MINI REVIEW

Microbiota and the plant immune system work together to defend against pathogens

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Abstract

Plants are exposed to a myriad of microorganisms, which can range from helpful bacteria to deadly disease-causing pathogens. The ability of plants to distinguish between helpful bacteria and dangerous pathogens allows them to continuously survive under challenging environments. The investigation of the modulation of plant immunity by beneficial microbes is critical to understand how they impact plant growth improvement and defense against invasive pathogens. Beneficial bacterial populations can produce significant impact on plant immune responses, including regulation of immune receptors activity, MITOGEN-ACTIVATED PROTEIN KINASE (MAPK) activation, transcription factors, and reactive oxygen species (ROS) signaling. To establish themselves, beneficial bacterial populations likely reduce plant immunity. These bacteria help plants to recover from various stresses and resume a regular growth pattern after they have been established. Contrarily, pathogens prevent their colonization by releasing toxins into plant cells, which have the ability to control the local microbiota via as-yet-unidentified processes. Intense competition among microbial communities has been found to be advantageous for plant development, nutrient requirements, and activation of immune signaling. Therefore, to protect themselves from pathogens, plants may rely on the beneficial microbiota in their environment and intercommunity competition amongst microbial communities.

Introduction

The interaction between innate immune receptors in plants and immunogenic elicitors originating from microbial communities controls the spatial–temporal crosstalk between plants and microorganisms. Microbe-triggered immunity (MTI) signaling begins when plant cell surface receptors, also known as pattern recognition receptors (PRRs), recognize the elicitors produced by bacteria, such as microbe-associated molecular patterns (MAMPs) (Couto and Zipfel 2016). The majority of the microbes that inhabit the plant leaves are non-pathogenic and are able to elicit PRR-mediated pattern-triggered immunity (PTI) responses. PTI mainly requires phytohormone signaling, ROS generation, and

MAPK cascade activation (Bigeard et al. 2015). In conclusion, bacterial immunogenic peptides are recognized by the plant PRRs, triggering plant defense.

The bacterial flagellum contains flagellin units that aid in bacterial motility and identification by plant PRRs. The FLAGELLIN SENSITIVE2 (FLS2) receptor, specific to plants and involved in MTI signaling, frequently detects the well-known microbial elicitor peptide flagellin-22 (flg22) (Chinchilla et al. 2006). Bacterial motility is affected by repeated modifications to the flg22 peptide region but not immunological recognition via FLS2 (Parys et al. 2021). Nevertheless, certain *Pseudomonas* bacteria have evolved specifically for certain mutations in crucial flg22 areas, enabling them to avoid immunological detection caused by FLS2 without exhibiting aberrant locomotion (Colaianni et al. 2021). This indicates a stability between plant and microbial adaptability that co-evolved in nature to prevent imbalance.

The interaction between plant–pathogens and the environment, particularly abiotic elements like light, temperature, water, and nutrients, is currently being recognized as a new

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area of study (Saijo and Loo 2020). Many these stresses may produce danger-associated molecular patterns (DAMPs), but it is unknown how these molecules are perceived. Due to the possibility that combinatorial stress responses could influence interactions between plants and their environment, it is plausible that DAMP binding to their cognate receptors could cause DAMP-triggered immunity (DTI). These environmental factors have a significant impact on how plants and microbes interact, but the underlying molecular pathways are still unknown. The majority of abiotic stressors make plants more susceptible to their pathogens (Bidzinski et al. 2016; Zarattini et al. 2021). They could play an important role by modulating the expression of a group of immune signaling genes. At low temperatures, the salicylic acid (SA)-signaling genes were found to be transcriptionally active, whereas the jasmonic acid (JA)-signaling genes were inhibited (Wu et al. 2019a, b). At high temperatures, the suppression of JA-signaling genes was restored. This suggests that abiotic and biotic stresses often crosstalk with each other and may have a profound impact on plant defense signaling.

Nevertheless, plant immune responses are also targeted by the pathogen-derived effectors. Plants have intracellular immune receptors from the NUCLEOTIDE-BINDING DOMAIN LEUCINE-RICH REPEAT (NLR) proteins family, which allow them to recognize such effectors with racialized immunity (Cesari 2018; Chen et al. 2022). Effector interactions with plant NLRs led to their oligomerization and initiate effector-triggered immunity (ETI) responses (Ahn et al. 2023). The hypersensitive reaction (HR), which causes localized cell death, is the most common ETI phenotype in plants. Pathogens are prevented from migrating outside of damaged plant tissues by HR. Therefore, both plants and microbes continuously challenge one another in a variety of ways under tight selection pressure. In this review, we have outlined the characterization of isolated commensal bacterial strains and their function in plant defense signaling by acting on its innate immune system.

The microbiome influences immune signaling pathways in plants

In the past, plant–pathogen interactions were used to decipher plant immune signaling pathways. However, the manipulation of plant defense by the microbiota has added a fresh line of research that has deepened our understanding of the control of plant–microbe interactions. This microbiota is often found to be associated with plants and may have the capacity to affect plant immunity (Fig. 1). The potential of pathogens to cause disease is resisted by these beneficial microbes (Table 1). It can directly combat the pathogen or indirectly by getting plants to manufacture antifungal chemicals to achieve microbiota-mediated plant protection. These microbes may be able to outcompete their niche competitors; e.g., *Pseudomonas piscium* inhibits the growth of the fungus *Fusarium graminearum* by targeting its histone acetyltransferases (Chen et al. 2018).

Plants begin an immune response against microbes after binding to the flagellum protein FliC, which is then deglycosylated and degraded by plant-derived enzymes (Boutrot and Zipfel 2017; Buscaill et al. 2019). As a result, the flg22 peptide is released into plant apoplastic space and interacts with the FLS2 receptor. This in turn causes FLS2 to associate with its co-receptor, BRI1-ASSOCIATED KINASE 1 (BAK1). This FLS2–BAK1 immune complex subsequently triggers ROS bursts and MAPK activation (Couto and Zipfel 2016). According to Vogel et al. (2016), MAMP recognition by PRRs activated their co-receptor BAK1 to trigger this immune response. Notably, this microbiota-mediated protection is no longer conferred by *bak1/bkk1* mutant plants. This shows that MTI signaling components also govern microbiota-induced immune signaling in plants. MAMP elicitation causes apoplastic ROS bursts that are mediated by the PRR, which are important pathways of MTI signaling in plants (Qi et al. 2017). *P. fluorescens* from the rhizosphere inhibits flg22-induced ROS bursts (Mavrodi et al. 2011). This shows that by reducing the short ROS surge, beneficial bacteria might successfully undermine plant immunity for their colonization. In addition, MAPK activation controls the production of transcription factors and defense-related genes, which is essential for immune signaling (Meng and Zhang 2013). Beneficial plant bacteria can target MAPKs, which will have negative on subsequent immune signaling events. A helpful microorganism named *Sinorhizobium* sp. strain NGR234 disrupts MAPK signaling and prevents the transcription of defense genes. The study found that this bacterium secretes a protein known as NopL that blocks the phenotype of MAPK-induced cell death (Ge et al. 2016). Pathogens, however, may hinder the plant PRRs' ability to recognize MAMPs by modifying, sequestering, and degrading MAMPs. *Pseudomonas syringae* DC3000 secreted protease can break down MAMP to prevent the MTI responses from being triggered (Pel et al. 2014). To prevent PTI activation, several fungi can conceal their chitin molecules. Additionally, their recognition is hindered by the conversion of chitin to chitosan (de Jonge et al. 2010). Since the microbiota exhibits these elicitors, it stands to reason that they can encourage colonization and immune modulation through related mechanisms. Microbiome association, on the other hand, may cause the activation of plant immunity. For instance, in response to the bacterial pathogen *P. syringae* DC3000, *Sphingomonas melonis* can increase the expression of immune signaling genes in Arabidopsis (Vogel et al. 2016). Therefore, the plant microbiome may stimulate immune modulation activity using identical strategies as pathogens.
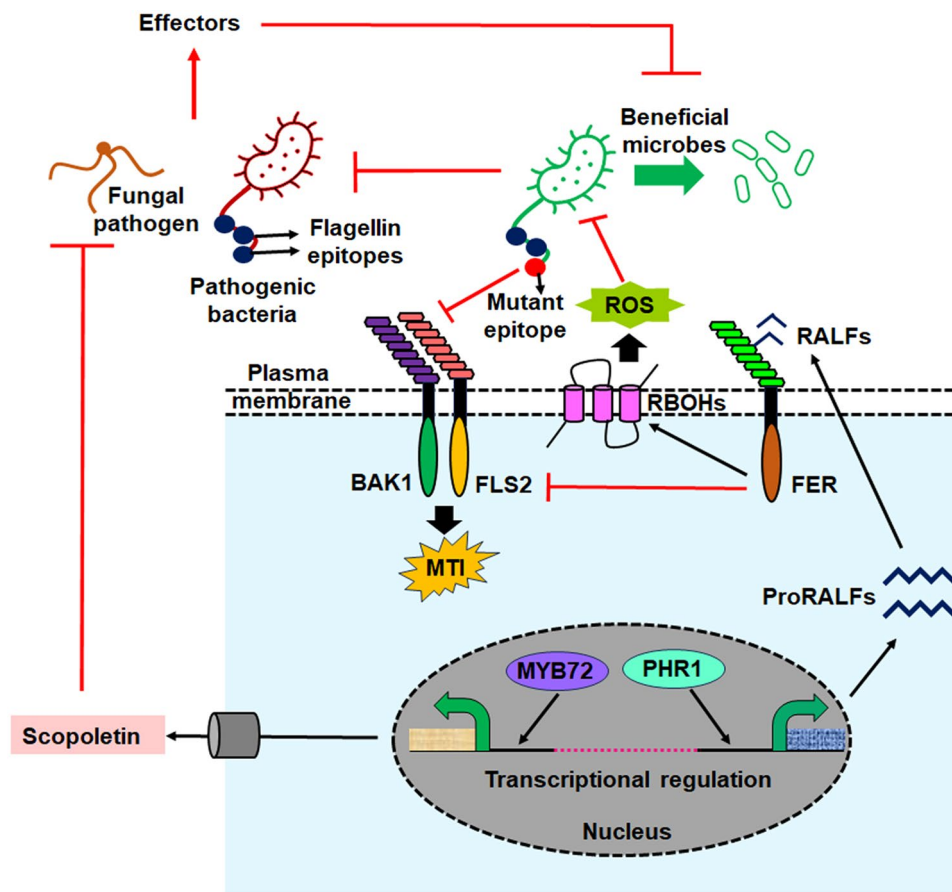
Fig. 1 Model depicting the microbiota-mediated manipulation of plant immune signaling pathways. Plant-associated beneficial bacteria acquire new mutations in their flagellin epitope, which prevent FLS2-BAK1-induced MTI signaling. Once microbiota suppress plant immune signaling, they encourage other beneficial bacteria to colonize plant tissues. These microorganisms can stimulate transcription factors like MYB72 to trigger the biosynthesis of antifungal compounds like scopoletin. PHR1 is another transcription factor that is induced by plant–microbiome interactions under Pi-starved conditions. It has also been known as an activator of *RALF* gene transcription, a ligand for FERONIA receptor kinase. RALF binding promotes FER activation, which causes RESPIRATORY BURST OXIDASE HOMOLOGS (RBOHs)-mediated ROS production. This FER-induced ROS burst in turn negatively regulates microbiota enrichment. FER also appears to function in receptor antagonism during plant–microbiota interactions. Contrarily, pathogens secrete effector proteins in plants that also affect the surrounding microbiota

Table 1 List of other beneficial bacteria and their role in plant resilience Indole-3-acetic acid, IAA

Name of the bacteria	Zone	Plant	Function	References
Rhizobium leguminosarum	Rhizosphere	Rice	Promote seedlings growth	Biswas et al. (2000)
Bacillus cereus	Rhizosphere	Wheat	IAA production and enhancing plant growth	Çakmakçi et al. (2006)
Sphingomonas sp.	Phyllosphere	Arabidopsis	Prevents *P. syringae* pv. tomato DC3000 infection	Innerebner et al. (2011)
Methylobacterium sp.	Phyllosphere	Lentil	Increase cytokinin levels to aid in plant growth	Jorge et al. (2019)
Paenibacillus polymyxa	Rhizosphere	Arabidopsis	Release of antimicrobial compounds and accelerates plant growth	Hong et al. (2016)
Streptomyces bikiniensis	Rhizosphere	Cucumber	Triggering ISR response against *Fusarium* sp.	Zhao et al. (2012)
Burkholderia cepacia	Rhizosphere	Pepper	Promotes plant growth and produces antifungal compound	Jung et al. (2018)
Burkholderia gladioli	Rhizosphere	Cotton	Plant growth increment, triggering of the ISR, and antifungal activity	Wang et al. (2023)
Bacillus amyloliquefaciens	Rhizosphere	Wheat	Exhibits profound fungicidal effects on *Fusarium graminearum*	Gong et al. (2015)

Microbiota on leaves protect against foliar diseases

Pathogenic and non-pathogenic microbes can also be found in leaf microbiomes. Plants' innate immune systems also interfere with their colonization in a species-specific manner. To colonize plant leaves, both helpful and harmful bacteria generated from phyllosphere go through particular adaption processes. The shift in the leaves environment depends on its physical and chemical characteristics, which makes its adaptation extremely distinct from that of the root microbiota (Chaudhry et al. 2021). A recent study discovered that HopM INTERACTOR 7 (MIN7) and CONSTITUTIVE ACTIVE DEFENSE 1 (CAD1) are the PTI signaling components control the development of the leaf endophytic bacteria (Chen et al. 2020). The endophytic microbial diversity in the leaves was altered in Arabidopsis mutants for these genes. It is also important to highlight that these elements are found in various plant species and are connected to vesicle trafficking during plant immunological responses. Previous studies have shown that phytohormone-mediated protection against fungi is activated by both proteobacteria and actinobacteria, suggesting that the soil-borne bacteria may trigger immunity against foliar pathogens (Ritpitakphong et al. 2016; Vergnes et al. 2020). Fungal microbiomes found on *Tricyrtis macropoda* leaves produced metabolic compounds and increase endophytic microbial populations (Wang et al. 2021a, b). The study has found that the green areas of leaves contain higher *Cercospora* fungi, less metabolites, and higher levels of lipids, organic acids, and amino acids. As metabolites build up, the color of the leaves may alter. These findings show that commensal microorganisms stimulate PTI in the leaves, promoting the growth of advantageous microbes that defend against pathogenic fungus.

Environmental stress, microbe–microbe interactions, and plant–microbe interactions are currently the main topics of research into microbe-mediated biocontrol in the phyllosphere. Therefore, both in vitro and field studies are needed to evaluate sustainable biocontrol methods against foliar diseases (Legein et al. 2020). For instance, the *Pseudomonas* genus is rich in the phyllosphere and comprises both commercial biocontrol strains and plant pathogens (Delmotte et al. 2009; Innerebner et al. 2011). Diverse *Pseudomonas* strains have been proven to suppress leaf-invading pathogens in the lab and field conditions (Romero et al. 2016; Simionato et al. 2017). *Bacillus* spp. are also commonly used as commercial biocontrol treatments because of their antagonistic actions on microbial rivals (Table 1). They produce polyketides and antipathogenic peptides that fight off diseases like *Sclerotinia*

sclerotiorum and *Fusarium* head blight (Fernando et al. 2007; Dunlap et al. 2013). Overall, plant microbiomes can benefit plant health through direct and indirect effects on foliar pathogens.

Rhizobacteria weaken root immunity, and promote microbiome association

Rhizobacteria usually inhibit root-specific immune responses in order to encourage the attachment of commensal bacteria to plant roots (Teixeira et al. 2021). It was found that *Pseudomonas simiae* WCS417 and *Bacillus subtilis* FB17, two isolated commensals, prevent the expression of MAMP-induced genes in Arabidopsis roots (Stringlis et al. 2018a; Lakshmanan et al. 2013). *P. simiae* WCS417 also produces scopoletin, a coumarin root exudate, under the control of transcription factor MYB72 (Fig. 1). Scopoletin promotes the recruitment of the root microbiome and has antimicrobial effects on soil-borne fungus *Fusarium oxysporum* and *Verticillium dahliae* (Stringlis et al. 2018b). *Pseudomonas capeferrum* WCS358, a different intriguing commensal bacterium, produced gluconic acid derivatives that lower the extracellular pH of the medium (Yu et al. 2019). Due to its acidity, *P. capeferrum* WCS35 was able to subvert the immune responses at the roots. The gluconic acid-induced pH decrease suppresses the flg22-triggered events, such as the ROS bursts and the expression of marker genes, to promote colonization of beneficial microbiota. As a result, the suppression in plant immune responses initiated by rhizobacteria encourages their colonization in the roots, which causes plants to produce antimicrobial compounds to fight off infections.

Soil mineral content determines the enrichment of microbiota in plants

Deficits in iron (Fe) and phosphate (Pi) can balance the relationship between immune activation and growth in plants. *P. simiae* WCS417 increases the absorption of Fe in Arabidopsis roots and initiates the systemic immune responses in the shoots (Verbon et al. 2019). However, it has been demonstrated that Fe deficit in Arabidopsis results in enhanced resistance against pathogens. *Botrytis cinerea* infection promotes the Fe deficiency response in roots, which in turn stimulates the production of ethylene (ET) in leaves and ultimately leads to resistance to *B. cinerea*. This resistance phenomenon to *B. cinerea* is further regulated by basic Helix–Loop–Helix (bHLH) transcription factors. Arabidopsis mutants lacking *bHLH* genes were susceptible to *B. cinerea* infection and exhibited a reduced level of ET synthesis. Moreover, they

found that two S-adenosyl methionine (SAM) members, i.e., SAM1 and SAM2, are associated with increased ET production in Arabidopsis leaves under Fe-deficient conditions. As a result, Fe availability regulates leaf resistance to *B. cinerea* via a bHLH-SAM-dependent mechanism (Lu and Liang 2023). Interestingly, the bacterial pathogen *Dickeya dadantii* also manipulates Fe uptake in plants. According to the study, the defense activation in Arabidopsis by *D. dadantii* depends on the Fe status of the plant (Kieu et al. 2012). Low Fe content results in reduced susceptibility of the Arabidopsis to *D. dadantii*. The reduced susceptibility has been found to be associated with increased levels of SA accumulation and defense gene expression. *P. syringae* effector AvrRps4 binds the plant Fe sensor protein BRUTUS (BTS) to promote Fe uptake and bacterial proliferation in Arabidopsis (Fig. 2). Additionally, AvrRps4-expressing *P. syringae* pv. *tomato* (*Pst*) DC3000 infection causes Fe accumulation in the apoplast of Arabidopsis *resistance to P. syringae 4* (*rps4*) and *enhanced Disease Susceptibility1* (*eds1*) mutants (Xing et al. 2021). This implies that NLR protein guards BTS, and its association with AvrRps4 results in RPS4-triggered immunity and low Fe accumulations in plant apoplast. Both beneficial and pathogenic bacteria have the ability to produce siderophores, which bind Fe. Bacterial pathogens receive Fe from plants through siderophores (Fig. 2). On the other hand, plant-beneficial bacteria also generate siderophores exhibiting high affinity Fe-binding activity, which prevents pathogens from obtaining Fe and eventually causing disease (Verbon et al.

2017). Beneficial *Pseudomonas* bacteria produce these siderophores, which trigger induced systemic resistance (ISR) in plants under Fe stress (Meziane et al. 2005; De Vleesschauwer et al. 2008). Recent research also suggests that root colonization by *Bacillus velezensis* SQR9 depends on secreted YukE protein. YukE protein enters plant plasma membrane, promoting Fe leakage and stimulate root colonization. The first instance of a helpful rhizobacterium exploiting a toxin delivery system to encourage colonization and subsequently plant–microbe interactions has been documented (Liu et al. 2023). Furthermore, Arabidopsis roots respond to Pi-limiting situations by reprogramming transcription to stop its defense signaling gene expression and overcome nutrient shortage. PHOSPHATE STARVATION RESPONSE 1 (PHR1), a transcriptional regulator, directs microbiome attachment to Arabidopsis roots while adversely modulating the expression of a subset of immune signaling genes under Pi stress. The expression of SA-responsive genes was increased in *phr1* mutants rather than JA-signaling genes. PHR1 therefore controls both the Pi starvation response (PSR) and plant immunity (Castrillo et al. 2017). The receptor-like kinase FERONIA (FER) is known to play a variety of roles in immune responses, plant growth, and development (Zhang et al. 2020). Under different mechanisms PHR1 directly binds to the *Rapid Alkalinization Factor* (*RALF*) gene promoters in *Arabidopsis thaliana*, activating the expression of these genes in Pi-starved environments (Fig. 1). Being a FER ligand, RALFs allow root bacteria to colonize by preventing the complex

Fig. 2 The Fe status of soil regulates plant immunity to microbes. Low levels of Fe can trigger plant immunity, while high levels of Fe promote susceptibility. Pathogenic microbes can stimulate Fe accumulation in plants, leading to enhanced susceptibility and disease development. By contrast, plant-beneficial microbes produce molecules with higher Fe-binding activity than pathogenic bacteria called siderophores. These siderophores retain Fe-scavenging properties and also trigger immune responses in plants. Moreover, pathogenic bacteria secrete effector proteins that target Fe regulatory proteins to cause Fe uptake and aid their colonization
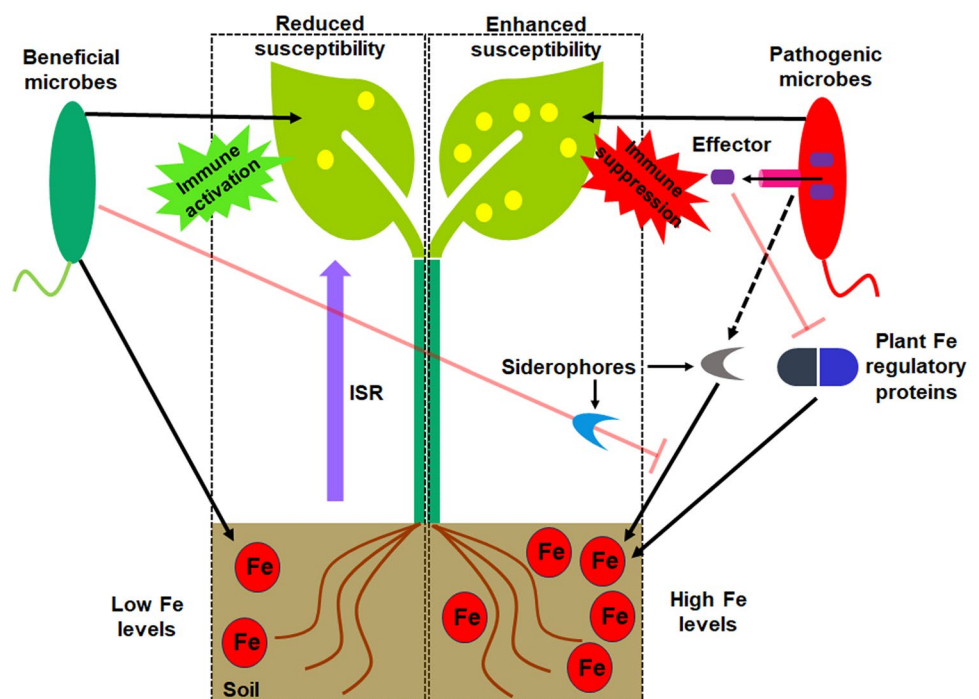
formation between the FLS2 and BAK1 and subsequently MTI signaling (Tang et al. 2022). According to Duan et al. (2010), RHO-like GTPases (ROP), which control the growth of root hairs, can be recruited by GUANINE NUCLEOTIDE EXCHANGE FACTORS (GEFs) through their interaction with the FER receptor-like kinase. To activate Rho GTPase in Arabidopsis, phosphatidylserine accumulates in the plasma membrane under the control of FER. Recently, it was found that FER-induced ROS generation also regulates the enrichment of advantageous pseudomonads in the rhizosphere microbiome (Fig. 1). In the study, it has been shown that reduced ROS levels enriched beneficial *Pseudomonas* population in the complex rhizosphere microbiome in the Arabidopsis *fer-8* mutants (Song et al. 2021). Therefore, by regulating ROS production, FER–GEFs–ROP signaling can control the development of root hairs and the accumulation of advantageous bacteria at roots. This shows that the mineral status of the soil affects the signaling pathways underlying plant immunity.

Rhizobacteria trigger ISR in plants to aboveground pathogens

ISR is a key plant defense tactic that is induced by commensal root-derived bacteria (Pieterse et al. 2014). ISR is commonly characterized by an early priming of defense against foliar infections, which is also an indirect process by which microbiota protect plants against disease-causing pathogens. Rhizobacteria commonly induced systemic defensive responses in plants to protect distal tissues from ongoing pathogen invasion (Shalev et al. 2022). Plants typically exhibit JA/ ET-mediated ISR rather than SA-induced systemic acquired resistance (SAR) responses following rhizobacteria inoculation (Pieterse et al. 1996, 1998; Pozo et al. 2008). The primary elicitors in rhizobacteria that trigger systemic defensive signals in plants are siderophores, flagella, and lipopolysaccharides generated from cell walls (Meziane et al. 2005). Several Arabidopsis mutants known to be defective in the JA and ET signaling pathways also affect ISR mediated by *P. fluorescens* (Pieterse et al. 1998; Pozo et al. 2008). On the other hand, rhizobacterial-induced systemic immune responses do not generate the accumulation of PR proteins, a precursor to SAR signaling in the distal tissues (Pieterse et al.1996). In a recent study, it was shown that azelaic acid (AZA), a mobile SAR signal, increases the accumulation of hybrid proline-rich proteins, which in turn regulates *P. simiae* WCS417 interactions with Arabidopsis roots (Banday et al. 2022). Therefore, rhizospheric bacteria contribute to

ISR, which works as the main plant defense mechanism, whereas SAR operates redundantly against pathogens.

Effector proteins affect the colonization of the plant microbiome

Effector proteins released by pathogens frequently have an impact on the colonization of plant microbiota (Fig. 1; Snelders et al. 2018). It is unknown if effectors produced by pathogens directly interact with plant microbiomes. VdAMP3, an antimicrobial effector protein from the fungus *Verticillium dahliae*, outcompetes its microbial competitors (Snelders et al. 2021). Brg11, a transcription activator-like effector (TALE) secreted from T3SS of *Ralstonia solanacearum*, raises polyamine levels in the host plant by activating arginine decarboxylase (ADC) gene expression. *R. solanacearum*'s growth was unaffected by the greater polyamine buildup caused by Brg11, although it inhibits other niche rivals (Wu et al. 2019a, b). Together, how effectors interact with the plant microbiome is governed by both their immune modulation activity in the plant and their antibacterial effects.

Additionally, commensal bacteria have toxin delivery mechanisms that lower interbacterial competition (Bernal et al. 2018). Horizontal gene transfer is the primary mechanism by which plant-associated bacterial populations retain such toxin delivery systems. *Pantoea ananatis*, *Burkholderia glumae*, *P. syringae* pv. *actinidiae*, and others have multiple toxin delivery systems with diverse roles (Shyntum et al. 2015; Kim et al. 2020; Wang et al. 2021a, b). For example, the commensal bacteria *Dyella japonica* MF79 uses type II effectors to drastically reduce root-specific immune responses in Arabidopsis (Teixeira et al. 2021). The beneficial rhizobacteria *P. simiae* WCS417 and *Pseudomonas defensor* WCS374 both include Type III toxin delivery systems (T3SS), which harbor putative effectors with unknown activities (Stringlis et al. 2019). After the injection of these microorganisms, tobacco leaves exhibited no ETI-induced cell death. The cause might be that these toxins are either not recognized or incapable of being delivered into tobacco leaves. Future research on the function of these effectors in interactions between plants and beneficial microorganisms may, therefore, be required.

Synthetic microbial communities (SynComs) may increase plant protection from diseases

It has been showed that the diverse communities of advantageous microorganisms that make up the microbiome can improve plant development and defense mechanisms. However, it is not known whether certain microbial combinations

or the entire microbiome are required to mediate the function that promote plant resilience. Studies have demonstrated that consortium prepared from bacteria associated with sugarcane and pine can speed up the development of maize (Puri et al. 2015; Armanhi et al. 2018). In this regard, it has been suggested to engineer and create SynComs, which are like microbiome inoculants (Liu et al. 2019). In recent years, SynCom has been successfully developed, employing microbial communities originating from the phyllosphere and rhizosphere (Castrillo et al. 2017; Chen et al. 2020). Plants already exposed to pathogens have been recovered after a SynCom application (Durán et al. 2018). According to the study, the capacity of phylogenetically unrelated bacteria from the Comamonadaceae and Pseudomonadaceae can protect Arabidopsis against harmful fungi and oomycetes. But how SynCom functions in varied environmental situations is still a mystery. The majority of the SynCom treatment was completed in a controlled setting to maintain all of the factors, including inoculum density, nutritional availability, and plant genotypic background. Despite that, it is still conceivable that diverse plant genotypes may utilize microbes that can adapt to varied ecological settings.

Conclusions and future directions

The microbiome determines how the plant immune system responds to pathogens and modulates its defense signaling. In addition to protecting against diseases, the innate immune system must function suitably for FLS2-mediated surveillance of commensal bacteria in the plant microbiota. According to recent studies, commensal bacteria can obstruct MTI, suggesting that flg22 mutations may be present in the commensal microbiota (Fig. 1). The majority of flg22 mutations in commensal bacteria enable them to take advantage of colonization (Colaianni et al. 2021). This shows that flg22 mutations also escape FLS2 recognition by plant microbiomes. As a result, flagellin's immunogenic and motility activities may conflict with commensal bacteria's ability to suppress MTI, leading to antagonistic pleiotropy (Parys et al. 2021).

Plants are also able to recruit beneficial bacteria at the roots when infected with foliar pathogens. Upon pathogen challenges, plants can modify their root microbiome and particularly promote a population of disease-suppressive and growth-promoting beneficial microorganisms, thereby increasing the chance that their progeny would survive. In the rhizosphere, *Arabidopsis thaliana* attracts helpful bacterial species that produce biofilms and induce ISR response against downy mildew pathogen *Hyaloperonospora arabidopsidis* (Berendsen et al. 2018). As a result, the subsequent generation of plants raised in the same soil develops resistance to the disease. This implies that the development of disease-suppressive soils results from the gathering of protective bacteria. Therefore, a complete understanding of the mechanisms that regulate the establishment and interaction of helpful microorganisms by plant roots would create new opportunities to increase agricultural productivity.

Microorganisms are important for plant function and can boost crop yield (Table 1). The fundamental problem in the study of plant–microbe interactions is enhancing plant health under environmental stress situations by utilizing naturally occurring microbiota. The microbiome can be manipulated to create SynComs that can be used to study the link between the root microbiome and plant phenotypes. Therefore, high-throughput experimental methods are needed to construct SynComs by understanding their microbiological features, such as microbial library preparation in accordance to their genomes (de Souza et al. 2020). However, SynComs research struggle to replicate real soil ecosystems because of their complexity. Additional study is required to authentically replicate rhizosphere ecosystems that can suppress plant diseases.

P. simiae WCS417 is a popular plant growth-promoting rhizobacterium (PGPR) that has been proven to cause ISR. It has been used in numerous studies on plant–microbe interactions, demonstrating the potential of PGPRs to manipulate the rhizosphere microbiome and protect plants from pathogens (Verbon et al. 2019). Rhizobacteria also play key role in regulating root-specific immune responses. Cucurbitacin B, a triterpenoid compound, is attracted to rhizospheric bacteria and inhibits the growth of pathogenic fungus (Zhong et al. 2022). These compounds promote antifungal activity, combat infections, and support the colonization of beneficial microbes. By contrast, pathogen deployed effectors can interact with the microbiome by activating plant immune signaling gene expression and antagonizing microbial competitors. *V. dahliae*, a pathogen, secretes VdAve1, a small protein that disables the plant's defense mechanisms, allowing pathogens to colonize and spread disease. VdAve1 also has the ability to modify the plant microbiomes (Snelders et al. 2020). However, the role of these effectors in interactions between plants and beneficial bacteria is still elusive.

Ecological studies and fundamental discoveries have improved our understanding of plant microbiomes. Microbiota interaction with diverse plant backgrounds in both stressed and non-stressed environments could fill knowledge gaps in plant–microbiome interactions research. The use of commercial agrochemicals may be replaced by microbe-mediated plant protection. Therefore, finding appropriate biocontrol agents that could have both direct and indirect favorable impacts on plant health must be a component of microbiome research. In comparison to the phyllosphere, the rhizosphere has a greater diversity and accumulation of microorganisms. As a result, it is probable that the environment will include large quantities of MAMPs that can

continuously cause plants to activate their immune systems. On the other hand, it is important to understand how plants selectively react and continue growth in MAMP-rich environments. Recently, rhizosphere microbiome management by plant genotypes have been examined using genome-wide association studies (GWAS) method (Deng et al. 2021; Wang et al. 2022). The research found a correlation between the microbial taxa of the rhizosphere in foxtail millet cultivars and the plant immune receptor FLS2 (Wang et al. 2022). This study demonstrates the use of GWAS to harness the microbiome for the development of high-yielding cultivars, with the potential for agricultural sustainability through the regulation of immune signaling gene expression in plants. However, substantial research is required to fully comprehend the molecular mechanisms of immune signaling pathways between plant genes and the rhizospheric bacteria.

Data availability Not applicable.

Declarations

Conflict of interest No conflict of interest declared.

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