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Rhizosphere microbiome regulation: Unlocking the potential for plant growth

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ARTICLE INFO

Keywords:

Rhizosphere microorganism
PGPR
Regulating microorganisms

ABSTRACT

Rhizosphere microbial communities are essential for plant growth and health maintenance, but their recruitment and functions are affected by their interactions with host plants. Finding ways to use the interaction to achieve specific production purposes, so as to reduce the use of chemical fertilizers and pesticides, is an important research approach in the development of green agriculture. To demonstrate the importance of rhizosphere microbial communities and guide practical production applications, this review summarizes the outstanding performance of rhizosphere microbial communities in promoting plant growth and stress tolerance. We also discuss the effect of host plants on their rhizosphere microbes, especially emphasizing the important role of host plant species and genes in the specific recruitment of beneficial microorganisms to improve the plants' own traits. The aim of this review is to provide valuable insights into developing plant varieties that can consistently recruit specific beneficial microorganisms to improve crop adaptability and productivity, and thus can be applied to green and sustainable agriculture in the future.

1. Introduction

The rhizosphere is a hotspot for plant-soil microorganism interactions, in which exudates released by plant roots are a main food source for microbial communities and a driving force of their population density and activities (Bulgarelli et al. 2013, Ibekwe et al. 2013, Schlaeppi et al. 2013, Bulgarelli et al. 2015). Bacterial community abundance in non-rhizosphere soil is approximately 6.91×10^8 , which dramatically increases in the rhizosphere to 6.44×10^9 and in the endosphere to 1.24×10^9 (Tkacz et al. 2018, Guo et al. 2020, Wang et al. 2020). Although the composition of microbial communities in rhizosphere soils has been reported to be consistent, mainly consisting of species in the phyla *Proteobacteria*, *Actinobacteria*, *Bacteroidetes*, and *Firmicutes*, there are notable differences in relative abundance at the level of phylum (Lundberg et al. 2012, Liu et al. 2019, Li et al. 2023).

As a recognized second genome of plants, the rhizosphere microbiome, with its enhanced microbial diversity and activity, is crucial for the growth, development, and health of plants (Berendsen et al. 2012). The abundant microbial communities in the rhizosphere can also use so-called rhizosphere sediments, such as nutrients, root exudates,

marginal cells, and mucus released from plant roots, as food and signals, and then interact with host plants and participate in biogeochemical cycles (Philippot et al. 2013). Rhizosphere engineering with plant growth-promoting rhizobacteria (PGPR) can enhance agricultural productivity and ecological sustainability by improving nutrient cycling, promoting plant growth, and providing biocontrol against pathogens (Hakim et al. 2021). However, soil microorganisms do not unconditionally enter the rhizosphere to interact with plants; their functioning can only be achieved through chemotaxis from the rhizosphere, root surface adhesion, root surface biofilm formation and endobiochemistry (Liu et al. 2024).

In view of the important role of rhizosphere microbial communities in promoting plant growth and health maintenance, it is of key importance to explore the regulatory mechanism of the rhizosphere microbial community assembly process and its functioning. Unraveling the secrets of the interaction between the rhizosphere microbiome and plants can then be applied to manipulating this microenvironment for specific production purposes. There are three main factors that affect the rhizosphere microenvironment: the host plant, the microbiome and the rhizosphere soil. They can each regulate the structure of rhizosphere

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<https://doi.org/10.1016/j.crmicr.2024.100322>

Available online 22 November 2024

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microbial communities (Park and Mannaa 2023). Host plants generate root signals, especially root exudates, that regulate the composition and function of rhizosphere microbial communities, and play an important role in shaping rhizosphere microbial communities (Zhalnina et al. 2018). In addition, the abundance and diversity of microorganisms in the rhizosphere depend on complex interactions, as well as root sediment quantity and quality, which are determined by each plant's particular genome (Bais et al. 2006), emphasizing the role that host

plants play in shaping rhizosphere microbial communities.

This paper reviews how the rhizosphere microbiome affects plant growth and health maintenance, as well as the main methods for regulating the composition and function of the rhizosphere microbiome. It also provides a comprehensive overview of how host plants can shape the rhizosphere microbiome at different genomic levels, recruit specific microorganisms, and play an important role in improving the plants' own traits. The ultimate goal of this review is to highlight the

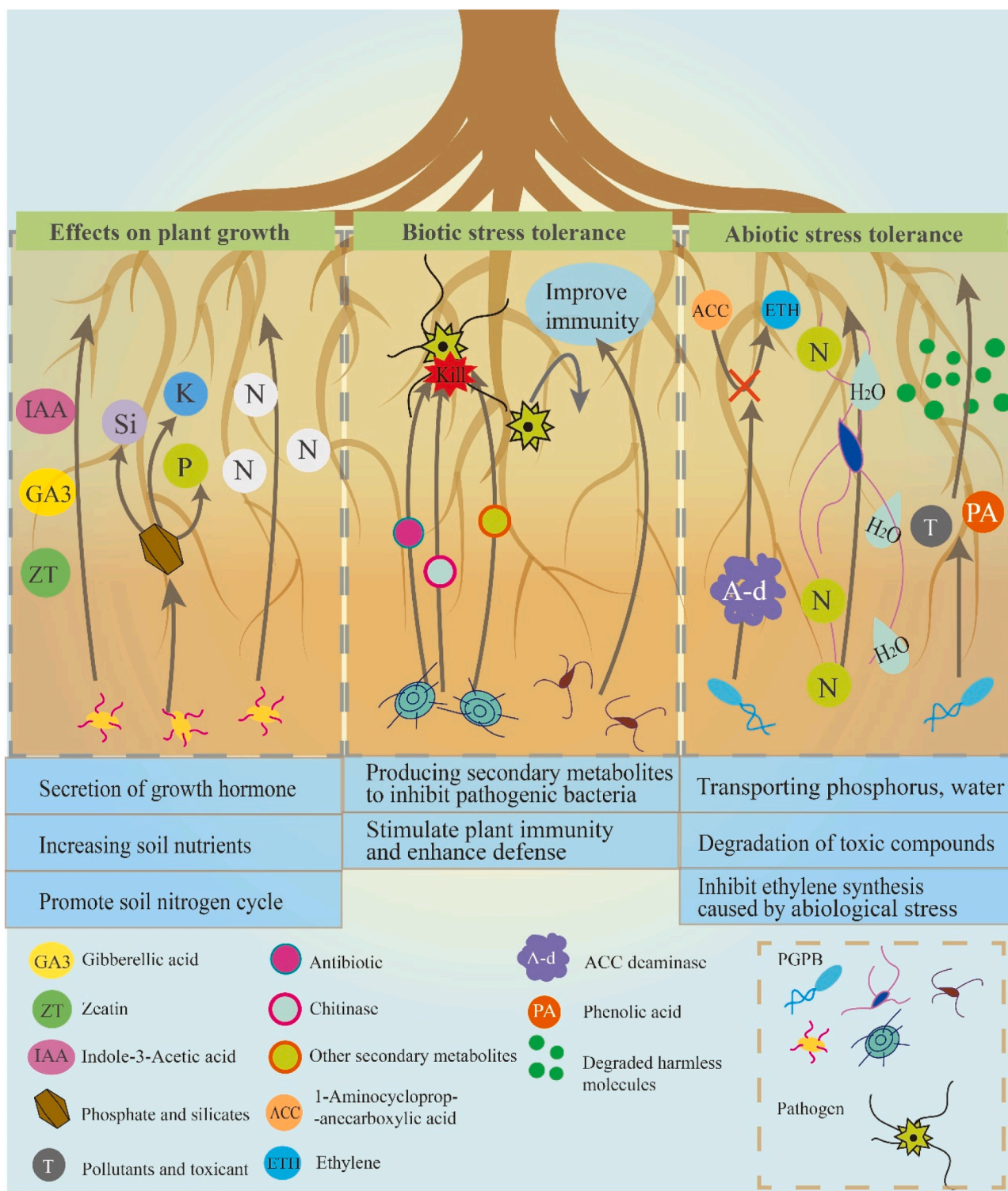


Fig. 1. The influence of the rhizosphere microbiome on plant phenotype remodeling.

importance of host plants in regulating their own rhizosphere microbial communities and the potential for recruiting specific beneficial microorganisms as new breeding traits, in order to deepen our understanding of the mechanism of plant-microbial interactions, and ultimately promote the development of environmentally friendly green agriculture.

2. The role of the rhizosphere microbiome in plant phenotypic remodeling

Based on the interaction characteristics with host plants, root-associated microorganisms can be categorized into mutualists, pathogens, and commensals (Brader et al. 2017, Thoms et al. 2021). Mutualists are microorganisms that form specialized symbiotic structures within plant roots to facilitate substance exchange. For example, arbuscular mycorrhizal fungi assist plants in absorbing phosphate, while rhizobia in the roots of leguminous plants provide essential nitrogen nutrients to their hosts. In return, these microorganisms receive, from the host plant, organic carbon sources necessary for their growth. Pathogens are microorganisms that can cause diseases in host plants upon colonization. Commensals represent a large portion of the root-associated microbiome; they exhibit low dependency on their host plants, and are often referred to as rhizosphere microorganisms. These organisms can have neutral or even detrimental effects on host plants, and may potentially become pathogens, but they can also provide beneficial effects. These effects can be divided into three types: effects on plant growth and development, effects on plant tolerance to abiotic stresses and effects on plant biotic stress tolerance. They include promoting nutrient absorption, producing plant growth regulators, and inhibiting harmful microorganisms, thereby contributing to a healthier plant ecosystem (Qu et al. 2020, Thoms et al. 2021) (Fig. 1). These organisms have wide range of functions and exhibit high diversity. Consequently, studying their classification, biological functions, and interactions with the environment, other microorganisms, and host plants has become a major research focus

2.1. Effects on plant growth and development

Beyond their fundamental cellular roles, rhizosphere microorganisms exhibit specialized functions that promote plant growth and development; these include, secretion of growth hormone, increasing soil nutrients and facilitating nutrient acquisition in plants. Plant growth regulators are signaling compounds that regulate crucial aspects of growth, development and environmental stress responses, they include abscisic acid, auxin, brassinosteroids, cytokinins, ethylene and gibberellins (Waadt et al. 2022). Among them, IAA, gibberellic acid and zeatin can promote plant growth and cell division, and improve plant stress resistance. In addition to the synthesis of these special compounds by plants themselves, rhizosphere microorganisms can also produce phytohormone-like substances. For example, fungi isolated from healthy plants can produce such substances that, when applied it to *Lolium multiflorum* seeds and seedlings under both in vitro and under greenhouse conditions, result in greatly enhanced plant growth traits.

In addition to the influence of plant hormone levels, the healthy growth of plants is closely related to there being sufficient nutrients in the soil. Elements such as nitrogen, phosphorus, potassium and silicon are essential for plant growth, but they are often present at low levels and are often unavailable because of being insoluble. Therefore, rhizosphere microorganisms that can provide and deliver nutrients should be isolated and utilized for plant growth. For example, *Enterobacter ludwigii* bacteria facilitate the dissolution of insoluble sulfates and silicate minerals, thereby increasing the availability of silicon, phosphorus, and other essential elements (Adhikari et al. 2020).

Moreover, in addition to increasing the nutrient content in the soil, microorganisms also assist plants in nutrient absorption, promote soil element cycling, and maintain soil homeostasis. Under conditions of low nitrogen availability, the relative abundance of slow-growing ammonia-

oxidizing bacteria (AOB) and *Bradyrhizobia* in the rhizosphere of *Lycium barbarum* increases, thereby enhancing nitrogen uptake and boosting the content of flavonoids, alkaloids, and amino acids (Li et al. 2023). Likewise, the maize rhizosphere enhances nitrogen assimilation by recruiting *Oxalobacteraceae* and utilizing the enzymes they secrete, creating highly active biological hotspots within the rhizosphere (Yu et al. 2021, Hao et al. 2022). The temporal complementarity of N utilization efficiency of wheat roots and root-associated microorganisms further demonstrates that rhizosphere microorganisms can promote plant uptake of nitrogen (Yang et al. 2022). Notably, arbuscular mycorrhizal (AM) fungi, with their extensive hyphae, act as an extended root system, facilitating the transport of distant phosphorus and water to the plant (Li et al. 2016).

Current research has revealed that bacteria often have the aforementioned growth promoting functions, thus facilitating plant growth. For example, *Bacillus*, a common genus of soil bacteria includes species that can deliver various 'services'. The species *Bacillus subtilis* can solubilize soil P, enhance nitrogen fixation, and produce siderophores that promote its growth and suppress the growth of pathogens. *Bacillus subtilis* enhances stress tolerance in its plant hosts by inducing the expression of stress-response genes, plant growth regulators, and stress-related metabolites (Hashem et al. 2019). However, a single growth-promoting bacterium is not sufficient for plant growth promotion. On the contrary, the more diverse and complex the rhizosphere microbial community, the more effective it is with respect to improving plant growth. For example, heightened microbial diversity in the rhizosphere of pear trees, with a notable increase in groups like *Gammaproteobacteria*, *Chlamydiae*, *Bacteroidetes*, and *Clostridia*, can stimulate increased branching, modulate growth patterns, and augment both the quantity and quality of fruit production, enhancing both taste and aroma (Shi et al. 2023). Furthermore, connections between microbial taxa have been found to promote nitrogen uptake by rice and ultimately to increase yield (Zhong et al. 2020)

For these reasons, plants benefit from recruiting useful rhizosphere microorganisms and establishing complex and diverse microbial communities to enhance growth (Hinsinger et al. 2009). The rhizosphere microbial community exhibits a pronounced successional dynamic that corresponds to the different developmental stages of plants. As plants transition from vegetative growth to reproductive growth, the community tends to stabilize (Chaparro et al. 2014, Gore et al. 2018), but the bacterial load significantly increases compared to the initial stage, especially in relation to *Bacteroidetes* (Wang et al. 2024). This suggests an intimate association between the composition of rhizosphere microbial communities and the development of plants. For example, specific soil microorganisms can influence the flowering phenology of *Boechera stricta*, a wild relative of *Arabidopsis thaliana*, and affect the flowering time of *Arabidopsis* (Wagner et al. 2014). Rhizosphere microorganisms increase and prolong the bioavailability of nitrogen through nitrification and convert tryptophan into the plant hormone indoleacetic acid (IAA). This process down-regulates the genes that trigger flowering, thereby stimulating further plant growth and delaying flowering (Lu et al. 2018). These revelations suggest that, through the judicious selection of relevant rhizosphere microorganisms, it is possible to modulate plant phenotypes, enabling them to adapt to the soil and climatic environments more effectively (Panke-Buisse et al. 2015).

2.2. Effect on plant biotic stress tolerance

In natural environments, the proliferation of diverse bacterial and fungal pathogens reflects the transition of plants from a healthy to a diseased state. Fungi are among the dominant causal agents of plant diseases, they kill their hosts and feed on dead material (necrotrophs), colonize the living tissue (biotrophs) or start the infection as biotrophs but later switch to necrotrophs (hemibiotrophs).

Rhizosphere microorganisms can directly kill pathogens, suppress their growth or limit their spread. For instance, *Pseudomonas putida*, P.

libanensis, *P. aeruginosa*, *Bacillus subtilis*, *B. megaterium*, and *B. cereus* isolated from chilli pepper rhizosphere could significantly suppress the infection of *Phytophthora capsici* (Hyder et al. 2020). Furthermore, there is a significant increase in the abundance of *Flavobacterium* among the rhizosphere microbes of loofah after root-knot nematode infection. Particularly noteworthy is the presence of *Streptomyces* species, which exhibit strong insecticidal activity against nematodes (Qu et al. 2023). Similarly, *Piriformospora indica* can successfully colonize the intercellular spaces of banana roots, inhibit the growth and spread of *Fusarium oxysporum cubense* tropical race 4, and promote lateral root formation. This significantly reduces the occurrence of *Fusarium* wilt in banana plants (Zhu et al. 2023). *Chitinophaga* and *Flavobacterium* in synthetic bacterial consortia (SynComs) suppress fungal diseases by degrading fungal cell walls through enhanced chitinolytic activity and producing antifungal secondary metabolites via specific NRPS-PKS gene clusters (Carrión VJ 2019). Mendes et al identified specific strains within the *Pseudomonadaceae* family which are recognized for their pronounced inhibitory impact on the fungal pathogen *Rhizoctonia solani* from sugar beet (Mendes R 2011).

Concurrently, the assembly of rhizosphere microbial communities, intimately linked to plant health, is related to disease progression. For example, in rice, the diversity of the rhizosphere microbiota initially declines with the onset of disease. However, as the disease progresses and stabilizes, the afflicted rice becomes associated with a richer array of key probiotic microbes, constructing a more intricate microbial network. This network functions to suppress pathogenic organisms and bolster the plant's innate immune response (Jiang et al. 2023). Small changes in the rhizosphere microbial community mediated by the host can have a significant impact on host health (Haney et al. 2015). However, this dynamic is not exclusively dictated by pathogens; it may also be influenced by other members of the rhizosphere microbiota. It has been reported that initially homogeneous soils can rapidly develop different rhizosphere microbiomes. Disease outcomes have been significantly predicted as early as two weeks before there was any difference in pathogen density between healthy and diseased populations, possibly due to divergence in rhizosphere microbiome assembly early in the onset of disease. More than 130 bacterial OTUs were found to be associated with plant health maintenance, and in particular, five enriched OTUs (*Lysinibacillus*, *Pseudarthrobacter*, *Bordetella*, *Bacillus*, and *Chryseobacterium*) reduced disease severity by 30.4–100 % when inoculated with pathogens (Gu et al. 2022). Collectively, these findings suggest that the pathogen-driven reshaping of the plant rhizosphere microbial communities could be instrumental in enhancing a plant's resistance to its own pathogens.

Recent studies have suggested that this increase in disease resistance is due to some key rhizosphere microbial groups reducing pathogen abundance or activating host plant systemic acquired resistance through various complex mechanisms, which is ultimately manifested by increased host plant disease resistance or reduced disease severity. Certain strains of rhizosphere bacteria have the capacity to augment systemic acquired resistance or specific resistance in plants through the activation of the host's immune system. For instance, AMF have been shown to induce substantial alterations in over 35 root exudates of the host plant, modulate enzymatic activities, diminish bacterial diversity, and improve resistance to specific pathogens (Ma et al. 2022). Similarly, two *Bacillus* strains from the rhizosphere, A8a and HA, generate multiple volatile organic compounds that significantly suppress pathogenic organisms like *Fusarium solani*, *F. kuroshium*, and *Phytophthora cinnamomi*. They also activate various hormonal signaling pathways associated with plant growth and defense mechanisms, including those for auxin, jasmonic acid (JA), and salicylic acid (SA) (Cortazar-Murillo et al. 2023). Upon encountering the downy mildew pathogen *Hyaloperonospora arabidopsidis*, *A. thaliana* selectively enriches beneficial bacterial communities within the rhizosphere, with a preference for *Xanthomonas*, *Stenotrophomonas*, and *Microbacterium*. These bacteria synergistically form biofilms to promote colonization and induce

systemic resistance (ISR) through pathways involving salicylic acid and jasmonic acid, thereby enhancing the plant's systemic disease resistance (Berendsen et al. 2018). Moreover, these plant growth regulators also engage in the rhizosphere to enlist beneficial microorganisms for the plant, including species such as *Rhodanobacter*, *Sphingomonas*, and *Micromonospora* (Zhu et al. 2022). The advantages of *Pseudomonas* strains are evident in their significant promotion of plant health and disease resistance, employing a range of mechanisms such as nutrient competition, pathogen parasitism, secondary metabolite production, and the induction of systemic resistance (Pieterse et al. 2014). This also suggests that the rhizosphere microbiome of plants after biological stress induction is associated with the improvement of self-tolerance.

To enrich the beneficial rhizosphere microorganisms, for instance, *Arabidopsis* roots selectively recruit *Bacillus subtilis* FB17 through dose-dependent secretion of L-malic acid induced by the pathogen *Pseudomonas syringae* pv. *tomato* (Pst DC3000), promoting FB17 binding and biofilm formation on the roots (Rudrappa et al. 2008). The *Streptomyces morookaensis* strain Sm4-1986 excretes a range of secondary metabolites, such as xerucinonin A and 6-pentyl- α -pyrone, which have the potential to enhance soil characteristics, augment the population of rhizosphere microorganisms that promote banana growth, and notably decrease the prevalence of *Fusarium* wilt in bananas (FWB) (Zhu et al. 2023). The *Pseudomonas brassicacearum* R401 strain produces 2,4-diacetylphloroglucinol (DAPG), a compound capable of inhibiting the proliferation of diverse bacterial species, while also secreting the iron chelator pyrazin [1,2-a] pyrazine-4,9-dione, known as pyoverdine, which can stimulate the growth of certain bacteria in iron-limited conditions. When these two compounds work together, they are able to inhibit the growth of rhizosphere-competing bacteria more effectively, thereby favoring the survival and success of specific bacterial populations (Getzke F 2023).

2.3. Effects on plant tolerance to abiotic stresses

Besides the severe threats to plant health posed by diseases, abiotic stresses introduced by severe environments and poisons are a significant impediment to plant growth and development. Unfortunately, severe environmental conditions, such as drought, high temperature or saline-alkali soil, are widely distributed worldwide. In these environments plants grow slowly and the cropping area is limited. Besides the challenging external physical conditions, toxic compounds produced by plants or introduced by humans are becoming a more serious threat. Like the elimination of disease-causing bacteria, rhizosphere microorganisms can also eliminate the harm caused by abiotic factors.

When facing the survival pressure brought about by unfavorable conditions such as drought, salt and alkalinity, plants increase ethylene synthesis from its precursor 1-aminocyclopropane-1-carboxylic acid (ACC). Low concentrations of ethylene can regulate plant growth to a certain extent, but an increase in concentration will eventually lead to plant death. Rhizosphere microorganisms can alleviate this phenomenon by secreting ACC deaminase to degrade ethylene synthesis precursors and improve plant tolerance (Chandwani et al. 2022).

In addition to the ACC deaminase that reduce the degree of host stress response. In response to different abiotic stresses, plants can recruit unique microorganisms and use their multiple mechanisms to help themselves. For example, under poor soil and drought conditions, corn attracts beneficial microorganisms by adjusting the composition of root exudates, such as root flavonoids, which can promote the enrichment of specific bacterial groups such as *Oxalobacteraceae* in the rhizosphere (Yu et al. 2021). In addition, the various enzymes they secrete not only help to deliver nutrients, but also increase the biological activity of the rhizosphere region, forming a so-called "hotspot" and promoting nitrogen acquisition in maize (Hao et al. 2022). Meanwhile, drought stress induces the production of 4-Methylumbelliferone (4-MU) from dwarf rootstocks, thereby regulating rhizosphere microbial diversity and promoting root structure, thus enhancing drought resistance in apples

(Zhang et al. 2023). Acetic acid is capable of enriching microorganisms related to nitrogen fixation, including nitrogen-fixing bacteria and *Pseudomonas* species, potentially improving the drought resistance of willow trees through the enhancement of their nitrogen absorption capacity (Kong et al. 2022).

With the expansion of human activities, soil pollution has become increasingly serious. The interaction between plant roots and rhizosphere microorganisms can change the rhizosphere microenvironment and reduce the content of heavy metals and their bioavailability in rhizosphere soil through adsorption, precipitation, and transformation (Qian et al. 2023). In cadmium contaminated soils, certain specific rhizosphere microorganisms are pivotal in alleviating the toxicity in *Solanum nigrum*. Notably, the phyla *Ascomycota*, *Glomeromycota*, *Proteobacteria*, and *Actinobacteria* enhance the plant's uptake and detoxification of cadmium. They achieve this by modulating various mechanisms, including plant hormone levels, signaling pathways, and nutrient uptake, facilitating the accumulation of cadmium in the roots. Iron-manganese oxidizing bacteria can form a blanket layer around plant roots, reducing arsenic accumulation in plant tissues. Bacteria can also help plants absorb iron from the soil by producing substances such as siderophores, which indirectly affect the uptake and migration of arsenic. In addition, rhizosphere bacteria may also affect arsenic behavior in the soil and plant uptake by altering the microbial community structure and nutrient cycling (Sun et al. 2023). The presence of the fungus *Piriformospora indica* affects the abundance of the arsenic-resistant bacteria *Lysobacter* and *Steroidobacter*, and effectively enhances arsenic tolerance in *Artemisia annua* by fixing arsenic in plant roots and improving iron transport in plant stems (Rahman et al. 2023). In saline-alkali soils polluted with heavy metals, the combination of bio-organic fertilizers and arbuscular mycorrhizal fungi (AMF) allows the accumulation of more heavy metals and salts in plants than without treatment or when one approach is used in isolation. The synergistic effect of the two is mainly due to the further improvement of soil nutrient levels and microbial activity, and the establishment of symbiotic relationships between clumps of mycorrhizal fungi and the host (Lu et al. 2023).

The rhizosphere and phyllosphere microbiomes of host plants possess the capacity to break down chemical agents, including pesticides and the phenolic acids excreted by plants. *Bacillus* strains, isolated from azoxystrobin-enriched soil, were found to harbor genes associated with pesticide degradation pathways, including *benC*, *pcag*, and *pcaH* (Kraxberger et al. 2023). Similarly, phenolic acids are known to contribute to the challenges of continuous cropping; these can, however, be degraded by specific *Bacillus* species present in continuous cropping peanut soil, potentially mitigating the issues (Liu et al. 2017).

3. Shaping and dynamic regulation of the rhizosphere microbiome by host plants

Since the discovery of disease-suppressive soils following monoculture wheat, the plant "cry for help" hypothesis has gradually gained ground (Gao et al. 2021). This hypothesis posits that plants can respond to pathogen invasion by specifically recruiting beneficial microorganisms to enhance their disease resistance. As research into how host plants recruit beneficial microorganisms at various genetic levels deepens, it has been found that host plants have significant potential in reshaping rhizosphere microbial communities to improve crop productivity.

3.1. Specific exudates of different plant species determine special rhizosphere microbial communities

From an ecosystem standpoint, a variety of factors influence the assembly of plant rhizosphere microbial communities, with plant species playing a significant role. Plant species can specifically shape the composition and function of their own rhizosphere microbial

communities. Zhang et al. determined that plant species independently contributed at a rate of 10.9 % to the formation of the rhizosphere microbial community, marking them as a crucial factor in the structuring of such communities within seasonal rainforests (Zhang et al. 2023).

There are significant differences in the diversity of microorganisms of different species. In a study of three endanger plants, although the coverage of bacteria and fungi in the rhizosphere soil of them is similar, there are remarkable differences in the Chao1 index of alpha diversity, which means that the abundance of specific microorganisms is the major factor contributing to microbial community differences (Xu et al. 2020). Under the same soil and soil microbial planting conditions, plants of different species can shape their unique preferred microorganisms. Wipfel et al. have established a microbiota library from bacteria found in the roots and nodules of *Lotus japonicus* and *A. thaliana*, which were then used to create synthetic communities (SynComs). These SynComs were employed in gnotobiotic reconstitution systems to explore various factors, including nitrogen-fixing nodule symbiosis, immunity, and root exudation, that influence the establishment of the root microbiota. Results show that *L. japonicus* and *A. thaliana* host distinct root microbiota that are clearly separated from the surrounding soil microbiota, indicating a host-species-specific recruitment process. These findings imply that the observed host preference patterns may be a result of microbial adaptation to conserved root features in a given host lineage, rather than a direct consequence of coevolution with the host plant. The plant immune system and root exudates may play a role in selecting commensal bacteria in a host-specific manner (Wipfel et al. 2021) (Fig. 2).

Similarly, the same plant species growing in different soils with different resident microorganisms, have similar rhizosphere microbiome assembly processes. By planting tomatoes in three soils for three cycles, it was found that although there were significant differences in the bacterial communities in different soils at the beginning, they had similar succession processes, and specific bacteria such as *Rhizobium*, *Flavobacterium* and *Beijerinckia fluminensis* GR2 were gradually enriched; this could promote heterologous biodegradation, Nutrients metabolize and inhibit the growth of *Ralstonia solanacearum* and protect plants from infection (Su et al. 2023). Similarly, the rhizosphere microbial communities of *Holcus lanatus* and *Jacobaea vulgaris* initially differed when grown in conspecific and heterospecific soils, but over time, they gradually became similar to the composition of conspecific soil (Steinauer et al. 2023).

Therefore, the mechanisms by which different host plants exhibit significant differences in the composition and function of their respective microbiomes are of interest. From the perspective of the plants themselves, different plants have specific root exudates to selectively recruit rhizosphere microorganisms, and these exudates are the main media for host plants to construct differentiated rhizosphere microbial communities that are conducive to their own growth. The interaction of root exudates and chemotactic strains may affect the cycling and availability of nutrients in the soil, as well as the adaptability of plants to multiple stresses, thereby enhancing the competitive advantage of plants. For example, L-theanine secreted by the roots of tea plants selectively shapes microbial assembly by altering the structure of rhizosphere microbial communities, reducing the abundance of genes associated with denitrification and complete nitrification (Xie et al. 2022). *Casuarina equisetifolia* attracts chemotactic strains by releasing specific chemicals such as 2,4-di-tert-butylphenol, methyl stearic acid, and arginine, which allow specific bacterial communities to aggregate and colonize rhizosphere soils (Lin et al. 2022). To confirm the importance of root exudates, Zhou et al. allowed the exchange of root exudates by restricting physical contact between tomato and potato or onion roots, and found that root exudates from potatoes and onions can change the structure of tomato rhizosphere bacterial communities, thereby enhancing the inhibitory effect on the soil-borne pathogen *Verticillium dahlia* (Zhou et al. 2023). Furthermore, Liu et al. discovered that integrating *Achyranthes bidentata* into the *Rehmannia glutinosa* cropping system as an intercrop can enrich the soil with beneficial

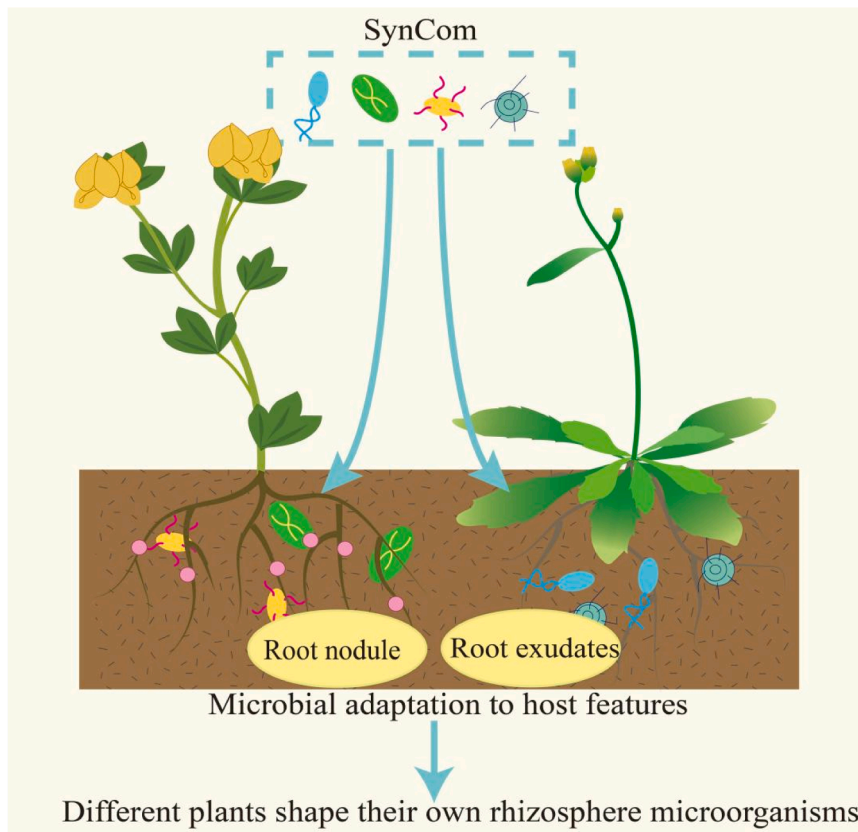


Fig. 2. *Lotus japonicus*(left) and *Arabidopsis thaliana*(right) shape their own rhizosphere microorganisms after the same SynCom treatment.

microorganisms like *Bacillus*, *Fictibacillus*, and *Bradyrhizobium* through root exudates, enhancing microbial diversity and suppressing the growth of the pathogenic microorganism *Fusarium* in the rhizosphere of *Rehmannia rehmannia* (Liu et al. 2022).

Furthermore, Wen et al. found a significant correlation between five metabolites—tocopherol acetate, citrulline, galactitol, octadecylglycerol, and behenic acid—in healthy and diseased watermelons and the shifts in their rhizosphere microbial communities. These metabolites weakened the autotoxin degradation function of bacteria like *Rhizobia*, *Streptomyces*, *Proteus*, *Pseudomonas*, and *Sphingomonas*, while promoting the activity of anaerobic *Microbacterium*, *Lysobacter*, *Nocardia*, *Flavobacterium*, and *Gemmatimonas* in metabolizing small molecule sugars and acids (Wen et al. 2022). Further studies showed that the difference in the content of root exudates can also lead to the change in the rhizosphere microbial community. For example, four poplar varieties secrete various content in luvangetin, salicylic acid, gentisic acid, oleuropein, strigol, chrysin and linoleic acid, which makes the strong impact on the core microbiome and drive the change in the rhizosphere microbial communities (Li et al. 2022). Disease-resistant banana varieties can produce much more Shikimic acid, D-(-)-ribofuranose and propylene glycol than the susceptible varieties do; these enriched metabolites exhibit strong inhibitory effect on the pathogen (Liu et al. 2023). In contrast to ordinary crops, the root-derived metabolites of medicinal plants are relatively diverse and allelopathy. However, the communities shaped by these secretions are not enough to metabolize and alleviate allelopathy, eventually leading to the occurrence of continuous cropping obstacles, which need exogenous supplementation of specific beneficial microorganisms to solve the obstacles (Liu et al. 2023, Qu et al. 2024). In summary, plant species and its root exudates play a crucial role in specifically shaping their own rhizosphere microbial communities. It is evident that specific root exudates are responsible for variations in the composition and functionality of rhizosphere microbial communities between different species.

3.2. Genotype and the functional genes of host plants affect the rhizosphere microbial communities

Apart from the differences between plant species, distinct genotypes within the same species also possess genetically specific root-associated core rhizosphere microbiomes. The variations in the rhizosphere microbiome among different varieties are primarily manifested in aspects of microbial diversity, composition and the relative abundance of specific microbial communities (Lundberg et al. 2012, Walters et al. 2018). More importantly, these differences contribute to the phenotypic differences between them.

It has been demonstrated that two soybean varieties and their recombinant inbred lines (RILs) with high and low nodulation traits are able to select different microorganisms from the soil to form their own unique rhizosphere bacterial community structure and symbiotic network (Zhong et al. 2019). Furthermore, the genotype of *Arabidopsis* significantly influences the abundance and activity of specific OTUs within the *Pseudomonadaceae* family (Haney et al. 2015). More obviously, Castellano-Hinojosa et al. have shown that different genotypes of citrus grafted rootstocks have a decisive impact on the species and number of active rhizosphere bacteria. These different genotypes recruit specific bacterial groups, mainly those known to promote plant growth, such as *Bacillus*, *Streptomyces*, *Pseudomonas*, *Mesorhizobium*, *Sphingomonas*, and *Rhizobium*. These bacteria have the ability to solubilize nutrients like phosphorus, sulfur, and calcium, and synthesize a range of plant growth regulators and siderophores, thereby facilitating nutrient absorption and translocation within plant roots (Castellano-Hinojosa et al. 2023).

The influence of microbial differences between varieties in relation to phenotype, however, goes beyond plant nutrition: other studies have found that the beneficial microbial species recruited by different genotypes are also compatible with their own stress resistance. For example, the rice mutant *sst* (seedling salt tolerant) with the better salt tolerance

exhibits the significant differences in the rhizosphere microbial community and also root exudates, compared to the wildtype (Lian et al. 2020). Furthermore, the low arsenic accumulation (LSA) and high arsenic accumulation (HSA) genotypes of Chinese cabbage (*Brassica rapa* ssp. *pekinensis*) may have differences in arsenic accumulation capacity that are closely related to the composition and function of their rhizosphere microbial communities. Significant differences are observed in the relative abundances of microbial groups such as *Acidobacteria*, *Rokubacteria*, *Patescibacteria*, and *Actinobacteria* between these genotypes (Sun et al. 2023). Similarly, wheat cultivars Jinan 17 (JN17) and Linmai 2 (LM2), with low cadmium and high zinc accumulation, have been found to enrich specific rhizosphere bacteria such as *Gemmatimonadaceae*, *Sphingomonadaceae*, and *Beijerinckiaceae*. These bacterial communities influence heavy metal accumulation and transfer through mechanisms like hormone stimulation and root hair growth (Liu et al. 2022). Different soybean varieties can recruit specific rhizosphere microorganisms that enhance growth and resilience. For instance, in the RM-Williams 82 variety, increased abundance of *Flavisolibacter* and *Caulobacter*, which alleviated molybdenum nanoparticle toxicity, boosting plant height, root length, biomass, and nitrogen fixation by 70.8 %, 80.7 %, 145.8 %, and 349.8 %, respectively (Zhou et al. 2023).

The disparity is particularly evident in the process of domestication, while humans shape new varieties in the process of pursuing high yield, disease resistance and other desirable traits, rhizosphere microorganisms are also constantly changing to adapt to and assist in the formation of new traits. Domestication has converted wild tetraploid wheat from a slow-growing, fungal-dominated community characterized by genes for carbon sequestration, into a rapidly growing, bacteria-dominated community replete with genes for carbon degradation. This transformation leads to a reduction in the prevalence of principal fungal groups and simultaneously augments the diversity of bacterial communities (Yue et al. 2023). Similarly, the rhizosphere microbial diversity of wild licorice (*Glycyrrhiza uralensis*) is significantly higher than that of licorice cultivated for one (C1) and three years (C3). PGPR such as *Rhizobium*, *Streptomyces*, and *Nitrososvibrio* in wild licorice enhance the expression of genes for synthesizing glycyrrhizin and glycyrrhizic acid (Zhong et al. 2022). Similarly, the rhizosphere bacterial community of *Cucumis* and its wild relative, *Cucumis metuliferus*, showed significant differences after root-knot nematode (RKN) infection. The wild species experienced drastic changes early in the infection, but with little change in bacterial composition and diversity. It recruited different probiotic species, displayed an increased abundance of the antagonistic genus *Pseudomonas*, and ultimately established a more intricate microbial network (Song et al. 2023). Such differences are probably a consequence of targeted genomic alterations during the selection of crop traits, resulting in modifications to the plant root structure and root exudates. In turn, these changes profoundly affect the composition and functionality of the plant rhizosphere microbiome (Pérez-Jaramillo et al. 2015).

In each environment, the construction of the host plant's rhizosphere microbiome is primarily determined by genomic information. Thus, the plant's ability to specifically recruit beneficial rhizosphere microorganisms is heritable. Yin et al. found that, in addition to possessing unique rhizosphere microorganisms different from susceptible counterparts, the resistant offspring HF12 can also shape a similar microbiota to maintain disease resistance. (Yin et al. 2022). Through association analysis of metagenomic information with host plant genomes, this genetic effect can be mapped to certain gene loci that potentially regulate the recruitment process of rhizosphere microorganisms. For instance, Escudero-Martinez et al. have pinpointed several loci that have a substantial effect on rhizosphere microbial communities via their examination of both wild and cultivated barley genomes. Notably, a locus termed QRMC-3HS, situated on barley's chromosome 3, has been recognized as the principal factor dictating the composition of microbial communities. Comparative root RNA sequencing analysis of sibling families with different alleles of QRMC-3HS and different microbial communities revealed three main candidate genes, namely a gene

encoding an unknown functional protein, a nucleotide-binding leucine-rich repeat (NLR) gene, and a xylooligosaccharide/hydrolase (XTH) enzyme gene. Among these, the NLR structure showed differences in different varieties, which may be a potential regulator. XTH expression is downregulated when exposed to high-density microbial communities, possibly promoting microbiota recruitment by modifying cell wall polysaccharides (Escudero-Martinez et al. 2022). Another study also found that the presence of quantitative trait loci (QTLs) in tomatoes is associated with changes in rhizosphere microbial community characteristics, particularly the abundance of *Streptomyces* and *Cellvibrio*, as well as genes involved in the metabolism of plant polysaccharides, iron, sulfur, trehalose, and vitamins. This includes a genomic region of about 6.31 trillion base pairs, covering over 60 gene screening regions related to the domestication process of tomatoes, including the iron-regulated gene *FIT* and the aquaporin *SITIP2.3*. In addition, ninety-eight root-specific plant genes are associated with *Streptomyces* (Oyserman et al. 2022).

Since the rhizosphere microorganisms recruited can be genetically inherited, the association between genes and microorganisms is worthy of further study. A recent study has shown that the RIPENING-INHIBITOR (RIN) transcriptional factor is not only a key regulator governing fruit ripening, but also enhances plant resistance to pathogens by influencing the composition of plant root exudates at the seedling stage, promoting the assembly of specific disease-resistant microbiota. RIN mutants have differentiated root exudates, which cause changes in the composition and diversity of rhizosphere microbial communities, in particular, the relative abundance of antibiotic-related genes and disease-suppressing actinomycetes (such as *Streptomyces*) in the rhizosphere of RIN mutant plants is significantly reduced. Recovery is, therefore, possible by administering compounds secreted in lower concentrations in RIN mutants, such as 3-hydroxyflavones and riboflavin (Yang et al. 2023) (Fig. 3).

In addition to microbial regulation through the production of root exudates, the interaction between plant functional genes and microorganisms is associated with the plant growth regulation process. For example, when light-induced soybean nodulation and infection line formation occur, the photoinducible factors such as soybean TGACG-binding factor 3/4 (GmSTF3/4) and flowering localization T (GmFTs) are produced. When calmodulin kinase (CCaMK) is activated by rhizobia phosphorylated GmSTF3, the GmSTF3 is triggered to form a complex with GmFT2a, which directly activates the root nodule formation signaling pathway 1 (NSP1). The expression of nodule organ initiation (NIN) and nuclear factors Y (NF-YA1 and NF-YB1) fosters the symbiosis between plants and rhizobia (Wang T 2021). Genes in the symbiotic pathway also indirectly affect other rhizosphere microorganisms, and by comparing the wild-type Baimai root and nodulation mutant Nod factor receptor 5 (*nfr5*), Nodule inception (*nin*) and Lotus histidine kinase1 (*lhk1*) genes, it was found that the mutant had significant changes in the bacterial community composition of at least two parts of the root and rhizosphere. In the *nfr5* and *nin* mutants, the infection process was either not initiated, or terminated at the microcommunity stage. Conversely, the *LHK1* mutant could initiate numerous root hair infection threads but ultimately failed to penetrate the cortical cells. Although these mutants are healthy in appearance, they are smaller in size and have slightly yellowish leaves (Zgadżaj et al. 2016). This indicates that these nodulation-related genes influence not only the formation of nodules and nitrogen utilization but also have an impact on other microorganisms within the rhizosphere. A similar phenomenon was found in non-leguminous plants, and the *NRT1.1B* gene affected the nitrogen use efficiency of rice by influencing the composition of rhizosphere microorganisms, thus suggesting a new strategic direction for improving the nitrogen efficiency of crops (Zhang et al. 2019).

When facing stress, host plants can adapt to distinct genes beyond their prior endogenous regulatory pathways, restructuring their rhizosphere microbial communities via mechanisms that bolster their own adaptability. For example, plants can optimize their growth and survival

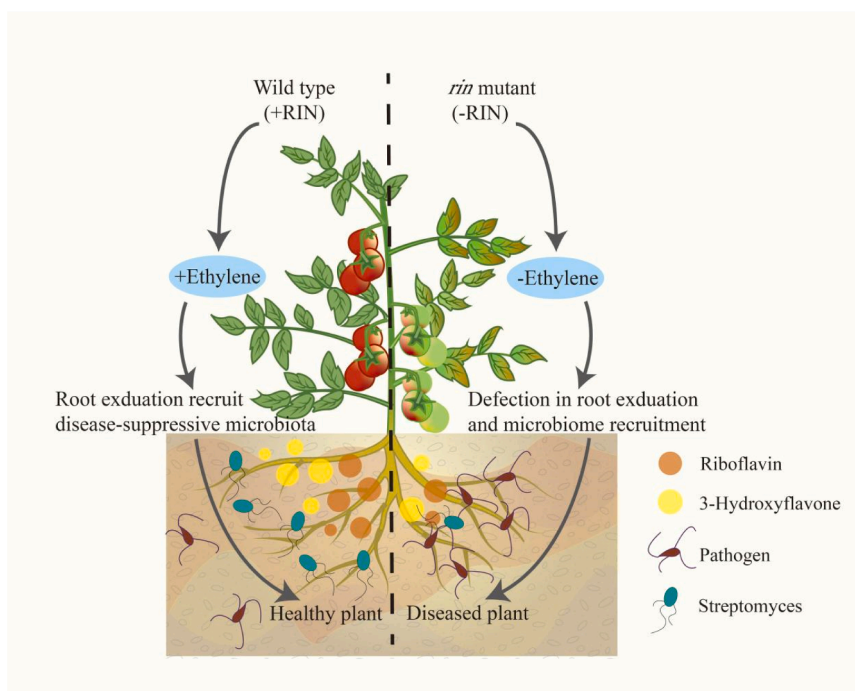


Fig. 3. RIN mutant tomato lacks exudates for the recruitment of microorganisms.

strategies through the microbe-root-shoot axis under unfavorable light conditions. Under low-light conditions, the signal detected by plant leaves is regulated over long distances by the transcription factor MYC2, which in turn manages the composition of the root bacterial community. This microbial partnership allows plants to minimize their investment in aboveground defense mechanisms and redirect resources essential for growth (Hou et al. 2021). When facing phosphorus deficiency, the phosphorus starvation response system (PSR) of *Arabidopsis thaliana* controls the colonization of *Colletotrichum tofieldiae*, a rhizosphere endophytic fungus, in the roots, thereby facilitating phosphorus transport to the aerial parts, promoting growth and improving fecundity. Moreover, PEN2-dependent indole glucoside metabolism, a branch of the plant endogenous immune response, is also functionally linked in the PSR system in regulating Ct (Hiruma et al. 2016). Even during non-phosphorus stress, the genetic network underlying the phosphorus stress response (PSR) can harmonize the balance between nutrition and defense, directly influencing the rhizosphere microbial composition via transcriptional regulators like PHR1, while curbing the plant's defense mechanisms and simultaneously enhancing phosphorus absorption and utilization (Castrillo et al. 2017). Research into mycorrhizal symbiosis in rice has uncovered a regulatory network pivoting on phosphorus starvation response (PHR) transcription factors, linking the promoters of 266 transcription factors and 47 genes related to mycorrhizal symbiosis. PHR transcription factors are key regulatory elements of mycorrhizal symbiosis in rice, and the genes related to symbiosis are directly regulated through the P1BS motif, thereby affecting the process of mycorrhizal symbiosis. In addition, SPX domain proteins inhibit mycorrhizal infections by inhibiting OsPHR2-mediated activation of symbiotic-related genes. However, plants overexpressing OsPHR2 showed improved mycorrhizal infection ability, partially resisting the inhibitory effect of phosphorus in regulating mycorrhizal symbiosis through the SPX-PHR central network (Shi et al. 2021). Similarly, Wang et al.'s study indicates that PHR2 is a major regulator of the phosphate starvation response in *Medicago*, enhancing the expression of phosphate starvation-induced genes. In addition, it promotes mycorrhizal colonization by inducing the expression of key symbiotic genes such as PT4, RAM1, and WR15a. However, they also found that overexpression of PHR2 leads to increased degradation of arbuscules. SPX1 and SPX3

control arbuscule degradation through mechanisms partly independent of PHR2. These findings suggest that the activity of PHR2 in arbuscule-containing cells needs to be tightly regulated. Under iron-limited conditions, coumarin compounds synthesized by Feruloyl-CoA 6'-hydroxylase 1 can provide signals and nutrients for microorganisms and change the composition of root microorganisms, promoting their participation in iron absorption and transport (Harbort et al. 2020). The transcription factor MYB72 specifically expressed by the MYB72 gene of *Arabidopsis thaliana* in roots controls the interaction between β -glucosidase BGLU42 and the beneficial rhizosphere bacterium *Pseudomonas simiae* WCS417 to mediate the production and secretion of the coumarin molecule kaempferol, which can inhibit soil fungus pathogens and improve iron nutrition (Stringlis et al. 2018). Transgenic soybean GsMYB10 can regulate the microbial composition of the soybean rhizosphere through the expression of its functional genes, mainly enriching some microorganisms that are beneficial to withstanding aluminum toxicity, such as *Pasteurus*, *Dyella*, *Aspergillus* and *Talaromyces*. These microorganisms help soybeans resist aluminum toxicity by altering functional genes controlling activities such as soybean cell wall biosynthesis and organic acid transport (Liu et al. 2023).

Analyzing the dynamic regulatory mechanisms of host plant functional genes with respect to their rhizosphere microbiome helps in a comprehensive understanding of plant-microbiome interactions and their role in stress responses. Identifying the regulatory genes involved in plant recruitment of rhizosphere microorganisms aids in molecular breeding, enabling the development of new plant varieties that can robustly recruit beneficial microbes to promote growth or alleviate stress.

4. Concluding remarks and future prospects

The rhizosphere is a crucial microenvironment that promotes plant growth and health. The potential of beneficial rhizosphere microorganisms to enhance plant growth and stress resistance has been well documented. This article provides an overview of the exceptional performance exhibited by rhizosphere microbial communities, delving into the critical role that host plants play in sculpting their own rhizosphere microbiomes to reap these advantages.

In summary, host plants, soil microorganisms, and soil properties collectively influence the assembly and function of rhizosphere microbiomes. This insight suggests three key ideas for engineering the composition and structure of rhizosphere microbial communities. Among them, microbial-mediated approaches are considered the most direct and effective methods.

Microbial-mediated strategies combat plant pathogens and enhance plant growth by introducing exogenous microorganisms to alter the rhizosphere's microbial community. (Berendsen et al. 2012). First, the soil adhering to the surface of plant roots (2-3mm) was collected as the rhizosphere soil sample, and then all sequences contained in the soil were obtained by high-throughput sequencing method. After careful assembly and annotation, a comprehensive data set suitable for in-depth bioinformatics analysis was compiled. Data analysis focused on confirming target microbial taxa by assessing microbial diversity, relative abundance, and functional analysis. According to the result determined by the analysis, these microorganisms were obtained from the rhizosphere soil by appropriate isolation method, and the characteristics were verified in the laboratory to filter useful strains. Finally, after rigorous validation through small-scale culture experiments, these promising strains were subjected to large-scale fermentation process for commercial application, thus providing an effective method to solve the challenges of plant growth and green agriculture. For example, Zolla et al. and Yergeau et al. improved plant growth under drought and in highly petroleum-contaminated soil conditions, respectively, through microbiome transplantation. Zhuang et al. and Kaur et al. each constructed microbial communities of six *Pseudomonas* strains and four bacterial strains, respectively, which significantly promoted the growth of garlic and cotton (Niu et al. 2017, Santhanam et al. 2019, Zhuang et al. 2020,

Kaur et al. 2022). In addition, Niu et al. constructed a community of seven strains that suppressed maize seedling blight pathogen. Santhanam et al. studied the biocontrol activity of five indigenous strains that inhibited sudden wilt disease in tobacco. The above functions prove that the application of microorganisms plays an important role in promoting the development of green agriculture (Fig. 4).

In contrast to microbe-driven approaches, host plants possess the ability to actively enlist beneficial microorganisms that are suited to the prevailing conditions, facilitated by the expression of specific functional genes. The reshaping of rhizosphere microbial communities by host plants can be studied at the levels of species, genotype, and specific functional genes, deepening our understanding of the mechanisms by which host plants regulate the assembly and function of rhizosphere microbiomes.

Although microbe-driven approaches are effective, the effects are not long-lasting and require repeated addition and application. Further research is needed to explore the genetic basis and molecular mechanisms by which host plants regulate rhizosphere microorganisms, laying a solid foundation for breeding new crop varieties that can consistently recruit beneficial rhizosphere microorganisms. While methodologies such as amplicon sequencing and metagenomics facilitate the analysis of how these factors influence shifts in rhizosphere microbial communities, considerable challenges remain. These include deciphering the effective spatiotemporal dynamics in crops, pinpointing the precise regulatory effects of host plant functional genes on rhizosphere microbiomes, and establishing the link between the restructured rhizosphere microbiomes and alterations in plant phenotypes.

In future applications, the combined use of synthetic microbial communities and crop varieties capable of robustly recruiting these

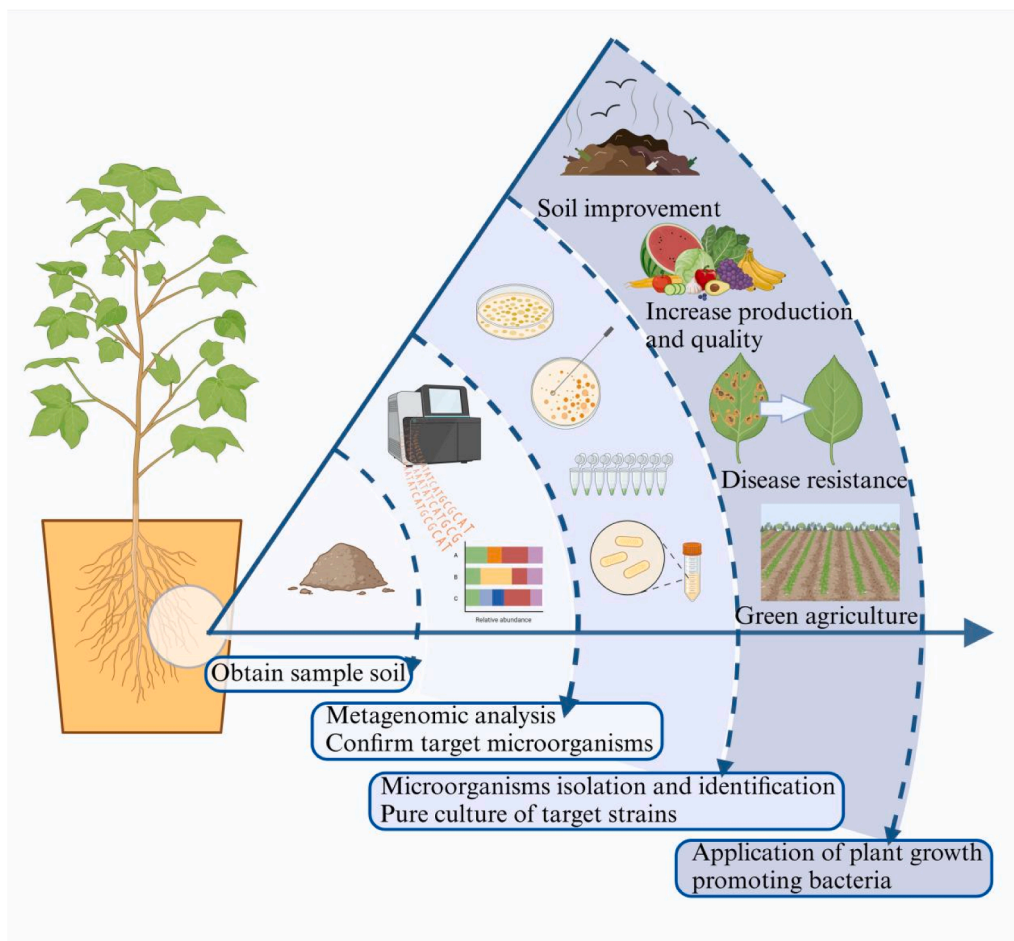


Fig. 4. Research and application process for the use of rhizosphere microorganisms (Created with BioRender.com).

beneficial microorganisms has the potential to enhance the success rate of enriching beneficial rhizosphere microorganisms. Eventually, an economical, effective, and environmentally friendly method for improving crop traits will be available.

Funding

This work was supported by the Strategic Priority Research Program of the Chinese Academy of Sciences, GrantNo. XDA0440000.

CRediT authorship contribution statement

Chenghua Luo: Writing – review & editing, Writing – original draft, Visualization. **Yijun He:** Writing – review & editing, Writing – original draft. **Yaping Chen:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Yaping Chen reports financial support was provided by Chinese Academy of Sciences, South China Botanical Garden, Guangdong Provincial Key Laboratory of Applied Botany. If there are other authors, they 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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