium ficifolium, Oenothera biennis,* and *Echinochloa crus-galli*)	(Jan et al., 2019)
Organic pollutants stress (Polyaromatic hydrocarbon Degrading, pyrene)	Polycyclic aromatic hydrocarbon (PAH) degradation, plant growth promotion (IAA, P-solubilization, N fixation, siderophore), ACC deaminase activity.	*K. pneumoniae* AWD5, *P. aeruginosa* PDB1, *A. faecalis* BDB4, *P. fragi* DBC and *Acinetobacter* sp. PDB4	Collected rhizosphere and non-rhizosphere soil samples from industrial waste sites.	(Singha et al., 2018)
Organic pollutants stress	Degrading phenanthrene absorbed into the plant, changing the phenanthrene-degrading enzyme activities and gene expression levels in rice.	*Phomopsis liquidambaris*	The inner bark of the stem of *Bischofia polycarpa*	(Fu et al., 2020)

(*continued on next page*)

Table 1 (*continued*)

Abiotic stress	Mechanisms	Strains	Soil/plant/tissue	Reference
Organic pollutants stress	Enhancing rice growth, root function, chlorophyll, adenosine triphosphate (ATP) energy, and resistance; boosting phenanthrene degradation through enzyme activity and gene expression.	*Phomopsis liquidambaris*	The stem of *Bischofia polycarpa*	(Fu et al., 2022)
Organic pollutants stress	Involving in the rapid inactivation of diazinon in rice plants treated with diazinon (in vivo degradation of diazinon).	*B. altitudinis* DB26–R and *B. subtilis* subsp. *Inaquosorum* B6–L	Endophytic bacteria (root, stem, and leaf) from diazinon treated and non treated rice	(Nasrollahi et al., 2020)
Organic pollutants stress	Reducing the quinclorac toxicity to microorganisms in soil.	*Streptomyces* sp. strain AH-B	Quinclorac-contaminated soils	(Lang et al., 2018)
Organic pollutants stress	Influencing the perspective of metabolites, the dynamics of degradation enzyme activity and the expression of key genes.	*Phomopsis liquidambaris*	The inner bark of the stem of *Bischofia polycarpa*	(Fu et al., 2018)
Salt stress	Producing various phytohormones such as IAA, GA, ABA, and organic acids.	*Curtobacterium oceanosedimentum* SAK1, *Curtobacterium luteum* SAK2, *Enterobacter ludwigii* SAK5, *Bacillus cereus* SA1, *Micrococcus yunnanensis* SA2, *Enterobacter tabaci* SA3	Endophytes from the roots of *Oenothera biennis L.*, *Artemisia princeps* Pamp, *Chenopodium ficifolium* Smith and *Echinochloa crus-galli*	(Khan et al., 2020)
Salt stress	Having PGP traits, in particular, ACC deaminase activity.	*Bacillus* spp.	The composite soil samples	(Misra et al., 2017)
Salt stress	Producing ACC deaminase and alleviating salt stress by reducing the production of stress ethylene.	*Burkholderia* sp. MTCC 12259	Rhizospheric soil samples	(Sarkar et al., 2018b)
Salt stress	Possessing ACC deaminase and preventing ethylene production. Having PGP traits, including P-solubilization, IAA production, siderophore production, hydrogen cyanide (HCN) production, etc.	*Enterobacter* sp. P23	The rhizospheric soil samples were collected from rice fields near the coastal belt of Odisha	(Sarkar et al., 2018a)
Salt stress	Promoting the growth of rice under salt stress by regulating antioxidant enzyme system, enhancing photosynthesis, and improving soil enzyme activities.	*Bacillus pumilus* JIZ13	The rice rhizosphere soil	(Wang et al., 2023)
Salt stress	Having PGP properties and promoted photosynthetic pigments, proline, and antioxidant production.	*Bacillus pumilus* JPVS11	Rhizosphere and non-rhizosphere soil samples were collected from salinity affected regions	(Kumar et al., 2021)
Salt stress	The functional groups of EPS can help to bind and chelate Na^+ in the soil and thereby reduces the plant's exposure to the ion under saline conditions.	*Bacillus tequilensis* UPMRB9 and *Bacillus aryabhattai* UPMRE6	Rice roots with adhered soil were collected from seven salt-affected rice fields	(Shultana et al., 2020a)
Salt stress	Producing EPSs to enhance the salt tolerance of rice seedlings.	*Pantoea alhagi* NX-11	The rhizosphere soil of sea rice on a beach	(Sun et al., 2019)
Salt stress	Having PGP traits (production of IAA, siderophores, N and HCN, P-solubilization, non-symbiotic N_2 fixation and anti-microbial or biocontrol activities) and EPS secretion.	*Halomonas* sp. Exo1	*Avicennia marina* Rhizosphere Soil	(Mukherjee et al., 2019)
Salt stress	Enhancing rice growth and salinity tolerance; improving assimilation and chlorophyll stability; regulating stress-related genes and proteins for signal processing and transcription.	*Fusarium* sp.	Isolated endophytes from 720 segments of leaves, roots, and seeds of salt-sensitive IR-64 and salt-tolerant Pokkali rice varieties	(Sampangi-Ramaiah et al., 2020)
Salt stress	Exhibiting the substantial potential for ACC deaminase activity on rice plants, alleviating the salinity effects by upregulation of the stress responsive *CIPK* genes	*Achromobacter* sp. FB-14	The rhizospheric soil sample of rice	(Shahid et al., 2020)
Salt stress	Inducing changes in expression of a considerable number of photosynthesis, hormone, and stress-responsive genes, cell-wall, and lipid metabolism-related genes under salt stress	*Bacillus amyloliquefaciens*sn13	Rhizobacteria SN13 isolated from alkaline soil	(Chauhan et al., 2019)

PGP, plant growth promoting; ACC, 1-aminocyclopropane-1-carboxylic acid; SOD, superoxide dismutase; CAT, catalase; IAA, indole-3-acetic acid; ABA, abscisic acid; JA, jasmonic acid; APX, ascorbate peroxidase; POD, peroxidase; EPS, exopolysaccharides; N, nitrogen; P, phosphorus; Cd, cadmium; SA, salicylic acid; PAH, polycyclic aromatic hydrocarbon; ATP, adenosine triphosphate; HCN, hydrogen cyanide.

pollutants' activity, lessening their detrimental effects on rice.

Fu et al. (2020) spotlighted the endophytic fungus *Phomopsis liquidambaris*, which forges a symbiotic relationship with rice, exhibiting the capability to degrade phenanthrene. This degradation process is underscored by congruent shifts in fungal genes and corresponding enzymatic activities, emphasizing the microbial genetic underpinning in organic pollutant mitigation (Fu et al., 2022). Nasrollahi et al. (2020) found that rice's endophytic bacteria not only degrade diazinon ex vivo but also contribute to its rapid inactivation in treated rice plants.

Moreover, beyond the plant matrix, microorganisms also offer environmental remediation. Lang et al. (2018) demonstrated that when *Streptomyces* sp. strain AH-B was added to soil with quinclorac, it sped up the herbicide's breakdown, reducing its negative impact on the soil's microorganisms. Emphasizing the duality of their role, bioremediative microorganisms produce enzymes converting pollutants to benign metabolites. These metabolites, innocuous to plants, further serve as growth substrates for the microorganisms themselves (Fu et al., 2018; Lang et al., 2018).

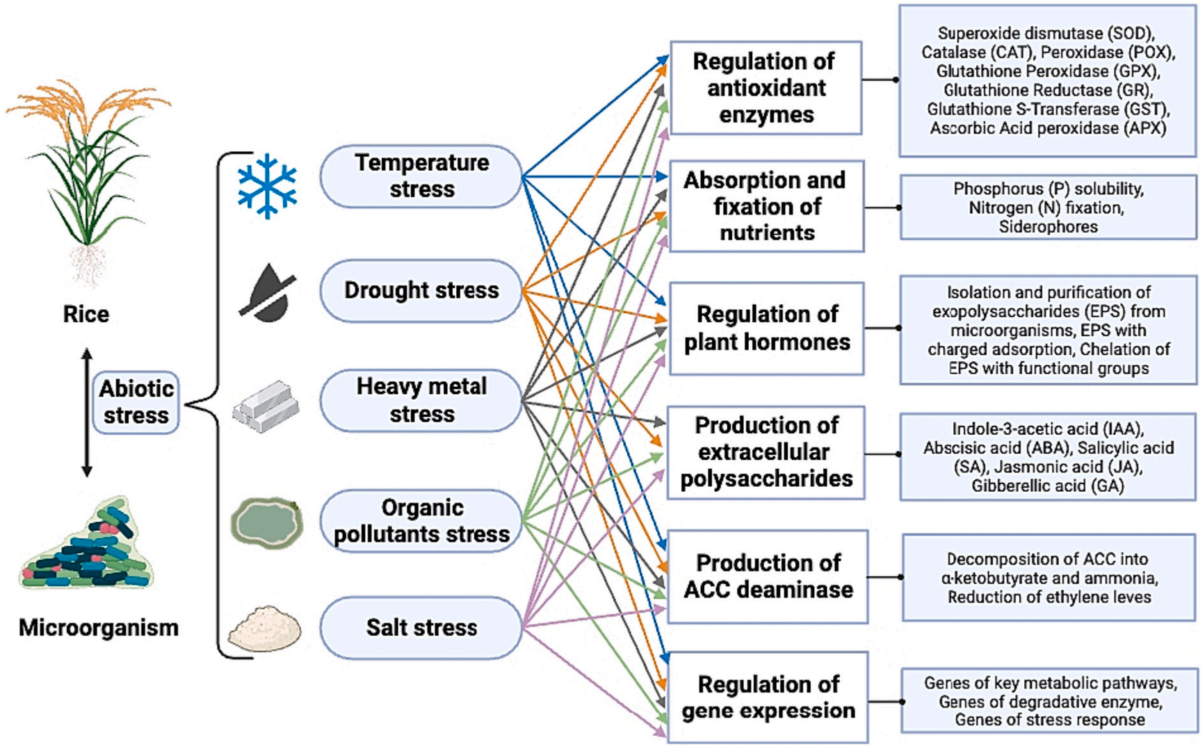


Fig. 3. Mechanisms via which microorganisms enhance rice's stress tolerance. Microbial interactions with rice bolster its tolerance against abiotic stressors through various means: modulation of antioxidant enzyme activity, nutrient absorption and fixation, regulation of plant hormones, synthesis of extracellular polysaccharides, production of ACC deaminase, and alterations in gene expression. Created with BioRender.com.

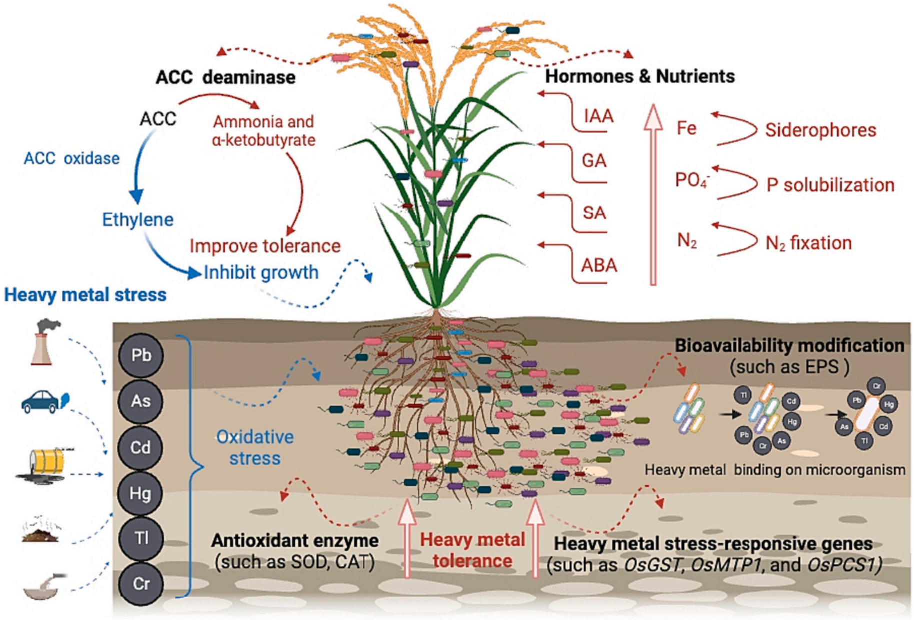


Fig. 4. Microbial mechanisms in alleviating heavy metal stress in rice. Environmental challenges have resulted in heavy metal contamination, leading to multiple physiological disruptions in rice, such as inhibited growth due to increased ethylene synthesis and oxidative stress (blue arrows). The synergy between microorganisms and rice bolsters the plant's resilience against heavy metal stress. This fortification arises from various mechanisms: the production of ACC deaminase, hormonal adjustments, improved nutrient uptake, enhanced antioxidant enzyme activities, regulation of gene expression, and adsorption of heavy metals mediated by extracellular polysaccharides (red arrows). Pb, lead; As, arsenic; Cd, cadmium; Hg, mercury, Tl, thallium; Cr, chromium; ACC, 1-Aminocyclopropane-1-carboxylic acid; IAA, indole-3-acetic acid; GA, gibberellin; SA, salicylic acid; ABA, abscisic acid; SOD, superoxide dismutase; CAT, catalase; EPS, exopolysaccharides. Created with BioRender.com.

In conclusion, strategically employing microorganisms not only enhances rice's resistance to organic pollutants but also integrates growth promotion with advanced bioremediation strategies, offering a promising approach for managing organic pollutants in rice cultivation.

4.5. Microbial strategies for enhancing salt tolerance in rice: hormonal synthesis, ACC deaminase, exopolysaccharides, and genetic adaptation

Improving salt tolerance in rice using microorganisms is a promising ecological approach, leveraging the combined strengths of specific microorganisms. Certain salt-tolerant rhizobacteria enhance rice growth by synthesizing plant hormones like IAA and GA, and modulating the internal ABA levels to counteract salt stress. These hormonal changes have significantly improved rice's ability to withstand salty conditions (Khan et al., 2020; Liu et al., 2022).

Interestingly, the enzyme ACC deaminase in some microorganisms helps reduce the increase in ethylene production under salt stress, which can otherwise harm the plant's health (Misra et al., 2017; Orozco-Mosqueda et al., 2020; Sarkar et al., 2018a/b). Microorganisms can adjust the plant's antioxidant enzymes, boost photosynthesis, and strengthen soil enzyme activity, helping rice thrive in salty conditions (Khan et al., 2020; Kumar et al., 2021; Wang et al., 2023).

Exopolysaccharides (EPS) produced by certain microbes act as osmoprotective agents, chelating salts and enhancing the osmotic resilience of the microbial strains. Furthermore, EPS supports plant health and increases rice's tolerance to salinity (Shultana et al., 2020a; Mukherjee et al., 2019; Sun et al., 2019). Additionally, when rice plants are exposed to these microorganisms, they change their genes in a way that helps them deal with salt. This includes changes in genes related to hormones, stress responses, and cell structures, which together help reduce damage from salt (Sampangi-Ramaiah et al., 2020; Shahid et al., 2020; Chauhan et al., 2019).

In synthesis, these intertwined mechanisms present a holistic, effective blueprint for augmenting rice's salt tolerance. Utilizing these microbial resources offers a sustainable approach for rice farming in salty areas. It combines hormonal, enzymatic, osmoprotective, and genetic strategies to provide strong solutions for growing rice in high-salinity conditions.

4.6. Microbial mechanisms in enhancing rice's tolerance to combined abiotic stresses

The interplay between rice and microorganisms is crucial, particularly under combined abiotic stresses. Microbes play a significant role in enhancing rice's tolerance to such stresses, notably through the modulation of plant hormones like GA, JA, and IAA. This hormonal regulation is instrumental in promoting root growth and enhancing antioxidant enzyme activities in rice, equipping the plant with a more robust defense mechanism (Raza et al., 2022).

Confronted with combined stresses, there's a marked increase in reactive oxygen species within rice, leading to oxidative stress. At this point, specific microbes support rice by providing antioxidant compounds or by boosting the rice's natural antioxidant defenses, aiding in its fight against oxidative stress (Singh et al., 2020). These microbes also enhance soil structure by secreting polysaccharides, enzymes, and other bioactive compounds, which facilitates better water and nutrient absorption by rice. Symbiotic relationships, such as those formed through mycorrhizal associations, are particularly effective in improving soil structure and thereby rice's stress tolerance (Wahab et al., 2023).

In summary, microorganisms are crucial in aiding rice to address the combined challenges of abiotic stresses, particularly in the face of environmental changes and climate variability. They harness a wide range of physiological and molecular mechanisms. A comprehensive understanding and continued research into these mechanisms are essential. Not only do they pave the way for innovative strategies to boost rice's resilience against these stresses, but they also ensure global food security and promote sustainable agricultural practices in an ever-changing climate.

5. Advancing the use of microbial inoculants in rice agriculture

Microbial inoculants, derived from beneficial microorganisms that help rice endure abiotic stresses, represent an eco-friendly approach to safeguard rice cultivation (Omomowo and Babalola, 2019; Alori and Babalola, 2018). With the growing interest in reducing the usage of chemical inputs in agriculture, these microbial solutions are gaining traction as sustainable alternatives to traditional pesticides and fertilizers (Khanna et al., 2022b; Kumar et al., 2022; Sessitsch and Mitter, 2015; Santos et al., 2019). The emphasis lies in the effective preparation, inoculation, and harnessing of these microorganisms for optimal benefit in both industrial and agricultural settings (Fig. 5).

This approach not only aligns with the global shift towards sustainable agriculture but also offers an avenue for enhancing crop resilience in an environmentally conscious manner. The implementation of microbial inoculants encompasses a range of practices, from selecting the right strains to optimizing application techniques, ensuring that these biological agents effectively contribute to healthier, more robust rice crops.

5.1. Developing microbial inoculants: crafting effective consortia for rice cultivation

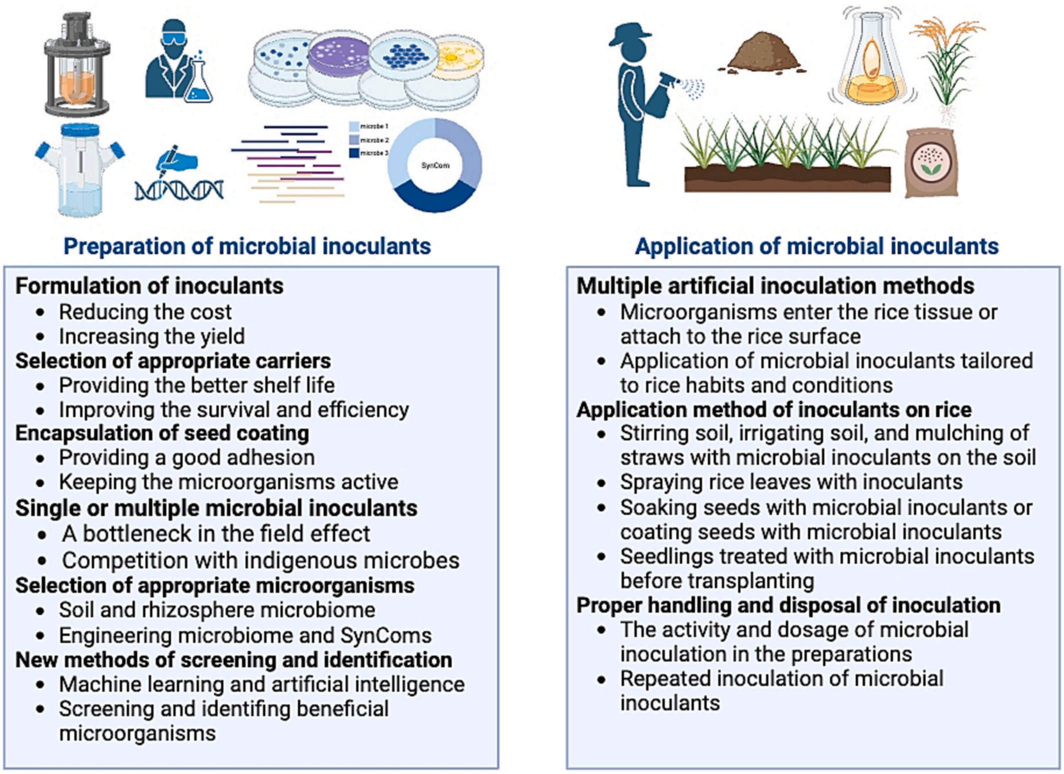
The creation of microbial inoculants involves selecting beneficial microbial strains and employing cost-effective carriers or seed coatings for agronomic use (Malusá et al., 2012). Crucial to their development is the selection of suitable carriers and seeds-coating encapsulation methods. To optimize microbial efficacy, the choice of carriers and inoculation techniques should prioritize microbial viability, appropriateness for rice cultivation, and practical applicability (Tabassum et al., 2017). Proper seed coating is crucial to maintain microbial activity over time and to maximize benefits during the initial growth stages of rice (Ma, 2019).

Industry trends highlight the prominence of both singular and composite microbial inoculants, primarily as biofertilizers or plant protectants (Lobo et al., 2019; Qiu et al., 2019). However, while promising in controlled settings, their field consistency remains a challenge (Etesami and Maheshwari, 2018). Additionally, the inoculants' efficacy in diverse microbial terrains requires assessment. Due to complex soil and rhizosphere interactions, inoculants might encounter competition and colonization challenges (de Souza et al., 2020; Pradhan et al., 2022; Qiu et al., 2019; Trivedi et al., 2017).

Emerging research on soil and rhizosphere microbiomes emphasizes the advantages of diverse microbial interactions over single-strain approaches (Carlström et al., 2019; Marín et al., 2021; Tsolakidou et al., 2019; Zhou et al., 2022). With deeper insights into SynComs, core microbiomes, and community systems, the importance of designing custom-tailored inoculants becomes evident. These inoculants aim to enhance sustainable agriculture by improving crop health and yield (Saad et al., 2020; Toju et al., 2018). Modern computational techniques, encompassing machine learning and artificial intelligence, are pivotal in discerning beneficial microorganisms. Integrating SynComs with microorganisms skilled in plant colonization and consistent beneficial interactions lays the groundwork for producing robust and effective agricultural inoculants (de Souza et al., 2020; Zhang et al., 2019).

5.2. Strategic implementation: optimizing microbial inoculant deployment in rice cultivation

While developing effective microbial inoculants is crucial, their strategic application is equally important. Tailoring these inoculants to the specific habits and conditions of rice cultivation is essential for enhancing growth and managing stress effectively. To maximize their benefits for rice growth and stress resistance, inoculants must be adapted to specific rice cultivation conditions and stress scenarios (Rojas-Sánchez et al., 2022). The method of application should be



Preparation of microbial inoculants

Formulation of inoculants
- Reducing the cost
- Increasing the yield

Selection of appropriate carriers
- Providing the better shelf life
- Improving the survival and efficiency

Encapsulation of seed coating
- Providing a good adhesion
- Keeping the microorganisms active

Single or multiple microbial inoculants
- A bottleneck in the field effect
- Competition with indigenous microbes

Selection of appropriate microorganisms
- Soil and rhizosphere microbiome
- Engineering microbiome and SynComs

New methods of screening and identification
- Machine learning and artificial intelligence
- Screening and identifing beneficial microorganisms

Application of microbial inoculants

Multiple artificial inoculation methods
- Microorganisms enter the rice tissue or attach to the rice surface
- Application of microbial inoculants tailored to rice habits and conditions

Application method of inoculants on rice
- Stirring soil, irrigating soil, and mulching of straws with microbial inoculants on the soil
- Spraying rice leaves with inoculants
- Soaking seeds with microbial inoculants or coating seeds with microbial inoculants
- Seedlings treated with microbial inoculants before transplanting

Proper handling and disposal of inoculation
- The activity and dosage of microbial inoculation in the preparations
- Repeated inoculation of microbial inoculants

Fig. 5. Application of microbial inoculants in rice cultivation. The utilization of abiotic stress-tolerant microorganisms in rice cultivation requires precise preparation and application of microbial inoculants to fully harness their beneficial attributes. Preparatory stages necessitate careful selection of the inoculant composition, a suitable carrier, and protective coating. As microbial inoculant development progresses, there's a need for adaptive screening techniques to identify ideal microorganisms for singular or composite inoculant formulations, tailored to diverse agricultural settings. During inoculant application in rice fields, it's paramount to choose optimal inoculation methods and timings, aligned with local agricultural practices, to guarantee the effective colonization, proliferation, and functional contribution of the microbes, especially during episodes of abiotic stress. Created with BioRender.com.

chosen to optimize microbial effectiveness (Chaudhary et al., 2022). Various inoculation techniques, including soil, seed, seedling, and foliar applications, can facilitate microorganism entry into rice tissues or adherence to their surfaces.

Even in the water-abundant environment of rice cultivation, soil application of microbial inoculants remains prevalent, with various methods for soil introduction. These microorganisms can be added to soil as suspensions, powders, or soaking solutions, either by blending them directly with the soil or dispersing them through irrigation (Al-Taweil et al., 2010). Enhancing straw return with microbial inoculants can boost yield and nutrient levels (Wang et al., 2020). Treating rice seeds with inoculants enables early colonization of functional microbes, which then inhabit various rice tissues throughout the growth cycle. Techniques like seed coating or soaking in microbial solutions enhance seeds' microbial exposure (de Souza et al., 2016; Singh et al., 2020). Foliar sprays enable microorganisms to penetrate through stomata, facilitating recovery under abiotic stress (Devarajan et al., 2021). Pre-transplant treatment of seedlings with bacterial solutions can foster microbial colonization and enhance stress tolerance in later growth stages (Shultana et al., 2020b). A holistic approach, employing multiple inoculation methods, is more effective in fortifying rice against abiotic stresses (Arun et al., 2020; Nascente et al., 2017).

Considering microbial activity and dosage is essential for effective treatment. Microorganisms should be capable of reproducing and establishing themselves in rice habitats or tissues (Gouda et al., 2018; Timmusk et al., 2017). Repeated applications may be necessary due to potential decreases in microbial populations over time (Tabassum et al., 2017). In summary, mindful application of microbial inoculants is necessary to avoid potential inefficiencies. In facing unpredictable abiotic stress, the timely adjustment and replenishment of microbial inoculants are vital for comprehensive stress management.

6. Concluding remarks and future perspectives

In the face of global climate change and anthropogenic disturbances, rice, a critical staple crop, confronts notable challenges to its yield and quality. This review extensively explored how abiotic stresses like temperature, drought, heavy metals, organic pollutants, and salinity impact rice growth. Through in-depth investigations of the origins of microbes interacting with rice, the critical role of microbes in enhancing the resilience of rice to these abiotic stresses has been established. Specifically, various microbial mechanisms, such as nutrient synthesis, hormone regulation, and antioxidative activations, are paramount in augmenting rice's tolerance to such stresses. Moreover, we highlighted the application and challenges of microbial inoculation techniques in rice cultivation, proposing a range of strategies on how to formulate, optimize, and implement these techniques.

With the rapid advancement of technologies like Next-Generation Sequencing (NGS), there is hoped to unveil more intricate interactions between microbes and rice and to identify more beneficial microbial species. The use of mixed microbial communities and “SynComs” is particularly promising. Future research should focus on optimizing the potential of microbes in these communities to enhance rice's tolerance to abiotic stresses. Given the economic and sustainability concerns of large-scale microbial inoculation techniques, further refinement and optimization are necessary. Interdisciplinary research methodologies, integrating microbiology, plant physiology, agronomy, ecology, and data science, will play a pivotal role in this context. Equally important is the practical application and training for farmers in microbial inoculation techniques, ensuring effective implementation in actual agricultural settings.

The evolving global climate underscores the importance of exploring how symbiotic relationships between rice and microbes can aid in adapting to these environmental shifts. While significant strides have been made in understanding these interactions, further research is imperative to delve deeper into the intricacies of microbial communities and their roles in diverse ecological settings. The future of rice cultivation hinges on effectively integrating these microbial strategies into contemporary agricultural practices. Emphasizing interdisciplinary research and employing cutting-edge methodologies will be crucial in harnessing this microbial potential. This approach will pave the way for more sustainable and resilient rice cultivation, enabling it to withstand and thrive amidst the challenges posed by a changing climate.

CRediT authorship contribution statement

Jintong Zhao: Investigation, Methodology, Writing – original draft. **Xiaoxia Yu:** Investigation, Methodology, Writing – original draft. **Chunyi Zhang:** Conceptualization, Supervision, Writing – review & editing. **Ligang Hou:** Supervision, Writing – review & editing. **Ningfeng Wu:** Funding acquisition, Project administration, Supervision. **Wei Zhang:** Supervision, Writing – review & editing. **Yuan Wang:** Supervision, Writing – review & editing. **Bin Yao:** Funding acquisition, Project administration, Supervision. **Pierre Delaplace:** Conceptualization, Supervision, Writing – review & editing. **Jian Tian:** Conceptualization, Project administration, Resources, Supervision, Writing – review & editing.

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.

Data availability

No data was used for the research described in the article.

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