

Review Article

Linking plant functional genes to rhizosphere microbes: a review

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Summary

The importance of rhizomicrobiome in plant development, nutrition acquisition and stress tolerance is unquestionable. Relevant plant genes corresponding to the above functions also regulate rhizomicrobiome construction. Deciphering the molecular regulatory network of plant-microbe interactions could substantially contribute to improving crop yield and quality. Here, the plant gene-related nutrient uptake, biotic and abiotic stress resistance, which may influence the composition and function of microbial communities, are discussed in this review. In turn, the influence of microbes on the expression of functional plant genes, and thereby plant growth and immunity, is also reviewed. Moreover, we have specifically paid attention to techniques and methods used to link plant functional genes and rhizomicrobiome. Finally, we propose to further explore the molecular mechanisms and signalling pathways of microbe-host gene interactions, which could potentially be used for managing plant health in agricultural systems.

Introduction

Environment-friendly production of crops is one of the challenges in agricultural systems to feed growing population (Yashveer *et al.*, 2014). Increasing evidences indicate that the soil rhizomicrobiome benefit plant growth and health and therefore play an important role in dealing with this challenge (Bai *et al.*, 2022; Goh *et al.*, 2013; Mueller and Sachs, 2015; Pieterse *et al.*, 2014; Raza *et al.*, 2021). The host-associated microbiota inhabits inside various plant tissues and on root surface to access soil nutrients (Bai *et al.*, 2022). Microbial community structure is largely shaped by the host plant and external environment (Dastogeer *et al.*, 2020; Friesen *et al.*, 2011; Raza *et al.*, 2021). When plants are subjected to biotic or abiotic stresses, they can recruit beneficial microorganisms to help them resist these stresses by secreting a range of chemical factors, which is known as the 'cry for help' strategy (Bai *et al.*, 2022; Bakker *et al.*, 2018; Carrión *et al.*, 2019; Liu *et al.*, 2020; Liu and Brettell, 2019). To understand the comprehensive 'cry for help' strategy of plants, it is vital to unravel the molecular mechanisms of microbiome recruitment in the rhizosphere (Rolfe *et al.*, 2019; Zancarini *et al.*, 2021).

The functions of the plant genes are crucial for understand the signalling cascades that control plant development and stress responses (Depuydt and Vandepoele, 2021). A large number of genes functions have been identified in the model plant *Arabidopsis thaliana*. Frequently, a single gene or several genes can largely regulate traits such as nutrient uptake, disease resistance, and resistance to abiotic stresses in plants (Liu

et al., 2009; Wei *et al.*, 2022; Zhao *et al.*, 2021). These genes were further validated in different crops such as wheat, rice, maize, soybean and sorghum (Li *et al.*, 2018; Liu *et al.*, 2016; Maron *et al.*, 2013; Wei *et al.*, 2022; Yokosho *et al.*, 2011). In recent years, plant functional genes have also been found to play important role in shaping the rhizomicrobiome (Cordovez *et al.*, 2019; Zhang *et al.*, 2019). The discoveries of plant-microbe interaction at the molecular level provide a new direction for genetic breeding (Kroll *et al.*, 2017; Nerva *et al.*, 2022). Further research on microbes mutually interacting with the host genes is expected to cultivate new germplasm resources (Kroll *et al.*, 2017). Plant functional genes could regulate root phenotypic traits and the secretion of root exudates, such as organic acids and hormones (Kaushal *et al.*, 2021; Wang *et al.*, 2013, 2020; Yu *et al.*, 2021), which have been found to drive microbial community assembly in rhizosphere (Zhalnina *et al.*, 2018). For example, the expression of plant organic acid channel protein genes can promote the production of organic acid, which could recruit beneficial rhizosphere microorganisms by forming stable metal chelate complexes and increasing soil pH (Zhang *et al.*, 2017).

Rhizosphere microorganisms can also confer health advantages to plants by inducing the expression of plant functional genes (Berendsen *et al.*, 2018; Liu *et al.*, 2017). It has been proved that the expression of genes related to nutrient uptake and stress resistance is affected by structural and functional changes in the rhizosphere microbiota. These microbes can regulate the expression of plant functional genes by secreting secondary metabolites, producing volatile compounds and competing for nutrients,

thereby directly or indirectly influencing plant growth and development (Hacquard *et al.*, 2017; Hou *et al.*, 2021; Kwak *et al.*, 2018; Netzker *et al.*, 2020; Yuan *et al.*, 2018). Thus, there exists a complex network of interactions between functional plant genes and rhizomicrobiome and both of them play key roles for plant survival and growth (Berendsen *et al.*, 2018; Depuydt and Vandepoele, 2021). However, whether plant genes or rhizobia have a greater influence on plant development is currently being debated, which necessitates particular plant-microbe contribution algorithms. Exploring this relationship will help us to develop crop varieties with strong adaptability and resistance to various stresses. So far, such studies are only the tip of the iceberg due to the complex mechanism of microbe-host gene interaction that involve multidisciplinary intersections (Rolfe *et al.*, 2019). Therefore, understanding how plant-microbe communication is established requires more experimental exploration using cutting-edge technologies.

Unprecedented technologies facilitate the investigation on the link of plant-specific genes to rhizosphere microorganisms (Fadiji and Babalola, 2020; Kumar *et al.*, 2019; Levy *et al.*, 2018; Liu *et al.*, 2020; Schaarschmidt *et al.*, 2020; Xu *et al.*, 2018). These technologies include plant-related CRISPR-Cas, transgenics and transgenic hairy roots and microbial-related 16S rRNA sequencing, GeoChip, metagenomics and synthetic communities. Using the 'top-down' and 'bottom-up' designed methods and relevant techniques, great progress has been made in the mechanism of plant functional gene-microbe interaction (Chi *et al.*, 2018; Ke *et al.*, 2021; Lawson *et al.*, 2019; Xu *et al.*, 2021b). Here, we summarized how plant-specific genes regulate rhizomicrobiome, and in turn how rhizomicrobiome influence the host genes, as well as the research methods used.

Most microorganisms in nature are unculturable (Kaeberlein *et al.*, 2002). Yet minute and complicated experimental conditions and media combinations have to be considered in the culturable ones, greatly obstructing the development of microbiomics (van Teeseling and Jogler, 2021; Xing *et al.*, 2017). To overcome the shortcomings of pure culture, the microbiome sequencing technology has been developed in recent years (Liu *et al.*, 2012). It became clear that the microbiome could not be fully characterized at the genetic and transcriptional levels (Gao and Chu, 2020). Thus, the development of metaproteomics and metabolomics is particularly necessary for microbial functional studies (White *et al.*, 2016). The unprecedented development of microbiome technologies mentioned above has enabled an in-depth analysis and understand the composition and function of host-associated microbiota (Shao *et al.*, 2021).

Plant functional genes regulate rhizosphere microorganisms

Plant-specific genes influence rhizomicrobiome based on molecular signalling, which is essentially a 'top-down' process. Increasing number of studies examine how plant functional genes affect microbes at the molecular level, such as the structure of rhizomicrobiome selected by cultivars with the same high nutrient use efficiency and stress resistance (Chen *et al.*, 2019; Qiao *et al.*, 2017; Shi *et al.*, 2020). Although some genes explain only a small part of the total variance in the rhizomicrobiome, the microbiome is increasingly considered as an important predictor of plant phenotype (Bai *et al.*, 2022; Ravanbakhsh *et al.*, 2019; Zancarini *et al.*, 2021). In this section, we will specifically address

rhizomicrobiome that are likely regulated by plant functional genes regarding nutrient uptake genes, disease and abiotic stress resistance genes.

Nutrient uptake-related genes affect rhizosphere microbes

Plant growth and development heavily depend on the availability of nutrients that the root system can access to, indicating that plants have to face enormous challenges in extracting nutrients for cellular activities, and any lack of nutrients may decrease the productivity (Morgan and Connolly, 2013; Sukumar *et al.*, 2013). As a result, some plant species have 'risen to the occasion' and attempted to recruit soil microorganisms by regulating nutrient uptake genes to enhance defence capability against nutrient deprivation (Millet *et al.*, 2010; Teixeira *et al.*, 2019; Zhang *et al.*, 2019). The main mechanism of nutrient-uptake-related-genes regulating rhizosphere microbes is its capability to increase root surface area, root hairs and lateral roots that are key factors to alter the rhizosphere microbial community (Figure 1a; Contesto *et al.*, 2010; Ditengou *et al.*, 2000; Felten *et al.*, 2009; Hirsch *et al.*, 1997; Yu *et al.*, 2021). For example, the maize (*Zea mays*) mutant rootless meristem 1 (*rum1*) is defective in the initiation of embryonic seminal roots and postembryonic lateral roots in primary roots. *Rum1* gene is an important checkpoint for auxin-mediated initiation of lateral and seminal roots in maize, which may participate in the molecular network of root formation by regulating auxin transport in primary roots and auxin perception in primary root pericytes and influencing lateral root formation (Woll *et al.*, 2005). Recently, it has been shown that the rhizosphere bacterial diversity along the root development region of the maize mutant *rum1* is significantly reduced compared to the wild type (Yu *et al.*, 2021). This is because the mutant *rum1* lacks lateral roots, limiting water and nutrient acquisition during early developmental stages. This suggests that root development-related genes can control the length and number of lateral roots by mediating a number of keys signalling substances, which in turn affect the microbial composition in the rhizosphere.

A number of genes related to nutrient uptake and transport have been identified, such as ammonium nitrogen, nitrate nitrogen and phosphate root transporters (Wei *et al.*, 2010; Zhu *et al.*, 2016). For instance, several plasma membrane transporters involved in NO₃⁻ have been identified in *Arabidopsis* and other crops (Hu *et al.*, 2015; Wang *et al.*, 2012). *NRT1.1B* was found that largely explain the differences in nitrogen utilization efficiency between indica and japonica, which are the two main rice subspecies rice in Asian (Hu *et al.*, 2015). Moreover, *NRT1.1* not only transports nitrate but also promotes uptake of the growth promotion hormone from the rhizosphere, which affects lateral root development (Krouk *et al.*, 2010; L eran *et al.*, 2013; Teng *et al.*, 2019). It has been found that wild-type rice has more rhizosphere microbes involved in the nitrogen cycle compared to the *NRT1.1B* mutant. *NRT1.1B* is associated with the relative abundance of root bacteria that harbour key genes in the ammonification process, and these microbes may catalyse the formation of ammonium in the rhizosphere environment and thus affect the acquisition of nitrogen in plants (Zhang *et al.*, 2019). Another example is that Adenosine triphosphate binding cassette (ABC) transporter proteins include a large family have been shown to be involved in membrane transport of endogenous secondary metabolites in plants (Badri *et al.*, 2008; Yazaki, 2005). Some of these members in this family are

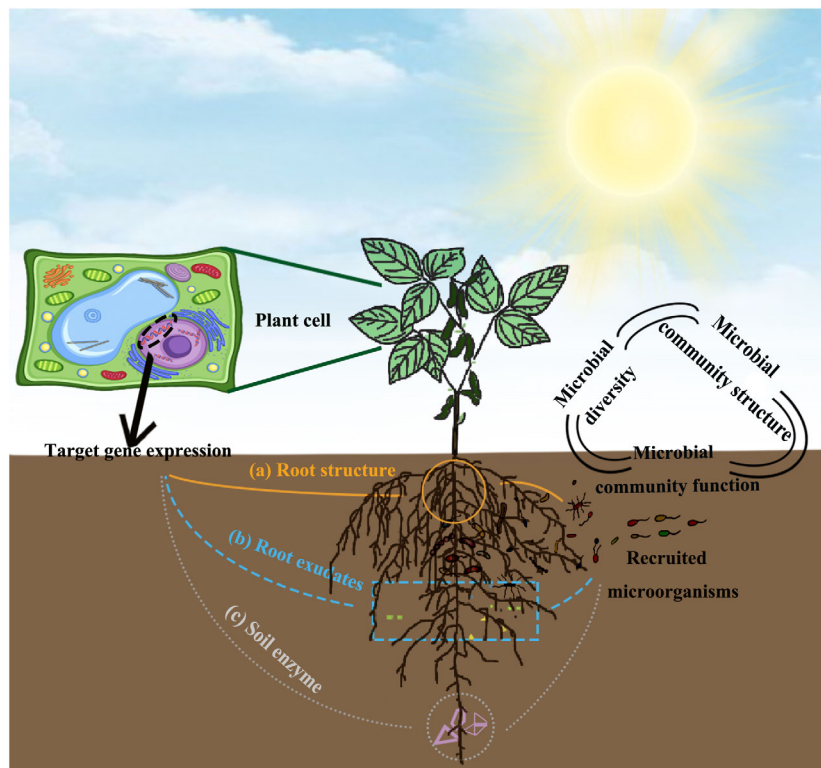


Figure 1 Plant functional genes regulate rhizosphere microbial diversity and function. (a) The development of root morphology (e.g., root length, number of lateral roots) is determined by the relevant plant genes, which usually regulate the synthesis of substances required for root morphology at the genetic and transcriptional levels. Changes in root structure imply differences in the ability of roots to supply nutrients, which affect the assembly of the rhizosphere microbial community to some extent; (b) Plant functional genes influence rhizosphere microbial diversity and structure through the control of root exudates (e.g., phenolics, flavonoids, hormones). (c) The expression of host-specific genes has a regulatory effect on soil enzyme activity, which in turn is closely related to microorganisms. However, whether plant functional genes can affect microbial diversity, and function by regulating soil enzyme activity remains to be further demonstrated by relevant studies. In short, plant genes can alter the diversity and assembly of rhizosphere microbes. Nevertheless, during these alterations of rhizosphere microorganisms, the functions of the original microbial community may be changed with the newly recruited microorganisms.

important in the secretion of antifungal diterpenes and heavy metal detoxification (Brunetti *et al.*, 2015; Jasiński *et al.*, 2001). Studies have shown that *Arabidopsis* mutants with damaged ABC transporter *abcg30* (*Atpdr2*) increase and decrease the secretion of phenols and sugars, respectively, forming a specific microbial community capable of resisting or degrading phenolic compounds enriched in *abcg30* plant secretions and thus reducing rhizobacterial diversity (Badri *et al.*, 2009; Cordovez *et al.*, 2019). Furthermore, karrikin (KAR)/KAR-like Signals (KLS)/D14L-ligand-responsive genes were proved to promote the production of strigolactones and flavonoids, which selectively modify the composition of the rhizomicrobiome (Wang *et al.*, 2020). These studies suggest that some nutrient uptake and transport-related genes can influence rhizomicrobiome composition by regulating root cell transporter protein activity, secreting root exudates (e.g., secondary metabolites, organic acids, hormones) and thus regulating plant nutrient utilization and altering root environmental conditions (e.g., soil pH, O_2 partial pressure, carbon source; Figure 1b; Kaushal *et al.*, 2021; Liu *et al.*, 2022; Wang *et al.*, 2013, 2020; Wen *et al.*, 2022; Yu *et al.*, 2021). Moreover, some root secretions can act as signals to initiate rhizosphere chemical communication recognition processes, thereby influencing microbial-based crop growth-defence trade-off strategies (Chen *et al.*, 2020; Lareen *et al.*, 2016; Vives-Peris *et al.*, 2020).

There exist some specific mechanisms in legumes by which nutrient uptake-related genes (e.g., genes that control nodulation and thus increase nitrogen uptake) regulate rhizomicrobiome. This is because symbiotic nitrogen fixation by rhizobia is a mutually beneficial symbiotic process established between legumes and rhizobia through the activation of rhizobia-induced signalling pathways and the expression of functional genes required for nodule primordium formation (Gao *et al.*, 2021; Yang *et al.*, 2022). Many important genes, including nodule initiation (NIN), nodule requirement (ERN1), Nod factor receptor 5, lotus root histidine kinase 1 and some micro(mi)RNAs, such as *MtmiR169a-MtNFYA1*, have been reported to be involved affect nodulation by regulating nodulation signalling pathways or mediating secreting of flavonoid and nitrate (affecting legume rhizobia infection; Combier *et al.*, 2006; Han *et al.*, 2020; Laloum *et al.*, 2014; Lorite *et al.*, 2018; Tsikou *et al.*, 2018). A recent study showed that overexpression of *miR169c* inhibited nodulation via targeting 3'-UTR of *GmNFYA-C*, while it promoted nodulation when *miR169c* lost its function (Xu *et al.*, 2021c). In the rhizosphere of prospective host legumes, rhizobia have a close cooperative or competitive relationship with soil microorganisms (Han *et al.*, 2020; Lorite *et al.*, 2018). For instance, exogenous rhizobia can increase the relative abundance of potentially beneficial microorganisms, thus altering the microbial

community structure and composition (White *et al.*, 2015; Xu *et al.*, 2020; Zgadzaj *et al.*, 2016; Zhong *et al.*, 2019). Moreover, *Bacillus cereus* group specifically promotes and suppresses the growth and colonization of *Sinorhizobia* and *Bradyrhizobia*, respectively (Han *et al.*, 2020). Therefore, legumes genes can also influence the establishment and modification of the rhizomicrobiome community by mediating rhizobial colonization and nodulation.

Overall, these studies suggest that nutrient-related genes can directly or indirectly influence the structure of rhizosphere microbial communities by altering root structure morphology, influencing plant nutrient use efficiency, regulating nodule colonization, and thus altering the rhizosphere microenvironment. These mechanisms can provide information for molecular breeding strategies to improve nutrient utilization and thus productivity in crops.

Disease resistance genes affect rhizosphere microbes

Plant growth in variable environment is threatened by various biotic stresses such as pathogen, and gradually domesticate the corresponding resistance mechanisms (Bakker *et al.*, 2018; Chen *et al.*, 2020; Li *et al.*, 2021; Liu *et al.*, 2020, 2021; Song *et al.*, 2021). When plants are invaded by pathogens, disease resistance genes will be activated, which in turn trigger plant-specific molecular immune recognition systems (Teixeira *et al.*, 2019). Previous studies have shown that the cell membrane receptor protein kinase FERONIA (*FER*) can regulate microbe-associated molecular patterns (MAMP)-induced reactive oxygen species (ROS) burst and basal ROS levels in roots through the small G protein (ROP2), which is a positive regulator of plasma membrane NADPH oxidase (Duan *et al.*, 2010; Stegmann *et al.*, 2017). After genetic analysis of different gene mutants, researchers found that ROP2-mediated basal level ROS regulation was essential for growth regulation of *Pseudomonas interrogans* (Bergonci *et al.*, 2014; Haruta *et al.*, 2014; Li *et al.*, 2016; Wang *et al.*, 2020; Zhu *et al.*, 2020). Researchers found that the *fer-8* mutant reduced basal levels of ROS in the root system after pathogen invasion and lacked NADPH oxidase mutants showed elevated rhizosphere *Pseudomonas* (Song *et al.*, 2021), suggesting that plants may mediate the plant immune system through the *RALF-FER* signalling pathway or affect the release of specific secretions that increase *Pseudomonas* populations to resist pathogen invasion (Figure 1b; Berendsen *et al.*, 2018; Liu *et al.*, 2017; Rudrappa *et al.*, 2008). As the most representative plant secondary metabolites, coumarins, benzoxazinoids and triterpenes play a pivotal role in improving plant disease resistance (Koprivova and Kopriva, 2022). Recently, it was found that two Multidrug and Toxic Compound Extrusion (MATE) transporter proteins (*CmMATE1* and *CIMATE1*) involved in the transport of their respective cucurbitacins (a triterpenoid unique to Cucurbitaceae). They further showed that the transport of cucurbitacin B from melon roots into the soil regulates the rhizosphere microbiome by selectively enriching two bacterial genera, *Enterobacter* and *Bacillus*, leading to strong resistance to the soil-borne wilt fungus *Fusarium oxysporum* (Zhong *et al.*, 2022; Zhou *et al.*, 2016). Together, these studies demonstrate that plants' disease resistance genes can recruit beneficial microorganisms or alter microbial community structure by activating the plant immune system or regulating the synthesis of several key metabolite in plants. These research efforts pave the way for the use of the

rhizosphere microbiome to improve resistance to soil-borne diseases.

Abiotic stress resistance genes affect rhizosphere microbes

In addition to biotic stresses, plant-microbial symbiotic organisms are also subjected to many abiotic stresses (Zhang *et al.*, 2020; Zhu, 2016), such as nutrient deficiency (i.e., nitrogen, iron and phosphorus) and high heavy metal (e.g., aluminium, cadmium and lead) stresses (Castrillo *et al.*, 2017; Fang *et al.*, 2020; Finkel *et al.*, 2019; Harbort *et al.*, 2020; López-Arredondo *et al.*, 2014; Ma, 2007; von Uexküll and Mutert, 1995). The *Arabidopsis* root-specific R2R3-type MYB transcription factor *MYB72* has become an important component of the induced systemic resistance (ISR) episode (Van der Ent *et al.*, 2008). In addition to its role in ISR, *MYB72* is also induced in *Arabidopsis* roots under growth conditions of iron limitation and distorted iron uptake (Buckhout *et al.*, 2009; Colangelo and Gueriot, 2004; van de Mortel *et al.*, 2008). It was strongly demonstrated that the transcription factor *MYB72* and *MYB72*-controlled β -glucosidase BGLU42 act key roles in regulating the beneficial rhizobacteria-ISR and iron-uptake responses, by regulating coumarin exudation to inhibit soil-borne fungal pathogens and promote the growth of growth-promoting and ISR-inducing rhizobacteria (Stringlis *et al.*, 2018). Rhizomicrobiome therefore have become a 'secret weapon' for plants to seize scarce soil iron resources, providing new ideas to regulate soil iron mobilization and activation, and promoting the widespread application of the plant functional gene-rhizosphere microorganism model in crop resistance to abiotic stresses (Stringlis *et al.*, 2018).

The plant MATE family transports a wide range of substrates such as organic acids, phytohormones and secondary metabolites (Magalhaes *et al.*, 2007; Seo *et al.*, 2012). The functions of many MATE transporter proteins have been illustrated in plants (Takanashi *et al.*, 2014), including the transport of secondary metabolites such as alkaloids (Shoji *et al.*, 2009), disease resistance regulation (Nawrath *et al.*, 2002; Sun *et al.*, 2011), iron translocation (Durrett *et al.*, 2007; Yokosho *et al.*, 2009) and Al detoxification (Wu *et al.*, 2014). MATE transporter proteins are also present and involved in Aluminium (Al) resistance and tolerance in crops such as rice, maize, soybean and sorghum (Liu *et al.*, 2016; Maron *et al.*, 2013; Yokosho *et al.*, 2011). When soybean was exposed to high Al stress, the expression of *GmMATE58* and *GmMATE1* genes increased, promoting the secretion of substances such as malic acid, oxalic acid and phenolic compounds (Chen and Liao, 2016; Li *et al.*, 2018; Liu *et al.*, 2016; Zhou *et al.*, 2018), which can recruit beneficial microorganisms to enhance soybean to resist Al toxicity. In particular, the recruited microorganisms, such as *Burkholderia*, can improve the solubility of phosphorus in the soil and undergo denitrification, thus improving soybean tolerance to Al toxicity (Lian *et al.*, 2019). Noteworthy, not only the normal or overexpression of genes but also the loss of plant functional gene can affect the host resistance to various stresses. Our recent research found that the rice could influence rhizosphere microorganisms by changing plant metabolites, such as salicin, arbutin, glycolic acid phosphate, after loss of the function of *sst* (seedling salt tolerant) gene and then assist host to resist salt stress (Lian *et al.*, 2020). These studies illustrated that, like nutrient-related genes, abiotic stress resistance genes can regulate rhizobia by inducing systemic stress resistance and regulating specific metabolites.

The expression of host-specific genes also has a regulatory effect on soil enzyme activities (Figure 1c; Chen *et al.*, 2011; Fließbach *et al.*, 2012). This mainly attributes to that soil enzymes are mainly derived from exudates of plant root (Guan *et al.*, 1986) and metabolites of microorganisms (Zimmermann and Frey, 2002). The amount and functions of microorganisms were closely related to the activities of soil enzymes (Durán *et al.*, 2018; Velmourougane and Blaise, 2017), including urease, sucrase and cellulase. The transgenic *AFPCI* disease-resistant sugar beet was found to have increased urease, dehydrogenase, protease, catalase, pronase, acid and alkaline phosphatase activities through greenhouse trials (Bezirganoglu and Uysal, 2017). However, it has been reported that tobacco planted with trans-antimicrobial protein gene and trans-null plasmid gene had some inhibitory effects on peroxidase and urease activities in purple soil at specific periods (Wang *et al.*, 2013). It remains to be further verified that plant disease resistance genes may affect the assembly of rhizosphere microorganisms by regulating the activity of soil enzymes.

Mechanisms of genes regulating the rhizosphere microbes

According to the description above, plant functional genes affect rhizomicrobiome mainly by regulating root structure morphology, plant nutrient use efficiency, rhizobial colonization, secondary metabolites and hormones, and activating the plant immune system, which in turn affect the rhizosphere microenvironment or directly signal to microorganisms (Egamberdieva *et al.*, 2017; Eichmann *et al.*, 2021; López-Ráez *et al.*, 2017). However, these mechanisms often act interactively in plants. For example, phytohormones can influence root structural morphology, plant-dependent defence processes and root exudate secretion (Eichmann *et al.*, 2021; Fu *et al.*, 2021). Growth hormone regulates *Arabidopsis* root development mainly through the growth hormone synthesis pathway and the polar transport carrier pathway. Deletion of the growth hormone synthesis genes *rt* (*rooty*) and *sur* (*super root*) can lead to excessive endogenous IAA synthesis, resulting in a high number of lateral roots (Boerjan *et al.*, 1995). Ethylene promotes *Arabidopsis* root hair growth by regulating the activity of EIN3/EIL1 and RHD6/RSL1 transcriptional complexes (Feng *et al.*, 2017). Moreover, plant immune system can be divided into two layers, and hormonal signals are essential for both layers (Aerts *et al.*, 2021). In the first layer, plants are damaged, recognize microorganisms/pathogens and release small molecule damage-associated molecular patterns that trigger immune signals leading to pattern-triggered immunity (PTI; Dangl *et al.*, 2013; Erb and Reymond, 2019). Gene expression in PTI immunity is almost always influenced by interactions between sectors (Hillmer *et al.*, 2017). In the second layer, pathogens secrete variable effectors that hinder PTI by inhibiting defence hormones, and resistant plants recognize the effectors, triggering effector immunity (ETI; Han and Kahmann, 2019). In ETI, all divisions can (partially) take over the response if one of them is inactive (Tsuda *et al.*, 2009). However, in the actual defence process, there is a complex crosstalk between molecular pathways of different hormones and this crosstalk is critical and complex for adjusting plant growth and development and thus affecting microorganisms (Aerts *et al.*, 2021). Furthermore, hormones can mediate the secretion of root exudates. It has been shown that disruption of ET signalling pathways leads to differences in the composition of root exudates, including

smaller amounts of esculetin, gallic acid, L-fucose, eicosapentaenoic acid, and higher amounts of β -aldehyde, and that these root exudate metabolites can affect the assembly and function of bacterial taxa (Fu *et al.*, 2021).

Effects of rhizosphere microbes on plant functional genes

Rhizosphere microorganisms can decompose soil organic matter into inorganic nutrients for plants and their physiological metabolic activities can also improve soil quality (Bhatti *et al.*, 2017; Li *et al.*, 2022; Li and Gong, 2021; Mishra *et al.*, 2017; Wang *et al.*, 2018). Rhizosphere microorganisms increase nutrient availability to plants, promote plant development and achieve the microbial ecological service function in farmland ecosystems. However, obtaining genetic varieties with high nutrient utilization and cross-stress resistance is the fundamental way to improve the yield and quality of farmland crops (Ali *et al.*, 2018; Anwar and Kim, 2020). Therefore, uncovering the mechanisms of 'bottom-up' regulation of plant functional genes by rhizosphere microbes is of great importance for agricultural production. In this section, the microbial effects on the expression of functional genes related to plant growth promotion, flowering, immune regulation and stress tolerance were reviewed.

Effects of rhizosphere microbes on plant growth and development genes

For decades, researches on beneficial plant-microbe interactions have formed a strong molecular framework (Lugtenberg and Kamilova, 2009; Saleem *et al.*, 2019). Microbes can up- or down-regulate the genes related to plant nutrient absorption by immobilizing nitrogen and to secondary metabolites, thus promoting or inhibiting plant growth (Figure 2). The main microorganisms associated with nitrogen fixation in the rhizosphere of specific plants include *Klebsiella*, *Paenibacillus* and *Azospirillum* (Grady *et al.*, 2016; Mehnaz *et al.*, 2007; Ryu *et al.*, 2020). Wang *et al.* (2021) pointed out that specific relationships exist between given host genetics and associated microbes. This is further supported by the results from synthetic communities (SynComs) application that can systemically regulate the transcription of genes involved in multiple facets of growth and nutrient metabolism, especially auxin responses and nutrient signalling pathways. The expression of nitrate transporter genes and nitrate reductase genes were down-regulated in plants treated with SynComs, which improved the biological fixation of N_2 , thereby inhibiting the direct absorption of nitrogen by roots and related metabolic pathways (Wang *et al.*, 2021). Many phosphorus starvation (*PSR*) genes, phosphate transport and metabolism genes are also activated by SynComs (Wang *et al.*, 2021; Wu *et al.*, 2013). This indicates that microorganisms not only contribute to phosphorus release from insoluble forms but also activate the *PSR* signalling system, thereby enhancing the absorption of environmental phosphorus and promoting inter-tissue phosphorus recycling (Desbrosses and Stougaard, 2011; Li *et al.*, 2019; Wu *et al.*, 2013; Zhong *et al.*, 2019). Additionally, GO analysis showed that auxin responsive genes were abundant among differentially expressed genes affected by SynComs application (Hinsinger *et al.*, 2011; Wang *et al.*, 2021). Recruited rhizosphere microbes can produce phytohormones to regulate plant flowering signalling pathways (Rodriguez *et al.*, 2019). A current focus is to decipher the link between rhizosphere microorganisms and plant functional genes on flowering time

(Figure 2). For one thing, microorganisms can produce IAA from tryptophan (Trp; Duca *et al.*, 2014; Molina *et al.*, 2018; Patten *et al.*, 2013; Treesubsuntonn *et al.*, 2018). One of the abundant rhizosphere microorganisms, *Arthrobacter*, has been reported to have the ability to produce IAA, which is beneficial for plant growth (Li *et al.*, 2018). IAA was the direct driver that down-regulated the expression of genes involved in flowering, which delays the flowering time (Lu *et al.*, 2018; Mai *et al.*, 2011). It was also found that the selectively enriched rhizosphere microorganism regulated the flowering time by affecting the available nitrogen content in autoclaved potting-mix soils (Ishioaka *et al.*, 1991; Panke-Buisse *et al.*, 2015). Notably, microbes also synthesize and emit many volatile organic compounds (VOCs) to perturb host flowering time (Hung *et al.*, 2013; Sánchez-López *et al.*, 2016b). VOCs are low molecular weight (<300 Dalton) molecules that are easily dispersed by air and water due to high vapour pressure and low boiling point (Bitas *et al.*, 2013; Schmidt *et al.*, 2016; Schulz and Dickschat, 2007). The appearance of floral buds in VOCs treated *ahk2/4* and *ahk3/4* plants occurred 3–4 days before non-treated *Arabidopsis*. In contrast, VOCs did not exert any significant effect on the time of floral bud appearance in both *ahk2/3* and *35S:CKX1* plants (*ahk2/4*, *ahk3/4* and *ahk2/3* are CK signalling mutants; *35S:CKX1* plants are CK oxidase/dehydrogenase1 over-expressing plants). These findings provide strong evidence that VOCs-promoted early flowering involves suppression of NO action through the scavenging of NO molecules by CKs (Riefler *et al.*, 2006; Sánchez-López *et al.*, 2016a; Werner *et al.*, 2008). Together, microbes synthesize a multitude of nutrients and hormones, that affect the expression of plant flowering-related genes, and may directly or indirectly regulate plant flowering time (De-la-Peña and Loyola-Vargas, 2014).

VOCs released from rhizomicrobiome can also improve multiple functions in ecosystems, such as plant growth and development (Gutiérrez-Luna *et al.*, 2010; Kanchiswamy *et al.*, 2015; Ortíz-Castro *et al.*, 2009; Schulz-Bohm *et al.*, 2018). A variety of bacteria or fungi have been identified to produce VOCs, such as *Bacillus*, *Pseudomonas* and *Serratia* spp. (Hassani *et al.*, 2018; Plyuta *et al.*, 2016; Xie *et al.*, 2020). Sun *et al.* (2020) found that treatment with *F.luteovirens* VOCs reduces primary root growth by aggravating auxin accumulation through the repression of the abundance of auxin efflux carrier *PIN-FORMED 2* (*PIN2*) protein, whereas it increases the lateral root number of *A. thaliana* seedlings. In addition to modulating root system architecture, treatment with *F. luteovirens* VOCs markedly increased above-ground growth. The transcriptomic and metabolomic analyses further supported the idea that *F. luteovirens* VOCs regulate plant growth and development by inducing up- or down-regulation of genes related to carbon/nitrogen metabolism and antioxidant defence (Sun *et al.*, 2020). Overall, these findings suggest that rhizosphere microbes can regulate plant growth-related gene expression by mobilizing nutrients, altering plant nutrient use efficiency and producing hormones such as IAA and volatile compounds.

Effects of rhizosphere microorganisms on plant resistance genes

As sessile organisms, plants have to cope with various biotic and abiotic stress for long-term domestication (Zhu, 2016). In this process, corresponding resistance genes and mechanisms have evolved continuously to resist adverse environmental conditions (Chong *et al.*, 2019; Frantzeskakis *et al.*, 2020). Recently, a

paradigm shift in the life sciences has emerged, in which microbial communities are viewed as core drivers of tolerance mechanisms (Cordovez *et al.*, 2019). Beneficial microbes were recruited to build defence signalling pathways (Figure 2), which are based on the interaction of plants, pathogenic bacteria and rhizomicrobiome in response to biotic stress, that is likely a survival strategy conserved across the plant kingdom (Liu *et al.*, 2019; Liu and Brettell, 2019). Durum wheat infected by the fungal pathogen *Fusarium pseudograminearum* (*Fp*) leads to an enrichment of the beneficial bacterium *Stenotrophomonas rhizophila* (SR80) in the rhizosphere. As an early warning factor, the assembled SR80 was able to promote the large-scale expression of pathogenesis-related (PR) genes involved in the salicylic acid and jasmonic acid signalling pathways, enhancing host immunity against crown rot disease (Liu *et al.*, 2016, 2021). Another case is that VOCs produced by *Fusarium culmorum* stimulated the production of flavonoid odoriferen VOCs of bacterium *Serratia plymuthica*, which induced the expression of associated defence genes in *Arabidopsis* (Raza *et al.*, 2021; Schmidt *et al.*, 2017).

Under abiotic stresses, the effect of rhizomicrobiome on plant genes might be more comprehensible. As for low phosphorus availability, the phosphorous starvation response induced by microbial invasion can promote the expression of master transcriptional regulator *Phr1* to alter orthophosphate (Pi) metabolism in plants. *Phr1* directly activates microbiome-enhanced response to phosphate limitation while repressing microbially driven plant immune system. It suggests that microbes have changed the transcription level of defence genes to enhance the immunity of plants (Castrillo *et al.*, 2017). Furthermore, rhizomicrobiome may change more defensive pathways to mitigate abiotic stress. Inoculation of *Arbuscular Mycorrhizal Fungi* (AMF) under drought stress condition has been found to be able to induce the expression of 1-pyrroline-5-carboxylic acid synthase (P5CS) gene. P5CS is a key enzyme involved in the proline synthesis, which can promote cell water retention, thus improving the ability of plants to resist osmotic stress (Hu *et al.*, 1992; Ruiz-Lozano *et al.*, 2006). At the same time, the AMF also enhance plant resistance to drought stress by regulating 9-cis-epoxycarotenoid dioxygenase (*NCED*) gene expression. *NCED* is an important enzyme in controlling abscisic acid (ABA) metabolism which catalyses the oxidative cleavage of epoxy carotenoids into xanthoxins (Chaufour *et al.*, 2019; Taylor *et al.*, 2000). As a whole, the evidence above suggests that microbes can regulate the expression of plant genes through multiple pathways, such as secreting hormones, producing VOCs, enhancing the plant immune system, and building defence signalling pathways, to help the host adapt to various stresses. These studies shed light on the important role of plant-associated rhizosphere microbiota for plant functions and broaden multiple ideas for manipulating host growth through microbial intervention.

Research methods of linking plant functional genes to rhizosphere microorganisms

The link of plant functional gene to rhizomicrobiome is complicated. Not only the 'functional genes-downstream, genes-metabolite or other signalling substances-microbe' pathway need to be considered but also factors such as inter-microbe, environments and plant residues (Chen *et al.*, 2019; Edwards *et al.*, 2018; Gao, Han, *et al.*, 2019; Gao, Karlsson, *et al.*, 2019; Geddes *et al.*, 2019; Pascale *et al.*, 2020; Trivedi *et al.*, 2021; Trubli

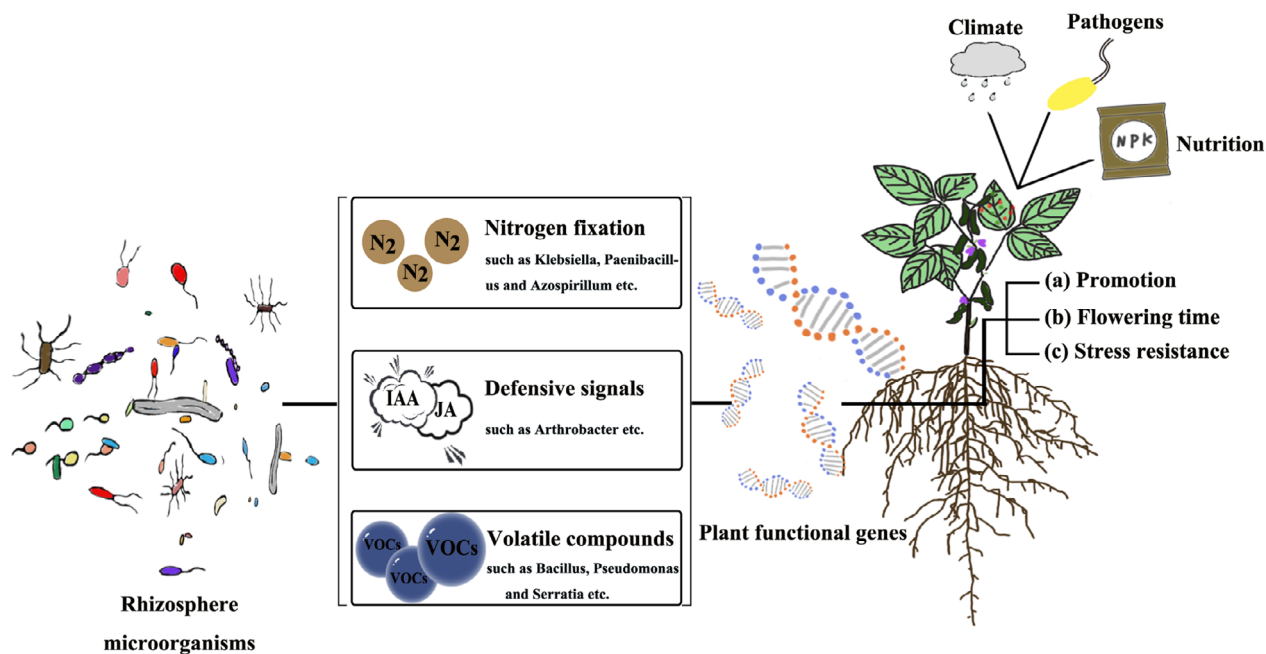


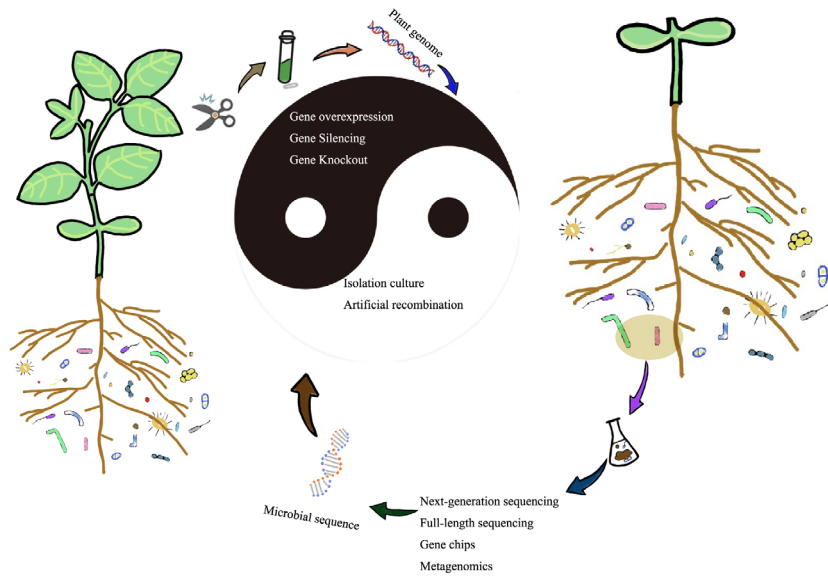
Figure 2 Rhizosphere microbes affect the plant functional genes related to growth and development, flowering time and stress resistance. (a) Microbes improved the biological fixation of N_2 . Microorganisms alter the content of various material components of the nitrogen cycle by stimulating the nitrogen cycle genes in the host, which in turn compensates for the material elements that the host is deprived of. In this way, microorganisms promote the nutrient uptake of the host and enable it to thrive. In addition to perceiving root secretions from plants, microbes themselves are capable of secondary metabolism to secrete specific substances, such as volatile compounds and hormones. Among them, volatile compounds have been shown to be direct drivers of plant growth hormone synthesis genes and photosynthesis genes. With the addition of plant growth hormone and photosynthesis, the growth of plants is affected. (b) Rhizosphere microorganisms directly or indirectly regulate the flowering time of plants. On the one hand, microbes secrete IAA to directly regulate flowering genes to influence flowering time; on the other hand, microbes indirectly influence flowering time by constraining plant nutrient requirements and secreting volatile compounds. (c) Under biotic and abiotic stresses, microorganisms influence the expression of defence genes (e.g., climate, pathogens, and nutrient deprivation), which in turn activate defence signalling pathways.

et al., 2018). These signalling substances, such as hormones and small RNA, are frequently exchanged between the host and the microorganism, triggering structural and functional changes on both sides (Huang et al., 2019; Middleton et al., 2021; Yang et al., 2016). The desired substantive function of microorganisms leads to healthy plant growth. The new findings suggest that the ultimate outcome of host health may depend on not only the exchange of substance between host and microbes but also the signalling and metabolic interactions among microbiome members (Durán et al., 2018; Finkel et al., 2019; Harbort et al., 2020; Xu et al., 2021b). Thus, understanding plant gene-microbe interactions may require examining these relationships at the level of host and microbial functional capacity, activity, and molecular exchange (Xu et al., 2021b). However, a larger reason for the slow progress in our understanding of the functionality of plant gene-microbe interactions may lie on our choice of methods and tools. How to integratively combine host-centric molecular technologies, such as CRISPR/Cas system (e.g., Cas9 and Cas12a), gene silencing (e.g., RNA interference) and gene overexpression, with microbial-centric histological sequencing technologies, such as amplicon sequencing, shotgun metagenomics, metatranscriptomics and metabolomics, are important to unlock complex mechanisms of plant gene-microbe interactions (Figure 3; Fitzpatrick et al., 2020).

Genome-Wide Association Studies (GWAS) well attach phytomics to microbiomics and demonstrate that host genomics does

influence the composition of the microbiome (Trivedi et al., 2021). GWAS were previously used to study the phyllosphere microbiome with quantitative methods to map microbiomes as phenotypes (Horton et al., 2014; Oyserman et al., 2022; Roman-Reyna et al., 2019; Wallace et al., 2018) and are increasingly focusing on the rhizosphere microbiomes of plants such as *Arabidopsis*, sorghum, barley, maize and tomato (Bergelson et al., 2019; Escudero-Martinez et al., 2022; Oyserman et al., 2018, 2022; Wagner et al., 2020). Compared to phyllosphere, the rhizosphere has proven to be the most promising part for unravelling the genetic power of the host microbiome (Deng et al., 2021). This may be owing to the high complexity of the rhizosphere microbiome and its strong colonization ability (Bano et al., 2021; Rico et al., 2014; Schlechter et al., 2019). GWAS break down the wall of the tripartite relationship between plant genotype phenotype-microbiome, thus identifying the link between plant phenotype and microbiome function (Horton et al., 2014; Vorholt et al., 2017). Therefore, the abundance and community structure of the rhizosphere microbiome can be used to infer the relevant genetic loci and plant genes (Deng et al., 2021; Escudero-Martinez et al., 2022). The inferred plant genes can be validated by artificially modified mutants to elucidate the potential host genetic causes of microbiome changes (Schäfer et al., 2022; Wagner et al., 2020). Even if candidate genes for microbial recruitment are identified, there are difficulties in reproducing and validating them (Zancarini

Figure 3 Connecting plant and microbes relegated technologies. Plant genomic data obtained from plant tissues and microbial sequence data obtained by various microbial sequencing techniques were used for plant functional gene and rhizosphere microbial function probes. The integration of plant gene-centred and rhizosphere microbial function-centred technologies is the key to promote the study of plant gene and rhizosphere microbial interactions.



et al., 2021). Conversely, host genotype data can also predict the composition of microorganisms, which determines whether there is inter- and intra-species variation in the microbiome in the host being tested (Deng *et al.*, 2021; Fitzpatrick *et al.*, 2018; Walters *et al.*, 2018). GWAS of plant microbiome associations promote a comprehensive understanding of the host molecular mechanisms of microbiome assembly and lay the foundation for microbiome characterization to be implemented into breeding programs. Notably, heritable rhizosphere microbes showed strong overlap in different host genotypes (Deng *et al.*, 2021). This fraction may be the few pivotal microorganisms that have stabilized on the species domestication and temporal evolutionary scales and subsequently regulate the proliferation of other members of the community (Brachi *et al.*, 2022). Furthermore, since environmental conditions are a major component of variability and plant genotypes can explain only a few microbial variations, GWAS need to develop more comprehensive models to reveal the effects of genotype, microbiome, environment and their interactions on plant phenotypes (Zancarini *et al.*, 2021).

For the microbial sequencing, the widely used technology is still second-generation sequencing, which has undoubtedly enabled researchers to gain a broad understanding of the structure of microbial community (Metzker, 2010; Niedringhaus *et al.*, 2011). Increasingly, studies are also focusing on the activity and function of microbes by incorporating metatranscriptomics and macrogenomics, gene chips and viral omics, with the potential for more advanced approaches to be developed later (McDonald *et al.*, 2022; Wang *et al.*, 2019; Xu *et al.*, 2021a; Zaramela *et al.*, 2021). Each of the technology mentioned above has its own advantages and disadvantages (Table 1), and researchers can choose the appropriate method according to the needs as well as the funding budget. It is worth noting that the gene impact on rhizomicrobiome is often accomplished through metabolism or small molecule signalling substances. Therefore, metabolomics and the detection of the transfer of small molecule signalling substances (i.e., miRNAs) becomes particularly important in this reciprocal process (Middleton *et al.*, 2021; Pang *et al.*, 2021). Therefore, data integration approaches are essential to unravel the relationship between plant functional gene and microbes. Pang *et al.* (2021) reviewed the statistical approaches developed

for integration of plant metabolites and microbiome data, and Zancarini *et al.* (2021) reviewed statistical approaches for integrating plant omics with microbiome data. It is certain that rapidly developing multi-omics combinatorial analyses may further elucidate mechanisms of interaction between genes and microbiomes.

A large amount of data is available based on the above methods to support the linkage between plant genes and microbial structure and function, but the validations of microbial functions are still lacking. Recently, artificial recombination has been increasingly used to validate microbial functions (Durán *et al.*, 2018; Zhuang *et al.*, 2021). We believe that the rapid development of technologies such as the high-throughput partitioning methods developed by Zhang *et al.* (2021) and computer-guided synthesis of artificial colonies could assist to explore the plant gene and microbe interaction. Specifically, there was a significant difference in root bacterial community composition between root diffusion barrier genotypes of *Arabidopsis* and wild type after inoculation with artificial bacterial communities (Salas-González *et al.*, 2021). These results suggest that the endothelial diffusion component of the *Arabidopsis* root system regulates the conformation of the microbial community (Zhou *et al.*, 2020). Furthermore, the synthetic population repressed the transcriptional response to ABA (cluster C2) by comparing differentially expressed genes in wild-type plants and mutant *myb36-2* roots, leading to the speculation that the microbiome regulates suberization and lignification through ABA-dependent pathways (Barberon *et al.*, 2016; Salas-González *et al.*, 2021). It is clear that synthetic biology is establishing transboundary links, as well as establishing molecular links between plant nutrition and defence (Berendsen *et al.*, 2018; Castrillo *et al.*, 2017; Liu *et al.*, 2020; Zhou *et al.*, 2012). However, recent developments in synthetic communities have ignored fundamental issues in microbiome studies, namely standardization and reproducibility (Zengler *et al.*, 2019). Little standardization in the culture systems is used to study complex microbial communities. Researchers typically use single strains or simple co-cultures, which are often poor models for complex and metabolically diverse microbial communities in nature (Ruby, 2008). While

Table 1 Commonly used technologies on plant functional gene and microbiome sequencing technologies

Techniques	Advantages	Disadvantages	References
Gene overexpression	Amplify gene function Commonly used for resistance to stress	Lethal effects	Dalman <i>et al.</i> (2017), Huo <i>et al.</i> (2021), Prabhu <i>et al.</i> (2017), Shalmani <i>et al.</i> (2021), Truong <i>et al.</i> (2021), Yang <i>et al.</i> (2017)
Gene knockout	High knockdown efficiency simple operation multiple targets can be edited simultaneously	Severe off-target property Prone to mutations	Ding <i>et al.</i> (2013), Gao <i>et al.</i> (2021), Irie <i>et al.</i> (2015)
Gene silencing	TGS:Genetic stability PTGS:High specificity Reproducibility easily manipulated	TGS:Mutants may have defects PTGS:positional effects transient incomplete gene knockouts	Ashfaq <i>et al.</i> (2020), Huang <i>et al.</i> (2021), Matzke and Mosher (2014), Sigman and Slotkin (2016), Tan <i>et al.</i> (2020)
Next-generation sequencing	High throughput low cost high efficiency	Low resolution difficult to detect low-abundance microorganisms at the genus level PCR preference	Metzker (2010), Niedringhaus <i>et al.</i> (2011), Shendure and Ji (2008)
Full-length sequencing	No PCR amplification required with ultra-long sequencing read length high precision no GC preference	High cost high error rate (15%–40%) low throughput	Gui-Feng and Hai-Yan (2020), Singer <i>et al.</i> (2016), Xu <i>et al.</i> (2019)
Gene chips	High density Rapid real-time detection automation	Too much information on hybridization slow processing and analysis of hybridization data specificity and sensitivity of hybridization need to be improved preparation of high-quality nucleic acid samples needs to be improved	Gabig and Wegrzyn (2001), Yang and Chen (2000)
Metagenomic	Allows access to large numbers of assembled genomes (MAGs) improves resolution of microbial community analysis Allows access to more diverse compositional and functional data	Expensive and host genes are vulnerable to contamination	Liu <i>et al.</i> (2021), New and Brito (2020)

these methods can provide a better understanding of the native microbiome, they lack reproducibility (even within a single laboratory) in the absence of microbial inoculate that are stable over time.

The care needs to be taken when using metagenomes to detect endophytes in leaves, stems and roots, as cross-contamination of host genes and microbial genes can occur (Liu *et al.*, 2021). To solve this problem, the host genome needs to be identified to remove the host gene contamination in subsequent analyses (Marotz *et al.*, 2018; Song and Xie, 2020). This has certainly limited much of the research from being carried out in some crops. In addition, choosing the appropriate time to sample is a challenge as there is often little or no a priori knowledge of when host and microbiome responses occur and how their interactions change as the plant grows (Xiong *et al.*, 2021). As some of the techniques involved above are expensive, we therefore recommend that researchers select multiple sampling time points and use suitable techniques to explore the dynamic processes of plant gene and microbial interactions in focal periods using a multi-omics approach. In addition, as soil type strongly influences microorganisms (Bai *et al.*, 2017; Girvan *et al.*, 2003; Pershina *et al.*, 2018), we suggest that experiments should be verified in different soil

types, so as to find general patterns of gene regulation of microorganisms.

Summary and outlook

Microbial communities with manipulated plant functional gene expression have great potential for bioengineering, agricultural and environmental remediation. There is clear evidence that functional plant genes and rhizomicrobiome can interact with each other. However, more fundamental studies are needed to decrypt the 'on or off' of functional genes in plant-microbe communication. There is no shortage of emerging technologies and methodological approaches that can be used to further explore the molecular mechanisms and signalling pathways of microbe-host gene interactions. However, it is still a long way to construct a complete network of plant functional genes and rhizosphere microbes, with a plethora of outstanding questions: (i) How to find plant genes that can regulate rhizomicrobiome on a large scale? GWAS may be a very good approach, considering that GWAS could be used to identify specific gene-regulated microorganisms; (ii) To what extent and how long can plant genes play a role in shaping the rhizospheric microbiota and its associated functions? Conversely, microorganisms to specific genes? (iii) Are there other signals, such as

miRNA, for the plant and microbe interaction besides metabolites? This knowledge will enable us to reshape the microbiome through genetic engineering, or to regulate the functional genes of plants through microbes, ultimately optimizing plant growth.

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Conflict of interest

The authors declare that they have no competing interests.

Author contributions

Tengxiang Lian, Jian Jin and Hai Nian designed the content and structure of the review. Qi Liu, Tengxiang Lian, Lang Cheng wrote the main manuscript. Qi Liu, Lang Cheng prepared Figures 1–3 and Table 1. The authors read and approved the final version of the manuscript.

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