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REVIEW ARTICLE

A review of root exudates and rhizosphere microbiome for crop production

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Abstract

Increasing crop yields and ensuring food security is a major global challenge. In order to increase crop production, chemical fertilizers and pesticides are excessively used. However, the significance of root exudates is understudied. Beneficial interactions between plant and rhizosphere microbiome are critical for plant fitness and health. In this review, we discuss the application and progress of current research methods and technologies in terms of root exudates and rhizosphere microbiome. We summarize how root exudates promote plant access to nitrogen, phosphorus, and iron, and how root exudates strengthen plant immunity to cope with biotic stress by regulating the rhizosphere microbiome, and thereby reducing dependence on fertilizers and pesticides. Optimizing these interactions to increase plant nutrient uptake and resistance to biotic stresses offers one of the few untapped opportunities to confront sustainability issues in food security. To overcome the limitations of current research, combination of multi-omics, imaging technology together with synthetic communities has the potential to uncover the interaction mechanisms and to fill the knowledge gap for their applications in agriculture to achieve sustainable development.

Keywords Plant-microbe interactions, · Multi-omics and visualization, · Fertilizers and pesticides, · Synthetic community, · Crop production, · Food security

Introduction

It has been challenging to solve food-related issues (Pischetsrieder 2018; Gao et al. 2021). Especially, global food demand is expected to increase by 70% by 2050 to meet the growing population (Singh et al. 2020). However, traditional agriculture practices cannot meet this requirement due to land degradation, widespread droughts, climate change and extreme weather (Singh et al. 2020). The rhizosphere is the narrow dynamic zone of soil that surrounds and is influenced by plants in which complex interactions occur between root exudates and soil microbiome (Coskun et al. 2017). Plant rhizosphere harbors diverse microbes, many of which benefit plants by assisting in nutritional acquisition and preventing infections by root pathogens (Beattie 2018). Deploying rhizosphere microorganisms to increase crop nutrient acquisition and stress resistance has great potential to solve the integral challenges for food security (Singh and Trivedi 2017). Furthermore, as an underground plant trait, root exudates have great promise to solve these challenges (Baetz and Martinoia 2014). Therefore, a comprehensive analysis of the abundance,

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structure, and functions of the plant microbiomes and their associated root exudates is of significance for designing effective, economical and environmentally-friendly approaches to achieve food security (Singh and Trivedi 2017).

Root exudates comprise a variety of compounds, including primary metabolites such as sugars, organic acids, amino acids, as well as plenty of unique secondary metabolites. However, the root exudation process remains understudied (Hartmann et al. 2008). Plants released 11–40% of total fixed carbon (C) through photosynthesis into the surrounding soils (Zhalnina et al. 2018), and the composition of exudates varies depending on plant species, genotype, developmental stage, root traits, nutrient availability, and environmental conditions (Zhang et al. 2019). Root exudates promote nutrient acquisition and drive plant-soil feedback on defense against pathogens via modulation of the root microbiome, and in this way reducing fertilizer and pesticide use (Preece and Penuelas 2020). Thus, future research should be targeted on optimizing and manipulating roots exudates to improve crop yields and reduce the use of fertilizers and pesticides. Progress has been made towards the characterization of root exudate components and/or rhizosphere microbiome in model and crop plant species, which includes but is not limited to *Arabidopsis* (Duran et al. 2018), rice (Sun et al. 2016), citrus (Xu et al. 2018), maize (Li et al. 2014), barley (Bulgarelli et al. 2015), wheat (O'Sullivan et al. 2016), sorghum (Subbarao et al. 2013a, 2013b), and sugarcane (Yeoh et al. 2016). However, fundamental understanding of how root exudates shape rhizosphere microbiome assembly to reduce fertilizer or pesticide is still unclear (Sasse et al. 2018). Establishing causal links between root exudate metabolites and root microbiome shifts remains challenging (Vorholt et al. 2017). To date, most of the reviews published on plant-microbe interactions focused on the factors affecting plant microbiome (Zhang et al. 2021), core microbiomes (Toju et al. 2018), and microbiome engineering (Arif et al. 2020), but few focused on how root exudates affected rhizosphere microbiome and the molecular mechanisms underlying the effect of plant-microbe interactions on promoting crop yield and food security. Preece et al. (2020) proposed that root exudate characteristics in crop wild relatives can be utilized to reduce the use of fertilizers and pesticides, but the mechanism of root-microbe interactions is not well-understood (Preece and Penuelas 2020).

Here, we highlight the research methods and recent progress on root exudates and rhizosphere microbiome functions, including the use of external artificial root exudates (ARE), multi-omics approaches such as metabolomics, metagenomics, isotopes labelling, imaging, and microfluidics technology. Furthermore, we review the recent progress regarding how root exudates shape the rhizosphere microbiome to improve agricultural output and reduce environmental pollution, and decrease our dependence on fertilizers and pesticides to achieve stratifying crop production. Finally, current challenges in root-microbe interactions and future directions are proposed.

A scientometric study of root exudates and rhizosphere microbiome

Over the past 20 years, more than 5000 papers are published on root exudates (Fig. 1). Publications on root exudates and rhizosphere microbiome generally increased from 2001 to 2020 (Fig. 1B). Especially, in the year of 2020 about 25% of the publications on root exudates were related to the rhizosphere microbiome, while in 2001 only about 6% of the publications on root exudates were related to rhizosphere microbiome. This revealed the growing research interest in root exudates and rhizosphere microbiome.

The top 15 research areas on root exudates are summarized in Fig. 1C. Studies on root exudates are closely related to plant sciences, agriculture, and environmental sciences ecology, which account to 39.13%, 35.01%, and 20.36% of the total publications, respectively. Similar results were found when the search was performed for both root exudates and rhizosphere microbiome (Fig. 1D). It should be clarified that these research areas are not mutually exclusive. For example, the first 2 research areas (i.e., Plant Sciences and Agriculture) largely overlap. The criteria used here are set by Web of Science instead of the authors. In other words, all these research areas are standard items in Web of Science. Furthermore, agriculture revealed a stronger relationship with rhizosphere microbiome, as agriculture replaces plant sciences and became No. 1. Furthermore, the percentage of microbiology increases greatly, i.e., from 7.72% to 17.91%, which discloses the fact that rhizosphere microbiome is part of microbiology. More details about the scientometric study are available in the Supplementary Information (Jiang et al. 2018, 2021; Ni et al. 2021).

Methods to study the effect of root exudates on rhizosphere microbiome

Root exudates mediate the interactions between plants and rhizosphere microorganisms and have been described to 1) regulate key processes of soil biogeochemical cycles (Philippot et al. 2013); 2) alter the soil structure, for example, elevated root exudation has the potential to increase biotic macro-aggregation of soils (Baumert et al. 2018); 3) release allelochemicals which have stimulatory and/or inhibitory effect on growth, health and behavior of neighboring plants (allelopathy) (Latif et al. 2017); 4) mobilize nutrients and complexate toxic metals (Chen et al. 2018; Kristiank et al. 2009; Shi et al. 2019); 5) establish plant-microbe and microbe-microbe interactions (Kurt et al. 2018); and 6) drive

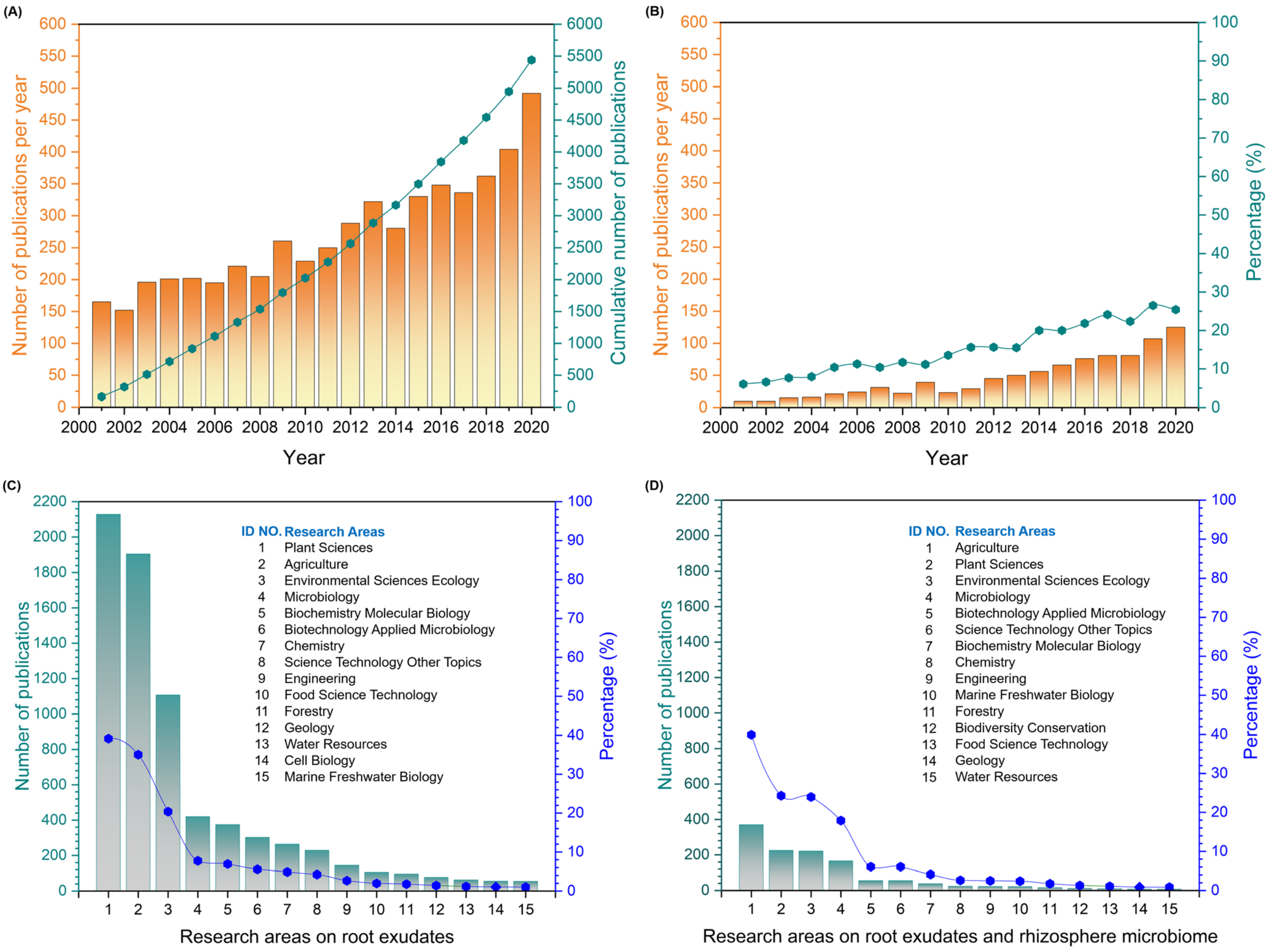

Fig. 1 Literature search on root exudates and rhizosphere microbiome from 2001 to 2020. (A) Number of publications per year and cumulative number of publications on root exudates. (B) Total Number and percentage of publications per year on root exudates and rhizosphere microbiome. Number of publications of the top 15 research areas on (C) root exudates and (D) root exudates and rhizosphere microbiome

the composition and function of rhizosphere microbial community (Zhalnina et al. 2018).

External addition of model root exudates

Because root exudates are comprised of an extremely diverse group of compounds, their compositions and associated effects on the rhizosphere microbiome are challenging to study. The collection and analysis of root exudates still remain imperfect (Oburger and Schmidt 2016). Because of the complexity and difficulty of sampling and identification, most studies focus on the mechanisms of primary exudates. The major role of primary exudates is to mobilize limiting and recalcitrant nutrients, such as phosphorous, and to detoxify heavy metals by releasing organic acid (Muller et al. 2016). However, not all of the primary metabolites are able to mobilize nutrients, such as sugars. Researchers added external artificial root exudates (ARE) containing different proportions of sugars, amino acids, and organic acids to the microcosms to disentangle the rhizosphere effect on bacterial communities (Landi et al. 2006; Langarica-Fuentes et al. 2018). Many studies have proved the "priming effect" of ARE, which could stimulate N cycles and/or shape soil microbial communities, and the effect depends on the compositions and proportions of ARE as well as other environmental conditions (Table 1). However, more research is needed to gain a better understanding of the roles of ARE on crop production.

Omics technologies for root exudate and rhizosphere microbiome profiling

The choice of metabolomics platform for root exudations detection relies on the component characteristics. Metabolomics is referred to untargeted analysis of as many metabolites as possible in one sample, and metabolomics tools separate, identify and quantify metabolites, which includes liquid chromatography (LC), gas chromatography-mass spectrometry (GC-MS), MS, nuclear magnetic resonance (NMR). In

Table 1 Some representative studies on the effect of ARE addition on the N cycle

ARE addition	Main findings	Reference
Maize mucilage solution (70 μg C/g dry soil)	Strong influence on the activity of denitrifying communities and little change on its diversity.	(Mounier et al. 2004)
Glucose and oxalic acid	A positive "priming effect" is likely to occur in oxalic acid-amended soils, but not in glucose-amended soils.	(Landi et al. 2006)
Solutions containing different proportions of sugar, organic acids, and amino acids (150 μg C/g soil)	ARE did not strongly affect the structure or the density of denitrifying communities, whereas potential nitrate reductase and denitrification activities were stimulated.	(Henry et al. 2008)
Organic acids (lactic, quinic, and maleic acids) and sugars (sucrose, glucose, and fructose)	A vital role in changing soil microbial communities and they may have an important impact on the plant growth.	(Shi et al. 2011)
Glucose, fructose, and sucrose; citric, succinic, fumaric and malic acid; and glycine, leucine, alanine, valine, serine, glutamic acid, lysine, aspartic acid, phenylalanine and arginine	Short-term ARE addition reduced the risk of N loss at all temperatures.	(Fisk et al. 2015)
A mixture of organic acids and simple sugars (3:1 by volume)	Exudates accelerates N-cycles by stimulating microbes to decompose labile soil organic matter.	(Meier et al. 2017)
Five sugars (glucose, fructose, sucrose, arabinose and ribose), five amino acids (valine, glycine, glutamine, alanine and serine) and five organic acids (malonic, malic, citric, fumaric and oxalic acid) at equimolar C concentrations.	The response and sensitivity of the different denitrifying communities to ARE addition is distinct at different target water-filled pore space.	(Langarica-Fuentes et al. 2018)

general, GC-MS is often used for the volatiles compounds and primary exudates detection, while water-soluble secondary exudates are analyzed on LC platforms or NMR (Zhang et al. 2012; Preece and Penuelas 2020). Recent advances in the broad-spectrum and highly sensitive metabolomics platforms allow us to detect and, to some extent, identify increasingly more of the secondary exudates and the organisms interacting with them in the rhizosphere, such as coumarins (Lundberg and Teixeira 2018; Stringlis et al. 2018), rosmarinic acid (Corral-Lugo et al. 2016), benzoxazinoids (Hu et al. 2018) and triterpene (Huang et al. 2019). These secondary exudates mostly function as signaling molecules, attractants, and/or inhibitors, and they often have a critical role in species-specific communication between interacting organisms (Hu et al. 2018). For example, flavonoids are widely studied and they are water-soluble secondary metabolite in exudates (Shaw et al. 2006), which need to be analyzed on LC platforms or NMR. Flavonoids are reported as chemotaxes and inducer of nodulation genes, and are known to mediate positive interactions between legume roots and N-fixing bacteria (Kudjordjie et al. 2019), and they often function actively at nanomole or micromole levels (Cooper 2004). Additionally, it can act as quorum sensing mimic of terrestrial plants and influence the microbial interactions of the microbe by promoting or inhibiting acyl-homoserine lactone (AHL) genes (Gao et al. 2003).

Based on profiling of marker genes or shotgun metagenome sequencing, cultivation-independent approaches allow us to gather considerable information on the microbial communities from various hosts (Levy et al. 2017). It is difficult to directly compare the results of these studies due to the different sampling methods and sequencing pipelines, but they have all revealed the core microbiome in the rhizosphere (Muller et al. 2016). For example, many independent studies have depicted *Proteobacteria* as predominant members of the rhizosphere (Xu et al. 2018), which is in accordance with fast-growing *Proteobacteria* possessing the ability to use a large number of root-derived C substrates (Philippot et al. 2013). Over the past decade, large-scale transcriptomics, metagenomics, proteomics, and combinations thereof were used to study composition of plant microbiome to explore environmental adaptation. Although metagenomic surveys allow the identification of enriched functional categories, complementary approaches are needed to verify the function via addressing gene expression patterns and dynamics (Muller et al. 2016).

Exploring the plant-microbe interactions with dynamic imaging and microfluidics

Different microhabitats formed by plant roots are colonized by adapted microbes ranging from beneficials to pathogens. However, spatial distributions at microscale, which are fundamental to explore the dynamics of root-microbe interactions, are usually lost during the sampling process for molecular analysis (Lugtenberg 2015). The bottleneck in the research of plant-microbe interactions is that the underground roots cannot be observed and studied without disturbance. One of the principal ways of overcoming this is adopt separation device such as rhizobox and artificial media, but they cannot explore the interactions in real time (Poole 2017). Therefore, it is useful to complement the indirect multi-omics with direct visualization methods, which could construct the relationships of temporal-spatial distributions of root exudates and microbiome. The most used visualization technology contains isotope imaging, chemical imaging, and microbial imaging (Oburger and Schmidt 2016). As for isotope imaging, nanoscale secondary ion mass spectrometry (NanoSIMS) could image the isotope distributions at individual cells (50-100 nm) level (Herrmann et al. 2007; Polerecky et al. 2012). Chemical imaging techniques comprising optical sensors enable real-time mapping dynamics and distributions of analyte concentrations around the rhizosphere, such as O_2, pH, and CO_2 (Koren et al. 2015; Oburger and Schmidt 2016). Recently, three-dimensional spatial distributions of root exudate were addressed by matrix-assisted laser desorption/ionization mass spectrometry imaging (MALDI-MSI), and a more complex metabolic view of plant–bacteria symbiosis within soybean nodules than previously hypothesized was established (Velickovic et al. 2018). With regarding to microbial imaging, the most reported fluorescence in situ hybridization (FISH) could identify, visualize, and quantity the single prokaryotic cells *in situ* (Amann and Fuchs 2008). The catalyzed reporter deposition combined with FISH (CARD-FISH) can further increase the signal intensity to achieve precise localizations for related host colonization strategies by microbe (Edwards et al. 2015).

To track the dynamics of interactions at high spatial resolution, the microfluidic technology could directly image of the interactions in real time. Microfluidics-based approach has been described for studying the real-time interactions between *Arabidopsis thaliana* and fluorescently labeled *Bacillus subtilis* at the microscale. The author showed the obvious chemotaxis of *B. subtilis* toward roots surface and exclusion of *Escherichia coli* after colonization (Massalha et al. 2017). Hence, this new technology holds the potential to broaden our understanding of the mechanisms underlying plant-microbe interactions and microbiome community assembly. At present, the application of this technology mainly stays in the interaction between plants and single cell.

Tracing rhizosphere biogeochemical processes with isotopes

The uptake and release of carbon (C) by plants can be traced by the radioactive and stable isotopes (Oburger and Schmidt 2016). Using isotopes of ^{14}C and ^{13}C, researchers have successfully uncovered the rhizosphere C cycling (Haichar et al. 2016). For example, $^{13}CO_2$ pulse labelling and phospholipid fatty acid stable isotope probing (PLFA-SIP) technique were used to study the effects of rice straw amendment on microbial consumptions of maize root exudates under rice-maize crop rotation, which demonstrated the presence of the rice straw decreased the utilization of root exudates by rhizosphere microorganisms (Maarastawi et al. 2019). Recently, DNA and RNA-SIP approaches combined with molecular biology methods allows to study metabolically active microbes that assimilate root exudates in detail (Oburger and Schmidt 2016). The fractionated DNA/RNA samples via ultracentrifuge allows in-depth analysis of active microbe that uptakes the enriched isotopes (Pett-Ridge and Firestone 2017; Yuan et al. 2016). SIP techniques are needed for analysis of root exudate–microbe interactions in depth (Oburger and Schmidt 2016).

Reduce fertilization by modulating the root microbiome for improving plant nutrient acquisition

The traditional agricultural systems depend on large-scale application of fertilizers, which causes a series of environmental problems (Coskun et al. 2017). Improving low N fertilizer use efficiencies and decreasing the N losses is vital for development of sustainable agriculture. Root exudates can recruit beneficial microbes helping the plants to take up more N via enriching diazotroph for biological N fixation (BNF), increasing N bioavailability, or promoting N conservation in soil by inhibiting microbial processes responsible for N losses (Fig. 2). In addition to N, root exudates can also increase the availability of phosphorus and iron in the rhizosphere, which will be discussed below.

Root exudates recruit beneficial microbes to acquire N

A wide range of microbes can convert atmospheric N (N_2) into ammonia, which could be assimilated by plants. To benefit from this function, various plants establish mutualistic interactions by releasing secondary metabolites for free-living N-fixing bacteria to enter the roots (Moreau et al. 2019). Among them, the symbiotic relationship between legume family members and *Rhizobium* family is the most studied beneficial plant-microbe interactions. *Rhizobium* enters the root cells legume and induces the formation of nodules, which fixes N_2 and converted it into ammonia. (Moreau et al. 2019). In addition to *Rhizobium*, legumes can symbiotically nodulate with *Bradyrhizobium*, *Sinorhizobium*, *Mesorhizobium*, and *Azorhizobium* in soils (Lugtenberg 2015). During this symbiosis, the plants secrete flavonoids into the rhizosphere, inducing the expression of nodulation genes of *Rhizobium* to synthesize nod factor, which

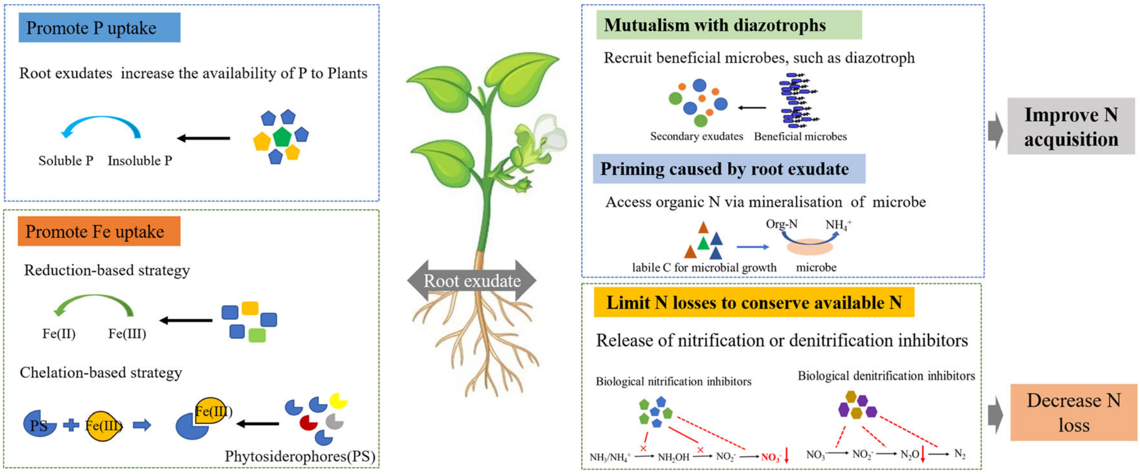

Fig. 2 Routes of beneficial interaction that root exudates could modify the rhizosphere microbiome to reduce dependence on fertilizers

recognized by plants. In addition, N_2-fixing bacteria, which do not form nodules are also be recruited by plants (Moreau et al. 2019). For instance, under N-depleted conditions, boreal feather mosses likely release chemo-attractants that induce N_2 fixing cyanobacteria which contribute to its N element (Bay et al. 2013). In N-depleted soils in Mexico, diazotrophs were enriched in the mucilage of maize aerial roots, and the major components of mucilage, such as arabinose, fucose and galactose, can be used by diazotroph as energy sources (Van Deynze et al., 2018). A recent study provides a new sight into positive relationships among an exotic endophytic fungus, crop nodulation, and N_2 fixation. *Phomopsis liquidambaris* was found to increase the expression of genes related with phenolic and flavonoid synthesis of peanut plant (*Arachis hypogaea* L.), and the root derived phenolics and flavonoids could effectively increase the expression of nodulation gene in *Bradyrhizobium* to increase the crop yields (Xie et al. 2019). Taken together, these findings highlight the potential of root exudates and microbes for improving N uptake. However, further investigations on the mechanisms underlying the recruitment of N-fixing bacteria by plants are needed.

Root exudates enhance microbial mineralization of soil organic N

Another strategy for plants to cope with N limitation is the rhizosphere priming, which refers to the stimulation/suppression of soil organic carbon decomposition by live roots and associated rhizosphere organisms compared to that by rootless soils when the environmental conditions are kept the same (Wang et al. 2020). The supply of fresh plant-derived C can suppress soil organic matter decomposition rates by 50% or stimulate it by 380% (Cheng et al. 2014). Rhizosphere priming is important for plants having access to organic N in soil (Moreau et al. 2019). Release of labile C from the root are shown to increase rhizosphere microbial growth and microbial N demand, and promoted mineralization of organic N in soil (Meier et al. 2017). The transformation of organic N to ammonia by microbes is the major process of soil N supply to plants (Landi et al. 2006). Therefore, the root-derived C might establish an evolutionary strategy between plants and rhizosphere microbiome, in which root-derived C could be used by microbes as energy sources, and, in turn, microbes benefit their hosts for N acquisition through enhanced mineralization of organic N in soil (Cheng et al. 2014).

Root exudates limit N losses to conserve available N

Biological nitrification inhibitors (BNI) in root exudates to minimize N losses as well as agricultural pollution are being actively studied (Coskun et al. 2017). The concept of BNI was first introduced by G. V. Subbarao (Subbarao et al. 2006). Since then, their presence and functions have been characterized in sorghum, wheat, *B. humidicola*, and rice (Pariasca Tanaka et al. 2010; Subbarao et al. 2013; O'Sullivan et al. 2016; Sun et al. 2016). To date, however, only few BNI have been isolated, such as Methyl 3-(4-hydroxyphenyl) Propionate (MHPP) (Zakir et al. 2008), Brachialactone (Subbarao et al. 2009), Sorgoleone, Sakuranetin, and 1,9-Decanediol. It is reported that BNI could restrain ammonia monooxygenase (AMO) while brachialactone, sorgoleone, and sakuranetin could restrain hydroxylamine oxidoreductase (HAO). The first and also the slowest step of nitrification is to oxidize ammonia into hydroxylamine, which is catalyzed by AMO, while the second step of nitrification is to oxidize hydroxylamine into nitrite, which is catalyzed by HAO. As a result, the nitrification process is restrained (Coskun et al. 2017). Previous studies on BNI have focused on its impact on ammonia oxidizing bacteria and archaea primarily because that ammonia oxidation is the rate-limiting step of nitrification. Laffite et al. (2020) discovered that BNI can directly inhibit the growth of *Nitrobacter hamburgensis* X14 from the litter or soil extracts of forest system trees (Laffite et al. 2019).

Denitrification is the other microbial process which leads to losses of mineral N from terrestrial ecosystems, however, the effects of root exudates on the denitrification process are largely unknown (Coskun et al. 2017). A previous study has found the denitrification potential in the root of invasive plant *Fallopia* sp. was low, and identified the biological denitrification inhibitor (BDI) (Bardon et al. 2014). This result indicated that invasive plants conserve the available N for growth to outcompete native plant species via inhibiting the denitrification process (Bardon et al., 2017). Plants can inhibit denitrification process by up to 80% via releasing procyanidins (Bardon et al. 2014; Bardon et al. 2016). The possible mechanism is that procyanidins could influence the stability of the cell membrane by acting as an allosteric inhibitor (Bardon et al. 2016). Besides, N losses could also be reduced via the dissimilatory nitrate reduction to ammonium (DNRA), a widely distributed process in soils which transformed the mobile nitrate into immobile ammonium by microbes. DNRA is probably a preferred process in the rhizosphere due to the higher C, which help plants conserve N in soils. This is supported by a research indicating that genes encoding enzymes responsible for DNRA were overrepresented in the rhizosphere in comparison with bulk soils (Li et al. 2014).

Root exudates promote phosphorus and iron uptake

In addition to N, root exudates can also promote the availability of other micronutrients such as phosphorus (P) and iron (Fe). P in the soil can react with cations in the soil (e.g., calcium ions) to form phosphates which are only sparingly soluble. As a result, the concentration of P in the soil is usually very low. Previous studies have shown that root exudates increase P availability in the system intercropping tomato and potato onion (Khashi u Rahman et al. 2021). In addition, when the soil is in deficiency of P, citrate and phytase present in the root exudates of tobacco were shown to improve the efficiency of P acquisition in tobacco (Giles et al. 2018). Furthermore, different root exudates were released in response to the of change P concentration (Pantigoso et al. 2020).

Fe is one of the most abundant elements in the soil, however, its availability to plants is usually limited due to the low solubility of its compounds. A lot of studies are conducted to reveal the role of root exudates in improving Fe acquisition. Generally, there are two strategies to improve iron acquisition, including reduction-based strategy and chelation-based strategy (Lo et al. 2016; Chen et al. 2017). Root exudates such as riboflavin, phenolic compounds, and phytosiderophores play important roles in Fe acquisition (Chen et al. 2017). Recently, it was found that coumarins, exudate by *Arabidopsis* root, play an important role in mobilizing Fe via reduction and chelation (Tsai and Schmidt 2017).

Reduction of pesticide dependence by shaping the rhizosphere microbiome to enhance plant defense

Biotic stresses, such as pests and pathogens, lead to significant decline in crop growth and yield, which threatens global food security worldwide (Liu et al. 2020). Roots of healthy plants are colonized by multi-kingdom microbial consortia, which help plants fight against pathogens and pests (Duran et al. 2018). However, so far, the knowledge of how specific plant root exudates recruit specific microbial taxa is limited (Bakker et al. 2018). The activation of the plant immune system under the attack of leaf pathogens led to the change of rhizosphere microbial community, indicating that plant immune signals and rhizosphere microbial community assembly are functionally related (Bakker et al. 2018).

Recently, with the development of metabolomics technology, more and more root metabolites have been identified, which play important roles in plant defense against pathogens (Table 2), and *Arabidopsis* is emerging as a valuable model system to address intricate relationships among the host and its colonizing microbes (Bakker et al. 2018; Muller et al. 2016). One of the strategies to strengthen plant defense is the root can release secretions to recruit beneficial microorganisms under pathogen attack, also referred to as “cry for help” (Bakker et al. 2018). The beneficial microbes may activate plant defense signaling pathways and/or restrain the virulence and growth of pathogens by secreting antibiotics (Liu et al. 2020) (Fig. 3). For example, on pathogen invasion, members of the *Chitinophagaceae* and *Flavobacteriaceae* were enriched in the root endosphere and protect plant against disease (Carrión et al. 2019). After *A. thaliana* is infected by *Pseudomonas syringae*, the root system secretes a large amount of malic acid and recruits *Bacillus subtilis* FB17, thereby activating the plant immune system (Yuan et al. 2018). Genus *Streptomyces* secrete secondary metabolites such as lantipeptides, which inhibit the *Fusarium* wilt of strawberry caused by *Fusarium oxysporum* (Kim et al. 2019). Under attack by pathogen *Pythium ultimum*, the secretion of vanillic acid, fumaric acid, and p-coumaric acid from barley root increased and they could induce *Pseudomonas fluorescens* CHA0 to colonize and synthesize antibiotic 2,4-diacetylphloroglucinol (DAPG) (Jousset et al. 2011). These results indicated that plants recruit beneficial microbes which produce antimicrobial compounds when attacked by pathogens. Plants root

Table 2 Root metabolites and their functions in plant defenses

Root metabolites	Functions	Reference
Malic acid	Recruits *Bacillus subtilis* FB17 and activates the plant immune system	(Yuan et al. 2018)
Salicylic acid	Immune signal or carbon source, mainly inhibits *Actinobacteria* and enrich *Proteobacteria*	(Sarah et al. 2015)
Jasmonic acid	Enriches bacteria for biological control	(Ruan et al. 2019)
Benzoxazinoids	Alter the root microbiome, decrease plant growth, increase jasmonate signaling and plant defenses, and inhibit herbivore in the next generation of plant.	(Hu et al. 2018)
Triterpene	Plant defense and antimicrobial activities, regulate the growth of root bacteria of *Arabidopsis thaliana*	(Huang et al. 2019)
Coumarin	Inhibits the soil-borne fungal pathogens *Fusarium oxysporum* and *Verticillium dahliae* by affecting assemble of rhizosphere microbiome	(Stringlis et al. 2018)
Rosmarinic acid	Functioned as an homoserine lactone mimic, and it is a plant defense mechanism to stimulate a premature quorum sensing response	(Corral-Lugo et al. 2016)
Salicylic acid	Defense phytohormone and act as a selective filter for rhizosphere microbiome	(Sarah et al. 2015)

metabolites, such as benzoxazinoids, triterpene, and coumarin, or their breakdown products were also found to repel some soil-borne bacteria and fungi (Cotton et al. 2019). A recent study by Hu et al. (2018) demonstrated that benzoxazinoids (BXs) altered root-associated fungal and bacterial communities, and promote jasmonate signaling to enhance plant defense, thereby inhibiting the effects of herbivores on the next generation of plants. Complementation experiments further demonstrated that the breakdown product 6-methoxy-benzoxazolin-2-one (MBOA) of benzoxazinone triggered the observed phenotypic changes (Hu et al. 2018).

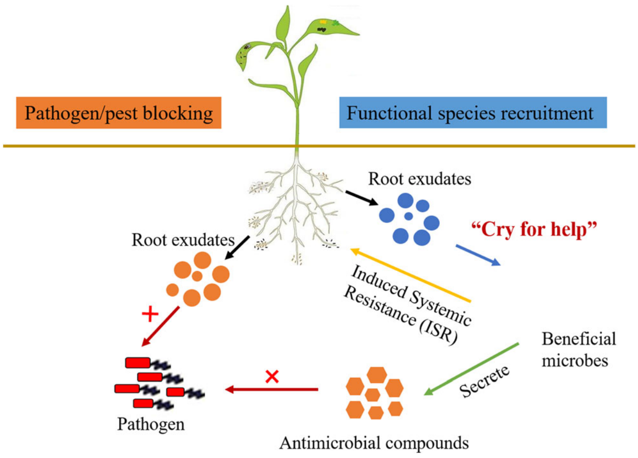

Fig. 3 Direct and indirect plant defense mechanisms mediated by root exudates. Direct plant defense means that root exudates could suppress pathogens and pests. Indirect plant defense refers to root exudates can drive plant-microbe feedbacks for defense by changing the rhizosphere microbiome by recruiting beneficial microbes, and these microorganisms can enhance plant defense through two pathways, one is to activate plant defense signaling pathways, the other is to secrete antimicrobial compounds to inhibit pathogens

Recently, a number of studies have tried to address the regulatory networks of plants genotypes for root metabolite biosynthesis involved in plants immune responses. Triterpenoids are plant-specific metabolites, which are involved in plant defense and signal transduction, and also have antibacterial activities. Huang et al. (2019) demonstrated that the triterpene biosynthesis network has the potential to synthesize more than 50 root metabolites. These root metabolites can selectively regulate *Arabidopsis* root microbiome by acting as antibiotics or proliferating agents. Cotton et al. (2019) compared the impact of three genetic mutations in different steps of BXs bio-synthesis pathway by non-targeted mass spectrometry analysis combined with amplicon sequencing, and established relationships between BX-regulated root metabolites and BX-dependent rhizosphere microbiome (Cotton et al. 2019). Adversely, when plant growth regulators and genotype are known, researchers focus on identifying the products of the transcription regulators and its effect on rhizosphere microbiome. In the model system of *Arabidopsis thaliana–Pseudomonas simiae* WCS417, the regulation mechanisms of root-specific transcription regulators MYB72 and the MYB72-controlled β-glucosidase BGLU42 on beneficial rhizobacteria-induced systemic resistance was explored. The antimicrobial scopoletin was identified as a dominant root exudate that is excreted into the rhizosphere regulated by MYB72- and BGLU42, and the scopoletin selectively inhibits soil-derived fungal pathogen *Verticillium dahliae* and *Fusarium oxysporum* (Stringlis et al. 2018).

However, root exudates also have negative effect on plant growth, and they mainly promote soil-borne diseases in two ways. One is that the autotoxins and allelochemicals secreted by plants can aggravate soil-borne diseases. For example, cinnamic, myristic and fumaric acids in tobacco root exudates was found to improve the expression of chemotaxis- and motility-related genes in *Ralstonia solanacearum*, and promoted *R. solanacearum* colonization and accelerate disease progression in tobacco (Li et al. 2017). The other is that they can promote the growth of pathogens through changing interactions between pathogens with other key species. For example, it was found that after the addition of sugar, the rapid growth and reproduction of *Fusarium* wilt pathogens were mainly due to the positive interactions between the keystone taxa with *Fusarium* wilt pathogens, which promoted the rapid growth and reproduction of pathogens (Ren et al. 2020). Therefore, the interaction mechanisms between rhizosphere pathogens and root exudates or other microbes are needed to clarify, which could also a basis for control technology of soil-borne diseases.

Current challenges and future directions

Multi-omics integration to reveal the root-microbe interactions

So far, there is limited understanding of how specific plant root exudates shape the microbiome to enhance plant growth and fitness. One major challenge in studying rhizosphere metabolites is to determine which composition in the samples can truly represent the root exudates *in situ*, because root exudates are affected by many factors, especially root microorganisms (Oburger and Schmidt 2016). Therefore, the application and optimization of metabolomics are required to identify real released secretions of plants *in situ* (van Dam and Bouwmeester 2016). Moreover, metabolomics, in combination of metagenomic and transcriptomic and stable isotope probing (SIP), are urgently needed to further comprehensively reveal the molecular regulation mechanisms of root exudates on microbiome assemble. More research in needed to clarify the role of genetic pathways in regulating plant immunity, and how does nutrient acquisition coordinate the selection of microbial traits (Bakker et al. 2018). It is meaningful to identify specific genes whose products interact with root-associated microbes, and to explain the role of genes in defining the functions (Lundberg and Teixeira 2018). When the functions of root metabolites are known, it is necessary to look up upstream for gene networks of plants that regulate root metabolites biosynthesis and secretion. Inversely, in order to identify the products of specific genes, future research should focus on exploring the types of root exudates showing significant response to the regulatory genes using metabolomics. Furthermore, wild-type plants and constructed mutants (unable to secret targeted root exudates) could be applied to reveal whether the effect mechanism on microbiome assemble is gene-specific (Fig. 4).

Imaging of root dynamic changes at continuous spatiotemporal scale

Visualization technologies can be used in agricultural decision support systems and prescriptive crop planning, which can finally improve crop production in agriculture (Poole et al. 2017; Gutiérrez et al. 2019). Nevertheless, currently, as the data acquisition is still a complex and cost-ineffective process, it is only limited to several times and sample points (Oburger and Schmidt 2016). Therefore, one future research direction is to continuously track and visualize the dynamic process under the influence of plant roots in space and time. Meanwhile, sufficient number of replicates and appropriate selection of the field of view are indispensable for critical interpretation of the obtained imaging results (Oburger and Schmidt 2016). Faster image acquisition, higher resolution, and time-lapse approaches are urgently needed to increase the amount of root image data (Downie et al. 2015).

Synthetic communities to uncover the causal relationships between plant phenotypes and microbiome assemble

Techniques like cultivation-independent profiling of rhizosphere microbiome have demonstrated the positive associations between microbes with host plants. However, the relationships of plant-microbe and microbe-microbe *in situ* are too complex to study the interaction mechanisms. For example, root exudates shape rhizosphere microbiome, and on the contrary, the compostion of rhizosphere microbiome alters root exudates profile (van Dam and Bouwmeester 2016). Thus, the interaction between root exudate and soil/rhizosphere microbiome causes difficulties in revealing the cause-effect relationship. More research is needed to elucidate the biological mechanisms involved in the causal relationships between plant phenotypes and microbiome assemble (Vorholt et al. 2017). It is necessary to complement the cultivation-dependent approach to study plant-microbe interactions with the aim to uncover the basic principles for application, such as synthetic communities (Fig. 5). Using bottom-up combined approach to construct synthetic communities by mixing selected strains and appling them to plants is a way of studying the interactions between plants and microbes, including identifying the specific

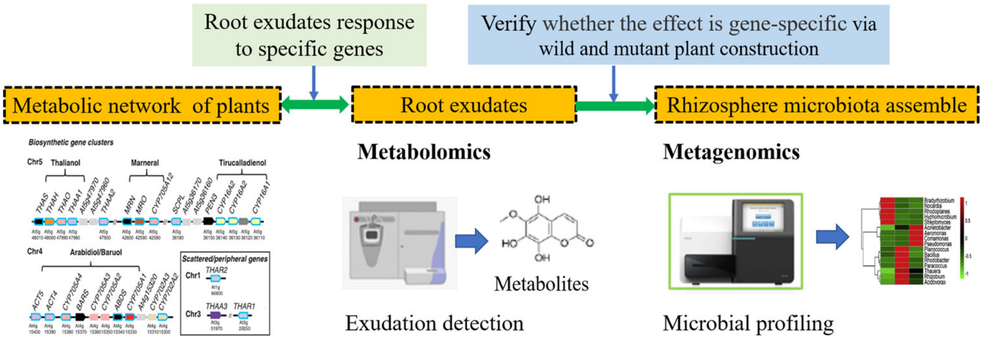

Fig. 4 An integrated tool for identifying the specific genes whose products interact with rhizosphere microbiome

mechanisms for micriobial assembly and the interaction between different members (Trivedi et al. 2020). These mechanisms could be then be translated into agricultural applications to optimise agricultural productivity and guarantee crop health (Vorholt et al. 2017). Another future direction is manipulating of the native microbiome by engineering plants that can recruit specific microbes via the production of root exudates (Fig. 5). Revealing the mechanisms between plant phenotypes and microbiome assemble could help harness genomic trait of plants to producing root exudate that attract beneficial microorganisms via gene editing (Singh et al. 2020). Especially, genetic manipulation of secondary metabolites biosynthesis pathways can provide new tools for rational manipulation of plant microbiome, and should be further studied to help the sustainable development of agriculture (Jacoby et al. 2021).

Conclusions

The effects of root exudates on shaping the rhizosphere microbiome, especially in the context of plant fitness and health, are poorly understood due to the inherent complexity of the biological system. Multifaceted approaches are needed to uncover the interaction mechanisms of root exudates and rhizosphere microbiome. Strategies for improving crop yield consist of breeding plants that select for beneficial microbes. Multi-omics and visulization techology, together with synthetic communities approach hold great potential for combining top-down and bottom-up studies to explain plant-microbe interactions and microbial community assembly. These fundamental principles and knowledge can be used to achieve sustainable development of the next-generation agriculture to solve the challenges of food security.

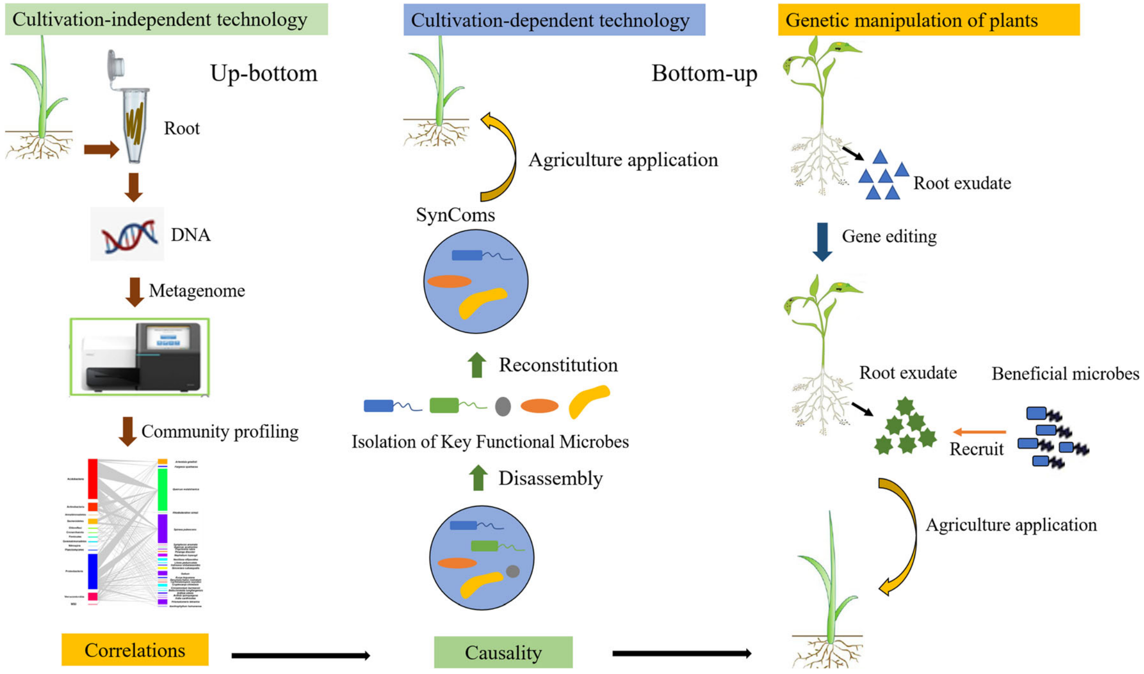

Fig. 5 Approaches to uncover the causal relationships between plant phenotypes and microbiome structure and functions and agricultural applications

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Data availability All data generated or analyzed during this study are included in this published article.

Declarations

Ethics approval and consent to participate Not applicable

Consent for publication Not applicable

Competing interests The authors declare no competing interests.

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