The root microbiome: Community assembly and its contributions to plant fitness[FA]

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ABSTRACT

The root microbiome refers to the community of microbes living in association with a plant's roots, and includes mutualists, pathogens, and commensals. Here we focus on recent advances in the study of root commensal community which is the major research object of microbiome-related researches. With the rapid development of new technologies, plant–commensal interactions can be explored with unprecedented breadth and depth. Both the soil environment and the host plant drive commensal community assembly. The bulk soil is the seed bank of potential commensals, and plants use root exudates and immune responses to build healthy microbial communities from the available microbes. The plant microbiome extends the functional system of plants by participating in a variety of processes, including nutrient absorption, growth promotion, and resistance to biotic and abiotic stresses. Plants and their microbiomes have evolved adaptation strategies over time. However, there is still a huge gap in our understanding of the regulatory mechanisms of plant–commensal interactions. In this review, we summarize recent research on the assembly of root microbial communities and the effects of these communities on plant growth and development, and look at the prospects for promoting sustainable agricultural development through the study of the root microbiome.

INTRODUCTION

Microbes colonizing the plant root, the root microbiome, are categorized as mutualists, pathogens, or commensals, depending on the character of their interactions with the plant (Brader et al., 2017; Thoms et al., 2021). However, there is some confusion about these terms, and it is necessary to clarify their differences. Mutualists are microbes that establish specific mutualistic structures with plants, such as arbuscular mycorrhizae, which assist in phosphate absorption (Toro et al., 1997; Ezawa and Saito, 2018), and rhizobia, which widely colonize legumes to form nitrogen-fixing root nodules (Masson-Boivin and Sachs, 2018; Lindstrom and Mousavi, 2020). Mutualists obtain essential carbon sources from the plants, which in turn can absorb mineral nutrients such as nitrogen and phosphorus via the mutualists.

Pathogens are microbes that lead to specific diseases after colonization such as *Pseudomonas syringae* (Nomura et al., 2005; Xin et al., 2018). Commensals constitute the majority of plant-associated microbes and include bacteria, fungi, archaea, viruses, and protozoa; they are loosely dependent on hosts but can be recruited in certain situations to influence hosts growth and development through neutral, beneficial or harmful interactions (Hooper and Gordon, 2001). However, with in-depth study, specific commensals may prove to be mutualists or pathogens. Because of the importance and diversity of the commensals, a major focus of root microbiome research has been to dissect their taxonomic structure and biological functions using multiomics techniques (Marchesi and Ravel, 2015), and to illuminate the interactions among environments, microbes, and hosts. Although research approaches, such as sequencing, also acquire information about mutualists and pathogens, commensals are the major interests of microbiome research.

The interactions between plants and commensals are complicated. Plants regulate root microbiota mainly through root exudates and the plant immune system, while root microbiota expands the habitable range and metabolic capacity of plants, and participate in diverse processes, such as plant development, nutrient absorption, and stress responses (Berendsen et al., 2012; Huang et al., 2014; Hiruma et al., 2016; Kwak et al., 2018; Zhang et al., 2019). Thus, a plant's phenotype is the co-product of the plant's genotype and its microbiome (Ravanbakhsh et al., 2019). Therefore, illuminating the molecular mechanisms of interactions between hosts and their microbiota is of great significance for using the microbial community to develop sustainable agriculture. Recently, the development of high-throughput sequencing and large-scale microbial isolation and identification have greatly promoted our understanding of the assembly, function, and interactions of the plant microbiome (Callahan et al., 2016; Knight et al., 2018).

Here, we summarize recent research advances on the root microbiome. Although fungi, viruses, and protozoa are important constituents of the root microbiota, we focus on the bacterial microbiome, including its assembly mechanisms and its functions in plant growth and development. Finally, we look ahead to promoting sustainable agricultural development by utilizing the root microbiome.

ROOT MICROBIOTA COMMUNITY STRUCTURE AND ASSEMBLY PATTERNS

Root-resident microbes include rhizosphere microbiota and endosphere microbiota, which colonize the region surrounding the roots and the internal tissues of the plant, respectively. The emerging information about root microbial communities of different plant species show that the composition of rhizosphere microbiota is similar to that of bulk soil microbiota. Moreover, the root microbial community mainly consists of species in the phyla Proteobacteria, Actinobacteria, Bacteroidetes, and Firmicutes (Bodenhausen et al., 2013; Bulgarelli et al., 2013, 2015; Guttman et al., 2014; Schlaeppi et al., 2014). However, the relative abundance of phyla differs among different plant species. For instance, the legume *Trifolium pratense* hosts a distinct root microbial community. The dominant phylum Proteobacteria accounts for 90.7% of the root microbiota and an operational taxonomic unit (OTU) identified as a *Rhizobium* is dominant among the Proteobacteria, accounting for 70% of the root microbiota (Hartman et al., 2017). This is consistent with the fact that *T. pratense* establishes a mutualistic relationship with rhizobia to fix nitrogen (Carlsson and Huss-Danell, 2003; Dhamala et al., 2017). Many factors affect the composition of the microbial community, including, in order of the magnitude of their effects, soil type, plant development stage, and plant genotype (Peiffer et al., 2013; Shakya et al., 2013; Schreiter et al., 2014; Bakker et al., 2015; Edwards et al., 2015; Zarraonaindia et al., 2015; Zhang et al., 2018; Xiong et al., 2021a). The regulation of the microbial community by soil type and plant genotype will be described in detail in the following sections. The microbial communities in different compartments change during vegetative growth and gradually stabilize during reproductive growth in different plants (Chaparro et al., 2014; Edwards et al., 2018; Zhang et al., 2018). There are significant differences in the amount of organic carbon released from roots during different stages of plant development, which has a stronger correlation with the bacterial community than the fungal community (Chen et al., 2019).

Studies demonstrate that microbiota diversity gradually decreases from the rhizosphere to the endosphere (Edwards et al., 2015). Bulgarelli et al. (2013) developed a two-step selection model based on previous studies. First, rhizodeposition drives microbes from the bulk soil to the rhizosphere and forms the rhizosphere microbiota. Second, rhizosphere microbes enter the endosphere under the regulation of the host genotype and the endosphere microbiota is established (Bulgarelli et al., 2013). Subsequently, Edwards et al. (2015) further divided the root microbiota among three compartments: rhizosphere, rhizoplane, and endosphere. At the same time, they emphasized a critical gating role for the rhizoplane and suggested that three or more steps are needed for microbes to move from the bulk soil to the endosphere.

MAIN FACTORS AFFECTING THE ROOT MICROBIOTA

The rhizosphere, rhizoplane (root surface), and endosphere represent different niches that can be occupied by root microbes. During colonization of the root, environment, plant–microbe interactions, and microbe–microbe interactions together shape the microbial communities formed in

the different niches by microbes from the bulk soil (Perez-Jaramillo et al., 2016; Adair and Douglas, 2017; Xiong et al., 2021b) (Figure 1).

Soil is a critical factor affecting the root microbiota

The bulk soil microbiota—A "seed bank" of plant root microbes

Soil is one of the most complex microbial ecosystems on earth (Gans et al., 2005). Many factors, such as climate, moisture availability, pore size, soil organic matter content, the total content of carbon and nitrogen, carbon–nitrogen ratio, and pH, make significant contributions to soil bacterial community diversity (Tecon and Or, 2017) (Figure 1). For instance, soil bacterial community diversity is significantly correlated with soil pH, being highest in neutral soil and lowest in acidic soil (Tecon and Or, 2017). The root microbial community is mainly derived from the bulk soil microbes by horizontal transfer, so bulk soil is regarded as the "seed bank" of the root microbial community (Bulgarelli et al., 2012; Lundberg et al., 2012). In some ways, the root microbial community can also be considered as a subset of the bulk soil microbial community (Zarraonaindia et al., 2015). Therefore, the bulk soil microbial community serving as the

initial inoculum of the root is an important factor affecting the establishment of the root microbial community (Bulgarelli et al., 2012; Lundberg et al., 2012; Peiffer et al., 2013; Edwards et al., 2015). There are significant differences in plant microbial communities in soils with different physicochemical properties under different climate conditions (Kang et al., 2019).

Soil physicochemical properties also affect root microbiota structure indirectly by affecting plants

The soil physicochemical properties, such as nutrient availability, also affect plant growth and development, and consequently further affect the composition of the root microbial community. Phosphorus is one of the most important macronutrients in plants. Although phosphorus is abundant in soil, phosphorus ions (Pi) easily form complexes with other ions, which are difficult to absorb by plants (Schachtman et al., 1998; Vance et al., 2003). Plants respond to phosphorus restriction through a series of morphological, physiological, and metabolic changes, defined as the phosphate starvation response (PSR). PHR1, a core transcription factor for balancing PSR and plant immune responses, directly regulates immunity-related genes and further inhibits microbe-induced immune responses under phosphorus
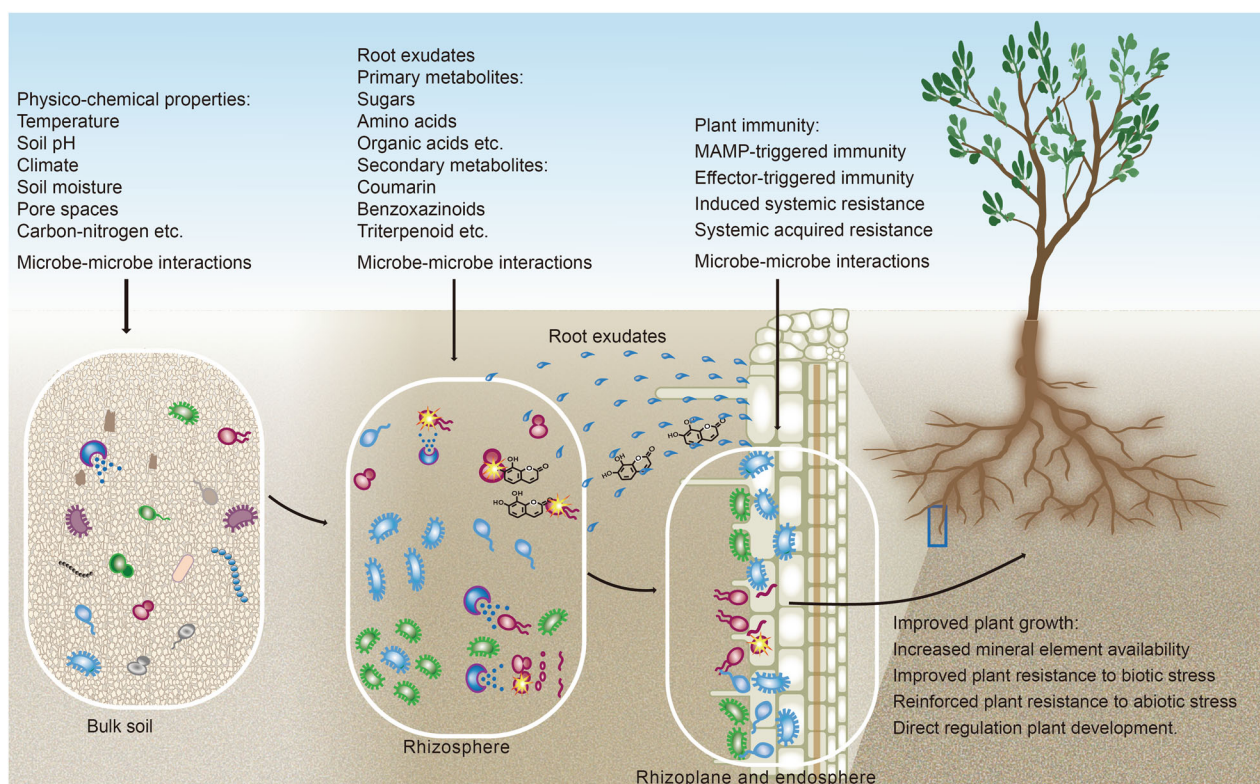

Figure 1. Factors affecting plant root microbial community structure and the subsequent effects on plant growth
The bulk soil microbial community is the seed bank for the plant root-associated microbiota. Soil physico-chemical properties, including soil pH, moisture, and soil composition affect the soil microbial community and consequently the root microbial community. Microbes are recruited from the bulk soil to the rhizosphere by root exudates, which include primary metabolites mainly responsible for attraction and secondary metabolites mainly responsible for screening the recruited microbes. Host genotypes influence the immune functions that control the entry of rhizosphere microbes into the endosphere. Microbe–microbe interactions also play roles at all stages of the process. The rhizosphere and endosphere microbes improve plant growth by increasing mineral nutrient availability and improving plant resistance to biotic and abiotic stress.

deficiency. The PSR affects the structure of the root microbiota, resulting in an atypical microbial community. Furthermore, the induction of genes involved in the PSR depends on the presence of microbes (Castrillo et al., 2017; Motte and Beeckman, 2017). Similarly, the amounts of inorganic nitrogen and iron in the soil also affect root microbiota structure through a similar mechanism (Zhang et al., 2019; Harbort et al., 2020).

The host regulates the root microbiota

Rhizosphere effects, the immune system, nutrient mobilization, and responses to stress determined by the host genotype regulate root microbial structure, which in turn influences the growth and developmental processes of the host.

Rhizosphere effects: root exudates drive microbiome assembly

Nearly 5%–20% of a plant's photosynthetically fixed carbon is secreted by the roots into the rhizosphere (Walker et al., 2003). Root exudates (e.g., sugars, amino acids, organic acids, fatty acids, and secondary metabolites) are important forms of communication between plants and microbes, and attract microbes to the rhizosphere from the bulk soil (Bais et al., 2006; Badri and Vivanco, 2009; Bulgarelli et al., 2013; Baetz and Martinoia, 2014). The effects of root exudates on the microbiota are defined as rhizosphere effects (Bulgarelli et al., 2013; Sasse et al., 2018; Zhalnina et al., 2018) (Figure 1). Using a combination of microbiome, comparative genomic, and exometabolomic approaches, researchers observed that plant root exudates have specific patterns associated with root growth and plant development (Zhalnina et al., 2018). By comparing the genomes of enriched and depleted rhizosphere bacteria and their ability to metabolize different root exudates during plant development, researchers further found that there is an interaction between microbial substrate uptake traits and plant exudation patterns. Rhizosphere bacteria have a preference for aromatic organic acids secreted by plants (nicotinic, shikimic, cinnamic, salicylic, and indole-3-acetic acids: IAAs) (Zhalnina et al., 2018). The interactions between microbial substrate uptake traits and plant exudation traits form the molecular mechanism by which plants can regulate microbial communities by modulating root exudates (Zhalnina et al., 2018). In terms of microbial adaptation to the root environment, rhizosphere-enriched genes were related to bacterial chemotaxis, biofilm formation, flagella assembly, and bacterial movement, suggesting that plants recruit microbes with root exudates (Xu et al., 2018a). Moreover, the fact that carbohydrate metabolism and amino acid metabolism-related functions were underrepresented in the rhizosphere core microbiome is consistent with the ability of these microbes to obtain simple carbon and nitrogen compounds from root exudates (Xu et al., 2018a).

Root exudates are significantly affected by many factors, such as plant species, developmental stage, root physiology, environment, nutrition, soil type, stress type, and stress degree (Sasse et al., 2018). For instance, a circadian clock with light as the main variable regulates metabolic function in plants. Plant carbohydrate metabolism and organic matter in the rhizosphere vary significantly during the day and night. There are significant differences in the bacterial community structure in the rhizosphere of wild-type *Arabidopsis* between light and dark conditions, and 13% of the rhizosphere community showed circadian rhythms (Staley et al., 2017). The Casparian strip (CS) in the endodermis, a physical barrier essential for controlling substance exchange between the root and its environment, plays an important role in regulating root exudates. Mutants with CS defects show that abnormal suberin deposition influences the release of root exudates, which in turn affects the recruitment of beneficial microbes and the final microbial community structure (Durr et al., 2021; Salas-González et al., 2021).

In addition to recruiting microbes by providing nutrients, roots also actively regulate rhizosphere microbial structure by secreting specific chemicals (Figure 1). For example, coumarin selectively inhibits some soil pathogens, while rhizosphere bacteria that promote growth and activate induced systemic resistance (ISR) have a high tolerance to coumarin. Coumarin stimulates the redox reaction to produce reactive oxygen species (ROS), which may be an important mechanism for the bacteriostatic effects of coumarin (Voges et al., 2019). The *Arabidopsis* mutant *f6 h1*, which is deficient in coumarin biosynthesis, assembles a distinct microbiome, indicating that the coumarin biosynthetic pathway is involved in shaping the root microbiome. Beneficial bacteria improve the colonization environment for themselves and supply immunity and growth benefits for the host after colonizing the root; these bacteria induce coumarin synthesis (Stringlis et al., 2018). The root-specific camalexin synthetic pathway helps regulate microbe–microbe interactions in the rhizosphere, contributing to sulfatase activity and plant growth promotion by beneficial microbes such as *Pseudomonas* ssp. CH267 (Koprivova et al., 2019). The benzoxazinoids (BXs) are a class of defensive secondary metabolites released by cereal roots. 6-methoxy-benzoxazolin-2-one (MBOA), a BX breakdown product, decreases plant growth, increases jasmonic acid (JA) signal transduction and plant defenses, and decreases herbivore performance in the next generation by regulating root-associated fungal and bacterial communities (Hu et al., 2018). Triterpenes are plant-specific metabolites, and *Arabidopsis* mutants with defects in triterpene biosynthesis form distinct root microbial communities compared with the wild type. Purified triterpenoids and representative triterpenoid mixtures selectively modulate the growth of 19 taxonomically diverse bacterial strains isolated from the root microbiota (Huang et al., 2019a). In short, plant roots recruit microbes from bulk soil and drive the assembly of microbial communities by supplying nutrients and releasing specific chemicals.

The plant immune system distinguishes "enemies" and "friends"

Plants have a sophisticated immune system that allows them to exclude harmful microbes while permitting commensals and mutualists to colonize their roots (Teixeira et al., 2019) (Figure 1). This process depends on recognition of highly conserved microbe-associated molecular patterns (MAMPs) and activation of MAMP-triggered immunity (MTI), which forms a primary defense against microbial colonization (Chisholm et al., 2006; Jones and Dangl, 2006). However, normal plant growth and development may be compromised during the immune process, a situation defined as "growth-defense tradeoffs" (Couto and Zipfel, 2016). So, how do beneficial microbes evade the plant immune system? Or, how do plants discriminate between harmful and beneficial microbes?

To establish interactions with plants, some microbes evade or suppress host immunity through various mechanisms (Yu et al., 2019b). For instance, researchers comparing the genomes of plant-associated versus non-plant-associated bacteria identified 64 plant-resembling plant-associated and root-associated domains (PREPARADOs) encoded by 11 916 genes in plant-associated bacteria (Levy et al., 2017). Moreover, some of these PREPARADOs are speculated to mimic as decoys to evade the host immune system, giving the microbes access to plant tissues (Trivedi et al., 2020). The biosynthesis and signaling pathways of the plant defense hormone salicylic acid (SA) are critical for shaping and maintaining a normal root microbiota through regulating colonization by certain bacterial families (Lebeis et al., 2015). Some root microbes, such as *Pseudomonas capeferrum* WCS358, lower their extracellular pH and inhibit root immunity by producing gluconic acid and its derivative 2-keto gluconic acid (Yu et al., 2019a). Other microbes overcome the plant immune system with their own secretions, such as *Bacillus velezensis* FZB42 (*B. velezensis*), a probiotic bacterium that secretes auxin. Bacterial auxin is essential for root colonization by *B. velezensis* and for its survival and replication by antagonizing ROS produced as part of the receptor EFR-triggered immune response. Meanwhile, ROS induces the synthesis of bacterial auxin (Tzipilevich et al., 2021).

Flg22, an N-terminal epitope of bacterial flagellin, is a typical MAMP triggering plant immune responses (Felix et al., 1999; Chinchilla et al., 2006). Colaianni et al. (2021) investigated the variability of flg22 peptides in commensals, and demonstrated that most commensal flg22 peptide variants failed to activate the pattern recognition receptor (PRR) FLS2 (64%) and did not significantly inhibit host growth (80%). Some flg22 peptide variants altered MTI signaling output by interfering with co-receptor enlistment and by another, unidentified mechanism that triggered the typical ROS response, resulting in modulation of plant immunity. Therefore, the commensal community has abundant flg22 diversity resulting in specific defense activation, pervasive evasion, and differential immune signal regulation, which may contribute to

community diversity and microbial homeostasis (Colaianni et al., 2021). In plants, FLS2 appears to be particularly vulnerable to evolutionary selection pressures. More than 100 amino acid changes in FLS2 have been identified using genome mining in >1,000 *Arabidopsis* accessions, indicating that FLS2 sequence variants seem to have evolved an ability to detect various flg22 variants to ensure proper immune activation (Parys et al., 2021; Stringlis and Pieterse, 2021). The diversified variants of flg22 evade the recognition of FLS2, while receptor FLS2 recognizes more flg22 variants through variation in amino acid, which shows the co-evolution between plants and microbes.

A recent study shows that the *Arabidopsis* root commensal community is involved in MTI regulation. Researchers identified a group of robust, taxonomically diverse strains that inhibited MTI. Both single strains and synthetic communities (SynComs) selectively regulated key immunogenes, including receptors, transcription factors, and biochemical executors, and increased the ability of other commensal bacteria to colonize roots (Teixeira et al., 2021). Similarly, based on their MTI-induced root growth inhibition (RGI) phenotypes, researchers divided SynComs into two types: those that induced RGI and those that did not, which modulated host sensitivity to root bacteria by inducing or inhibiting MTI responses, respectively. MTI activation altered the structures of RGI-inducing SynComs, which were attenuated in the presence of RGI-suppressing strains. Furthermore, non-RGI strains also altered the expression of 174 core host genes, including a subset of specifically down-regulated genes related to plant immunity (Ma et al., 2021). These results are consistent with those of Teixeira et al. (2021). This evolved mechanism balances the fight against pathogens by the immune system with growth-defense tradeoffs, resulting in host-commensal homeostasis (Ma et al., 2021).

Commensals prevent growth inhibition by suppressing immunity, but plants also actively ignore colonization by harmless bacteria. In the differentiated outer cell layers of *Arabidopsis* roots, the expression of PRRs is low and responsiveness to MAMPs is lost, so the immune response is not activated in the presence of beneficial or harmless microbes. However, neighboring cells show high expression of PRRs and rapid response to MAMPs if they are damaged, which is known as the damage-gate. The damage-gate precisely activates immunity at the infection site depending on plant cell damage signaling triggered by pathogens (Zhou et al., 2020). To sum up, the plant immune system actively overlooks colonization by beneficial microbes, and these microbes evade or suppress host immunity, which contributes to the interactions between hosts and commensals.

Other host genes regulating the assembly of root microbiome

Other genetic mechanisms also regulate microbial community assembly of roots. Bergelson et al. (2019) analyzed the root microbiomes of 196 *Arabidopsis* accessions and found that the host genotype seemed to have a stronger

effect on fungi than on bacteria. Moreover, they identified associations between the abundance of individual strains and plant genotypes using genome-wide association studies, and located some important quantitative trait loci (QTL) related to species richness and community structure. These QTL are involved in cell-wall integrity, plant immunity, and root and root hair development (Bergelson et al., 2019). By reanalyzing the same dataset, He et al. (2021) identified hub fungi and bacteria that are critical for assembling the microbial community. Likewise, they identified 91 hub host QTL involved in plant growth and development, root growth, pathogen resistance, and abiotic stress resistance (He et al., 2021). A recent study suggests that FERONIA (FER), a cell membrane receptor protein kinase, is involved in regulating microbiota structure. *Pseudomonas fluorescens* was enriched in the rhizosphere of the *Arabidopsis* mutant *fer-8* without microbial dysbiosis at the phylum level. FER negatively regulates colonization by beneficial *P. fluorescens* by regulating root ROS levels (Song et al., 2021). There is host preference in microbial community colonization (Wippel et al., 2021). *Lotus japonicus* and *Arabidopsis* root microbiota have 16 families in common, and a SynCom was built using 32 strains from the 16 shared families (16 strains each for *Lotus* and *Arabidopsis*). After both hosts were inoculated with the SynCom, the relative abundance of the strains originally isolated from *Arabidopsis* was higher on *Arabidopsis* root, while the strains originally from lotus were more abundant on lotus root. Based on these data combined with plant transcriptomic analysis, the host commensal preferences were mainly determined by plant immunomodulatory factors, MAMP receptor kinase, and ethylene response factors (Wippel et al., 2021).

Microbial colonization alters plant gene expression, an effect defined as the general non-self response (GNSR) (Maier et al., 2021). One study showed that when bacterial colonization occurred, 24 core GNSR genes were up-regulated to modulate plant metabolism, especially of tryptophan-derived secondary metabolites involved in plant defense. Using mutants, they further demonstrated that some GNSR genes make vital contributions to pathogen resistance (Maier et al., 2021). Plant epigenetic regulation may affect root microbial structure. For instance, mutant *dcl234*, an *Arabidopsis* triple mutant with defects in the RNA-directed DNA methylation (RdDM) pathway, had a reduced abundance of Aeromonadaceae and Pseudomonadaceae and an increased abundance of other families in the root microbial community. However, this regulation was independent of RdDM, and may have been caused by a series of modulations of cell-wall components, root exudates, and plant defenses (Kaushal et al., 2021). Comparing the root microbiome of three rice mutants defective in histone methylation, researchers found that histone methylation may have modulated the microbiome structure and composition by affecting the abundance of hub species (Lv et al., 2021).

Microbe–microbe interactions during microbial community assembly

Microbe–microbe interactions also are involved in root microbial community assembly (Figure 1). Niu et al. (2017) constructed a highly simplified maize SynCom from seven representative bacterial strains to test how microbial interactions affect community assembly. Experiments in which single strains were dropped out of the SynCom showed that elimination of *Enterobacter cloacae* but none of the other strains caused the SynCom to collapse, indicating that *E. cloacae* is a key member during community assembly. By analyzing bacteria, fungi, and oomycetes from different compartments in different *Arabidopsis* accessions, researchers built a network of microbial interkingdom interactions and identified two hub microbes that served as mediators between abiotic factors, host factors, and colonization by other microbes (Agler et al., 2016). The microbial community structure changed significantly after one or more strains were dropped from this SynCom. However, once a community was established, the structure was not significantly altered when the drop-out strains were subsequently added back, indicating that their priority effects occurred during bacterial colonization (Carlstrom et al., 2019). The vascular wilt pathogen *Verticillium dahlia* co-opts VdAMP3, an effector protein with antibacterial properties, to manipulate host microbiota to facilitate invasion (Snelders et al., 2021). Microbe-microbe interactions can improve plant resistance to biotic stress. For example, in *Arabidopsis*, the root bacterial community reshaped the fungal and oomycetal community structure to protect plants from them. The biocontrol ability of the bacterial root microbiota is a redundant trait that enhances plant survival (Durán et al., 2018).

THE EFFECTS OF ROOT MICROBIOTA ON PLANT DEVELOPMENT

The root microbiota contributes to plant nutrient absorption and resistance to biotic and abiotic stresses (Mueller and Sachs, 2015; Vandenkoornhuyse et al., 2015; Compant et al., 2019; Liu et al., 2020; Choi et al., 2021; Zhang et al., 2021a). Importantly, the function of the microbial community is closely associated with the regulation of the microbial community by the host (Figure 1). Under a particular stress condition, the host could form a specific root-related microbial community, and this microbiota may improve the resistance of plants to corresponding stress.

Root microbiota facilitates the uptake of mineral elements by plants

The root microbiota helps plants absorb mineral elements such as iron and nitrogen (Zhang et al., 2019; Harbort et al., 2020; Yu et al., 2021). Iron is an essential mineral nutrient for plants and acts as a catalyst in many biological processes, including photosynthesis and respiration (Balk and

Schaedler, 2014; Krohling et al., 2016). Iron deprivation causes plant chlorosis and affects growth and development (Morrissey and Guerinot, 2009). The root microbiota alleviates plant iron starvation, relying on changes in plant coumarin secretion and iron import. Both coumarin secretion and the root microbial community have profound effects on the plant's transcriptional response to iron deficiency. Moreover, the interactions between coumarins and commensals improve plant performance by enhancing iron absorption and regulating a set of defense-related genes (Harbort et al., 2020). Despite studies in rice showing that the nitrogen-utilizing efficiency of indica varieties is better than that of japonica varieties, the involvement of microbiome regulation has only recently been revealed (Koutroubas and Ntanos, 2003; Rakotoson et al., 2017; Zhang et al., 2019). Indica varieties recruited more bacteria with nitrogen metabolism functions than did japonica varieties, and a rice variety with *NRT1.1B*, a rice nitrate transporter and sensor gene, recruited bacteria with more ammonification activity than those recruited by the corresponding *nbt1.1b* mutant. When rice was grown on inorganic nitrogen, a SynCom made from indica-enriched bacteria promoted growth more than a SynCom made from japonica-enriched bacteria (Zhang et al., 2019). Besides enriching more bacteria with ammoniating active, flavones derived from maize root recruited more rhizosphere Oxalobacteraceae, which in turn promote nitrogen utilization and maize lateral growth (Yu et al., 2021). From a broader perspective, the root endodermis controls mineral absorption and exudate efflux, which is crucial for mineral balance in plants. The root microbiota affects mineral nutrient balance and abiotic stress tolerance by regulating the development of diffusion barriers in the endodermis, especially suberin deposition. This process depends on the inhibition of abscisic acid signal transduction by microbes (Salas-González et al., 2021). Therefore, microbes can not only directly promote the absorption of mineral elements in plants, but also indirectly help maintain the balance of mineral nutrition by regulating the establishment of the diffusion barrier in the root endodermis.

Root microbiota improves plant resistance to disease

Root commensals help plants resist pathogen invasion through various mechanisms, including niche competition, antibiotic secretion, and ISR induction (Compant et al., 2005; Lugtenberg and Kamilova, 2009; Beneduzi et al., 2012; Teixeira et al., 2019). A classic example is the existence of suppressive soils, which maintain the healthy growth of plants even in the presence of pathogens. Importantly, this ability is due partly to plant root microbial community (Weller et al., 2002). Some microbes may help directly by producing antibacterial substances that suppress pathogens or indirectly by inducing ISR in plants. *Pseudomonas syringae* pathovar *tomato* (*Pst*) is a pathogen that infects leaves; infected plants increase malic acid secretion from their roots and recruit *Bacillus subtilis*, resulting in a stronger immune response to *Pst* (Rudrappa et al., 2008). When *Arabidopsis*

leaves are infected with the downy mildew pathogen *Hyaloperonospora arabidopsidis*, three beneficial microbes, including *Xanthomonas* sp., *Stenotrophomonas* sp., and *Microbacterium* sp., are recruited in the rhizosphere to improve systemic resistance and enhance the resistance of the next generation of plants growing in the same soil (Berendsen et al., 2018). Similarly, after five successive generations of *Pst*-infected *Arabidopsis* grown in the same soil, the sixth generation showed increased JA level and disease resistance. This increased resistance may be partly due to changes in root exudation profiles, such that beneficial microbes are recruited and improve the disease resistance of the aboveground part of the plant (Yuan et al., 2018). Therefore, plants infected by pathogens are able to "cry for help" to the root microbiota and selectively enrich beneficial microbes. This phenomenon, in which plants benefit from previous generations grown in the same soil, is called the soil-borne legacy (Raaijmakers and Mazzola, 2016; Bakker et al., 2018). Given the above, plant resistance to pathogens is at least part by recruiting beneficial microbes from the soil.

Root microbiota enhances plant performance under abiotic stress

The root microbiota also helps plants resist abiotic stress. The improved plant resistance to abiotic stress is provided either directly by specific members of the root microbial community or indirectly through microbe–microbe interactions (Hartman and Tringe, 2019; Liu et al., 2020). Drought is an increasingly severe problem in agriculture. Interestingly, root microbiome improves the adaptation of hosts to drought stress (Xu and Coleman-Derr, 2019). A recent study showed that the rice root microbiome structure changed dramatically under short-term drought, but largely recovered to its pre-stress structure after rewatering. Nonetheless, prolonged drought caused severe and lasting effects on the endosphere community, which were not fully reversed after rewatering. After prolonged drought, Actinobacteria were enriched significantly and accounted for more than 80% of the post-drought bacterial community. Furthermore, *Streptomyces* sp. SLBN-177, isolated from most abundant OTU in the root microbiota, was able to promote root growth under drought conditions (Santos-Medellín et al., 2021). Similarly, the root microbiome changed significantly in sorghum under drought conditions, with Actinobacteria being moderately enriched and significantly promoting root growth (Xu et al., 2018b). Genome-resolved metagenomics and comparative genomics showed that the copy number of genes involved in iron transport and metabolism increased significantly in the Actinobacteria genomes. Moreover, Streptomyces promoted plant growth under drought conditions but this effect was reversed in the presence of exogenous iron, suggesting that iron metabolism plays an important role in drought-induced rhizosphere microbiome dynamics (Xu et al., 2021). Some bacteria isolated from grapevine promoted leaf biomass, shoot biomass and length, and photosynthetic activity under drought conditions in the greenhouse and also promoted root

biomass under field conditions (Rolli et al., 2015). These findings suggest that some commensals enhance plant resistance to drought.

Soil salinization is a global threat to agriculture. Due to the improper management of fertilizers and water, the area of saline-alkali soil is increasing. Using the microbial community to ameliorate salt stress is a promising method. Inoculation of asparagus with *Hypoxylon* spp. (Sj18), a fungus isolated from pecan roots, altered its endophytic community, such that the low abundance, salt-tolerant bacterial genus *Halomonas* became dominant. Meanwhile, inoculation with Sj18 improves salt tolerance in *Arabidopsis* (Huang et al., 2019b). Salt-induced root microbes alleviate salt stress in salt-sensitive and salt-insensitive Curcurbitaceae species, decreasing the Na^+ concentration in plants and promoting nutrient absorption. *In situ* microbial community isolated from salt-stressed host is more effective in alleviating host salt stress than that isolated from non-host plants. Meanwhile, ameliorating salt stress relies on species diversity, indicating that the beneficial regulatory mechanisms may involve synergies among different microbe species (Li et al., 2021).

Commensals also help regulate plant growth under low light. Perception of light in the leaves produces signals that regulate the root microbial community, which in turn regulates plant growth and development under the corresponding light conditions. Under low photosynthetically active radiation, plants favor growth at the expense of weaker defenses through a microbiota-root-shoot circuit. The growth-defense trade-off under low light is regulated by the root microbial community and the host transcription factor MYC2 (Hou et al., 2021). The above evidence suggests that root microbiota contributes to abiotic stress resistance and helps plants survive in harsh environments.

Root microbiota contributes to regulation of plant growth and development

Microbes directly regulate plant growth and development in addition to performing specific functions for corresponding physiological processes. Microbial modifications of ethylene levels in plants alter plant phenotypes, depending on growth-defense tradeoffs. *Pseudomonas putida* UW4 promotes plant growth by reducing ethylene levels, but at the cost of hypersensitivity to stress (Ravanbakhsh et al., 2019). Finkel et al. (2020) found that a single bacterial genus (*Variovorax*) reversed the severe inhibition of root growth caused by other bacterial strains and a SynCom composed of them. *Variovorax* species regulated the effects of the inhibitory SynCom on root growth by manipulating IAA levels. The researchers also identified a genomic hotspot 33, containing atypical IAA degradation operons, which is conserved in all available *Variovorax* genomes and is necessary and sufficient for reversal of RGI. Specific soil microbes can alter flowering time in *Arabidopsis* (Wagner et al., 2014; Panke-Buisse et al., 2015). Nitrification by rhizosphere microbes increased and prolonged nitrogen bioavailability, thereby promoting vegetative growth and delaying flowering. Moreover, rhizosphere *Arthrobacter* species also converted tryptophan in root exudates to IAA to delay flowering (Lu et al., 2018). Surprisingly, the microbial community mediates heterosis in maize. Hybrid maize lines performed only as well as their inbred parental lines under sterile conditions, but showed heterosis of root biomass when inoculated with a highly simplified SynCom. Importantly, these results were replicated in natural soils, indicating that the microbial community robustly mediates plant heterosis throughout the environment (Wagner et al., 2021). Although the specific molecular mechanisms of microbial regulation of plant growth and development are still unclear, there is no doubt that the microbial community is involved in plant growth and development. As more evidence emerges, the purposeful use of microbes will be achieved.

ADVANCES IN TECHNIQUES BOOST OUR UNDERSTANDING OF THE MICROBIOME

Research into the root microbiome mainly consists of culture-dependent, culture-independent, and reductionist SynCom approaches (Figure 2). Initial studies relied on isolating and purifying microbes and identified the cultured species and their abundances through colony morphology and number. However, it is difficult to reproduce natural conditions suitable for the growth of many microbes under laboratory conditions and a large proportion of microbes are not culturable, resulting in a lack of information about the true microbial community (Hill et al., 2000). Nonetheless, culture-dependent approaches remain important for microbiome research, such as the reductionist SynCom approach relying on high-throughput cultivation and identification (Bai et al., 2015; Zhang et al., 2021b). Subsequently, culture-independent approaches (e.g., DNA fingerprinting, phospholipid fatty acid analysis) were developed to study the diversity and composition of the entire community; however, these techniques have lower throughput and provide less information compared with emerging high-throughput sequencing and meta-omics approaches (Bossio and Scow, 1998; Jo et al., 2020). By using high-throughput sequencing approaches, researchers have gained an understanding of the composition of microbial communities with unprecedented breadth and precision (Bulgarelli et al., 2012; Lundberg et al., 2012; Liu et al., 2019, 2021). In addition, emerging metagenomics, metatranscriptomics, and metaproteomics technologies allow us to systematically understand the function of microbiomes (Caporaso et al., 2010; Liu et al., 2021).

Census approach (e.g., amplicons and metagenomic statistics) provides a holistic understanding of plant microbial communities, which is crucial for reviewing the fact of natural microbiomes, while the reductionist SynCom approach connects the fields of microbial ecology and plant molecular biology (Inceoglu et al., 2011; Bulgarelli et al., 2012, 2015; Knief et al., 2012; Lundberg et al., 2012; Guttman et al., 2014; Mendes et al., 2014; Edwards et al., 2015; Liu et al., 2019). Census experiments
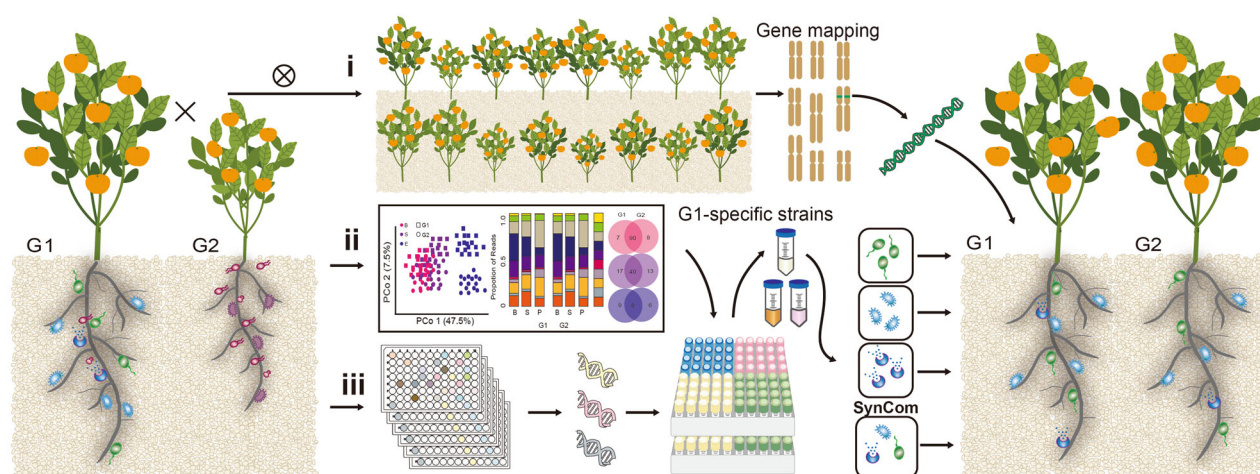
Figure 2. Microbiome research approaches

(i) Map plant genes that regulate bacterial colonization based on microbiome differences or related phenotypes. **(ii)** Use census experiments to identify potential functional bacterial strains that cause differential phenotypes in plants. **(iii)** Isolate and identify strains from root-associated microbiota to build a bacterial bank. Guided by census results, build synthetic communities (SynComs) using strains from the bacterial bank. Perform reductionist experiments in which a SynCom is added to sterile plants to investigate whether the SynCom has the expected biological functions. Dissect the molecular mechanisms of key host genes regulating colonization by specific strains, ultimately to elucidate the molecular mechanism of plant recruitment of specific strains and the effects of their regulation on plant growth and development.

provide information for the reductionist study of plant–microbiome interactions. Combining these data with that from isolated strains with relatively clear genetic information, researchers construct a wide variety of representative SynCom (Bulgarelli et al., 2012; Vorholt et al., 2017) (Figure 2). Bai et al. (2015) built a bacterial bank including most families of the root and leaf microbiota of *Arabidopsis* and sequenced the genomes of representative strains, paving the way for exploring the assembly and function of these microbial communities. Using the SynComs, interactions between plants and microbial communities are simulated under controlled conditions to repeatedly analyze the factors driving microbial community assembly and to verify their regulatory functions and molecular mechanisms during plant growth and development (Bodenhausen et al., 2014; Bai et al., 2015; Lebeis et al., 2015; Castrillo et al., 2017; Chen et al., 2020; Finkel et al., 2020). In short, great progress has been made on plant microbiome research through combining culture-dependent and culture-independent approaches. Holism Census approaches and reductionism SynCom approach each have their own advantages, and either method alone cannot truly reveal the mechanism of microbiome construction. Therefore, the comprehensive application of multiple research methods will be an effective way to understand and utilize the microbiome in future research.

FUTURE PERSPECTIVES: MICROBIOME APPLICATIONS IN MODERN AGRICULTURE

Despite great progress in understanding the root microbiome, utilizing the microbiome to improve crop growth and development is in its initial stages. The microbes that promote plant growth under experimental conditions tend to perform poorly in the natural environment (Sessitsch et al., 2019). Perhaps the added growth-promoting strains fail to become dominant and are unable to promote growth due to priority effects during microbial community reconstruction. Fortunately, emerging information about hub strains and keystone species in the microbial community provides further guidance for utilizing beneficial microbes (Agler et al., 2016; Niu et al., 2017). Hub species are microbes which establish more connections with other microorganisms within a microbial network, with some playing a crucial role in structuring the composition of the whole community and are defined as keystone species (Berry and Widder, 2014). We propose that it is possible to make use of keystone species in modern agriculture systems as illustrated below. On the one hand, direct addition of keystone species with growth-promoting function to a less healthy microbial community could potentially improve the composition and structure of that community, making it healthier. On the other hand, some keystone species themselves do not promote plant growth, but act as a mediator that indirectly curates a healthier community; these keystone species could also be used to improve crop performance.

The effects of plant genotype on plant root exudates and the immune system play important roles in regulating the establishment of root microbial communities (Hacquard et al., 2017; Sasse et al., 2018; Nobori and Tsuda, 2019). Even though researchers have shown that some specific genotypes can recruit certain beneficial microbes, relevant research progress is still rare. It is necessary to pay more attention to plant genes that favor colonization by specific beneficial microbes and select for these genes during the

process of crop breeding. Promoting the establishment of beneficial root microbial communities through host modification is a potentially effective way to promote plant growth and development. The pioneer work of integrating beneficial microbes in crop breeding needs more attention and support from government and breeding companies. Through comprehensive utilization of SynComs containing keystone strains and directed plant breeding, the microbiome will play a more active role in sustainable agriculture.

ACKNOWLEDGEMENTS

CONFLICTS OF INTEREST

The authors declare they have no conflicts of interest associated with this work.

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