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# RESEARCH PROGRESS ON THE REGULATORY MECHANISMS OF RHIZOSPHERE MICROORGANISMS IN ENHANCING PLANT TOLERANCE TO BIOTIC AND ABIOTIC STRESSES

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## ABSTRACT

Frequent human activities have led to the increased occurrence of environmental stresses, such as soil salinization, drought, plant diseases, heavy metal pollution, and low temperatures, severely constraining regional natural and socioeconomic development. Due to their sessile growth habit, plants are chronically exposed to multiple stresses. Although they can mount defense responses through physiological and biochemical adaptations, their inherent regulatory capacity remains limited. In recent years, with the advancement of ecological restoration projects, the role of rhizosphere microorganisms in modulating plant stress adaptation has become increasingly prominent. The rhizosphere serves as a critical interface for plant–soil–microbe interactions, where microorganisms regulate plant physiological functions through their metabolic activities, thereby assisting plants in establishing resistance and tolerance mechanisms against both biotic and abiotic stresses. To promote ecological restoration and alleviate human–land conflicts, this paper systematically reviews research progress on how rhizosphere microorganisms enhance plant tolerance to drought, cold, salinity, heavy metals, and diseases. By integrating typical case studies, we comprehensively discuss the underlying mechanisms, aiming to provide a theoretical reference for the application of rhizosphere microorganisms in agricultural development and ecological restoration.

**KEYWORDS:** rhizosphere microorganisms; environmental stress; microbial function; microbial community; bioremediation

## INTRODUCTION

Due to their sessile growth habit, plants are chronically exposed to both biotic and abiotic stresses. Their survival depends on rapid physiological, biochemical, and molecular network responses to environmental changes. In terrestrial ecosystems, plants act as primary producers, delivering organic compounds to the soil through photosynthesis and providing carbon sources for soil microorganisms. Meanwhile, soil microorganisms, as decomposers, convert organic matter into inorganic nutrients for plant uptake. The interaction between plants and microorganisms is fundamental to the stable functioning of ecosystems (Bais et al., 2006). With advances in soil microbiology research, the critical role of rhizosphere microorganisms in helping plants cope with environmental stresses has become increasingly evident. The term "rhizosphere" was first proposed by German scientist Hiltner in 1904 to refer to the soil region influenced by plant roots (Bakker et al., 2013). Kuzyakov and colleagues further delineated this zone as the soil area within 0.5–4.0 mm of the root surface. The rhizosphere serves as an important interface for material exchange and energy transfer between plants and soil. Rhizosphere microorganisms play a key role in this zone, directly influencing plant growth, development, metabolism, and other physiological and biochemical processes (Kuzyakov and Razavi, 2019).

Rhizosphere microbial communities mainly originate from the horizontal migration of bulk soil microorganisms; thus, the bulk soil microbial community is considered the "seed bank" for the rhizosphere microbial community. Through root exudates and immune responses, plants recruit and establish rhizosphere microbial communities from the bulk soil. These communities participate in various physiological and biochemical processes, promoting plant nutrient uptake, improving plant growth, and enhancing plant tolerance to both abiotic and biotic stresses (Bai et al., 2022). Rhizosphere microorganisms can be classified into three categories:beneficial, neutral, and harmful. The root exudates of some plants can inhibit harmful microorganisms, while those of others can recruit beneficial microorganisms. The composition of root exudates is influenced by plant physiological status, plant species, and the structure of the rhizosphere microbial community (Ahemad and Kibret, 2014). Beneficial rhizosphere microorganisms include plant growth-promoting rhizobacteria (PGPR), mycorrhizal fungi, and rhizobia, which can enhance plant tolerance to harsh environments such as drought and salinity (Zeng et al., 2018). Therefore, in ecosystem restoration research, plants and microorganisms should not be regarded as independent entities but rather as a holobiont consisting of the host and its associated microorganisms. Furthermore, rhizosphere microbial communities are extremely diverse, and the presence of other microorganisms may alter the function of any single rhizosphere microorganism. Hence, attention should also be paid to the overall structure and function of the rhizosphere microbial community (Figueredo et al., 2018).

In agricultural production and ecological restoration, adverse environmental conditions such as soil salinization, drought, and plant diseases severely constrain the sustainable development of agriculture. Irrational land use practices, including the excessive application of chemical fertilizers and pesticides as well as continuous cropping, have led to a decline in soil microbial community diversity, compromised crop quality, and even triggered ecological degradation. Although numerous studies have reported on plant adaptation to environmental stresses, research on the interaction between rhizosphere microorganisms and plants to enhance plant adaptation to abiotic and biotic stresses is still in its early stages. This paper systematically reviews the roles of plant growth-promoting microorganisms (PGPM) and rhizosphere microbial community composition in helping plants respond to environmental stresses from five aspects:enhancing plant tolerance to drought, cold, salinity, and heavy metals, as well as improving disease resistance. The aim is to provide a scientific basis for utilizing rhizosphere microorganisms in ecological restoration.

## Rhizosphere Microecological Mechanisms of Plant Response to Drought Stress

Drought is a major factor constraining crop production and the stability of ecological structures. Water deficiency leads to stomatal closure, reduced biomass, and decreased crop quality, exerting extensive negative impacts on agriculture and natural economies. Under drought stress, plants respond through various physiological and biochemical processes, including the reduction of root and shoot growth, decreased leaf water potential and transpiration rate, and increased levels of reactive oxygen species (ROS) and abscisic acid (ABA) (Gupta A et al., 2020). Studies have shown that the adaptive mechanisms of plants under drought stress may not be limited to their own physiological and biochemical regulation but may also benefit from interactions with other organisms, particularly soil microbial communities that respond rapidly to environmental changes. Among these, rhizosphere microorganisms play a crucial role in assisting plants to cope with drought stress (Lau and Lennon, 2012).

### Affect Water Use Efficiency

Water is an essential element for plant survival. Plant growth-promoting microorganisms (PGPM) can respond to drought stress by regulating plant water uptake, transpiration, and water use efficiency. Augé et al. analyzed 460 studies on the relationship between arbuscular mycorrhizal (AM) fungi and stomatal regulation and found that the stomatal conductance of host plants colonized by AM fungi was altered under drought conditions. Under different soil moisture conditions, the stomatal conductance of non-mycorrhizal plants was 24% lower than that of mycorrhizal plants. Under moderate soil moisture conditions, AM fungi promoted stomatal conductance more than twice as much as under well-watered conditions; under low soil moisture conditions, this effect was more than fourfold. Furthermore, dicotyledonous plants colonized by AM fungi exhibited slightly higher stomatal conductance than monocotyledonous plants, and C3 plants colonized by AM fungi showed higher stomatal conductance than C4 plants (Augé et al., 2015). These findings indicate that AM symbiosis enables plants to maintain higher stomatal conductance under drought stress and that the response to AM fungi varies among different plant functional groups. Ruth et al. inoculated barley (*Hordeum vulgare* L.) with Glomus intraradices and found that the fungal hyphae increased the contact area between roots and soil, contributing approximately 20% to total plant water uptake through both direct and indirect mechanisms (Ruth et al., 2011). Collectively, these results demonstrate that rhizosphere microorganisms can regulate plant water relations by altering plant traits, thereby improving water use efficiency, which is of great significance for enhancing plant growth under drought stress.

### Regulate the Antioxidant System

Plant growth-promoting rhizosphere microorganisms can also enhance plant tolerance to drought by regulating the antioxidant system. A study by Yaghoubian et al. showed that under drought stress conditions, wheat (Triticum aestivum cv. Azar2) plants inoculated with the arbuscular mycorrhizal fungus Glomus mosseae and the endophytic fungus Piriformospora indica exhibited reduced hydrogen peroxide content and lipid peroxidation rates, as well as increased activities of antioxidant enzymes such as catalase (CAT), ascorbate peroxidase (APX), and peroxidase (POD), along with increased leaf chlorophyll content. Highly active antioxidant enzymes can scavenge free radicals, protect plant cell membranes, and prevent DNA damage (Yaghoubian et al., 2014). Sarma et al. found that mung bean (*Vigna radiata* (L.) R. Wilczek) plants treated with Pseudomonas aeruginosa GGRJ21 showed increased activities of superoxide dismutase (SOD) and ascorbate peroxidase, whereas catalase activity initially increased and then decreased (Sarma and Saikia, 2014). Armada et al. inoculated lavender (Lavandula angustifolia Mill.) with Bacillus thuringiensis and found that under drought stress, this bacterium enhanced plant drought tolerance by reducing glutathione reductase (GR) and APX activities in lavender. The differences among the above research results may be attributed to the interactive effects of different plant species combined with various growth-promoting microorganisms (Armada et al., 2014).

### Regulation of Stress-Responsive Gene Expression

Plant growth-promoting rhizosphere microorganisms can also induce plant drought tolerance by regulating the expression of drought stress-responsive genes. Sherameti et al. found that after inoculating Arabidopsis thaliana with Piriformospora indica, the expression levels of stress-related genes such as phospholipase Dδ (PLD), calcineurin B-like protein 1 (CBL1), and histone acetyltransferase (HAT) were increased, thereby enhancing the drought tolerance of Arabidopsis (Sherameti et al., 2008). Kazerooni et al. discovered that after inoculating pepper with Bacillus amyloliquefaciens, the expression of the hydrolase (Xth) gene was enhanced, while the expression of the WRKY2, BI-1, PTI1, and binding immunoglobulin protein (Bip) genes was reduced, thereby increasing seedling growth rate and improving the physicochemical characteristics of pepper (Kazerooni et al., 2021). The expression of drought stress-responsive genes may vary depending on the bacterial strain and plant species. In summary, plant growth-promoting rhizosphere microorganisms can enhance plant tolerance to drought stress by regulating the expression of stress-responsive genes.

### Assembly of Rhizosphere Microbial Communities Enhances Plant Drought Tolerance

Plant responses to drought stress rely more on rapid changes in belowground microbial communities than on the rapid evolution of plant traits (Lau and Lennon, 2012). Drought stress can alter soil nutrient cycling, thereby affecting the structure and function of soil microbial communities and ultimately influencing plant growth and development. Plants depend on the metabolic activities of soil microorganisms to enhance the bioavailability of soil nutrients. Santos-Medellín et al. reported that under short-term drought stress, the rhizosphere microbial community structure of rice changed significantly and largely recovered to its pre-stress state after rewatering. Following drought stress, Actinobacteria accounted for more than 80% of the bacterial community. Furthermore, Streptomyces sp. SLBN-177, isolated from the most abundant OTU in the rhizosphere microbial community, promoted root growth under drought conditions (Santos-Medellin et al., 2021). These findings are consistent with the results of Xu et al., who found that drought significantly altered the rhizosphere microbial community composition of sorghum and that moderate enrichment of Actinobacteria significantly promoted root growth (Xu et al., 2018). This indicates that the enrichment of specific rhizosphere microorganisms can enhance plant resistance to drought by promoting root growth. In addition, Sukweenadhi et al. reported that after inoculating Arabidopsis thaliana with plant growth-promoting rhizobacteria (PGPR) such as Bacillus, Paenibacillus, Brevibacillus, and Micrococcus under drought stress, the metabolites of these growth-promoting bacteria induced the expression of the AtRAB18 and AtLT178 genes in Arabidopsis, both of which are involved in plant responses to drought stress via the ABA signaling pathway (Sukweenadhi et al., 2015). This demonstrates that rhizosphere microorganisms can enhance plant tolerance to drought stress by inducing the expression of drought tolerance-related genes. In summary, rhizosphere microorganisms can improve plant adaptation to drought stress through three important pathways:altering plant morphological characteristics, regulating the antioxidant system, and modulating stress-responsive gene expression. This understanding helps overcome the limitations of traditional breeding and transgenic technologies and holds significant theoretical and practical implications for agricultural production.

### Rhizosphere Microorganisms Promote Plant Cold Tolerance

Low temperature is one of the major factors limiting the geographical distribution of agriculture. Different plants have varying temperature requirements. Based on their tolerance to low temperatures, plants can be classified into chilling-sensitive plants and chilling-insensitive (or chilling-resistant) plants. Chilling-resistant plants can survive at certain low temperatures, whereas chilling-sensitive plants struggle to survive in low-temperature environments. Spring cold events often cause significant losses in crop production; therefore, exploring methods to improve crop cold tolerance is particularly important. Studies have shown that plant adaptation to low-temperature environments mainly involves three aspects:(1) the adaptation of biological traits such as plant structural characteristics and chlorophyll content; (2) physiological adaptation including cell membrane permeability and the antioxidant system; and (3) the adaptation of secondary metabolites such as terpenes and phenolic compounds. Yarzábal found that microorganisms can still survive in low-temperature environments and that these cold-tolerant microorganisms have evolved various adaptive mechanisms that hold promise for improving agricultural development in cold regions (Yarzábal, 2020). Current research on how rhizosphere microorganisms promote plant adaptation to low-temperature stress focuses primarily on the following three categories:(1) arbuscular mycorrhizal fungi (AMF); (2) plant growth-promoting rhizobacteria (PGPR); and (3) rhizobia.

### Arbuscular Mycorrhizal (AM) Fungi

Arbuscular mycorrhizal (AM) fungi are a group of soil symbiotic fungi, and their symbiosis with plants represents one of the most widespread and successful symbiotic relationships on Earth. AM fungi not only improve soil quality but also promote plant growth and enhance plant tolerance to cold stress. Paradis et al. found that under low-temperature treatment at 5 °C, wheat inoculated with Glomus mosseae exhibited significantly increased biomass and chlorophyll content (Paradis et al., 1995). The results indicate that AM fungi enhance plant adaptation to cold stress by regulating plant physiological and metabolic activities.

### Plant Growth-Promoting Rhizobacteria (PGPR)

Plant growth-promoting rhizobacteria (PGPR) are a group of beneficial bacteria that can directly or indirectly promote plant growth, enhance plant productivity, or improve plant stress tolerance. Studies have shown that PGPR can increase plant tolerance to low-temperature environments. Mishra et al. demonstrated that after inoculating wheat seedlings with Pseudomonas under low-temperature conditions, the biomass and nutrient content of the seedlings increased significantly. Meanwhile, the levels of metabolites such as free proline, nutrients, and amino acids were also significantly elevated, effectively enhancing the resistance of wheat seedlings to low-temperature stress (Mishra et al., 2011). These findings suggest that PGPR may improve plant growth under low-temperature conditions by regulating physiological and biochemical responses as well as the production of secondary metabolites in plants.

### Rhizobia

Leguminous plants fix atmospheric nitrogen ($N_2$) through symbiotic bacteria residing in their root nodules. These symbiotic bacteria are called rhizobia (e.g., Rhizobium meliloti). The plants provide nutrients for the growth and reproduction of rhizobia, while the rhizobia supply nitrogen to the plants through nitrogen fixation, forming a mutually beneficial symbiotic relationship. In addition, rhizobia can enhance plant cold tolerance. Liu et al. demonstrated that under low-temperature conditions, after inoculating alfalfa (Medicago) with the Rhizobium meliloti strain Dormal, the accumulation of soluble proteins and sugars increased significantly. Meanwhile, the expression of the cold stress-responsive gene CBF2 was upregulated, and the expression of the gene encoding the cold acclimation-specific protein Cas was maintained, thereby enhancing the growth capacity and cold tolerance of alfalfa in cold regions (Liu et al., 2019). This indicates that rhizobia can improve plant tolerance to low temperatures by regulating plant nutrient elements and the expression of cold stress-responsive genes. Currently, research on how rhizosphere microorganisms promote plant adaptation to cold stress remains relatively limited. Future efforts should strengthen the investigation of the molecular mechanisms underlying the interactions between rhizosphere microorganisms and plants in low-temperature environments to provide new methods and insights for crop cultivation and ecological restoration in cold regions.

### Rhizosphere Microecological Mechanisms of Plant Response to Salt Stress

Saline-alkali land is widely distributed across the globe. Due to its poor environmental carrying capacity, it severely hinders natural and socio-economic development. The high concentration of $Na^+$ in saline-alkali soil impedes plant uptake of water and nutrients, leading to water deficiency and nutrient imbalance, which in turn induces osmotic stress and ionic stress. To cope with high salt stress, plants can respond through various physiological and biochemical mechanisms, including regulating intracellular ion balance, activating the osmoregulatory system, and modulating hormone signaling (Zhao et al., 2021). Traditional methods for improving plant salt tolerance have mainly relied on a combination of breeding and genetic engineering. However, genetic engineering technology currently faces considerable controversy, and the introduced tolerance genes often exhibit poor stability and are prone to mutation. Therefore, this approach has not yet achieved ideal results in enhancing plant salt tolerance. With advances in research on plant stress resistance, it has been found that rhizosphere microorganisms can alleviate the negative effects of salt stress on plants. Rhizosphere microorganisms help plants establish resistance or tolerance mechanisms to adapt to high-salt environments by regulating nutrient uptake, phytohormone levels, and the content of antioxidant active substances. In addition, rhizosphere microorganisms can also improve plant salt tolerance by regulating the expression of salt stress resistance genes in plants.

### Promoting Plant Uptake of Nutrient Elements

Nutrient elements such as nitrogen and phosphorus are essential for plant growth. Rhizosphere microorganisms enhance plant survival in salt-stressed environments by improving plant uptake of nutrients such as phosphorus and nitrogen. Egamberdieva et al. inoculated licorice (Glycyrrhiza uralensis Fisch.) with Pseudomonas and Mesorhizobium under salt stress, which significantly increased the biomass, nodule number, and nitrogen content of licorice, indicating that rhizosphere microorganisms can promote nitrogen uptake in licorice under salt stress (Egamberdieva et al., 2017). Furthermore, rhizosphere microorganisms can also promote nutrient uptake by plants in high-salt environments through the production of siderophores, organic acids, and other substances. Li et al. inoculated tomato (*Solanum lycopersicum* L.) with the Rahnella aquatilis strain JZ-GX1 and found that JZ-GX1 was still able to produce indole-3-acetic acid (IAA) and siderophores under salt stress and possessed the ability to solubilize inorganic phosphorus, thereby enhancing plant phosphorus uptake and consequently improving plant tolerance to salt stress (Li et al., 2021).

### Regulation of Phytohormone Secretion

Under high-salt environments, the physiological and biochemical activities of plants undergo significant changes, and rhizosphere microorganisms enhance plant salt tolerance by regulating the levels of phytohormones such as abscisic acid (ABA), gibberellins (GA), and indole-3-acetic acid (IAA). High-salt environments induce the accumulation of endogenous ABA in plants, and ABA, as a water-regulating hormone, can enhance plant resistance to high salt stress. Arkhipova et al. inoculated wheat with Bacillus subtilis IB-22 and Pseudomonas mandelii IB-Ki14 and found that the IB-Ki14 strain increased the ABA content in wheat roots, thereby enhancing wheat salt resistance (Arkhipova et al., 2020). However, other studies have shown that rhizosphere microorganisms can reduce plant sensitivity to water deficiency by decreasing ABA content in plant roots (Jiang et al., 2012). This indicates that rhizosphere microorganisms can enhance plant resistance to high-salt environments by increasing ABA content, but ABA accumulation may vary depending on the bacterial strain and plant species. Furthermore, rhizosphere microorganisms also have the ability to secrete gibberellins. Under stress conditions, gibberellin signaling in plants is a key factor in inhibiting cell apoptosis. Khan et al. inoculated the soybean rhizosphere with Arthrobacter woluwensis AK1, Microbacterium oxydans AK2, Arthrobacter aurescens AK3, Bacillus megaterium AK4, and Bacillus aryabhattai AK5. Under 200 mmol/L NaCl stress, inoculation with these rhizosphere microorganisms significantly improved plant growth characteristics, increased chlorophyll content, and elevated the levels of gibberellins (GA), indole-3-acetic acid (IAA), and siderophores, thereby improving soybean growth under salt stress conditions (Khan et al., 2019). This suggests that the phytohormones produced by rhizosphere microorganisms are not of a single type but may involve the synergistic action of multiple hormones to promote plant growth. Moreover, under high-salt environments, rhizosphere microorganisms can induce IAA production in plants. IAA plays a crucial role in various cellular and developmental responses throughout the plant life cycle, regulating stem growth, inhibiting lateral bud germination, and promoting root formation. Li et al. inoculated rapeseed with the salt-tolerant Enterobacter cloacae, which increased endogenous IAA content in rapeseed and enabled it to tolerate 50 mmol/L and 100 mmol/L NaCl stress (Li et al., 2017). Therefore, salt stress-resistant microorganisms also represent a potential biofertilizer that can alleviate the adverse effects of salt stress on plants by regulating phytohormones. However, current research on rhizosphere microorganism-mediated phytohormone regulation under salt stress has mostly focused on IAA, with fewer studies on hormones such as GA and ABA. Future efforts should strengthen comprehensive research on multiple phytohormones under salt stress conditions.

### Regulation of Stress-Responsive Gene Expression

Rhizosphere microorganisms can also improve plant growth under salt stress conditions by regulating the expression of plant salt stress-responsive genes. Santos et al. found that under 250 mmol/L NaCl, certain strains of Stenotrophomonas and Exiguobacterium exhibited halophilic and plant growth-promoting characteristics. Co-inoculation of soybean (Glycine) with these two strains not only increased soybean seed germination rates but also upregulated the expression of the soybean growth marker gene Glyma.03G226000 and the salt stress-responsive genes Glyma.02G228100, Glyma.04G180400, Glyma.08G189600, and Glyma.17G173200 in the roots (Santos et al., 2023). Khan et al. inoculated soybean with Arthrobacter woluwensis AK1 under 100, 200, and 300 mmol/L NaCl conditions, which upregulated the expression of the tolerance genes GmLAXs and GmST involved in cell signaling (Khan et al., 2019). These results indicate that rhizosphere microorganisms can improve plant growth under salt stress conditions by regulating the expression of plant stress-responsive genes.

### Assembly of Rhizosphere Microbial Communities Enhances Plant Salt Tolerance

Accumulating evidence suggests that rhizosphere microorganisms play a crucial role in helping plants adapt to saline stress environments. Growth-promoting microorganisms may assist plants in establishing resistance mechanisms against high salinity by influencing the structure of the rhizosphere microbial community. Shao Meiqi inoculated tomato plants withBacillus subtilis NCD-2 under NaCl stress conditions and observed significant growth-promoting effects. Under 100 mmol/L NaCl stress, analysis of the bacterial and fungal community composition in the tomato rhizosphere following NCD-2 treatment revealed that NCD-2 significantly increased the relative abundance of bacterial genera such as Arthrobacter, Bacillus, Sphingomonas, and Microvirga. It also significantly increased the relative abundance of fungal phyla/groups, including Mortierella, Glomeromycota, and Chytridiomycota, while significantly reducing the relative abundance of pathogenic fungi such as Aspergillus and Fusarium. These results indicate that under salt stress, the NCD-2 strain may promote tomato growth by increasing the relative abundance of beneficial bacterial genera, including Arthrobacter, Bacillus, and Sphingomonas, and by reducing the relative abundance of pathogenic fungi such as Aspergillus and Fusarium.

These findings suggest that the assembly of plant rhizosphere microbial community structures may contribute to the establishment of tolerance mechanisms against salt stress. However, current research on how rhizosphere microbial community assembly enhances plant salt tolerance under saline conditions remains limited. Future efforts should strengthen the study of the structure and function of plant rhizosphere microbial communities under salt stress.

In summary, rhizosphere microorganisms can help plants enhance their tolerance to salt stress through various pathways, including promoting plant nutrient uptake, regulating plant hormone levels, modulating stress-responsive gene expression, and influencing the assembly of the rhizosphere microbial community. As population growth continues to make food scarcity a key research priority, further in-depth investigation into the interactions between rhizosphere microorganisms and plants, as well as their mechanisms of adaptation to salt stress in saline soils, remains an important topic worthy of continued exploration.

### Rhizosphere Microecological Mechanisms of Plant Response to Heavy Metal Stress

Some heavy metals are essential trace elements for plant growth and development. They not only serve as cofactors for enzymes but also play important roles in the structural domains of protein macromolecules. However, excessive intake of heavy metals can impair the physiological and biochemical processes of plants. Heavy metal stress induces the production of large amounts of reactive oxygen species (ROS) free radicals in plants, which in turn triggers the peroxidation of lipid membranes and macromolecular substances, leading to metabolic damage in plant cells and even causing cell death. Under heavy metal stress, plants undergo changes in biochemical molecules and physiological morphology throughout their growth process to mitigate heavy metal-induced cellular damage. However, in-depth research has revealed that rhizosphere microorganisms play an important role in helping plants establish resistance mechanisms to alleviate heavy metal stress. Rhizosphere microorganisms and their metabolites (such as abscisic acid, gibberellins, and other phytohormones) improve plant growth under heavy metal stress by promoting the uptake of various nutrients. Additionally, they can alter the bioavailability of heavy metals through mechanisms such as modifying the release of chelating agents (e.g., organic acids and polyphosphates) and mediating oxidation/reduction reactions, thereby enhancing plant tolerance to heavy metal stress.

### Promoting Plant Uptake of Nutrient Elements

Nitrogen (N) is an essential element for plant growth, but atmospheric nitrogen cannot be directly utilized by plants. Nitrogen-fixing microorganisms in the soil convert atmospheric nitrogen into plant-available forms through a series of reactions. Symbiotic nitrogen-fixing microorganisms such as Bradyrhizobium sp., Pseudomonas sp., and Ochrobactrum cytisi can supply essential nitrogen to plants by fixing $N_2$, thereby promoting plant growth under heavy metal stress (Dary et al., 2010). Hao et al found that in lead (Pb)-contaminated soil, alfalfa *(Medicago sativ*a L.) inoculated with the rhizobium Glomus mosseae (G) and the arbuscular mycorrhizal fungus Rhizobium meliloti (R) exhibited significantly enhanced uptake of nitrogen and phosphorus, along with increased nodulation rate and mycorrhizal infection rate, which promoted plant growth and enhanced tolerance to lead pollution (Hao et al., 2025). Phosphorus is also an essential element for plant growth; however, the only plant-available forms in soil are $H_2PO_4^-$ and $HPO_4^{2-}$, with the majority of phosphorus existing in insoluble forms (Bhattacharyya and Jha, 2012). A large number of phosphate-solubilizing microorganisms exist in soil and can convert insoluble phosphorus into available phosphorus, thereby promoting plant phosphorus uptake. Ma et al. inoculated castor bean (Ricinus communis) and sunflower (Helianthus annuus) with Psychrobacter sp. SRS8 and found that SRS8 promoted phosphorus uptake in both plant species in nickel-contaminated soil (Ma et al., 2010). By enhancing plant uptake of nutrients such as nitrogen and phosphorus, rhizosphere microorganisms improve plant growth under heavy metal stress, which is of great significance for the reclamation of abandoned mines.

### Secretion of Phytohormones

During their metabolic activities, rhizosphere microorganisms secrete a range of metabolites into the soil, including phytohormones such as indole-3-acetic acid (IAA) and gibberellins (GA), which directly promote plant cell growth and division, thereby enhancing plant growth. Carlos et al. reported that ten bacterial strains, including Enterobacter, Serratia, Klebsiella, and Escherichia, were all capable of synthesizing IAA in the presence of heavy metals such as copper, arsenic, lead, nickel, cadmium, and manganese, thereby promoting the growth of sunflower (Carlos and Stefani, 2016). Efe et al. also reported that a strain of Bacillus vallismortis possesses IAA-synthesizing properties and promotes plant growth (Efe, 2020). Furthermore, rhizosphere microorganisms can produce multiple phytohormones that synergistically promote plant growth. Currently, research on phytohormone secretion by rhizosphere microorganisms under heavy metal stress has mostly focused on IAA, with fewer studies on other hormones. Future efforts should strengthen comprehensive research on the secretion of multiple phytohormones by rhizosphere microorganisms under heavy metal stress.

### Regulation of the Antioxidant Enzyme System

The plant antioxidant enzyme system, including superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD), can scavenge excess reactive oxygen species (ROS) free radicals induced by heavy metal stress, thereby protecting cells from damage and reducing the detrimental effects of heavy metals on plants. Garg et al. demonstrated that after inoculating pigeon pea [Cajanus cajan (Linn.) Millsp.] with the arbuscular mycorrhizal fungus Glomus mosseae, the activities of antioxidant enzymes such as superoxide dismutase, catalase, and peroxidase were increased under single or combined stress of cadmium and lead, thereby helping plants resist heavy metal damage (Garg and Aggarwal, 2012). Babu et al. reported that inoculating Pinus sylvestris with Trichoderma sp. PDR1-7 significantly promoted the dissolution of heavy metals in mine tailings, improved nutrient availability in the plant rhizosphere soil, increased chlorophyll content and antioxidant enzyme activities, and reduced the production of malondialdehyde (MDA)—an important marker of stress response—thereby improving plant growth under heavy metal stress (Babu et al., 2014).

### Oxidation-Reduction Reactions

In nature, some heavy metals exist in different valence states. Microorganisms can alter the valence states and chemical forms of heavy metal ions through a series of metabolic activities, thereby reducing their toxicity and indirectly enhancing plant tolerance to heavy metal stress. Wu Jia found that the toxicity of arsenic and its compounds varies depending on the valence state of arsenic and the composition of the compounds. As(V) is more toxic to plants than As(III). The arsenate-reducing bacteria Ts33 and Ts41, which are rhizosphere microorganisms, promoted the reduction of As(V) to As(III) in the soil, reducing the rhizosphere As(V) content by 9.97% to 18.64%. After transformation, the toxicity of arsenic was reduced, and the resulting damage to plant cells was correspondingly diminished (Suhadolnik et al., 2017). Srivastava et al. also reported that a strain of Serratia sp. can convert Cr(VI), which is highly toxic to plants, into Cr(III), which has lower toxicity (Srivastava and Thakur, 2012).

### Assembly of Rhizosphere Microbial Communities Enhances Plant Tolerance to Heavy Metal Stress

In the rhizosphere soil microecosystem, plants respond to heavy metal stress by recruiting specific microbial taxa to form functionally specialized rhizosphere microbial communities that help them cope with adverse environments. Gao Peng investigated the non-rhizosphere, rhizosphere, and endophytic microbial communities of *Pteris vittata* L. and found that the microbial community structure of P. vittata was significantly influenced by its spatial location but showed no significant relationship with arsenic concentration. Among these, the core rhizosphere microorganisms included beneficial microbes with high arsenic tolerance and plant growth-promoting capabilities, such as uncultured Xanthobacteraceae and the unclassified KD4-96 of Chloroflexi, which play important roles in alleviating arsenic toxicity in P. vittata . The rhizosphere serves as the interface for plant-microbe interactions and is an active zone for nutrient and energy exchange between soil and plants. In soils subjected to heavy metal stress, the rhizosphere may act as an important barrier preventing metal uptake. Core rhizosphere microorganisms are key components of the rhizosphere microbial community, and identifying these core microorganisms is of great significance for understanding the stability, plasticity, and function of complex microbial communities. Sun et al. collected rhizosphere soil samples from maize (*Zea mays* L.), rice (*Oryza sativa* L.), and soybean [*Glycine max* (L.) Merr.] grown in farmland surrounding a mining area that was co-contaminated with vanadium (V), chromium (Cr), copper (Cu), antimony (Sb), lead (Pb), cadmium (Cd), and arsenic (As). Using Illumina sequencing and co-occurrence network analysis, they found that the structuring of rhizosphere microbial communities was primarily determined by the levels of V and Cr. OTUs related to Gaiellaceae (an unclassified genus within the class Actinobacteria of the phylum Actinobacteria) participated in interactions with other bacterial species in the co-occurrence networks of soybean and rice and could co-exist with multiple metals, suggesting potential metal resistance (Sun et al., 2018). These studies indicate that the assembly of plant rhizosphere microbial communities may enhance plant tolerance to heavy metal stress. However, current research on how rhizosphere microbial community assembly enhances plant tolerance to heavy metals under heavy metal stress remains limited. In summary, rhizosphere microorganisms can enhance plant tolerance to heavy metal stress through multiple mechanisms, including regulating their own metabolites, mediating oxidation/reduction reactions, and influencing the assembly of rhizosphere microbial communities. Currently, research on the secretion of multiple phytohormones by rhizosphere microorganisms under heavy metal stress is insufficient, and the role of rhizosphere microbial community assembly in plant responses to heavy metal stress requires further investigation. Therefore, strengthening research on rhizosphere microorganisms will contribute significantly to the process of heavy metal remediation in contaminated sites such as mining areas.

### Rhizosphere Microecological Mechanisms of Plant Response to Diseases

The widespread use of chemical pesticides has led to continuously increasing resistance of pathogens in farmland ecosystems, while a large number of natural enemy organisms have been killed. This has allowed pathogens to proliferate extensively, seriously disrupting the ecological balance. Chemical pesticides not only pollute the air, water, and soil but may also remain in animals and plants, entering the human body through the food chain and endangering human health. Therefore, the development of environmentally friendly plant disease control technologies has become a research hotspot for scientists. Microbial remediation has attracted considerable attention due to its minimal disturbance to the natural environment and its relatively good control efficacy. Currently, significant breakthroughs have been achieved in research on the use of beneficial rhizosphere microorganisms for disease control. Numerous studies have shown that beneficial rhizosphere microorganisms can not only effectively control diseases but also significantly promote plant growth and development. For example, Gowtham et al. reported that the plant growth-promoting rhizobacterium Bacillus amyloliquefaciens exhibited a significant control efficacy of 71% against anthracnose in pepper (*Capsicum annuum* L.), and inoculation with this strain also enhanced the vigor and nutritional parameters of pepper seedlings (Gowtham et al., 2018). These plant growth-promoting rhizosphere microorganisms primarily help plants resist diseases through two mechanisms:inducing plant resistance and producing antimicrobial substances.

### Inducing Plant Resistance

Beneficial rhizosphere microorganisms help plants resist various diseases by inducing plant resistance, a mechanism that primarily involves systemic acquired resistance (SAR) and induced systemic resistance (ISR). SAR is typically triggered after a pathogen attacks the host via a salicylic acid (SA)-dependent pathway, whereas ISR is activated by certain rhizosphere microorganisms through jasmonic acid (JA) and ethylene (ET) signaling pathways (van Loon et al., 1998; Durrant and Dong, 2004). Yoo et al. reported that tomato (*Solanum lycopersicum* L.) seeds treated with the fungus Aspergillus terreus JF27 were able to inhibit bacterial spot disease caused by a pathogenic strain of Pseudomonas syringae. In the leaves of JF27-treated tomato plants, the expression level of the SAR marker gene PR1 (pathogenesis-related gene 1) was higher, indicating that JF27 may enhance tomato tolerance to spot disease by inducing SAR (Yoo et al., 2018). Tonelli et al. reported that Bacillus sp. CHEP5 induced ISR in peanut (Arachis hypogaea L.), which was highly effective in protecting peanuts against infection by the pathogen Sclerotium rolfsii (Tonelli et al., 2011).

### Production of Antimicrobial Substances

During their metabolic activities, rhizosphere microorganisms produce a variety of volatile organic compounds (VOCs). These VOCs diffuse through soil pores and play an important role in antagonistic interactions among microorganisms occupying the same ecological niche. Yuan et al. reported that VOCs produced by Bacillus amyloliquefaciens NJN-6 inhibited the growth and spore germination of Fusarium oxysporum f. sp., the causal agent of banana (Musa nana Lour.) wilt disease (Yuan et al., 2012). The effective VOCs produced by these biocontrol bacteria include benzenes, phenols, ketones, and alkanes; however, the quantity and composition of VOCs vary depending on the bacterial strain and are also influenced by environmental factors. Furthermore, during their metabolic activities, rhizosphere microorganisms can secrete extracellular enzymes that inhibit the growth of pathogenic microorganisms. Shen et al. found that Streptomyces hygroscopicus B04 can utilize various carbon sources and produce chitinase and protease, thereby reducing the incidence of root rot by inhibiting the growth of Fusarium oxysporum (Shen et al., 2016). Chitinase degrades fungal cell walls and stops hyphal growth by destroying the chitin in the hyphae of pathogenic fungi, making it an ideal biocontrol agent. It is worth noting that although various metabolites produced by biocontrol microorganisms have biocontrol effects, metabolites such as antibiotics may remain on crops and pose risks to human health.

### Assembly of Rhizosphere Microbial Communities Enhances Plant Disease Resistance

The rhizosphere soil harbors extremely abundant microbial communities, and the presence of other microorganisms may alter the plant signaling pathways activated by a single microorganism. Figueredo et al. co-inoculated and singly inoculated peanut (*Arachis hypogae*a L.) with Bradyrhizobium sp. SEMIA6144, Bacillus sp. CHEP5, and Sclerotium rolfsii (the causal agent of peanut stem rot) and found that co-inoculation with SEMIA6144 and CHEP5 significantly improved peanut resistance to S. rolfsii. However, indicators such as peroxidase activity and phenolic compound content differed between co-inoculation and single inoculation treatments. This result indicates that the interactions among rhizosphere microorganisms are highly complex and that the enhancement of plant tolerance to pathogens is not determined by a single rhizosphere microorganism (Figueredo et al., 2018). Rhizosphere microbial communities can enhance plant resistance to pathogens by producing antimicrobial substances that inhibit pathogens or by indirectly inducing ISR in plants. Berendsen et al. reported that when *Arabidopsis thaliana* (L.) Heynh. leaves were infected by the downy mildew pathogen Hyaloperonospora arabidopsidis, the rhizosphere recruited three beneficial microorganisms—Xanthomonas sp., Stenotrophomonas sp., and Microbacterium sp.—which enhanced the systemic resistance of the plants and thereby improved the resistance of progeny plants to the pathogen (Berendsen et al., 2018). Lee et al. analyzed the rhizosphere microbial communities of healthy and bacterial wilt-infected tomato plants and found that in diseased rhizosphere soil (DRS), the relative abundances of Actinobacteria and Firmicutes were lower than those in healthy rhizosphere soil (HRS), while the population of the pathogenic bacterium Ralstonia solanacearum remained unchanged. Four bacterial strains—Brevibacterium frigoritolerans HRS1, Bacillus niacini HRS2, Solibacillus silvestris HRS3, and Bacillus luciferensis HRS4—were isolated from HRS. These strains activated plant immunity, rendering the plants more immunocompetent against pathogens (Lee et al., 2021). A stable and abundant beneficial microbial community in the plant rhizosphere is more conducive to plant growth and the prevention of pathogen invasion. As the rhizosphere microbial community grows, the increase in population density leads to changes in its physiological and biochemical characteristics, exhibiting features that are not present in a small number of strains or a single strain. Quorum sensing (QS) signal molecules from rhizosphere bacteria can activate multiple plant defense genes, including MPK3, MPK6, WRKY22, and WRKY29 (Hartmann and Schikora, 2012). These results indicate that in response to pathogen infection, the plant rhizosphere recruits beneficial microorganisms and alters the structure and function of the rhizosphere microbial community, thereby enhancing plant resistance to diseases. In summary, rhizosphere microorganisms enhance plant disease resistance through important mechanisms such as inducing plant resistance, producing antimicrobial substances, and regulating the assembly of rhizosphere microbial communities. Currently, research on the biological control of diseases using rhizosphere microorganisms has achieved many results, but there are still shortcomings. With the development of metagenomic technologies, the close relationships among the composition, structure, and function of rhizosphere microbial communities and plant growth and disease occurrence are gradually being revealed. However, research on how rhizosphere microbial community assembly enhances plant disease resistance remains limited. Future efforts should strengthen the study of microbial community structure and function to further provide a theoretical basis for plant disease resistance.

## CONCLUSION AND OUTLOOK

With the development of ecological engineering and agriculture, rhizosphere microorganisms play a critical role in helping plants adapt to various abiotic and biotic stresses. Through multiple pathways, they promote the regulation of a series of biological traits and physiological and biochemical responses in plants, thereby assisting plants in coping with adverse environments and ensuring their growth and development. Although significant progress has been made in understanding how rhizosphere microorganisms help plants withstand environmental stresses, research gaps remain regarding their roles under five types of stress—drought, cold, salt, heavy metals, and diseases—particularly in the following three aspects:

1) Molecular mechanisms remain unclear. The molecular mechanisms by which rhizosphere microorganisms mediate plant adaptation to abiotic stress are still poorly understood. Future research should integrate transcriptomics, metabolomics, microbiome analysis, and molecular biology approaches to elucidate the molecular mechanisms underlying changes in rhizosphere microbial communities during plant responses to environmental stress.

2) Research on phytohormone regulation is incomplete. Current studies on the regulation of phytohormones by rhizosphere microorganisms under stress conditions have mainly focused on indole-3-acetic acid (IAA). However, how other hormones such as gibberellins (GA) and abscisic acid (ABA) participate in regulating plant–environment interactions, as well as how rhizosphere microorganisms modulate hormone levels to prevent excess (since excessive phytohormones can inhibit plant growth), require further investigation.

3) The balance mechanism between microbial community structure and function urgently needs to be explored. How do the structure and function of rhizosphere microbial communities balance the relationship between plant growth and stress resistance? During this balancing process, how do rhizosphere microorganisms influence plant uptake and utilization of nitrogen and phosphorus? These questions also require further investigation.

Therefore, future efforts should focus on strengthening research in the above three areas in order to provide new approaches and methods for ecological restoration and agricultural development.

### Authors' contribution

Q.F. Wu Writing original draft.; Z.M. Li and X.H. Pan analysis Data; X.H. Zeng and L.X. Zhou Writing-review and editing. All authors read the final manuscript and have given final approval of the version to be published.

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