



Plant-microbiome crosstalk and disease development

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Abstract

Plants harbor a complex immune system to fight off invaders and prevent diseases. For decades, the interactions between plants and pathogens have been investigated primarily through the lens of binary interactions, largely neglecting the diversity of microbes that naturally inhabit plant tissues. Recent research, however, demonstrates that resident microbes are more than mere spectators. Instead, the plant microbiome extends host immune function and influences the outcome of a pathogen infection. Both plants and the interacting microbes produce a large diversity of metabolites that form an intricate chemical network of nutrients, signals, and antimicrobial molecules. In this review, we discuss the involvement of the plant microbiome in disease development, focusing on the biochemical conversation that occurs between plants and their associated microbiota before, during and after infection. We also highlight outstanding questions and possible directions for future research.

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Introduction

When attacked by pathogens, plants activate a complex array of biochemical responses to prevent disease establishment and spread [1]. Immune receptors, antimicrobial proteins, and secondary metabolites have been widely investigated and characterized as key

components of the plant immune system [2]. However, recent research indicates that there is more to it: microbes that live in association with plants (i.e., the microbiome) can often extend plant immune function and comprise an additional layer of protection against diseases [3–5]. The molecular mechanisms that underlie these protective effects are still largely unknown, but they seem to fall into two general categories: (I) inhibition of pathogens as a result of competitive microbe–microbe interactions (direct effect), and (II) stimulation of the plant immune system by the microbiome (indirect effect) [3]. Importantly, the microbial populations that colonize plant tissues are not a random subset of the microbes that inhabit the surrounding environment. Instead, plants can actively recruit specific microorganisms as a strategy to mitigate a variety of stresses, including diseases [6]. Recruitment of beneficial microorganisms can occur even before the disease onset [7,8], and the beneficial effects of this recruitment can be inherited by the next generations of plants [9].

To recruit commensal microorganisms, plants use metabolites, such as carbohydrates, organic acids, phenolic-related compounds, and amino acids [10–12]. These metabolites are abundantly released through plant shoots and roots and serve as a source of nutrients that sustain microbial growth. In turn, recruited microbes can improve plant resistance against stresses, such as nutrient deficiencies, drought, or diseases [6]. The composition of these exuded metabolite pools is influenced by environmental factors, the plant nutritional status, age, and genotype, leading to a complex and specific response of the microbial community [13–18]. On the other hand, microorganisms can also release compounds that modulate plant exudation [19,20]. Thus, these molecules dictate the (highly complex) communication between plants and their associated microbiota, playing a central role in the response to adverse conditions.

Due to the ecological and agronomic importance of the communication established between plants and their microbiota, many studies have sought to identify metabolites that are involved in this interaction as well as understand how they contribute to plant protection against adverse conditions. By dissecting the functions of these molecules in the communication between

plants and microorganisms, we may be able to develop methods and strategies to protect plants against stresses. Here, we discuss the most recent studies on the communication network in plant–microbiome interactions in the context of diseases. This review highlights how host plants modulate their microbiota to prevent or mitigate infections, or even leave a legacy of protection for future generations (Figure 1).

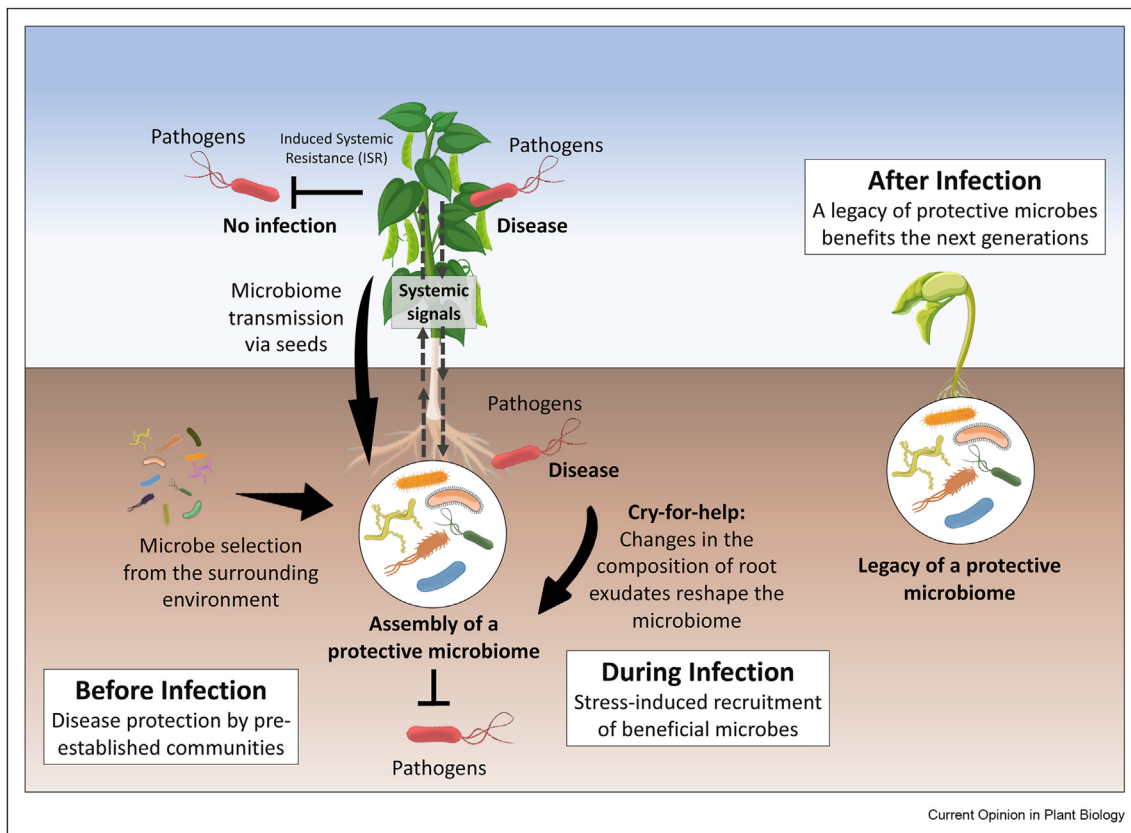
Before infection: pre-existing microbial communities can prevent diseases

Under natural field conditions, the spread of an incoming virulent pathogen is typically fast and highly destructive to genetically homogeneous plant populations. Yet, healthy individuals can often be found within close proximity to diseased ones, even though they are genetically compatible with the pathogen. Although the dynamics of disease outbreaks are complex and poorly

understood, this apparently stochastic behavior under homogeneous agricultural conditions is often attributed to uneven pathogen load, differences in plant physiological state, and heterogeneous soil physicochemical properties [21–23]. Recently, however, the microbiome has emerged as an important contributing factor.

Exciting new research demonstrates that the initial microbiome composition of a plant can predetermine the outcome of pathogen infection and, thus, disease dynamics. For instance, a rice seed endophyte (*Sphingomonas melonis* ZJ26) confers resistance against the seed-borne pathogen *Burkholderia plantarii* [24]. This protective effect can be transmitted across generations and is mediated by anthranilic acid, a secondary metabolite produced by the endophyte that interferes with the activation of virulence factors in the pathogenic strain. Importantly, plants of the same cultivar lacking the

Figure 1



The plant microbiome can determine the outcome of pathogen infections. The image illustrates how plant-associated microorganisms can influence disease development before, during and after infection. Plants may establish interactions with protective microbes before pathogens arrive, preventing the onset of diseases. Plant exudates containing primary or secondary metabolites are usually responsible for attracting these beneficial microbes from the surrounding environment. In some instances, protective microbes can be transmitted through seeds. During infection, plants “cry-for-help” and change the composition of their exudates, sometimes favoring the recruitment of beneficial microbes. After infection, the recruited microbial community may persist in the soil, establishing a legacy that protects the next generations of plants. The crosstalk underpinning these interactions among plants, protective microbes and pathogens has a significant role in determining disease outcomes and plant health. It should be noted that studies on plant microbiomes and their chemical communication with the host have largely focused on roots. Further research is needed to understand the extent to which the knowledge gained from the rhizosphere microbiome can be applied to the phyllosphere microbiome.

endophyte are susceptible to the pathogen, highlighting the sufficiency of the indigenous microbiota in preventing disease. Indeed, increasingly studies indicate that resistant and susceptible genotypes of the same plant often harbor distinct native microbiota. In the tomato cultivar Hawaii 7996, resistance against *Ralstonia solanacearum* has been associated with the prevalence of a specific *Flavobacterium* strain [25]. Interestingly, direct inoculation of flavobacteria or rhizosphere transplantation from resistant plants suppressed disease symptoms in the Moneymaker tomato cultivar, which is susceptible to the pathogen. Similarly, disease resistance in specific cultivars of wheat [26], strawberry [27], common bean [28], and potato [29] has been associated with the presence of a protective microbiota.

Plants can modulate the composition and function of microbial communities in their surrounding environments through the release of a variety of chemically diverse metabolites [10–12]. Because metabolite pools are determined by environmental and genetic factors, microbial communities associated with plant tissues are highly plastic and vary across environments and individuals [13,30–32]. While many molecules function as attractants, others can be harmful to specific microorganisms, including pathogens. Thus, plants modulate their microbiome not only with “carrots” but also with “sticks”. This is well exemplified by coumarins, a class of molecules that mediate iron uptake by the roots, but also exhibit broad antimicrobial activity [33,34]. Exudation of coumarins reshape the *Arabidopsis* root microbiome, causing the proliferation of some microbes in detriment of others [35,36]. Interestingly, root exudation of the coumarin scopoletin is induced by beneficial bacteria that are highly tolerant to it [36]. This suggests that some microbes may stimulate the exudation of specific plant antimicrobial metabolites to clear the rhizosphere of competitors. In return, plants could benefit from the elimination of potential pathogens from their rhizosphere and, in the case of coumarins, from an enhanced ability to respond to iron shortages.

A much larger diversity of molecules, including primary and secondary metabolites, can regulate the composition and function of plant microbiomes [37–39]. For instance, the amino acid glutamic acid has been shown to shift the microbial communities associated with strawberry and tomato plants, promoting the enrichment of specific bacterial taxa that presumably enhance resistance against fungal pathogens [40]. The plant specialized metabolites triterpenes and camalexins are also involved in microbiome assembly. A group of specific triterpenes (i.e., thalianin, thalianyl fatty acid esters, and arabinin) can selectively modulate the bacterial community in *Arabidopsis* roots and may contribute to species-specific variations in microbiome composition

[41]. Similarly, root-specific camalexin biosynthesis has been shown to be important for plant growth promotion by the beneficial rhizobacterium *Pseudomonas* ssp. CH267 in *Arabidopsis* [14]. Modulation of microbial communities is also illustrated by benzoxazinoids, a class of specialized metabolites that are exuded in large quantities by the roots of many cereal crop species [42]. Exudation of benzoxazinoids has been shown to attract and stimulate the colonization of maize roots by the growth-promoting bacterium *Pseudomonas putida* KT2440 under controlled conditions [43], while it has consistently reduced the abundance of Flavobacteriaceae and Comamonadaceae in maize roots under natural field conditions [44]. Furthermore, maize mutants deficient in benzoxazinoid production display large changes in both fungal and bacterial communities in their rhizospheres [45,46], which has been associated with reduced defense responses against herbivory [46]. Such studies demonstrate that specific plant metabolites play a significant role in shaping the composition of the microbiome, thereby contributing to plant health. Genetic, environmental and developmental factors that modify the pool of metabolites produced by a plant can lead to changes in microbiome composition and, consequently, affect plant health and development.

Recently, an elegant study showed that variation in the initial rhizosphere microbiome of tomato plants explains the future outcome of infection with the soil-borne pathogen *R. solanacearum* [8]. In a parallel to medical cohort studies, the authors repeatedly evaluated the same plants throughout their life cycle under natural field conditions. The final disease outcome was then linked to the initial microbiome composition, revealing that those plants that remained healthy had been significantly more colonized by pathogen-suppressing bacteria. Furthermore, disease outcome in this system could be predicted at the level of individual plants based on the composition of the rhizosphere microbiome, even before changes in pathogen density were detected [7]. Although it is remarkable that microbiome composition can diverge into different states with contrasting outcomes for disease resistance, a fundamental question remains unanswered: Why did some individuals develop a protective microbiome while others did not? Presumably, plant-derived metabolites contributed to the recruitment of specific microbes during community assembly. Understanding how the communication between plants and protective microbes occurs is a critical topic for future research and may allow for microbiome manipulation towards beneficial communities.

During infection: stress-induced recruitment of protective microbes

Research over the past few years has shown that plant-associated microbial communities can change significantly in response to stresses [6]. Although the precise

mechanisms and genes involved are often unknown, these changes have been largely associated with the release of specific plant metabolites that promote the recruitment and proliferation of beneficial microbes. Enrichment of specific groups of Actinobacteria, mainly *Streptomyces*, has been observed in the root system of plants submitted to drought [31,47–51]. Remarkably, some enriched strains have been shown to alleviate the drought stress, underscoring the role of recruited microbes in the response to adverse conditions. Likewise, plants submitted to nutrient deficiency, high salinity, metal toxicity, salt stress, light limitation, variable temperature, and pH variation display microbiome shifts [35,36,52–56].

Biotic stresses also reshape the plant microbiome. In a pioneer study, Rudrappa et al. (2008) demonstrated that infection of Arabidopsis leaves by *Pseudomonas syringae* pv. tomato DC3000 stimulated root colonization by the protective bacterium *Bacillus subtilis* strain FB17 [57]. This recruitment was mediated by the exudation of malic acid, which acted as an attractant for the beneficial strain. Since then, it has been well established that plants exposed to aboveground infections can recruit beneficial microbes from the rhizosphere via root exudates, a phenomenon denominated “cry-for-help” [9]. For instance, infection of Arabidopsis leaves with the oomycete *Hyaloperonospora arabidopsidis* resulted in the recruitment of three beneficial bacteria to the rhizosphere. When applied to the soil, these strains promoted disease protection through Induced Systemic Resistance (ISR), a form of immunity triggered in the aboveground parts by root-colonizing microbes [58]. In a recent study, a field experiment showed that the abundance of the protective bacterium *Stenotrophomonas rhizophila* SR80 in wheat roots was highly correlated with the presence of the pathogen *Fusarium pseudograminearum*, suggesting that this beneficial strain was recruited under natural conditions [59]. Importantly, systemic recruitment of beneficial partners is not restricted to infections by microbial pathogens. Aboveground infestation of pepper and cabbage by herbivorous insects also promoted the establishment of protective communities in the roots, leading to subsequent resistance against pathogens or pests [60–63]. Furthermore, the “cry-for-help” response also appears to occur when roots are attacked by pathogens. In this regard, systemic microbiome recruitment has been observed within the root systems of cucumber, tomato, and barley. In split-root experiments, inoculation of a pathogen on one side changed the composition of the root exudate at a spatially separated part, leading to the recruitment of protective microbes away from the infection site [64–66]. Together, these studies highlight the importance of bidirectional chemical communication between plants and their microbiota during biotic stress. Although the number of studies showing disease-induced assembly of protective communities is rapidly

increasing in the literature, examples of specific plant molecules that mediate microbiome remodeling remain scarce. Thus, a promising and relevant avenue for future research is the identification and characterization of such molecules.

In addition to the systemic effects highlighted above, recent research also indicates that diseases affect the resident microbiota that exist at the site of infection. For instance, the microbial community of citrus leaves infected with the fungal pathogen *Diaporthe citri* shifts towards the enrichment of members predicted to harbor antimicrobial traits [67]. Indeed, several bacteria isolated from diseased plants showed protective activity under controlled experimental conditions. Likewise, infection of rice leaves with *Magnaporthe oryzae* resulted in changes in the local communities of bacteria and fungi [68]. Also, infection of Arabidopsis with the obligate biotrophic oomycete *Albugo* sp. caused significant alterations in the leaf microbiome [69]. Remarkably, a recent work showed that Arabidopsis plants infected with powdery mildew exhibit extensive changes in the leaf microbiota, including a shift in microbial community composition and a two-fold increase in bacterial load, while the root microbiota remains relatively unchanged [70]. It has to be noted, however, that none of these studies identified what caused the local microbiome rearrangements during pathogen infection. In particular, the extent of the participation of plant molecules in reshaping the microbiome at the infection site remains unknown. Identifying such metabolites will be highly informative and could support the development of new strategies to interfere with diseases through the enrichment of protective microbes at infection sites.

Consistent with the notion that plants can modify their exudates in response to biotic stresses, comparative studies have shown that root exudates of infected plants are often more effective in attracting microbes than the exudates of uninfected individuals. For instance, maize plants infected with the fungus *Fusarium graminearum* were more efficient in attracting the beneficial strain *Bacillus amyloliquefaciens* OR2-30 to their roots than uninfected controls [71]. In another elegant study, infection of *Carex arenaria* roots with *Fusarium culmorum* led to the emission of volatile organic compounds (VOC) that stimulated the migration of bacteria with antifungal properties from distant areas in the soil [72]. The blend of VOC emitted by uninfected plants had a weaker attractant activity.

As expected of a chemical conversation, plant-associated microorganisms also release metabolites that modulate the composition of plant exudates [19,20]. Although still poorly investigated in the context of biotic stresses, this process might play a direct role in the outcome of plant diseases. The interference of microbes in the composition or secretion of plant exudates with

antimicrobial activity has already been reported, as exemplified by the exudation of coumarins by *Arabidopsis* roots in response to the beneficial bacterium *Pseudomonas simiae* WCS417 [36]. In addition, the biocontrol activity of *Bacillus cereus* AR156 has been associated with its ability to induce the production of antimicrobial molecules (i.e., lactic acid and hexanoic acid) by tomato roots [73]. Likewise, the growth-promoting bacterium *Pseudomonas* sp. strain RP2 induced changes in the root exudates of groundnut plants, causing a higher exudation of benzoic acid and salicylic acid, which inhibit the growth of the pathogenic fungus *Sclerotium rolfsii* in plants inoculated with this bacterium [74]. These studies indicate that members of the plant microbiome may promote disease protection by manipulating the composition and/or secretion of root exudates. Microbial molecules that mediate this effect, however, are yet to be described, but are likely key components of the conversation established between plants and their microbiomes during pathogen infection.

After infection: the legacy

As highlighted above, plants exposed to biotic stresses can actively recruit disease-suppressive microbes from the surrounding soil. This strategy may not only benefit the individuals that are under attack but may also provide protection to the next generations of plants, establishing a “memory” or “legacy” effect [9]. This phenomenon has been well-illustrated in *Arabidopsis* infected with the downy mildew pathogen *H. arabidopsidis* [75]. In this study, beneficial bacteria that were recruited by infected plants persisted in the soil and conferred enhanced disease protection to a subsequent generation of plants. This concept was further extended by the cultivation of successive generations of *Arabidopsis* plants infected with the leaf pathogen *P. syringae* pv *tomato* in the same soil [76]. After five generations, plants grown in this preconditioned soil showed an altered microbial community in their roots and displayed enhanced disease resistance. Thus, plants can inherit beneficial microbiomes from previous generations as a ‘soil-borne legacy’ [9], a fascinating idea that relates with the long-recognized concept of ‘disease suppressive soils’.

As the name suggests, disease suppressive soils are characterized by the low incidence of diseases caused by soilborne pathogens and typically develop following severe outbreaks in fields maintained as continuous monocultures of susceptible hosts [77–80]. The suppressive activity is largely determined by the microbiota composition and, therefore, these soils are a rich resource of beneficial microorganisms with plant protective traits. A pioneering study evaluated the microbial composition of a suppressive soil and revealed that the protection provided against the fungal root pathogen *Rhizoctonia solani* in sugar beets was due to the prevalence of bacterial

taxa enriched in antifungal activity [81]. Many subsequent studies validated and extended this conclusion, presenting, in some cases, the molecular mechanisms involved in pathogen inhibition [82–85]. Notably, plant metabolites released onto the rhizosphere during biotic stress are considered critical for the assembly of a beneficial microbial legacy and, consequently, for the establishment of disease-suppressive soils.

Plant microbiota can also be inherited by the next generation through seed colonization. Thus, microorganisms with beneficial characteristics can be selected from different plant tissues (pollen granules, flowers, or rhizosphere) and colonize different environments on the seed [86]. During germination, seed-associated microorganisms can be transmitted to the rhizosphere through cotyledon defoliation and root development [87]. Recent studies have shown that the microbiota present in seeds may contain members with beneficial characteristics and can promote plant growth or inhibit pathogens [88]. For example, Matsumoto *et al.* (2021) demonstrated that rice genotypes with varying degrees of resistance to *B. plantarii* infection harbor distinct seed microbiota, with resistant plants showing high abundance of bacteria of the genus *Sphingomonas* [24]. Interestingly, a *S. melonis* strain isolated from the seed-endophytic community of the disease-resistant rice genotypes restored resistance in susceptible plants. Importantly, the presence of these and other protective bacteria in seeds can also help in the establishment of an initial rhizospheric community, which will protect the seedling in its early stages of development [86]. While it is clear that the seed microbiome can have a role in plant resistance, it remains to be determined whether microbiome shifts in infected plants can also be transmitted through seeds to the next generation.

Concluding remarks and future directions

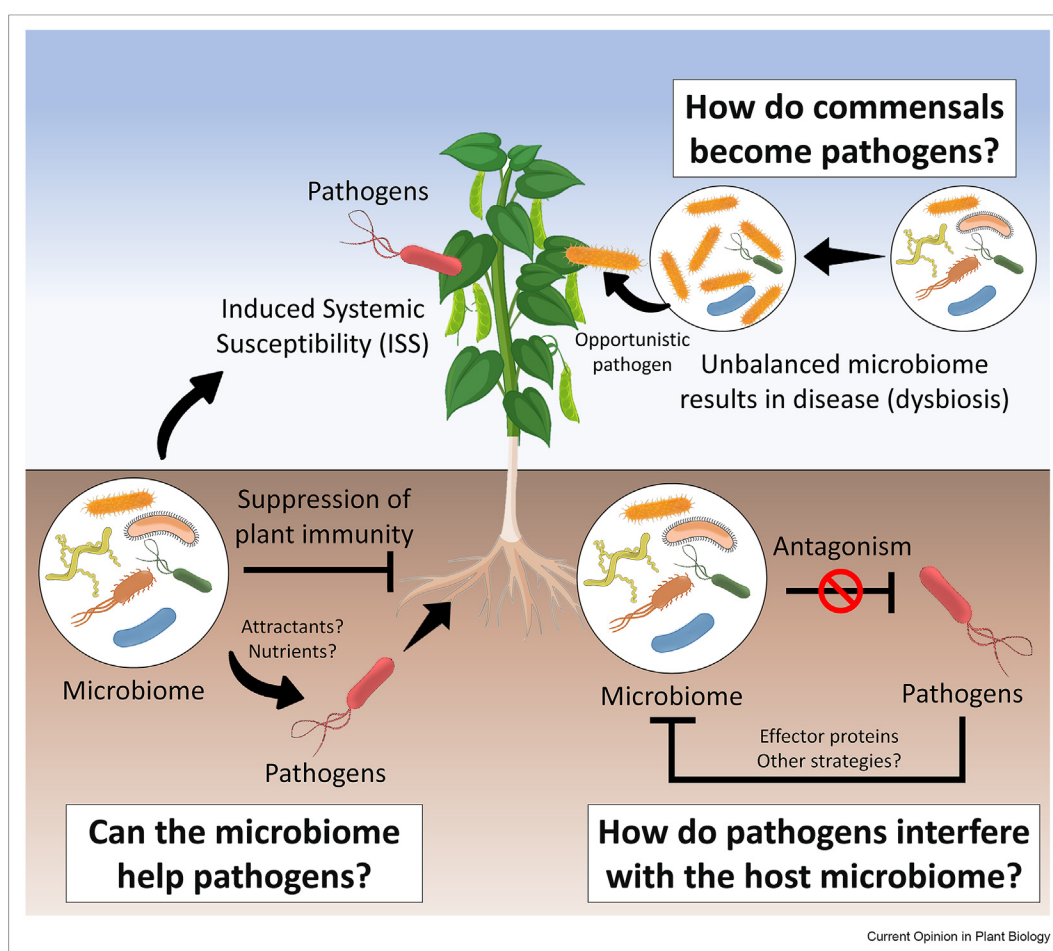
Research over the past 30 years has unveiled the molecular basis of the plant immune system and established generalizable rules that govern the outcome of plant–pathogen interactions. Although reports of disease protection mediated by specific microorganisms date back over 100 years [89], it was only in the last 10 years that the plant microbiome has become widely recognized as an additional layer of protection against diseases by plant immunologists. A wealth of recent studies now shows that commensal microbes extend the plant immune system and improve host health. In this context, it has become apparent that a large diversity of metabolites produced by both the plants and the microbes is central for this microbiome-mediated disease protection. The underlying mechanisms often include priming of the plant immune system by beneficial microbes or direct inhibition of pathogens through the production of antimicrobial compounds. Recent studies have also shown that microbiome-mediated pathogen

suppression can occur through competition for shared resources (e.g., space or nutrients) in a colonization-dependent manner [90,91]. Nonetheless, there is still much to learn about the involvement of the plant microbiome in disease development. In this regard, we highlight below three outstanding questions that, in our view, illustrate relevant knowledge gaps and constitute avenues for future research (Figure 2).

(I) *Can the microbiome help pathogens?* It is now widely accepted that many microbes can help plants to fight off diseases. However, it is logical to imagine that some pathogens may benefit from certain microbial communities. Indeed, studies in animals

have shown that the host microbiota can sometimes facilitate pathogen infection and worsen disease severity [92]. In plants, an early study showed that certain bacterial strains increased the pathogenicity of the fungus *Stagonospora nodorum* in co-inoculation assays in wheat leaves [93]. More recently, some root-associated bacteria have been shown to promote Induced Systemic Susceptibility (ISS) to specific pathogens and pests in Arabidopsis by interfering with the crosstalk of defense hormones [94–96]. Furthermore, recent research has shown that commensal microbes can suppress the plant immune system during root colonization [97–99]. Although not yet

Figure 2



Involvement of plant microbiomes in disease outcomes. Three questions that summarize some gaps in our current knowledge are highlighted. (I) Can the microbiome help pathogens? Although just barely explored, we anticipate that certain resident microbes may favor pathogen infection and worsen disease severity. Possible mechanisms include the activation of Induced Systemic Susceptibility (ISS) in the host, the suppression of the plant immune system, or the creation of favorable niches for pathogens through the production of metabolites (nutrients, attractants, etc.). (II) How do pathogens interfere with the host microbiome? Successful pathogens suppress or evade immune responses in their hosts. Since the microbiome constitutes an additional layer of immunity in plants, it is likely that pathogens have evolved a wide diversity of mechanisms to manipulate the plant microbiome as a virulence strategy. (III) How do commensals become pathogens? The plant microbiome harbors commensal microbes that, under specific conditions, display a pathogenic behavior and cause disease. Microbiome homeostasis is central for plant health, but how it is maintained is not well-defined. Finally, it is crucial to extend mechanistic studies on plant microbiomes to other parts of the plant, beyond the rhizosphere.

investigated, some pathogens may be “free riders” and take advantage of this immune suppression.

(II) *Do pathogens interfere with the host microbiome as a virulence strategy?* It is well-established that pathogens possess a large arsenal of molecular tools to interfere with plant immunity and, thus, facilitate infection [1]. Since the microbiome is an extension of the plant immune system, it is reasonable to assume that pathogens have evolved a wide diversity of strategies to counteract the positive effects of the microbiome on plant health and resistance. Indeed, recent studies demonstrated that the fungal pathogen *Verticillium dahliae* employs effector proteins to selectively suppress competitor bacteria and fungi associated with its host plants [100–102]. Additional research should help elucidate if such a strategy is widely employed by other plant pathogens, possibly revealing additional mechanisms of host microbiota manipulation.

(III) *How do commensal microbes become pathogens?* Recent research has shown that, just like animals, imbalanced microbiota can also lead to diseases in plants [103]. This phenomenon, known as dysbiosis, occurs when key protective members of the microbiota are lost, allowing the proliferation of opportunistic pathogen strains. In Arabidopsis, immunocompromised plants grown under high humidity show disease-like lesions due to the overproliferation of specific groups of bacteria in the leaf interior [104,105]. Proliferation of opportunistic strains has also been identified in *rbohD* knockout plants, which have impaired production of extracellular oxygen reactive species during immune responses [106]. In addition to demonstrating the role of the plant immune system in maintaining the homeostasis of native microbial communities, these findings show that some microbes can become pathogenic under specific conditions. Future research should explore how members of the microbiome are normally kept “under control”, but may become pathogenic during dysbiosis.

Declaration of competing interest

The authors declare the following financial interests, which may be considered as potential competing interests: Paulo José Pereira Lima Teixeira reports financial support from São Paulo Research Foundation (FAPESP), International Centre for Genetic Engineering and Biotechnology (ICGEB), Instituto Serrapilheira, and Aprosoja. Leticia Bianca Pereira reports financial support from FAPESP.

Data availability

No data was used for the research described in the article.

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References

Papers of particular interest, published within the period of review, have been highlighted as:

- * of special interest
- ** of outstanding interest

1. Jones JDG, Dangl JL: **The plant immune system.** *Nature* 2006, **444**:323–329.
2. Zhou J-M, Zhang Y: **Plant immunity: danger perception and signaling.** *Cell* 2020, **181**:978–989.
3. Teixeira PJP, Colaianni NR, Fitzpatrick CR, Dangl JL: **Beyond pathogens: microbiota interactions with the plant immune system.** *Curr Opin Microbiol* 2019, **49**:7–17.
4. Vannier N, Agler M, Hacquard S: **Microbiota-mediated disease resistance in plants.** *PLoS Pathog* 2019, **15**, e1007740.
5. Berendsen RL, Pieterse CMJ, Bakker PAHM: **The rhizosphere microbiome and plant health.** *Trends Plant Sci* 2012, **17**: 478–486.
6. Liu H, Brettell LE, Qiu Z, Singh BK: **Microbiome-mediated stress resistance in plants.** *Trends Plant Sci* 2020, **25**: 733–743.
7. Gu Y, Banerjee S, Dini-Andreote F, Xu Y, Shen Q, Jousset A, Wei Z: **Small changes in rhizosphere microbiome composition predict disease outcomes earlier than pathogen density variations.** *ISME J* 2022, **16**:2448–2456.
8. Wei Z, Gu Y, Friman V-P, Kowalchuk GA, Xu Y, Shen Q, Jousset A: **Initial soil microbiome composition and functioning predetermine future plant health.** *Sci Adv* 2019, **5**, eaaw0759.
9. Bakker PAHM, Pieterse CMJ, de Jonge R, Berendsen RL: **The soil-borne legacy.** *Cell* 2018, **172**:1178–1180.
10. Pascale A, Proietti S, Pantelides IS, Stringlis IA: **Modulation of the root microbiome by plant molecules: the basis for targeted disease suppression and plant growth promotion.** *Front Plant Sci* 2019, **10**:1741.
11. Sasse J, Martinoia E, Northen T: **Feed your friends: do plant exudates shape the root microbiome?** *Trends Plant Sci* 2018, **23**:25–41.
12. Bais HP, Weir TL, Perry LG, Gilroy S, Vivanco JM: **The role of root exudates in rhizosphere interactions with plants and other organisms.** *Annu Rev Plant Biol* 2006, **57**: 233–266.
13. Wang P, Lopes LD, Lopez-Guerrero MG, van Dijk K, Alvarez S, Riethoven J-J, Schachtman DP: **Natural variation in root exudation of GABA and DIMBOA impacts the maize root endosphere and rhizosphere microbiomes.** *J Exp Bot* 2022, **73**:5052–5066.

This work is a remarkable example of how the plant genotype determines the composition of root exudates. The authors identified inbred lines of maize that differ in root exudate concentrations of GABA

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and DIMBOA and, consequently, present different bacterial communities in their roots.

14. Koprivova A, Schuck S, Jacoby RP, Klinkhammer I, Welter B, Leson L, Martyn A, Nauen J, Grabenhorst N, Mandelkow JF, *et al.*: **Root-specific camalexin biosynthesis controls the plant growth-promoting effects of multiple bacterial strains.** *Proc Natl Acad Sci U S A* 2019, **116**:15735–15744.

The authors identify a cytochrome P450 gene (*CYP71A27*) in Arabidopsis, which is involved in camalexin biosynthesis, specifically in roots. They also show that this metabolite affects the microbiome composition and the plant interaction with growth-promoting bacteria.

15. Zhalnina K, Louie KB, Hao Z, Mansoori N, da Rocha UN, Shi S, Cho H, Karaoz U, Loqué D, Bowen BP, *et al.*: **Dynamic root exudate chemistry and microbial substrate preferences drive patterns in rhizosphere microbial community assembly.** *Nat Microbiol* 2018, **3**:470–480.

This work shows that the chemical composition of the root exudates from *Avena barbata* is dynamic and varies during plant development. Microbials in the rhizosphere showed distinct substrate preferences, explaining their succession in response to the growing plant root.

16. Pii Y, Penn A, Terzano R, Crecchio C, Mimmo T, Cesco S: **Plant-microorganism-soil interactions influence the Fe availability in the rhizosphere of cucumber plants.** *Plant Physiol Biochem* 2015, **87**:45–52.
17. Chaparro JM, Badri DV, Vivanco JM: **Rhizosphere microbiome assemblage is affected by plant development.** *ISME J* 2014, **8**:790–803.
18. Chaparro JM, Badri DV, Bakker MG, Sugiyama A, Manter DK, Vivanco JM: **Root exudation of phytochemicals in Arabidopsis follows specific patterns that are developmentally programmed and correlate with soil microbial functions.** *PLoS One* 2013, **8**, e55731.
19. Korenblum E, Dong Y, Szymanski J, Panda S, Jozwiak A, Massalha H, Meir S, Rogachev I, Aharoni A: **Rhizosphere microbiome mediates systemic root metabolite exudation by root-to-root signaling.** *Proc Natl Acad Sci U S A* 2020, **117**:3874–3883.

The authors show that the rhizosphere microbiome induces specific changes in the chemical composition of tomato root exudates. This phenomenon was found to be systemic and referred to as systemically induced root exudation of metabolites (SIREM).

20. Phillips DA, Fox TC, King MD, Bhuvaneshwari TV, Teuber LR: **Microbial products trigger amino acid exudation from plant roots.** *Plant Physiol* 2004, **136**:2887–2894.
21. Pagán I, García-Arenal F: **Tolerance of plants to pathogens: a unifying view.** *Annu Rev Phytopathol* 2020, **58**:77–96.
22. Bostock RM, Pye MF, Roubtsova TV: **Predisposition in plant disease: exploiting the nexus in abiotic and biotic stress perception and response.** *Annu Rev Phytopathol* 2014, **52**:517–549.
23. Campbell CL, Noe JP: **The spatial analysis of soilborne pathogens and root diseases.** *Annu Rev Phytopathol* 1985, **23**:129–148.
24. Matsumoto H, Fan X, Wang Y, Kusstatscher P, Duan J, Wu S, Chen S, Qiao K, Wang Y, Ma B, *et al.*: **Bacterial seed endophyte shapes disease resistance in rice.** *Native Plants* 2021, **7**:60–72.

This study shows that disease resistance can be determined and transmitted by the seed microbiome in rice. Seeds carrying a strain of *Sphingomonas melonis* are resistant to the seed-borne pathogen *Burkholderia plantarii* due to the production of anthranilic acid by the protective strain.

25. Kwak M-J, Kong HG, Choi K, Kwon S-K, Song JY, Lee J, Lee PA, Choi SY, Seo M, Lee HJ, *et al.*: **Rhizosphere microbiome structure alters to enable wilt resistance in tomato.** *Nat Biotechnol* 2018, <https://doi.org/10.1038/nbt.4232>.

The authors show that the rhizosphere microbiome contributes to resistance against *Ralstonia solanacearum* in the tomato variety Hawaii 7996.

26. Wu C, Wang F, Zhang H, Chen G, Deng Y, Chen J, Yang J, Ge T: **Enrichment of beneficial rhizosphere microbes in Chinese wheat yellow mosaic virus-resistant cultivars.** *Appl Microbiol Biotechnol* 2021, **105**:9371–9383.

27. Lazcano C, Boyd E, Holmes G, Hewavitharana S, Pasulka A, Ivors K: **The rhizosphere microbiome plays a role in the resistance to soil-borne pathogens and nutrient uptake of strawberry cultivars under field conditions.** *Sci Rep* 2021, **11**:3188.
28. Mendes LW, Raaijmakers JM, de Hollander M, Mendes R, Tsai SM: **Influence of resistance breeding in common bean on rhizosphere microbiome composition and function.** *ISME J* 2018, **12**:212–224.
29. Kobayashi A, Kobayashi YO, Someya N, Ikeda S: **Community analysis of root- and tuber-associated bacteria in field-grown potato plants harboring different resistance levels against common scab.** *Microb Environ* 2015, **30**:301–309.
30. Meier MA, Xu G, Lopez-Guerrero MG, Li G, Smith C, Sigmon B, Herr JR, Alfano JR, Ge Y, Schnable JC, *et al.*: **Association analyses of host genetics, root-colonizing microbes, and plant phenotypes under different nitrogen conditions in maize.** *Elife* 2022, **11**, e75790.

This study defined the rhizosphere microbial communities associated with 230 maize genotypes cultivated under high and low nitrogen conditions. It is an interesting example of how host genetics and environmental conditions determine the composition of plant microbiomes.

31. Fitzpatrick CR, Copeland J, Wang PW, Guttman DS, Kotanen PM, Johnson MTJ: **Assembly and ecological function of the root microbiome across angiosperm plant species.** *Proc Natl Acad Sci USA* 2018, **115**:E1157–E1165.
32. Haney CH, Samuel BS, Bush J, Ausubel FM: **Associations with rhizosphere bacteria can confer an adaptive advantage to plants.** *Native Plants* 2015, **1**, 15051.
33. Stassen MJJ, Hsu S-H, Pieterse CMJ, Stringlis IA: **Coumarin communication along the microbiome-root-shoot Axis.** *Trends Plant Sci* 2021, **26**:169–183.
34. Stringlis IA, de Jonge R, Pieterse CMJ: **The age of coumarins in plant-microbe interactions.** *Plant Cell Physiol* 2019, **60**:1405–1419.
35. Voges MJEEE, Bai Y, Schulze-Lefert P, Sattely ES: **Plant-derived coumarins shape the composition of an Arabidopsis synthetic root microbiome.** *Proc Natl Acad Sci USA* 2019, **116**:12558–12565.
36. Stringlis IA, Yu K, Feussner K, de Jonge R, Van Bentum S, Van Verk MC, Berendsen RL, Bakker PAHM, Feussner I, Pieterse CMJ: **MYB72-dependent coumarin exudation shapes root microbiome assembly to promote plant health.** *Proc Natl Acad Sci USA* 2018, **115**:E5213–E5222.
37. Koprivova A, Kopriva S: **Plant secondary metabolites altering root microbiome composition and function.** *Curr Opin Plant Biol* 2022, **67**, 102227.
38. Jacoby RP, Koprivova A, Kopriva S: **Pinpointing secondary metabolites that shape the composition and function of the plant microbiome.** *J Exp Bot* 2021, **72**:57–69.
39. Canarini A, Kaiser C, Merchant A, Richter A, Wanek W: **Root exudation of primary metabolites: mechanisms and their roles in plant responses to environmental stimuli.** *Front Plant Sci* 2019, **10**:157.
40. Kim D-R, Jeon C-W, Cho G, Thomashow LS, Weller DM, Paik M-J, Lee YB, Kwak Y-S: **Glutamic acid reshapes the plant microbiota to protect plants against pathogens.** *Microbiome* 2021, **9**:244.
41. Huang AC, Jiang T, Liu Y-X, Bai Y-C, Reed J, Qu B, Goossens A, Nützmann H-W, Bai Y, Osbourn A: **A specialized metabolic network selectively modulates Arabidopsis root microbiota.** *Science* 2019, **364**, eaau6389.

This study elucidates a specialized metabolic network involving triterpenes, which modulates the assembly of a specific microbiome in Arabidopsis roots. The work also suggests that triterpenes may play a role in the varying microbiome composition among different species.

43. Neal AL, Ahmad S, Gordon-Weeks R, Ton J: **Benzoxazinoids in root exudates of maize attract *Pseudomonas putida* to the rhizosphere.** *PLoS One* 2012, **7**, e35498.
44. Cadot S, Guan H, Bigalke M, Walser J-C, Jander G, Erb M, van der Heijden MGA, Schlaeppi K: **Specific and conserved patterns of microbiota-structuring by maize benzoxazinoids in the field.** *Microbiome* 2021, **9**:103.
45. Cotton TEA, Pétriacq P, Cameron DD, Meselmani MA, Schwarzenbacher R, Rolfe SA, Ton J: **Metabolic regulation of the maize rhizobiome by benzoxazinoids.** *ISME J* 2019, **13**: 1647–1658.
46. Hu L, Robert CAM, Cadot S, Zhang X, Ye M, Li B, Manzo D, Chervet N, Steinger T, van der Heijden MGA, *et al.*: **Root exudate metabolites drive plant-soil feedbacks on growth and defense by shaping the rhizosphere microbiota.** *Nat Commun* 2018, **9**:2738.
- This work illustrates the effects of benzoxazinoids exudation on the composition of the root-associated maize microbiome. The study also shows that this metabolite has a soil legacy effect via its derived product MBOA (6-methoxy-benzoxazolin-2-one), which shapes the microbiome and confers herbivore resistance to the next generation of plants.
47. Qi M, Berry JC, Veley KW, O'Connor L, Finkel OM, Salas-González I, Kuhs M, Jupe J, Holcomb E, Glavina Del Rio T, *et al.*: **Identification of beneficial and detrimental bacteria impacting sorghum responses to drought using multi-scale and multi-system microbiome comparisons.** *ISME J* 2022, **16**: 1957–1969.
48. Santos-Medellín C, Liechty Z, Edwards J, Nguyen B, Huang B, Weimer BC, Sundaresan V: **Prolonged drought impacts lasting compositional changes to the rice root microbiome.** *Native Plants* 2021, **7**:1065–1077.
49. Fitzpatrick CR, Mustafa Z, Viliunas J: **Soil microbes alter plant fitness under competition and drought.** *J Evol Biol* 2019, **32**: 438–450.
50. Xu L, Naylor D, Dong Z, Simmons T, Pierroz G, Hixson KK, Kim Y-M, Zink EM, Engbrecht KM, Wang Y, *et al.*: **Drought delays development of the sorghum root microbiome and enriches for monoderm bacteria.** *Proc Natl Acad Sci USA* 2018, **115**:E4284–E4293.
51. Naylor D, DeGraaf S, Purdom E, Coleman-Derr D: **Drought and host selection influence bacterial community dynamics in the grass root microbiome.** *ISME J* 2017, **11**:2691–2704.
52. Yu P, He X, Baer M, Beirincx S, Tian T, Moya YAT, Zhang X, Deichmann M, Frey FP, Bresgen V, *et al.*: **Plant flavones enrich rhizosphere Oxalobacteraceae to improve maize performance under nitrogen deprivation.** *Native Plants* 2021, **7**: 481–499.
- This is a comprehensive study demonstrating that root-derived flavones enrich the rhizosphere with bacteria from the Oxalobacteraceae family. These bacteria promote maize growth under nitrogen deprivation.
53. Li H, La S, Zhang X, Gao L, Tian Y: **Salt-induced recruitment of specific root-associated bacterial consortium capable of enhancing plant adaptability to salt stress.** *ISME J* 2021, **15**: 2865–2882.
54. Finkel OM, Salas-González I, Castrillo G, Conway JM, Law TF, Teixeira PJPL, Wilson ED, Fitzpatrick CR, Jones CD, Dangl JL: **A single bacterial genus maintains root growth in a complex microbiome.** *Nature* 2020, <https://doi.org/10.1038/s41586-020-2778-7>.
55. Timm CM, Carter KR, Carrell AA, Jun S-R, Jawdy SS, Vélez JM, Gunter LE, Yang Z, Nookaew I, Engle NL, *et al.*: **Abiotic stresses shift belowground *populus*-associated bacteria toward a core stress microbiome.** *mSystems* 2018, **3**:e00070. e00017.
56. Castrillo G, Teixeira PJPL, Paredes SH, Law TF, de Lorenzo L, Feltcher ME, Finkel OM, Breakfield NW, Mieczkowski P, Jones CD, *et al.*: **Root microbiota drive direct integration of phosphate stress and immunity.** *Nature* 2017, **543**:513–518.
57. Rudrappa T, Czymmek KJ, Paré PW, Bais HP: **Root-secreted malic acid recruits beneficial soil bacteria.** *Plant Physiol* 2008, **148**:1547–1556.
58. Pieterse CMJ, Zamioudis C, Berendsen RL, Weller DM, Van Wees SCM, Bakker PAHM: **Induced systemic resistance by beneficial microbes.** *Annu Rev Phytopathol* 2014, **52**:347–375.
59. Liu H, Li J, Carvalhais LC, Percy CD, Prakash Verma J, Schenk PM, Singh BK: **Evidence for the plant recruitment of beneficial microbes to suppress soil-borne pathogens.** *New Phytol* 2021, **229**:2873–2885.
60. Friman J, Karssemeijer PN, Haller J, de Kreek K, van Loon JJA, Dicke M: **Shoot and root insect herbivory change the plant rhizosphere microbiome and affects cabbage-insect interactions through plant-soil feedback.** *New Phytol* 2021, **232**: 2475–2490.
61. Kong HG, Kim BK, Song GC, Lee S, Ryu C-M: **Aboveground whitefly infestation-mediated reshaping of the root microbiota.** *Front Microbiol* 2016, **7**:1314.
62. Lee B, Lee S, Ryu C-M: **Foliar aphid feeding recruits rhizosphere bacteria and primes plant immunity against pathogenic and non-pathogenic bacteria in pepper.** *Ann Bot* 2012, **110**:281–290.
63. Yang JW, Yi H-S, Kim H, Lee B, Lee S, Ghim S-Y, Ryu C-M: **Whitefly infestation of pepper plants elicits defence responses against bacterial pathogens in leaves and roots and changes the below-ground microflora.** *J Ecol* 2011, **99**:46–56.
64. Lombardi N, Vitale S, Turrà D, Reverberi M, Fanelli C, Vinale F, Marra R, Ruocco M, Pascale A, d'Errico G, *et al.*: **Root exudates of stressed plants stimulate and attract *trichoderma* soil fungi.** *Mol Plant Microbe Interact* 2018, **31**:982–994.
65. Liu Y, Chen L, Wu G, Feng H, Zhang G, Shen Q, Zhang R: **Identification of root-secreted compounds involved in the communication between cucumber, the beneficial *Bacillus amyloliquefaciens*, and the soil-borne pathogen *Fusarium oxysporum*.** *Mol Plant Microbe Interact* 2017, **30**:53–62.
66. Dudenhöffer J-H, Scheu S, Jousset A: **Systemic enrichment of antifungal traits in the rhizosphere microbiome after pathogen attack.** *J Ecol* 2016, **104**:1566–1575.
67. Li P-D, Zhu Z-R, Zhang Y, Xu J, Wang H, Wang Z, Li H: **The phyllosphere microbiome shifts toward combating melanose pathogen.** *Microbiome* 2022, **10**:56.
- This work is an example of how a leaf pathogen changes the local microbiome. Here, citrus leaves infected with the fungus *Diaporthe citri* present an altered community of bacteria, with enrichment of strains with putative antifungal traits.
68. Dastogeer KMG, Yasuda M, Okazaki S: **Microbiome and pathobiome analyses reveal changes in community structure by foliar pathogen infection in rice.** *Front Microbiol* 2022, **13**, 949152.
69. Agler MT, Ruhe J, Kroll S, Morhenn C, Kim S-T, Weigel D, Kemen EM: **Microbial hub taxa link host and abiotic factors to plant microbiome variation.** *PLoS Biol* 2016, **14**, e1002352.
70. Durán P, Reinstädler A, Rajakrut AL, Hashimoto M, Garrido-Oter R, Schulze-Lefert P, Panstruga R: **A fungal powdery mildew pathogen induces extensive local and marginal systemic changes in the *Arabidopsis thaliana* microbiota.** *Environ Microbiol* 2021, **23**:6292–6308.
- This work shows that infection of *Arabidopsis* with the powdery mildew pathogen *Golovinomyces orontii* changes the leaf microbiome. Interestingly, no major changes were observed in the roots, indicating that the disease has no obvious systemic effect on the root microbial community.
71. Xie S, Jiang L, Wu Q, Wan W, Gan Y, Zhao L, Wen J: **Maize root exudates recruit *Bacillus amyloliquefaciens* OR2-30 to inhibit *Fusarium graminearum* infection.** *Phytopathology* 2022, **112**: 1886–1893.
72. Schulz-Bohm K, Gerards S, Hundscheid M, Melenhorst J, de Boer W, Garbeva P: **Calling from distance: attraction of soil bacteria by plant root volatiles.** *ISME J* 2018, **12**:1252–1262.
- This work shows that *Carex arenaria* roots infected with the fungal pathogen *Fusarium culmorum* produce volatile organic compounds that stimulate the migration of distant bacteria in the soil.
73. Wang N, Wang L, Zhu K, Hou S, Chen L, Mi D, Gui Y, Qi Y, Jiang C, Guo J-H: **Plant root exudates are involved in *Bacillus cereus* AR156 mediated biocontrol against *Ralstonia solanacearum*.** *Front Microbiol* 2019, **10**:98.

This is an interesting example of how beneficial microbes can alter the composition of plant exudates. Here, tomato roots colonized by *Bacillus cereus* AR156 produce antimicrobial molecules associated with *Ralstonia solanacearum* control.

74. Ankati S, Rani TS, Podile AR: **Changes in root exudates and root proteins in groundnut–*Pseudomonas* sp. interaction contribute to root colonization by bacteria and defense response of the host.** *J Plant Growth Regul* 2019, **38**:523–538.
75. Berendsen RL, Vismans G, Yu K, Song Y, de Jonge R, Burgman WP, Burmölle M, Herschend J, Bakker PAHM, Pieterse CMJ: **Disease-induced assemblage of a plant-beneficial bacterial consortium.** *ISME J* 2018, **12**:1496–1507.
76. Yuan J, Zhao J, Wen T, Zhao M, Li R, Goossens P, Huang Q, Bai Y, Vivanco JM, Kowalchuk GA, et al.: **Root exudates drive the soil-borne legacy of aboveground pathogen infection.** *Microbiome* 2018, **6**:156.
77. Gómez Expósito R, de Bruijn I, Postma J, Raaijmakers JM: **Current insights into the role of rhizosphere bacteria in disease suppressive soils.** *Front Microbiol* 2017, **8**:2529.
78. Schlatter D, Kinkel L, Thomashow L, Weller D, Paulitz T: **Disease suppressive soils: new insights from the soil microbiome.** *Phytopathology* 2017, **107**:1284–1297.
79. Raaijmakers JM, Mazzola M: **ECOLOGY. Soil immune responses.** *Science* 2016, **352**:1392–1393.
80. Weller DM, Raaijmakers JM, Gardener BBM, Thomashow LS: **Microbial populations responsible for specific soil suppressiveness to plant pathogens.** *Annu Rev Phytopathol* 2002, **40**:309–348.
81. Mendes R, Kruijt M, de Bruijn I, Dekkers E, van der Voort M, Schneider JHM, Piceno YM, DeSantis TZ, Andersen GL, Bakker PAHM, et al.: **Deciphering the rhizosphere microbiome for disease-suppressive bacteria.** *Science* 2011, **332**:1097–1100.
82. Carrión VJ, Perez-Jaramillo J, Cordovez V, Tracanna V, de Hollander M, Ruiz-Buck D, Mendes LW, van Ijcken WFJ, Gomez-Exposito R, Elsayed SS, et al.: **Pathogen-induced activation of disease-suppressive functions in the endophytic root microbiome.** *Science* 2019, **366**:606–612.
83. Carrión VJ, Cordovez V, Tyc O, Etalo DW, de Bruijn I, de Jager VCL, Medema MH, Eberl L, Raaijmakers JM: **Involvement of Burkholderiaceae and sulfurous volatiles in disease-suppressive soils.** *ISME J* 2018, **12**:2307–2321.
84. Cha J-Y, Han S, Hong H-J, Cho H, Kim D, Kwon Y, Kwon S-K, Crüsemann M, Bok Lee Y, Kim JF, et al.: **Microbial and biochemical basis of a Fusarium wilt-suppressive soil.** *ISME J* 2016, **10**:119–129.
85. Chapelle E, Mendes R, Bakker PAHM, Raaijmakers JM: **Fungal invasion of the rhizosphere microbiome.** *ISME J* 2016, **10**:265–268.
86. Samreen T, Naveed M, Nazir MZ, Asghar HN, Khan MI, Zahir ZA, Kanwal S, Jeevan B, Sharma D, Meena VS, et al.: **Seed associated bacterial and fungal endophytes: diversity, life cycle, transmission, and application potential.** *Appl Soil Ecol* 2021, **168**, 104191.
87. Kong HG, Song GC, Ryu C-M: **Inheritance of seed and rhizosphere microbial communities through plant-soil feedback and soil memory.** *Environ Microbiol Rep* 2019, **11**:479–486.
88. Berg G, Raaijmakers JM: **Saving seed microbiomes.** *ISME J* 2018, **12**:1167–1170.
89. Baker KF: **Evolving concepts of biological control of plant pathogens.** *Annu Rev Phytopathol* 1987, **25**:67–85.
90. Wang NR, Wiesmann CL, Melnyk RA, Hossain SS, Chi M-H, Martens K, Craven K, Haney CH: **Commensal *Pseudomonas fluorescens* strains protect Arabidopsis from closely related *Pseudomonas* pathogens in a colonization-dependent manner.** *mBio* 2022, **13**, e0289221.
91. Vogel CM, Potthoff DB, Schäfer M, Barandun N, Vorholt JA: **Protective role of the Arabidopsis leaf microbiota against a bacterial pathogen.** *Nat Microbiol* 2021, **6**:1537–1548.
92. Stevens EJ, Bates KA, King KC: **Host microbiota can facilitate pathogen infection.** *PLoS Pathog* 2021, **17**, e1009514.
This is a review article that discusses how microbiota can facilitate pathogen infections in animals. A good starting point for researchers interested in the same phenomenon in plants.
93. Dewey FM, Wong YL, Seery R, Hollins TW, Gurr SJ: **Bacteria associated with *Stagonospora (Septoria) nodorum* increase pathogenicity of the fungus.** *New Phytol* 1999, **144**:489–497.
94. Beskrovnaya P, Melnyk RA, Liu Z, Liu Y, Higgins MA, Song Y, Ryan KS, Haney CH: **Comparative genomics identified a genetic locus in plant-associated *Pseudomonas* spp. that is necessary for induced systemic susceptibility.** *mBio* 2020, **11**:e00575–e00620.
This work demonstrates that some root-associated bacteria can promote induced systemic susceptibility (ISS) to foliar pathogens. The authors identify bacterial genes required for the ISS phenotype.
95. Haney CH, Wiesmann CL, Shapiro LR, Melnyk RA, O'Sullivan LR, Khorasani S, Xiao L, Han J, Bush J, Carrillo J, et al.: **Rhizosphere-associated *Pseudomonas* induce systemic resistance to herbivores at the cost of susceptibility to bacterial pathogens.** *Mol Ecol* 2018, **27**:1833–1847.
96. Pineda A, Zheng S-J, van Loon JJA, Dicke M: **Rhizobacteria modify plant-aphid interactions: a case of induced systemic susceptibility.** *Plant Biol* 2012, **14**(Suppl 1):83–90.
97. Teixeira PJL, Colaianni NR, Law TF, Conway JM, Gilbert S, Li H, Salas-González I, Panda D, Del Risco NM, Finkel OM, et al.: **Specific modulation of the root immune system by a community of commensal bacteria.** *Proc Natl Acad Sci U S A* 2021, **118**, e2100678118.
98. Ma K-W, Niu Y, Jia Y, Ordon J, Copeland C, Emonet A, Geldner N, Guan R, Stolze SC, Nakagami H, et al.: **Coordination of microbe-host homeostasis by crosstalk with plant innate immunity.** *Native Plants* 2021, **7**:814–825.
99. Yu K, Liu Y, Tichelaar R, Savant N, Lagendijk E, van Kuijk SJJ, Stringlis IA, van Dijken AJH, Pieterse CMJ, Bakker PAHM, et al.: **Rhizosphere-associated *Pseudomonas* suppress local root immune responses by gluconic acid-mediated lowering of environmental pH.** *Curr Biol* 2019, **29**:3913–3920.e4.
100. Snelders NC, Boshoven JC, Song Y, Schmitz N, Fiorin GL, Rovenich H, van den Berg GCM, Torres DE, Petti GC, Prockl Z, et al.: **A highly polymorphic effector protein promotes fungal virulence through suppression of plant-associated Actinobacteria.** *New Phytol* 2022, <https://doi.org/10.1111/nph.18576>.
101. Snelders NC, Petti GC, van den Berg GCM, Seidl MF, Thomma BPHJ: **An ancient antimicrobial protein co-opted by a fungal plant pathogen for in planta mycobiome manipulation.** *Proc Natl Acad Sci U S A* 2021, **118**, e2110968118.
102. Snelders NC, Rovenich H, Petti GC, Rocafort M, van den Berg GCM, Vorholt JA, Mesters JR, Seidl MF, Nijland R, Thomma BPHJ: **Microbiome manipulation by a soil-borne fungal plant pathogen using effector proteins.** *Native Plants* 2020, **6**:1365–1374.
This article shows that the fungal pathogen *Verticillium dahliae* suppresses specific bacteria from the host microbiome as a virulence strategy. The pathogen employs effector proteins with antimicrobial activity to selectively eliminate antagonistic strains.
103. Paasch BC, He SY: **Toward understanding microbiota homeostasis in the plant kingdom.** *PLoS Pathog* 2021, **17**, e1009472.
104. Chen T, Nomura K, Wang X, Sohrabi R, Xu J, Yao L, Paasch BC, Ma L, Kremer J, Cheng Y, et al.: **A plant genetic network for preventing dysbiosis in the phyllosphere.** *Nature* 2020, **580**:653–657.
105. Xin X-F, Nomura K, Aung K, Velásquez AC, Yao J, Boutrot F, Chang JH, Zipfel C, He SY: **Bacteria establish an aqueous living space in plants crucial for virulence.** *Nature* 2016, **539**:524–529.
106. Pfeilmeier S, Petti GC, Bortfeld-Miller M, Daniel B, Field CM, Sunagawa S, Vorholt JA: **The plant NADPH oxidase RBOHD is required for microbiota homeostasis in leaves.** *Nat Microbiol* 2021, **6**:852–864.