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REVIEW

Plant-root microbiota interactions in nutrient utilization

Haoran XU[1], Weidong LIU[1], Yuhang HE[2], Di ZOU[2], Jinghang ZHOU[2], Jingying ZHANG (✉)[1], Yang BAI (✉)[3]

1 Institute of Genetics and Developmental Biology, Chinese Academy of Sciences, Beijing 100101, China.
2 School of Life Science, Yunnan University, Kunming 650504, China.
3 Peking-Tsinghua Center for Life Sciences, College of Life Sciences, Peking University, Beijing 100871, China.

KEYWORDS

Root microbiota, plant gene, interaction, nutrient utilization

HIGHLIGHTS

- Soil nutrient conditions shape the root microbiota composition.
- Plant nutrient-utilizing genes drive the assembly of root microbiota.
- Root microbiota enhances nutrient availability for plants.
- Root microbiota modulates plant gene expression to promote nutrient utilization efficiency through phytohormone.
- Microbiome genome- and microbiome-wide association studies offer novel approaches to deeply explore the interactions between plants and their root microbiota.
- Utilizing root microbiota is a promising strategy to improve crop nutrient utilization in agriculture.

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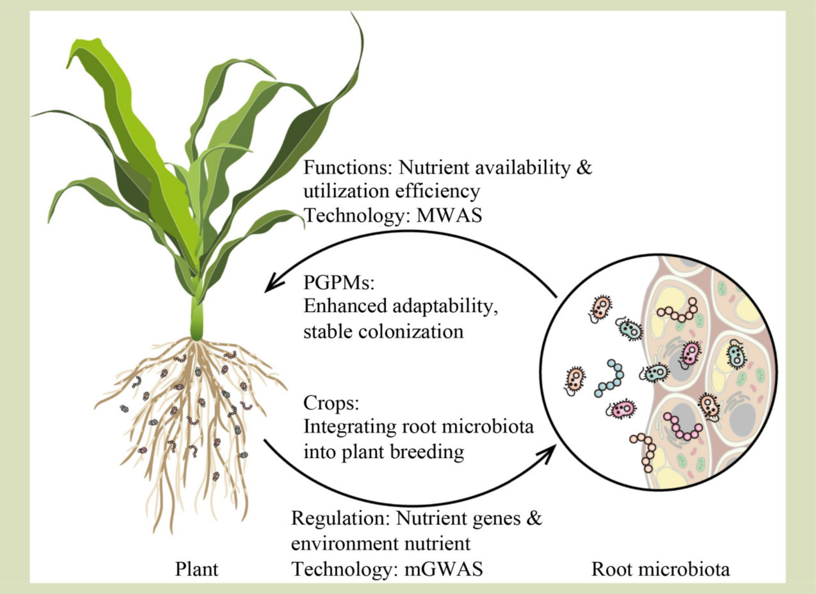
Correspondences: jyzhang@genetics.ac.cn,
ybai@genetics.ac.cn

GRAPHICAL ABSTRACT



ABSTRACT

Natural plant roots enrich a diverse array of soil microbes, collectively known as the root microbiota. This microbiota interacts synergistically with plants, modulating various physiological processes, including nutrient utilization, which influences plant growth and health. Environmental nutrient conditions and plant nutrient-related genes have been reported to regulate the composition of the root microbiota. Innovative analytical methods, such as microbiome genome- and microbiome-wide association studies, have advanced understanding of the relationships between plants and root microbiota. These methods systematically reveal the interactions between root microbiota and plant nutrient utilization, providing a theoretical foundation for applying root microbiota in agriculture.

1 Introduction

In natural environments, plant roots selectively enrich a diverse array of microbes. These microbes, known as root microbiota, accompany the plant throughout its life cycle[1], and substantively enhance nutrient utilization[2,3]. Plants absorb essential minerals and elements from the soil through their roots, then convert and distribute them to various tissues to support healthy growth. Emerging evidence underscores a close correlation between root microbiota and nutrient utilization in plant[4–8]. The influence of root microbiota on nutrient availability and uptake efficiency is critical for plant health and productivity. The symbiotic relationship between plants and root-associated microbes is dynamic and complex, significantly contributing to the optimization of the plant nutrient utilization[9].

The exploration of plant nutrient utilization has long focused on plant genes related to nutrition. Researchers have identified the roles and mechanisms of key nutrient-related genes, including those involved in nutrient signal sensing, response, uptake transporters, and the distribution, metabolism and conversion of nutrients[10]. Functional studies of these crucial nutrient genes have examined their regulatory effects on root microbiota. For example, genes related to nitrogen and phosphorus utilization regulate root microbiota composition[4,11]. Increasingly, studies report the functional diversity of plant growth-promoting microorganisms (PGPMs). These beneficial microorganisms help plants enhance nutrient availability and utilization efficiency[12]. PGPMs include bacteria and fungi, such as nitrogen-fixing bacteria that help plants fix atmospheric nitrogen, phosphorus-solubilizing bacteria that convert insoluble soil phosphorus into a bioavailable form, hormone-producing bacteria that regulate plant growth and arbuscular mycorrhizal fungi (AMF) that enhance nutrient uptake by extending root surface area and facilitating phosphorus acquisition from soil[13,14]. However, the synergistic mechanisms between these beneficial microbes and plants have not been adequately explored. Some studies have used microbiome genome-wide association studies (mGWAS) and microbiome-wide association studies (MWAS) to systematically analyze the relationships between root microbiota, plant genes and nutrient phenotypes[15,16]. These studies further leverage plant mutant systems to validate the regulatory roles of plant genes on root microbiota and isolate plant root microbes to verify the effects of root microbiota on plant nutrient phenotypes. This research has provided a solid foundation for mechanistic studies of plant-root microbiota interactions and significantly advance the application of functional root microbiota in agriculture.

This review explores the interactions between plants and their root microbiota, including the regulatory effects of environmental nutrient conditions and plant nutrient-related genes on root microbiota, and the beneficial roles of root microbiota in plant nutrient utilization. The achievements of new technologies such as mGWAS and MWAS in revealing the relationships between plants and root microbiota are summarized. It discusses the opportunities and challenges of applying these interactive relationships in agriculture, offering insights into leveraging these findings to improve crop nutrition and productivity.

2 Nutrient-mediated regulation of the plant root microbiome

External nutrient status, plant gene responses, and their interactions determine the diversity and homeostasis of root microbiota (Fig. 1). Soil, as the major source of root microbiota, directly affects community composition and structure by altering microbial transmission from soil to roots[17]. Plant nutrient utilization genes significantly regulate root microbiota to improve plant survival and health[18].

2.1 Environmental nutrient conditions shape the root microbiota composition

Soils serve as a primary reservoir for root microbiota. Microbes undergo initial screening and community differentiation in rhizodeposits, which include root-released tissue cells, exudates, lysates, volatile compounds and more[19,20]. Some microbes further colonize the rhizosphere and rhizoplane, forming close interactions with plants. Consequently, changes in soil nutrient composition and availability lead to variations in root microbiota, affecting their function and capacity for nutrient utilization by plants.

The soil microbiome undergoes dramatic changes after fertilizer application. Nitrogen fertilization strongly negatively regulates nitrogen cycle-related genes (*nirK*, *amoA*, *nosZ-I* and *nosZ-II*), reducing nitrogen transformation in soil[21]. These changes in the soil microbiome subsequently affect the microbial assembly process from soil to root. A study on rhizosphere microbiota following increased nitrogen fertilization showed a decreasing trend in α diversity (Shannon and Chao 1 indices) of the rice (*Oryza sativa*) microbial community, altering soil carbon, nitrogen and phosphorus properties, and related enzyme activity levels[22]. Unbalanced fertilization strategies (e.g., deficient in N, P or K) exhibit diverse assembly patterns in the root microbiota of soybean

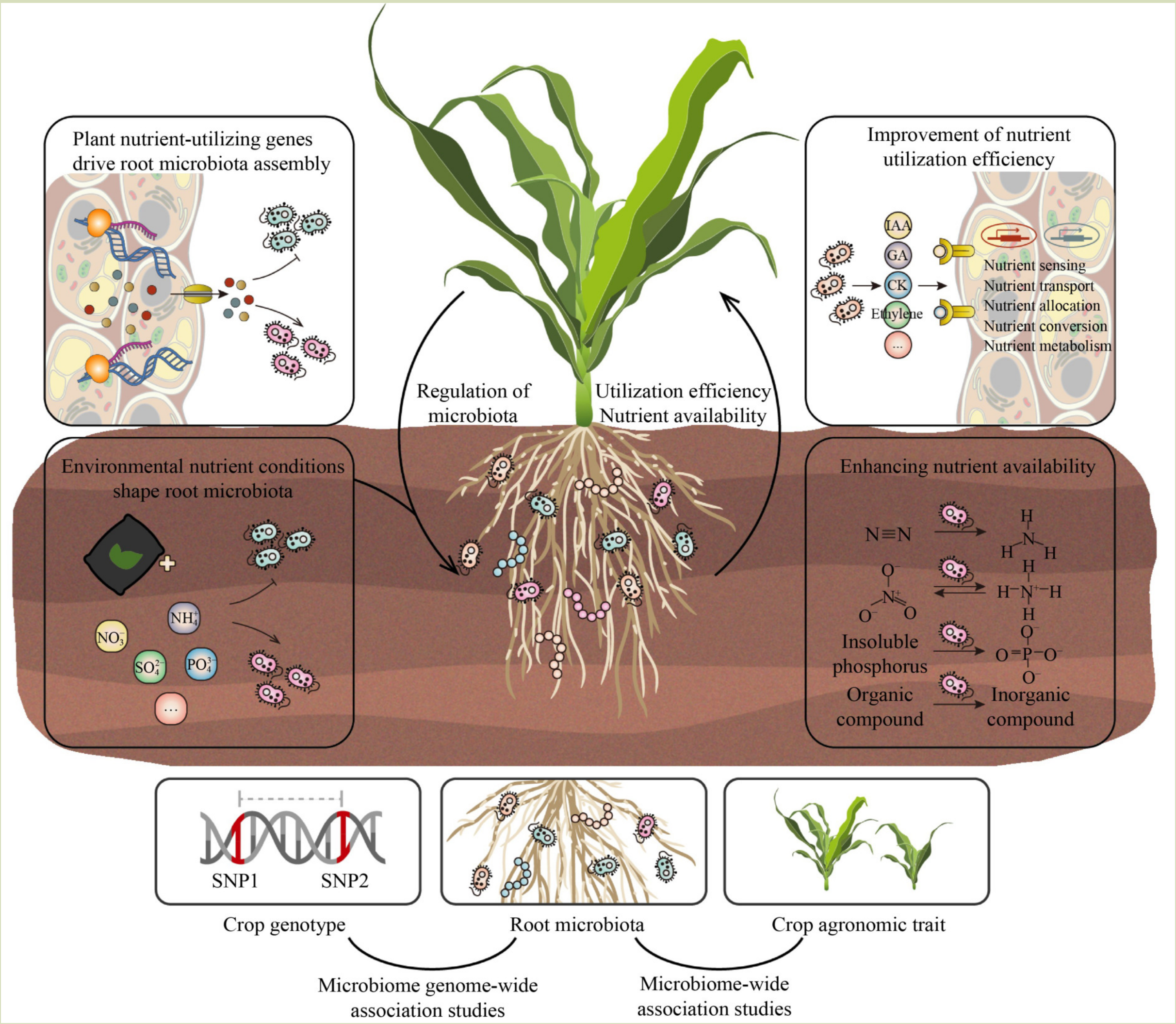


Fig. 1 Plant and root microbiota coregulation nutrient utilization.

(*Glycine max*); the bacterial community differs in the absence of N fertilizer compared to fertilized plants[23]. Similarly, root microbiota in wheat (*Triticum aestivum*) showed significant differences in microbial structure under four different N levels. Several genera, such as *Arthrobacter*, *Bacillus* and *Devosia*, shifted in response to N fertilization and are described as plant growth-promoting rhizobacteria that respond positively to N fertilizer. Studies on P fertilizer indicate that three different P fertilization treatments lead to significant changes in the structure of bacteria and fungi in the root microbiota of maize (*Zea mays*) and sorghum (*Sorghum bicolor*)[24], whereas the absence of phosphorus fertilizer impedes the total load and turnover rate of root microbiota[23]. Additionally, sulfur fertilizer application enriches sulfur-reducing bacteria in the rice rhizosphere, lowering rhizosphere soil pH, promoting cadmium absorption and increasing rice yield[25]. A survey of fungal communities within the endosphere, rhizosphere and bulk soil in wheat fields fertilized for 35 years showed that long-term fertilizer application significantly affects soil fungal community composition, correlating with soil P and zinc contents[26]. Similarly, organic and mineral fertilization significantly impact root microbiota in lettuce (*Lactuca sativa*)[27]. These studies demonstrate that soil nutrient conditions significantly influence the initial assembly of root microbiota, which may subsequently impact their role in regulating plant nutrient uptake.

2.2 Genetic control of root microbiota by plant nutrient-related genes

Plant nutrient-related genes regulate plant growth status, and also control the root microbiota. Some studies have reported that nutrient-utilizing genes or genetic network drive distinct root microbiota assembly patterns. *NRT1.1B,* an important nitrate-transporter gene, possesses natural variations between *indica* and *japonica* rice, mediating different nitrogen-use efficiency in theses subspecies[28]. *Indica* and *japonica* variants carrying different variation of *NRT1.1B* assemble distinct root microbiota, and *indica* regulates more nitrogen-cycling bacteria in the root microbiota than the *japonica*, helping utilization for less suitable organic nitrogen sources[11]. Structural differentiation of this functional root microbiota can also be found in *NRT1.1B* functionally deficient mutants and near-isogenic lines. This suggests that the functional root microbes of *indica* and *japonica* are mediated by *NRT1.1B*[11]. *CIPK2* (encoding an calcineurin B-like interacting protein kinase 2), is crucial in nitrogen uptake and root development. Overexpression of *CIPK2* enriches *nifH* gene, which codes for the ferric protein subunit of the nitrogenase complex of diazotrophs in the rice root microbiota. A synthetic community of six nitrogen-fixing strains enriched in the *CIPK2* overexpression line significantly improves rice growth and nitrogen uptake in nitrogen-deficient soils[29]. Overexpression *Malus domestica* NO^{3-} transporter (*MdNRT2.4*) in apple rootstocks and seedlings root enrich more microbes with nitrogen metabolic functions. *Rhizobium* ARR11 isolated from apple rootstocks enhances apple seedling growth[30]. PHOSPHATE STARVATION RESPONSE 1 (PHR1) is a major transcription factor in the phosphate starvation response (PSR) in *Arabidopsis*[31]. Loss of function in genes such as *PHR1*, *SPX1*, *SPX2*, *PHF1*, *PHO2* and *NLA* in the PSR pathway leads to variations in root microbiota composition. Constrained ordination revealed significant differences between bacterial communities by these PSR mutants[32]. The regulation of root microbiota by *PHR1* assist in phosphate utilization and alleviate phosphate starvation[4]. PSRs are also essential for establishing mycorrhizal symbiosis, governing Pi-sensing pathways to help plants mitigate phosphate starvation[33]. Pathways driving coumarin synthesis and secretion in the rhizosphere regulate the structure of *Arabidopsis* root microbiota, and the regulated root microbiota improves host iron absorption[6]. Sugar uniporters SWEETs mediate the spatial colonization of microbiota in *Arabidopsis* root[34]. The increasing studies demonstrate that the regulation of the root microbiota by plant nutrient-related genes is essential for optimizing plant nutrient uptake and assimilation.

3 Role of the root microbiota in plant nutrient utilization

The root microbiota comprises numerous functional genes[35], often referred to as the plant's second genome. These microbes improve plant nutrient utilization in the rhizosphere in two ways: microbes can convert unusable nutrient elements into forms preferred by plants or enhance nutrient uptake efficiency by producing signaling substances (Fig. 1).

3.1 Enhancing nutrient availability

Root microbes balance various nitrogen forms in the rhizosphere through nitrogen fixation, ammonification, nitrification, denitrification and ammonia oxidation, ensuring plants grow healthily in an optimal nitrogen environment, and preventing damage from nitrogen deficiency or excess[36]. Nitrogen fixation is facilitated by root bacteria and archaea with nitrogenase enzymes, converting N_2 to NH_3 for plant use. Rhizobia, a diverse group of nitrogen-fixing bacteria, form symbiotic relationships with legumes. Bacteria recognize legume signals like flavonoids and invade root tissues to form symbiotic structures. These structures offer a microaerobic environment, preserving nitrogenase activity and improving fixation efficiency. In addition, *Cyanobacterium*[37], *Azoarcus*[38], *Herbaspirillum*[39] and *Azospirillum*[40], widely present in cereal crop rhizospheres, can establish loose nitrogen-fixing associations with plants without forming nodule-like structures. The stem xylem of maize selectively recruits highly conserved microbes dominated by Gammaproteobacteria, which have a large number of nitrogenase genes (*nifH*) and enhance nitrogen accumulation in maize[41]. Root-associated bacteria in the family Oxalobacteraceae are selectively enriched in maize roots under N deprivation, promoting lateral growth by increasing nitrogen absorption capacity[42]. Ammonium and nitrate are the main nitrogen forms absorbed by plants, the balance between ammonium and nitrate is maintained by a series of microbe-mediated chemical reactions, including ammonification, which converts organic nitrogen to ammonia[43], and nitrification, a two-step process that converts ammonia via nitrite to nitrate[44]. These processes convert inorganic nitrogen into different forms through various metabolic pathways[45], ensuring a dynamic nitrogen balance in the rhizosphere. In addition, microbes convert complex organic nitrogen into small molecules through enzymatic reactions, making these molecules available for plant uptake. Extracellular enzymes are the primary means by which soil microbes degrade complex organic nitrogen compounds into assimilable small molecules[46]. Some small molecules (e.g., amino acids) are directly absorbed and utilized by plants, while others are further converted into inorganic forms through microbial ammonification[43].

Root microbiota can also make a substantive contribution to converting phosphorus to available forms in the soil[47], mainly through inorganic phosphate solubilization and organic phosphate mineralization. Microbes metabolize organic acids or secrete hydrogen ions into the rhizosphere through proton pumps to dissolve insoluble inorganic phosphates such as calcium phosphate, aluminum phosphate and iron phosphate. These organic acids promote phosphorus dissolution through chelation and proton exchange[48]. Numerous studies have identified *Bacillus*, *Pseudomonas* and *Burkholderia* in crop rhizospheres as having strong phosphorus-solubilizing capacities[49,50]. In addition, microbes secrete acidic or alkaline phosphatases to promote organic phosphate mineralization, hydrolyzing organic phosphorus compounds into inorganic phosphorus for plant uptake[51]. *Pseudomonas* can release inorganic phosphorus by secreting glycerol phosphodiesterases that degrade phospholipids in the soil[52]. *Bacillus* can solubilize insoluble phosphorus in the soil by secreting organic acids such as gluconic, lactic, acetic, succinic and propionic acids[53]. Maize can select actinobacteria associated with facilitating P acquisition[54]. Members of the fungal order Helotiales are consistently enriched by the root of *Arabis alpina* (Brassicaceae) in P-deficient soils, promoting host growth and P uptake[55].

Many studies have reported that root-associated bacteria aid plants in obtaining iron. The root microbiota aids in the absorption and utilization of available iron, facilitated by root-secreted scopoletin and fraxetin[6]. For example, *Pseudomonas* isolated from the peanut (*Arachis hypogaea*) root microbiota secretes the siderophore pyoverdine, which improves iron nutrition in both greenhouse and field experiments[56]. Another study identified seven bacterial strains with a high capacity to produce siderophores in the rhizosphere of crops. Among the *Pseudomonas* strains, *Pseudomonas monsensis* RMC4 exhibited the maximum iron complexation capacity[57]. *Fusarium oxysporum* FO12 promotes the production of phytosiderophores and rice growth while upregulating Fe-related genes in rice[58].

3.2 Phytohormone-driven modulation of plant gene expression

Recent studies have revealed that root-associated microbes substantially contribute to elevating the efficiency of plant nutrient uptake by influencing gene expression. For example, inoculation with three synthetic communities, composed of bacteria from the soybean root community and carrying genes for indole-3-acetic acid synthesis, nitrogen fixation or phosphate solubilization, significantly regulates N and P signaling networks, thereby facilitating N and P acquisition and plant growth[59]. AMF significantly upregulate the expression of specific phosphate transporter family genes, increasing P uptake efficiency and yield in cotton (*Gossypium hirsutum*)[14]. These microbial performances in nutrient utilization efficiency may be achieved by manipulating plant hormone levels or downstream signaling responses. The root microbiota contains many genes that synthesize and secrete various hormones, including auxin, gibberellic acid, cytokinin, ethylene and abscisic acid[60–63]. These hormones and their complex interactions regulate plant physiologic processes related to nutrient utilization at very low concentrations, such as root growth, root hair development and cell division[50,64]. Metagenomic data show that rhizobacteria have stronger indole-3-acetic acid synthesis capabilities than bacteria from other environments[65]. The gibberellic acid biosynthetic pathway is also present in root microbiota members such as *Bradyrhizobium japonicum* and *Sinorhizobium fredii*[66,67]. Additionally, gibberellic acid is a crucial signaling molecule in plant-microbe symbiosis, especially between legumes and Rhizobia[68]. Various PGPMs such as *Azospirillum*, *Bacillus*, *Methylobacterium*, *Pseudomonas* and rhizobia produce cytokinin, which is vital for regulating nutrient absorption[69,70]. Some studies have found that root microbiota influence plant responses to hormones by manipulating hormone levels. For example, *Variovorax* can degrade auxin, reversing the negative effects of microbial-produced auxin on root development[71]. In summary, root microbiota regulate plant nutrient absorption by producing or metabolizing plant hormones in the rhizosphere, maintaining high nutrient utilization efficiency in complex environments.

4 Exploring root microbiota-plant nutrient phenotype relationships through large-scale association studies

Initial investigations into plant-microbe symbiosis for nutrient acquisition concentrated on one-on-one interactions with beneficial root microbes, such as the well-documented roles of rhizobia in nitrogen fixation and AMF in phosphorus uptake. The focus of plant-microbe research has since been revolutionized by next-generation sequencing, enabling a detailed characterization of the interplay between plant genotypes and root microbiome composition in nutrient regulation. Recent advances have leveraged genome-wide association studies (GWAS), typically used to dissect plant-genotype-phenotype relationships, to explore the intricate connections among the root microbiome, plant genotypes and nutrient-related plant phenotypes. This integrative approach will enable a deeper understanding of the complex dynamics within the plant-root microbiota interactions (Fig. 1).

4.1 Microbiome genome-wide association studies

GWAS have become a cornerstone in plant biology, elucidating the genetic architecture underlying phenotypic diversity across plant populations[72]. These studies have been instrumental in pinpointing genomic regions associated with plant growth, offering insights into the genetic basis of agronomic traits. The evolution of GWAS has extended its reach to the plant microbiome, revealing the subtle interplay between plant genomes and the composition of root microbiota. Pioneering work by Beilsmith et al.[73] has standardized the approach to plant microbiota association analysis, streamlining the identification of genotype-microbiota correlations across diverse plant species.

The application of GWAS to microbiome research has opened new avenues for understanding how specific plant genes modulate the abundance of PGPMs, thereby influencing plant health and development. For example, a comprehensive analysis of the phyllosphere microbiota in over 300 maize cultivars has mapped genetic loci that govern bacterial taxa and their metabolic functions, shedding light on the genetic control of microbial community assembly[74]. In switchgrass, mGWAS has linked plant loci involved in immune responses and signaling pathways to the composition of the root microbiome, highlighting the genetic basis of plant-microbe interactions based on an extensive data set of nearly two thousand samples[75]. Similarly, a deep dive into *Arabidopsis* root microbiota samples has identified key quantitative trait loci that harbor genes implicated in plant growth, development, and stress responses, further underlining the genetic regulation of the root microbiota[76]. The case of the maize gene *Zm00001d048945* exemplifies the power of mGWAS in dissecting gene-microbe relationships. This gene, encoding a TPX2 domain-containing protein akin to the WAVE-DAMPENED2 microtubule binding protein, has been shown to regulate the colonization of the bacterium *Massilia*, with mutant studies confirming its role in modulating *Massilia* and supporting lateral root development under nitrogen-deficient conditions[77]. Variations in root microbial abundance among 230 maize cultivars under contrasting nitrogen regimes underscore the impact of natural genetic variation on microbiome assembly[78]. Collectively, these studies underscore the utility of mGWAS in systematically unraveling the regulatory effects of plant genetics on the microbiota.

4.2 Microbiome-wide association studies

To deconstruct the intricate roles of microbes in plant nutrition, MWAS have been developed to link microbiota characteristics, including community diversity, composition and specific taxonomic abundances, with nutrition-related plant phenotypes[79]. MWAS offers a robust framework for the identification of PGPMs. Through large-scale association analysis, it is possible to discover numerous root microbes that exhibit strong correlations with pivotal plant nutrient phenotypes, such as plant stature, biomass, nitrogen sequestration and yield. Subsequent targeted screening of these microbes can elucidate the PGPMs that enhance plant vigor and well-being. For example, an MWAS in foxtail millet (*Setaria italica*) correlated 257 rhizoplane microbial biomarkers with six critical agronomic traits, including the width of the top second leaf, and validated the causal link between these biomarkers and growth-promoting traits in controlled and sterilized soil environments[15]. Additionally, an MWAS of the phyllosphere microbiota across 30 cassava cultivars revealed an inverse relationship between the abundance of *Lactococcus lactis* and leaf aluminum content, coupled with a positive correlation with leaf potassium levels. Inoculation with *L. lactis* was shown to significantly mitigate endogenous aluminum levels while enriching potassium levels[80].

While MWAS has been used to reveal extensive correlations between the root microbiota and plant nutritional phenotypes, the potential for false positives with low-abundance microbes necessitates rigorous validation through inoculation experiments using defined synthetic communities or monocultures. Focusing on the analysis of core root microbiota members, especially those that are consistently present and abundant across various soil conditions and plant genotypes, provides an effective strategy to minimize false positives and solidify the biological significance of observed associations[29].

5 Challenges in the agricultural application of root microbiota

With breakthroughs in the study of interactions between plants and root microbiota enhancing nutrient utilization, more attention is focused on utilizing these interactions to achieve desirable yield traits in the field. Despite the presence of numerous beneficial microbes promoting nutrient utilization in the rhizosphere, only a few microbial inoculants, such as Rhizobia, AMF, *Bacillus* and *Pseudomonas*, are successfully commercialized and consistently effective under complex field environments[81]. The primary limitation is that subsequently inoculated PGPMs often lack host preference and struggle to colonize the host due to stable interactions between the host and the preestablished community after synergistic coevolution[82]. Soil animals, including protists and nematodes, regulate plant-root microbiota interactions, affecting the stable relationship of nutrient absorption between plants and PGPMs[83]. To address the challenges of PGPMs application, several strategies can be used (Fig. 2).

Enhancing the adaptability and colonization of PGPMs. Culturing and identifying root microbes from natural environments systematically enriches an *in situ* PGPMs resource, giving them with enhanced stability and tailored functions for nutrient utilization in analogous settings. The resilience of bacterial inoculants is shaped by nutrient-scarce conditions and the niche-specific signals and nutrients secreted by roots, which selectively favor certain microbial taxa[84,85]. Facilitating robust PGPMs colonization involves the strategic manipulation of the microenvironment to favor the establishment of these beneficial microbes, including the modulation of pH, secondary metabolite profiles, and the management of competitive antagonism[86]. In the realm of agricultural production, methodologies such as inoculant formulation, large-scale propagation, and the careful selection of strains and carriers can orchestrate a microenvironment conducive to PGPMs colonization. For established crop cultivars, conflicts arising from the interaction between incoming inoculants and the entrenched microbial community or plant defense responses can be mitigated through the genetic engineering of the inoculant strains. For example, an engineered *Bacteroides* strain, provided with a unique gene cluster for metabolizing a marine polysaccharide (porphyrin), has demonstrated the capacity to stably colonize the murine gut by exploiting a metabolic advantage. This innovative approach bolsters the competitive edge of the introduced microbes against the resident microbiota within the same metabolic niche, facilitating their integration and potential replacement[87]. The application of this method in plant-microbiota studies will enhance the colonization and adaptation capabilities of PGPMs.

Integrating root microbiota into plant breeding. The incorporation of genes that modulate beneficial root microbes represents a frontier in plant breeding strategies[88]. The intricate regulatory interplay between plant genes and specific PGPMs within the root microbiome has been well-documented. Through correlation analysis, it is possible to delineate plant genotypes that are compatible with particular PGPMs. Synthesizing these findings with synthetic community inoculation experiments allows for the functional validation of prospective PGPMs. Seedling microbiota engineering provides an efficient method for screening the compatibility between plants and PGPMs. By assessing seedling growth and PGPMs colonization, plant genotypes that match PGPMs can be identified expeditiously[89]. The interaction obtained by mGWAS was used to breed new plant cultivars that are more adaptable to environmental microorganisms. Concurrently,

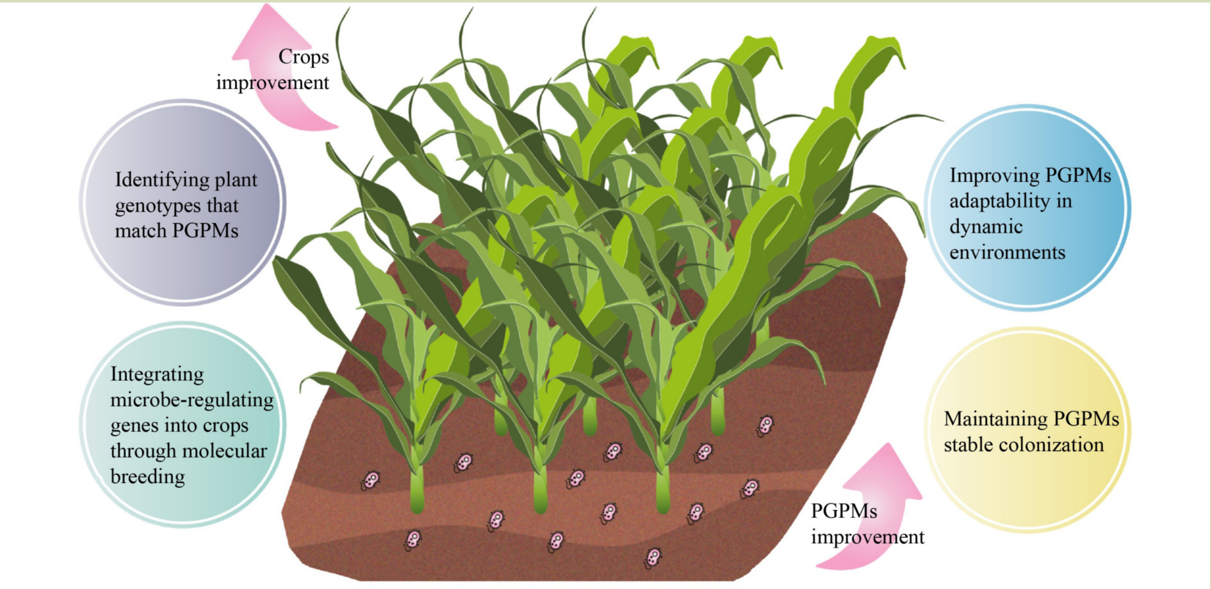


Fig. 2 Applying root microbiota to agriculture through crops and plant growth-promoting microorganisms improvement.

genes identified through mGWAS can be harnessed as novel breeding targets aimed at enhancing desirable plant traits. By integrating host genetic regulation with the inoculation of exogenous strains, it should be possible to amplify the agricultural utility of PGPMs, forging a symbiotic relationship that bolsters both plant and microbial performance.

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Compliance with ethics guidelines

Haoran Xu, Weidong Liu, Yuhang He, Di Zou, Jinghang Zhou, Jingying Zhang, and Yang Bai declare that they have no conflicts of interest or financial conflicts to disclose. This article does not contain any studies with human or animal subjects performed by any of the authors.

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