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Understanding microbiome shifts and their impacts on plant health during pathogen infections

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Abstract

Pathogen infections can drastically reshape plant-associated microbiomes, yet the mechanisms underlying these shifts and their consequences for plant health remain elusive. In this review, we integrate recent advances to delineate how pathogen attack drives local and systemic microbiome restructuring via 3 major processes: (i) collateral effects of the plant immune system, including alterations to the local physicochemical niche; (ii) active recruitment of beneficial microbes through pathogen-induced root exudates (primary and secondary metabolites, volatiles, and organic compounds); and (iii) pathogen-mediated manipulation of the host microbiome through microbial effectors, antimicrobial production, or niche competition. By contrasting adaptive outcomes (enrichment of disease-suppressive taxa) with detrimental consequences (dysbiosis, mutualist loss, or proliferation of disease-promoting microbes), we emphasize the need for time-resolved, mechanistic studies that move beyond correlative surveys. Although the enrichment of protective microbes is a recurring theme in current literature, it is important to recognize that not all microbiome shifts are adaptive or host directed. Considering alternative explanations is critical to avoid survivorship bias and to accurately interpret microbiome dynamics in the context of plant–pathogen interactions. Building on these insights, we discuss the rational design of microbiome-based interventions to enhance crop resilience, including synthetic microbial consortia and elicitor-mediated recruitment of beneficial microbes. Notably, integrating microbiome dynamics into plant pathology offers a promising path toward sustainable disease management, transforming the microbiome from a passive background into an active, designable component of plant immunity.

Introduction

Every year, plant pathogens are responsible for substantial crop losses worldwide (Savary et al. 2019; Ristaino et al. 2021). Such losses threaten food security and environmental sustainability, a concern that is particularly urgent as the world population is projected to reach nearly 9.8 billion by 2050. Addressing this challenge requires innovative disease control strategies, as conventional approaches alone may not suffice to ensure a stable and sustainable food supply. A promising approach lies in harnessing the plant microbiome, a diverse community of microorganisms living in and around plants. These microbes can function as an extension of the plant immune system, offering an additional layer of protection against pathogens (Berendsen et al. 2012; Hacquard et al. 2017; Teixeira et al. 2019; Vannier et al. 2019; Pereira et al. 2023).

The plant immune system consists of a sophisticated array of defense mechanisms that enable plants to detect and combat invading organisms (Jones and Dangl 2006; Zhou and Zhang 2020; Ngou et al. 2022a). Pathogen detection is initially mediated by cell surface pattern recognition receptors that perceive highly conserved microbe-associated molecular patterns (MAMPs). This recognition triggers pattern-triggered immunity, effectively restricting most pathogens (Snoeck et al. 2025). However, certain pathogens have evolved strategies to evade or suppress pattern-triggered immunity by secreting virulence molecules known as *effectors* (Toruño et al. 2016; Buscaill and van der Hoorn 2021). In turn, an intracellular class of innate immune receptors—primarily from the nucleotide-binding and leucine-rich repeat receptor family—is activated upon effector recognition, resulting in a more robust response called *effector-triggered immunity* (Contreras et al. 2023). While this 2-layered immune system is essential for plant survival, viewing plant immunity in the context of a binary association between a host and a pathogen misses an important piece of the puzzle: the plant microbiome.

Plants form close associations with diverse microorganisms, including bacteria, fungi, archaea, and protists, which colonize different plant compartments (Vorholt 2012; Bulgarelli et al. 2013; Fitzpatrick et al. 2020; Trivedi et al. 2020). These microbial communities not only coexist with plants but actively contribute to their health. Generally, they enhance nutrient acquisition, alleviate environmental stresses, and provide protection against pathogens through direct and indirect mechanisms (Hiruma et al. 2016; Vogel et al. 2021; Qi et al. 2022). Beneficial microbes can directly interact with other microorganisms by producing antimicrobial compounds or competing for essential resources such as nutrients and space (Gu et al. 2020; Getzke et al. 2023). Indirectly, they can suppress pathogens via activation of the plant immune system (Vogel et al. 2016; Vishwanathan et al. 2020). In this way, the microbiome can actively shape the outcome of plant–pathogen interactions, ultimately influencing plant resistance and productivity.

The composition of the plant microbiome arises from a complex interplay of biotic and abiotic factors. Each plant forms a complex habitat, offering a unique physicochemical environment to which certain microbes are better adapted than others. Importantly, rather than passively acquiring their microbiome, plants can

selectively recruit specific microorganisms by secreting a variety of molecules (Yang et al. 2025). For example, primary and specialized metabolites in root exudates serve as chemical signals that attract beneficial microbes or repel harmful ones (Berendsen et al. 2018; Stringlis et al. 2018; Cotton et al. 2019; Thoenen et al. 2023). This selective recruitment enables plants to fine-tune the structure and function of their microbial community to better withstand various adverse conditions, including diseases (Liu et al. 2020; Gao et al. 2021). Beyond plant-driven selection, microbes themselves play an active role in microbiome composition. Some microbes may release molecules that modulate the secretion of plant metabolites or mediate microbial interactions, such as quorum-sensing signals and antimicrobial compounds (Chepsergon and Moleleki 2023; Compant et al. 2025). Additionally, microbiome dynamics are influenced by environmental conditions, host-specific factors (e.g. plant tissues, age, species), and microbial genetic traits related to nutrient acquisition, motility, stress tolerance, and host adaptation (Chaparro et al. 2014; Wagner et al. 2016; Cole et al. 2017; Levy et al. 2018; Knights et al. 2024; Mo et al. 2024). Therefore, plant-associated microbial communities are not merely a reflection of the microbes present in the surrounding environment. Instead, they emerge from a multifaceted association among plants, microbes, and environmental factors (Cheng et al. 2019; Compant et al. 2025). Understanding these processes is essential for unlocking the microbiome potential in sustainable agriculture.

The concept of disease-suppressive soils provides a foundation for our current understanding of pathogen-induced microbiome shifts (Mazzola 2002; Weller et al. 2002; Haas and Défago 2005; Raaijmakers et al. 2009; Schlatter et al. 2017; Spooren et al. 2024). Disease suppression, often observed in long-term monoculture soils, refers to the natural ability of soil microbial communities to limit disease incidence despite the presence of virulent pathogens. Foundational studies demonstrated that suppression emerges from the enrichment of specific microbial taxa and functions that antagonize pathogens or enhance plant health (recently reviewed by Spooren et al. 2024). In these systems, repeated pathogen pressure favors the proliferation of beneficial microbes that directly suppress pathogens or prime host defenses, insights largely revealed through classical soil transfer experiments, genomics, transcriptomics, and microbiome profiling (Mendes et al. 2011; Cha et al. 2016; Chialva et al. 2018; Li et al. 2023; Zhou et al. 2023). More recently, Carrión et al. (2019) provided a mechanistic demonstration of this process, showing that pathogen infection of roots activated disease-suppressive traits within the endophytic microbiome. Together, these studies established a conceptual framework that underpins current research on pathogen-induced microbiome shifts and microbiome-mediated plant defense.

Although research on the plant microbiome has advanced significantly in recent years, the significance of microbial shifts and the factors governing them have not been fully explored. Stress conditions such as disease are known to alter microbial communities (Hu et al. 2018b; Carrión et al. 2019; Seybold et al. 2020; Gao et al. 2021), yet the molecular mechanisms underlying these changes are still poorly characterized. Furthermore, the biological consequences of these shifts are equally unclear. While insights from disease-suppressive soils have been instrumental in revealing how pathogen pressure can enrich protective microbes (Spooren et al. 2024), our understanding on disease-induced microbiome shifts remains incomplete, particularly in aboveground tissues, where the principles established in soils and roots may not fully apply. Many studies attribute the enrichment of specific microbes in infected plants to their protective roles (Berendsen et al. 2018; Liu et al. 2020, 2021a; Yang et al. 2020; Goossens et al. 2023). However,

alternative explanations must be considered. Are these shifts always beneficial to plant health, or are they sometimes merely a consequence of infection? Could some changes be neutral, having no effect on disease progression? Or could some shifts even be detrimental, inadvertently favoring pathogen establishment? Without a deeper mechanistic understanding of these processes, it is challenging to determine the functional implications of microbiome alterations in plant health and disease. In this review, we compile current knowledge on microbiome functions in plant–pathogen interactions, identify major gaps in the field, and outline directions for future research as well as for the development of microbiome-informed strategies for sustainable agriculture.

Microbiome responses to pathogen invasion

Plant diseases trigger dynamic structural and functional shifts in host-associated microbial communities, mirroring patterns observed in animal systems (Box). Advances in high-throughput sequencing and multi-omics technologies have enabled detailed characterization of these changes across diverse plant–pathogen interactions. A recurring finding is the alteration of microbial alpha diversity (species richness and evenness) and beta diversity (community composition) during infections. For instance, the soil-borne pathogens *Ralstonia solanacearum* in tomato and *Fusarium oxysporum* in watermelon significantly reduce bacterial alpha diversity in the rhizosphere, accompanied by structural reorganization of microbial networks (Wei et al. 2018; Tong et al. 2024). In contrast, *Magnaporthe oryzae* and *Xanthomonas oryzae* in rice leaves have been associated with increased bacterial alpha diversity (Yang et al. 2020; Tian et al. 2021), highlighting context-dependent outcomes. Changes in beta diversity, indicative of microbiome restructuring, are nearly ubiquitous, with distinct microbial taxa either enriched or depleted in diseased plants.

Microbiome shifts in response to infection can be systemic or local (Fig. 1). Systemic shifts occur at sites distant from the infection, often affecting belowground microbial communities in response to foliar pathogens. For example, *Pseudomonas syringae* DC3000 infection in the leaves of *Arabidopsis thaliana* (hereafter Arabidopsis) leads to the enrichment of *Bacillus subtilis* FB17 in the roots, a bacterial strain with protective functions (Rudrappa et al. 2008). Similarly, infection by *Hyaloperonospora arabidopsidis* (*Hpa*) promotes the enrichment of *Xanthomonas*, *Microbacterium*, and *Stenotrophomonas* in the root microbiome. A synthetic consortium composed of these bacteria reduces *Hpa* susceptibility and enhances plant growth, indicating a protective role (Berendsen et al. 2018). Other foliar infections, whether caused by fungal or bacterial pathogens (even herbivory), can alter root microbiomes (Yuan et al. 2018; Friman et al. 2021; Zhu et al. 2021). These systemic effects are largely mediated by the release of specific metabolites into root exudates, supporting the concept that plants can actively recruit beneficial microbes in response to stress (Rudrappa et al. 2008; Bakker et al. 2018; Vismans et al. 2022).

Local shifts, in contrast, occur at the infection site. An early study demonstrated that the oomycete pathogen *Albugo candida* disrupts bacterial networks in Arabidopsis leaves, acting as a key driver of phyllosphere microbiome shifts (Agler et al. 2016). More recently, Goossens et al. (2023) found that repeated *Hpa* infections in Arabidopsis for pathogen propagation in different laboratories drive convergence in the phyllosphere microbiota across genetically diverse accessions. This *Hpa*-associated microbiota is enriched with bacteria exhibiting antagonistic effects against the pathogen. Notably, many of these protective microbes appear

Box. Microbiome shifts in plant and animal diseases

Animals and plants harbor complex, dynamic microbial communities that play central roles in nutrient acquisition, immune homeostasis, and protection against pathogens. While both systems host distinct microbial assemblages, core taxa and their functions show important parallels that reveal shared principles of host–microbiome biology. Pathogen infection, immune dysfunction, or other stressors commonly perturb these systems, reducing diversity, eliminating functionally important commensals, and favoring opportunistic expansions of fast-growing groups (Ilyaskina et al. 2025). In animals, acute infections by enteric pathogens such as *Salmonella* provoke inflammation and toxin production, which deplete protective short-chain fatty acid producers such as *Faecalibacterium* and *Roseburia*. The resulting collapse of these niches promotes blooms of opportunistic Proteobacteria such as *Clostridioides difficile* and *Escherichia coli*, perpetuating inflammation and compromising colonization resistance (Drumo et al. 2015; Caballero-Flores et al. 2023; Gupta and Dey 2023). Dysbiosis is also a hallmark of chronic inflammatory disorders, such as inflammatory bowel disease and autoimmunity, where depletion of commensals that sustain mucosal homeostasis coincides with Proteobacteria enrichment, fueling persistent inflammation and tissue damage (Chen et al. 2021). Beyond the gut, disease-associated microbiome shifts are observed in other tissues: for example, *Staphylococcus aureus* overgrowth in atopic dermatitis, *Pseudomonas* dominance in cystic fibrosis airways, and *Gardnerella* blooms in bacterial vaginosis (Aggarwal et al. 2023). Interestingly, comparable processes also occur in plants. Fungal infection can trigger *Pseudomonas* proliferation, which thrive in nutrient-rich, stressed tissues (Seybold et al. 2020), echoing opportunistic microbial expansions in inflamed animal guts. In addition, *Arabidopsis* mutants with impaired immunity display striking reductions in microbiome diversity and overgrowth of Proteobacteria such as *Pseudomonas* (Chen et al. 2020; Paasch and He 2021). Transferring these dysbiotic communities into healthy plants is sufficient to induce disease symptoms, closely paralleling fecal microbiota transplantation experiments in animals where dysbiotic communities alone can drive pathology (Paasch and He 2021). Despite these convergences, plants display a unique adaptive capacity. Rather than triggering exclusively detrimental outcomes, pathogen attack and other stressors can reprogram root exudation and systemic signaling to actively recruit beneficial microbes. For example, *Ralstonia* infection in tomato enriches root-associated bacteria with wilt disease-suppressing activity (Yang et al. 2023), a "cry for help" response absent from animal systems, where disease-associated microbiome shifts have been more consistently linked to negative consequences. Together, these parallels suggest that insights from one system can inform the other, opening opportunities for cross-kingdom strategies to harness the microbiome for improved health and resilience.

to originate from the rhizosphere, suggesting the occurrence of root-to-shoot microbial exchanges during disease progression.

A growing body of evidence indicates that microbiome shifts during infection may enrich beneficial microbes, directly influencing disease outcomes. However, causality remains a central challenge: Are enriched microbes actively recruited by the host to mitigate disease, or do they opportunistically colonize niches disrupted by infection? Three major non–mutually exclusive factors likely shape these dynamics (Fig. 2):

- **Collateral effects of plant immunity:** Activation of the plant immune system alters the conditions of the rhizosphere and phyllosphere (Piasecka et al. 2015). These changes, such as the secretion of antimicrobial compounds or shifts in pH, create new ecological niches that may be unfavorable to some microbes but conducive to the proliferation of others that are less affected by host defenses. Additionally, physiologic changes commonly associated with immune responses or pathogen colonization, including altered nutrient availability, can further influence microbial community composition by favoring certain taxa over others.
- **Active recruitment of beneficial microbes by the plant:** Plants can modulate biochemical outputs, such as specific root exudates, volatile organic compounds, and other signaling molecules, to attract microbial partners with beneficial functions (Rolfe et al. 2019). This active remodeling of the plant microbiome serves as a strategic adaptation to endure stressful conditions, including pathogen attack.
- **Pathogen manipulation of the host microbiome:** Pathogens may manipulate the host environment to reshape the associated microbial community in their favor. By secreting effector proteins and altering host metabolic processes, pathogens can suppress beneficial microbes and potentially create conditions that promote the proliferation of their own supportive microbial allies (Mesny et al. 2024). This manipulation can lead to a dysbiotic microbiome, weakening the host defense and facilitating more effective colonization by the pathogen.

While the enrichment of protective microbes is a recurring theme in the current literature, it is unlikely that all altered taxa are host selected or beneficial. Recognizing alternative hypotheses is essential to avoid perpetuating a form of survivorship bias. Studies disproportionately emphasize microbes with identifiable protective roles because they offer agronomically relevant mechanistic explanations, while the majority of taxa altered during infection (whose ecologic roles remain unknown) are often overlooked. This bias may distort our understanding of microbiome dynamics, as the functional significance of most microbial shifts, whether adaptive, incidental, or even detrimental, remains unresolved. Reductionist frameworks that attribute microbiome shifts solely to host-driven recruitment of protective microbes risk oversimplifying the ecologic complexity of plant–microbiota–pathogen interactions. For instance, plant defense molecules, pathogen-derived metabolites, and effector proteins can independently and synergistically reshape microbial communities (Jin et al. 2024), and neutral ecologic processes such as random colonization, demographic drift, or priority effects may also drive community shifts in some contexts (Nemergut et al. 2013; Zhou and Ning 2017). Additionally, ecologic cascades triggered by the depletion of keystone taxa may destabilize microbial networks (Agler et al. 2016). Thus, the enrichment of protective microbes may not be a universal consequence of infection. Recognizing survivorship bias and the tendency to focus on "success stories" is critical for advancing this field. Therefore, a comprehensive understanding of the mechanisms driving microbiome shifts is essential for developing targeted strategies to manipulate
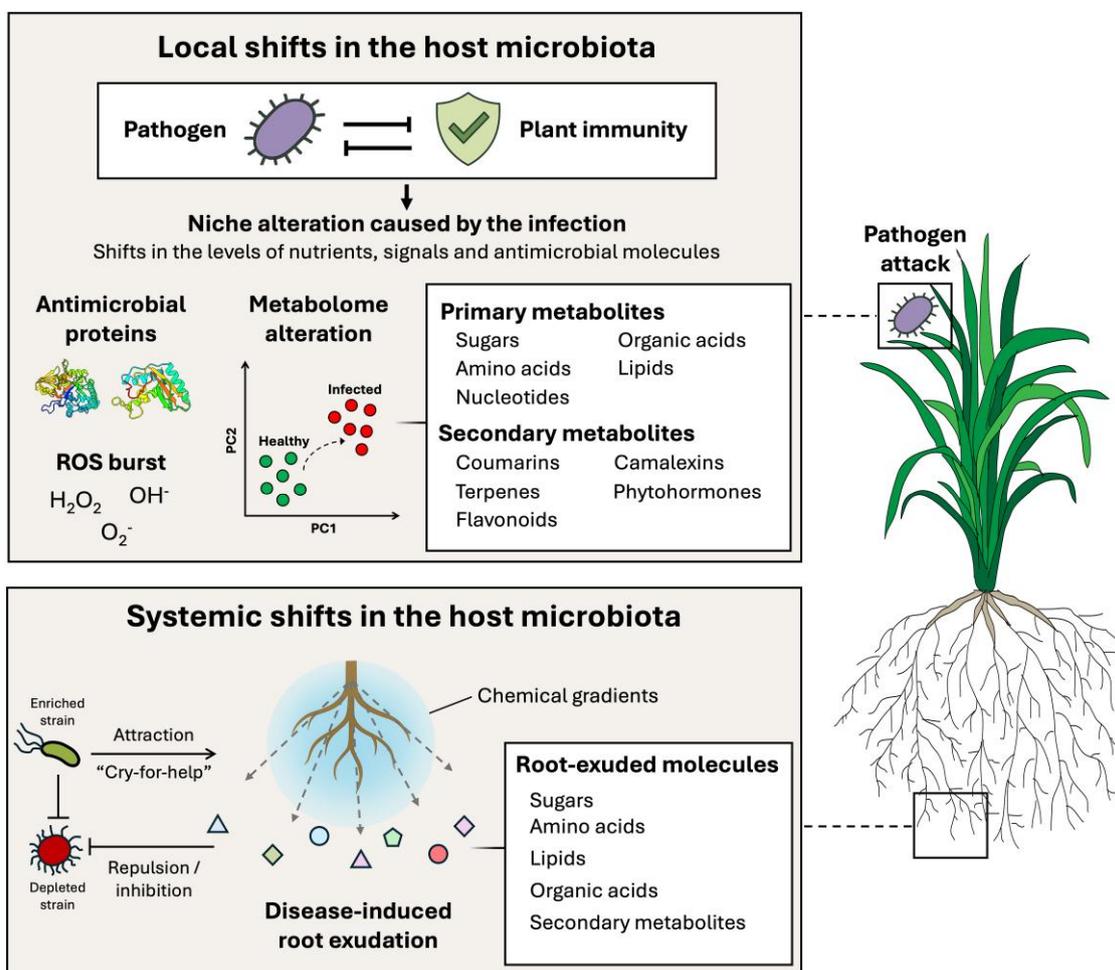
Figure 1. Disease-induced microbiome shifts occur locally and systemically. The interaction between the plant immune system and an invading pathogen disrupts local niche conditions in host tissues by altering nutrient availability, signaling molecules, and antimicrobial compounds. These local changes reshape the metabolome, modifying levels of primary and secondary metabolites, and thereby select for microbial strains that can tolerate or exploit the altered environment while suppressing less-adapted taxa. Simultaneously, infection in 1 organ (e.g. leaves) can trigger systemic shifts in distant tissues (e.g. roots) by inducing the exudation of specific metabolites into the rhizosphere. These root-exuded compounds establish chemical gradients that either attract some microbes, including beneficial partners, or repel and inhibit other strains. In this way, infection can produce a "cry for help" that recruits protective microbes systemically while depleting those unable to withstand pathogen-induced changes.

plant-associated microbial communities, whether to enhance disease resistance, promote plant growth, or improve agricultural sustainability. In the following sections, we explore the causes and consequences of microbiome shifts in plant disease ecology.

Causes of microbiome shifts during pathogen infection

Collateral effects of plant immunity on the microbiome

Pathogen invasion triggers plant immune responses, which deploy a multifaceted defense system that may inadvertently reshape host-associated microbial communities. Upon detecting invaders, plants activate immune pathways that generate signaling molecules and antimicrobial compounds (Zhou and Zhang 2020; Nguyen et al. 2022). These include antimicrobial proteins and peptides (Huang et al. 2021), reactive oxygen species (ROS; Torres et al. 2006), phytohormones (e.g. salicylic acid, jasmonic acid, and ethylene; Pieterse et al. 2012), specialized secondary metabolites (e.g. flavonoids, alkaloids, and phenolics; Piasecka et al. 2015; Nguyen et al. 2022), and regulatory microRNAs

(Wang et al. 2016; Cai et al. 2018). While these defense mechanisms aim to curb pathogen spread, they also create a dynamic chemical environment that imposes selective pressures on resident microbes (Fig. 1). Commensal taxa sensitive to certain antimicrobials or oxidative stress may decline, while resilient species that detoxify these compounds or exploit new ecologic niches can thrive (Stringlis et al. 2018; Thoenen et al. 2023, 2024; Zhang et al. 2023). Notably, even in the absence of active infection, plants with constitutively active immune responses exhibit altered microbial communities, underscoring the pervasive influence of defense pathways on microbiome assembly (Lebeis et al. 2015; Pfeilmeier et al. 2021; Lv et al. 2022; Vincent et al. 2022; Song et al. 2023). This collateral effect highlights the duality of plant immunity: while effectively defending against pathogens, it can reshape the microbiome, potentially enriching or depleting specific taxa, altering microbial functions, or even promoting opportunistic pathobionts. Whether these changes are side effects or directly regulated by the plant remains unclear in many cases. In what follows, we illustrate how specific defense molecules mediate the balance between pathogen suppression and microbiome structure, emphasizing the ecologic trade-offs inherent in plant–microbe interactions during disease.
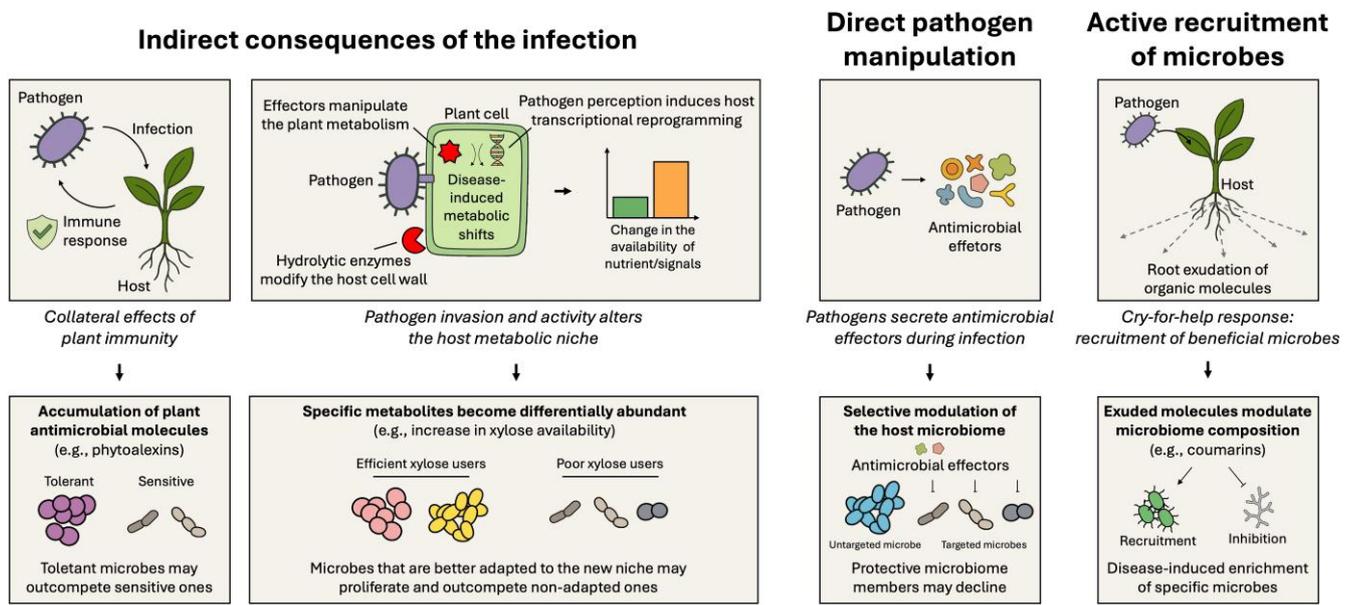
Figure 2. Drivers of microbiome shifts during pathogen infections in plants. Multiple processes contribute to changes in microbial community composition during disease. Some shifts may be indirect consequences of infection, arising as collateral effects of plant immunity or as a result of host metabolic reprogramming. Immune responses, such as the production of reactive oxygen species, antimicrobial proteins, and secondary metabolites, can inadvertently suppress sensitive microbial taxa, favoring the proliferation of tolerant ones. For example, glucosinolates produced by plants in response to herbivores or necrotrophic pathogens may affect the native microbiome (Russ et al. 2025). Pathogen invasion further alters the host metabolic niche, modifying nutrient availability and signaling landscapes. For instance, *Xanthomonas* strains acting as opportunistic pathogens secrete hydrolytic enzymes via the type II secretion system, leading to cell wall degradation and shifts in nutrient profiles. These changes favor microbes that are better adapted to the new niche, contributing to dysbiosis (Entila et al. 2024; Pfeilmeier et al. 2024). Beyond indirect effects, pathogens can directly manipulate the host microbiome through the secretion of antimicrobial effectors, which may selectively inhibit protective microbial taxa and weaken the defensive barrier provided by the resident community. For example, *Verticillium* species produce antimicrobial effectors that suppress specific members of the root microbiome, facilitating colonization (Snelders et al. 2020). Finally, plants can actively shape their microbiome during disease through the "cry for help" response, which involves the exudation of organic molecules from roots. These exudates can recruit beneficial microbes while limiting the growth of harmful taxa. For example, Arabidopsis secretes coumarins that promote the recruitment of protective bacteria while inhibiting fungal pathogens (Stringlis et al. 2018). Together, these host- and pathogen-driven mechanisms illustrate the dynamic reshaping of plant microbiomes during infection. Although enrichment of protective microbes can occur during infection, the ecologic consequences of disease-induced microbiome shifts are complex and often nonadaptive. Many taxa whose abundances change may not contribute to host defense, and some shifts could even be neutral or detrimental. Therefore, to fully understand the causes and ecologic consequences of disease-induced microbiome changes, it is essential to examine these dynamics in a detailed and unbiased manner for each plant–pathogen interaction.

Camalexin

Camalexin is an indole alkaloid phytoalexin produced by Arabidopsis and other crucifers in response to pathogen attack (Glawischnig 2007). This molecule accumulates upon MAMP perception and exhibits broad-spectrum toxicity against bacteria, oomycetes, and fungi (Rogers 1996; Schlaeppi et al. 2010; Lemarié et al. 2015; Khare et al. 2017). Beyond pathogen suppression, camalexin can shape plant-associated microbial communities. Arabidopsis mutants deficient in root-specific camalexin biosynthesis display altered rhizosphere microbiomes, with community shifts correlating with camalexin concentration and microbial strain sensitivity (Koprivova et al. 2019). Strikingly, camalexin is required for the growth promotion effect triggered by certain beneficial bacteria, indicating that it facilitates plant interactions with specific microbes and modulates microbiome function (Koprivova et al. 2019). Camalexin has also been implicated in induced systemic resistance (ISR), a form of immune response that is activated by beneficial microbes colonizing the roots (Van De Mortel et al. 2012; Nguyen et al. 2022). The roles of camalexin extend to seed–microbe interactions: while it inhibits the seed-borne pathogen *Alternaria brassicicola* in Brassicaceae, it enriches resistant seed-associated fungi, likely due to microbial detoxification pathways and niche specialization (Lerenard et al. 2024). These findings indicate that camalexin acts as a direct antimicrobial agent and a selective mediator of microbiome assembly,

possibly balancing pathogen suppression with the recruitment of tolerant microbes.

Coumarins

Coumarins are phenolic compounds synthesized by plants, microorganisms, and some animals, with roles in iron homeostasis, defense, and microbiome modulation (Stringlis et al. 2019). In plants, these metabolites are well-known iron-mobilizing agents, exuded in large quantities by roots under nutrient-limiting conditions to enhance iron bioavailability (Stringlis et al. 2019; Robe et al. 2021). Coumarins also function as defense molecules and accumulate during pathogen attack, directly inhibiting microbial growth or disrupting virulence strategies such as biofilm formation and quorum sensing (Helman and Chernin 2015; El-Sawy et al. 2024; Zaynab et al. 2024). A role for coumarins in shaping microbiome composition has only recently emerged. Arabidopsis mutants defective in root coumarin exudation exhibit an altered rhizosphere microbiome under iron deficiency, with specific commensal genera being differentially affected, likely due to variation in their tolerance to coumarin toxicity (Stringlis et al. 2018; Voges et al. 2019). Notably, root-exuded coumarins suppress fungal pathogens (e.g. *F. oxysporum*) while promoting colonization by tolerant beneficial bacteria (e.g. *Pseudomonas simiae* WCS417), illustrating their selective antimicrobial effects on microbiome composition (Stringlis et al. 2018). Interestingly, the Arabidopsis

transcription factor MYB72, which regulates coumarin biosynthesis, is required for rhizobacteria-mediated ISR, directly linking coumarin production to immune priming (Zamioudis et al. 2015). By suppressing specific taxa (including pathogens), recruiting beneficial microbes, and optimizing iron availability, coumarins exemplify how plant defense metabolites can govern microbiome shifts in response to different stress conditions.

Triterpenes

Triterpenes are a structurally diverse class of secondary metabolites that act as antimicrobial agents against pathogens and modulators of plant-associated microbial communities (Thimmappa et al. 2014). While constitutively produced during normal plant development, their biosynthesis is often induced upon pathogen attack, serving as a first chemical barrier against invaders (Polturak et al. 2022). Beyond direct antimicrobial activity, emerging evidence highlights their influence on the assembly and function of plant-associated microbial communities (Huang et al. 2019; Zhong et al. 2022). Arabidopsis mutants defective in the biosynthesis of root-specific triterpenes exhibit shifts in microbial community composition, displaying enrichment and depletion of certain taxa, underscoring a selective effect of these compounds (Huang et al. 2019). In cucurbits, root-exuded cucurbitacins provide protection against the soil-borne pathogen *F. oxysporum* by shifting the rhizosphere microbiota toward the enrichment of beneficial bacteria (Zhong et al. 2022). These findings illustrate how plant molecules such as triterpenes create niche opportunities for resilient microbes, thereby shaping microbiome structure and function.

Benzoxazinoids

Benzoxazinoids (BXs) are indole-derived secondary metabolites predominantly found in Poaceae (De Bruijn et al. 2018). They accumulate in aboveground tissues and in the soil, contributing to direct defense against insect herbivores and pathogens, as well as mediating interactions with commensal microbes (De Bruijn et al. 2018; Hu et al. 2018b; Kudjordjie et al. 2019). Similar to coumarins, BXs contribute to iron mobilization by facilitating the solubilization and uptake of this micronutrient in the rhizosphere (Hu et al. 2018a; Schlaeppi et al. 2021; Bass 2024). Genetic disruption of the BX biosynthetic pathway in maize results in altered microbial communities on shoots and roots and within the rhizosphere, demonstrating the role of BXs in shaping the plant-associated microbiome (Kudjordjie et al. 2019). In wheat, leaf infection by the fungal pathogen *Zymoseptoria tritici* triggers systemic suppression of immune-related metabolites, including BXs (Seybold et al. 2020). Remarkably, these pathogen-induced changes in the wheat metabolome correlate with significant shifts in the leaf microbiome (Seybold et al. 2020), illustrating how an altered chemical milieu during disease drives the restructuring of plant-associated microbial communities. Furthermore, maize roots actively secrete BXs into the soil, thereby modulating the composition of bacterial and fungal communities. These soil microbiome shifts are linked to the regulation of salicylic acid and jasmonic acid signaling pathways, ultimately contributing to the suppression of herbivores such as the caterpillar *Spodoptera frugiperda* (Hu et al. 2018b).

Glucosinolates

Glucosinolates are a diverse class of sulfur-containing secondary metabolites found predominantly in plants of the order Brassicales. Best known for their role in plant defense, these compounds serve as chemical deterrents against herbivores and microbial pathogens (Kim and Jander 2007; Stotz et al. 2011). Apart from their function as defense compounds, glucosinolates and their breakdown products have been shown to modulate plant microbial communities (Chhajed et al. 2020; Yang et al. 2024). In Arabidopsis, the assembly of bacterial and archaeal communities in the rhizosphere is influenced by the biosynthesis and breakdown pathways of glucosinolates (Wolinska et al. 2021; Chroston et al. 2024). In addition, tryptophan-derived indole glucosinolates released from roots shape microbial community assembly (Basak et al. 2024). Siebers et al. (2018) also demonstrated that soil exposure to rapeseed-derived glucosinolates alters microbial community composition and promotes the enrichment of plant growth–promoting microorganisms. Interestingly, efflux pumps were recently shown to play an important role in the ability of commensal bacteria to colonize Arabidopsis shoots, possibly helping them to withstand the collateral toxicity of glucosinolate breakdown products generated during defense against herbivores and necrotrophic pathogens (Russ et al. 2025). These studies suggest that glucosinolates function not only as defense compounds but also as microbial drivers, potentially selecting beneficial microbes.

Reactive oxygen species

Upon MAMP recognition, plants rapidly initiate a cascade of biochemical responses that characterize pattern-triggered immunity. A hallmark of this response is the accumulation of ROS, which play key roles in restricting pathogen growth and suppressing virulence (Torres et al. 2006; Tripathy and Oelmüller 2012). In addition to targeting pathogens, ROS affect commensal microbes, likely contributing to shifts in microbiome composition during pathogen infection. These effects on microbial communities appear to be highly context dependent. Arabidopsis *rbohD* mutants, which display impaired ROS production during immune responses, exhibit pronounced microbial dysbiosis in the leaves and increased susceptibility to opportunistic *Xanthomonas* strains (Pfeilmeier et al. 2021, 2024; Entila et al. 2024). This dysbiosis is primarily driven by the overproliferation of these pathogen strains, which secrete plant cell wall–degrading enzymes that likely alter nutrient availability and influence the growth of surrounding microbes (Entila et al. 2024; Pfeilmeier et al. 2024). This illustrates how pathogen-induced niche modifications can reshape microbial community structure. Interestingly, plant-derived ROS production is essential for successful colonization of Arabidopsis roots by a beneficial *Bacillus velezensis* strain (Tzipilevich et al. 2021). Conversely, reduced basal ROS levels are required for the growth of beneficial pseudomonads in Arabidopsis roots (Song et al. 2021). These observations challenge the assumption that immune responses primarily target and terminate the growth of pathogens; instead, they suggest that immune signaling pathways can facilitate the establishment of mutualistic microbes. ROS can also interact with plant secondary metabolites to further modulate microbiome dynamics. Root-exuded coumarins generate ROS, which selectively inhibit specific microbial taxa, particularly under iron-deficient conditions (Voges et al. 2019). These studies highlight the multifaceted role of ROS at the interface between plant immunity and microbiome assembly.

Beyond the antimicrobial compounds detailed here, plants deploy an array of complementary strategies to ward off pathogens. These include structural defenses, such as cell wall reinforcement (Wan et al. 2021) and the accumulation of protective cuticle and wax layers (Bourdenx et al. 2011; Aragón et al. 2021), as well as physiologic adaptations, such as nutrient scavenging and reallocation (Stolpe et al. 2017; Liu et al. 2021b). Furthermore, plants can interfere with microbial quorum sensing, a process that regulates virulence in pathogens. For example, many bacterial pathogens utilize

N-acylhomoserine lactones to regulate their virulence factors (Venturi and Fuqua 2013), and plants have evolved mechanisms to disrupt these signals, thereby impeding pathogen colonization and disease establishment (Joshi et al. 2016; Pun et al. 2021). Notably, beneficial microbes employ similar N-acylhomoserine lactone systems to facilitate colonization, which in turn can promote plant growth or enhance disease control (González and Marketon 2003; Helman and Chernin 2015; Hartmann et al. 2021). Given the shared reliance on quorum sensing for host colonization by pathogenic and commensal bacteria, plant strategies designed to disrupt pathogen communication may inadvertently alter the composition or function of nontarget microorganisms during immune responses.

Active recruitment of beneficial microbes by the plant

Plants are not passive victims during disease; they actively remodel their microbiome as part of an integrated defense strategy. In response to aboveground biotic stress from pathogens or herbivores, plants release a suite of root exudates that influence surrounding microbial communities, a mechanism commonly referred to as the "cry for help" (Bakker et al. 2018). These exudates are rich in primary and secondary metabolites, volatile organic compounds, and other signaling molecules that attract beneficial microbes from the soil (Rudrappa et al. 2008; Kulkarni et al. 2024). For example, maize plants infected by pathogens exhibit an altered root metabolic profile that favors the enrichment of beneficial Bacillus species (Xia et al. 2024). Also, tomato plants infected with R. solanacearum secrete compounds such as 3-hydroxyflavone and riboflavin to recruit Streptomyces strains, effectively suppressing wilt disease (Yang et al. 2023). Interestingly, the cry-for-help mechanism can be triggered by metabolites of nonpathogenic microbes, indicating that the recruitment of beneficial microorganisms is not dependent on disease occurrence (Liu et al. 2024).

The selective recruitment of protective strains can bolster local plant defenses and trigger ISR, which often occurs without incurring the energy costs associated with constitutive immune activation (Verhagen et al. 2006; Pieterse et al. 2021). For instance, Arabidopsis plants attacked by the foliar downy mildew pathogen H. arabidopsidis attract a consortium of rhizospheric bacteria that collectively prime its immune system (Berendsen et al. 2018). Interestingly, mutant plants unable to produce or perceive salicylic acid did not exhibit microbiome-mediated immune priming when grown in soil conditioned by infected plants, indicating that this protective effect requires salicylic acid signaling in the responding plant (Vismans et al. 2022). Similarly, in wheat, recruitment of Stenotrophomonas rhizophila under Fusarium pseudograminearum infection activates defense signaling pathways even though the bacterium does not directly inhibit the pathogen (Liu et al. 2021a).

These examples illustrate that the cry-for-help response is a highly dynamic and targeted process. The most notable outcome is the enrichment of specific protective strains in the root microbiome, yet secondary shifts (i.e. attraction of nonprotective microbes) may also occur, potentially influencing a broader spectrum of microbial interactions. This active recruitment underscores the sophisticated role of plants in shaping their associated microbial communities during disease, transforming microbiome shifts from a by-product of infection into a strategic defense mechanism. Although plants exhibit this notable adaptive capacity, the mere presence of enriched taxa does not necessarily indicate a functional or beneficial response. For example, recent work in Arabidopsis showed that drought suppresses plant immunity and iron uptake, leading to

the consistent enrichment of Streptomyces in roots across diverse soils (Fitzpatrick et al. In press). However, this proliferation was uncoupled from direct benefits to the host. Similarly, drought-induced Streptomyces enrichment in sorghum failed to correlate with host benefits (Fonseca-Garcia et al. 2025), suggesting that not all stress-associated microbiome shifts reflect targeted recruitment or a plant's "cry for help." These findings underscore the complexity of plant–microbe interactions and caution against interpreting microbial enrichment solely as an adaptive defense strategy.

Pathogen disruption of plant-associated microbial communities

To successfully colonize their hosts, pathogens must overcome the plant's innate immune system and the resident microbiota that compete for space and nutrients (Mesny 2023). Many of these resident microbes also protect the plant by directly antagonizing pathogens or priming host immunity (Teixeira et al. 2019; Pereira et al. 2023). Consequently, it is plausible that pathogens have evolved strategies to manipulate the plant microbiome and create a niche more conducive to infection. Emerging studies indicate that certain pathogens can indeed directly influence plant-associated microbial communities through the secretion of antimicrobial effector proteins. For example, the pathogenic fungus Verticillium dahliae produces effectors that specifically suppress groups of microorganisms capable of antagonizing its growth (Snelders et al. 2020, 2021, 2023). In addition to V. dahliae, other pathogens have been shown to manipulate the microbiota of their hosts. For instance, the soil-borne fungus Rosellinia necatrix encodes effectors with antimicrobial activity that disrupt plant microbial communities during cotton infection (Chavarro-Carrero et al. 2024). Likewise, the oomycete A. candida releases antimicrobial proteins into the apoplast, which alter the composition of leaf-associated bacterial community in Arabidopsis (Gómez-Pérez et al. 2023). While these examples provide valuable insights into how pathogens may actively reshape plant-associated microbial communities, the overall prevalence of such pathogen-driven disruptions remains to be fully determined.

Consequences of microbiome shifts on plant health

Recruitment of disease-suppressive microbes

Pathogen attack induces intense biochemical and physiologic changes that extend beyond the primary site of infection (Jones and Dangl 2006; Ngou et al. 2022b; Hönig et al. 2023). Upon infection, the host plant is transformed into a distinct niche characterized by the accumulation of antimicrobial molecules, altered nutrient availability, and shifts in key signaling molecules, such as phytohormones and peptides (Torres et al. 2006; Nguyen et al. 2022; Hönig et al. 2023). These changes substantially modulate the composition and functionality of the plant-associated microbiome (Teixeira et al. 2019). Depending on the initial microbial community, host genotype, and environmental conditions, such microbiome shifts may yield different outcomes for plant health (Wang et al. 2022; Andargie et al. 2023). One especially promising outcome, with significant agricultural implications, is the enrichment of disease-suppressive microbes (Fig. 3).

As described earlier, a growing body of evidence supports the cry-for-help hypothesis as a cause of microbiome shifts during pathogen attack. Consequently, infected plants may actively recruit protective microorganisms as a defense strategy. For example, foliar infection of Arabidopsis by P. syringae pv. tomato triggers the secretion of malic acid from the roots, selectively
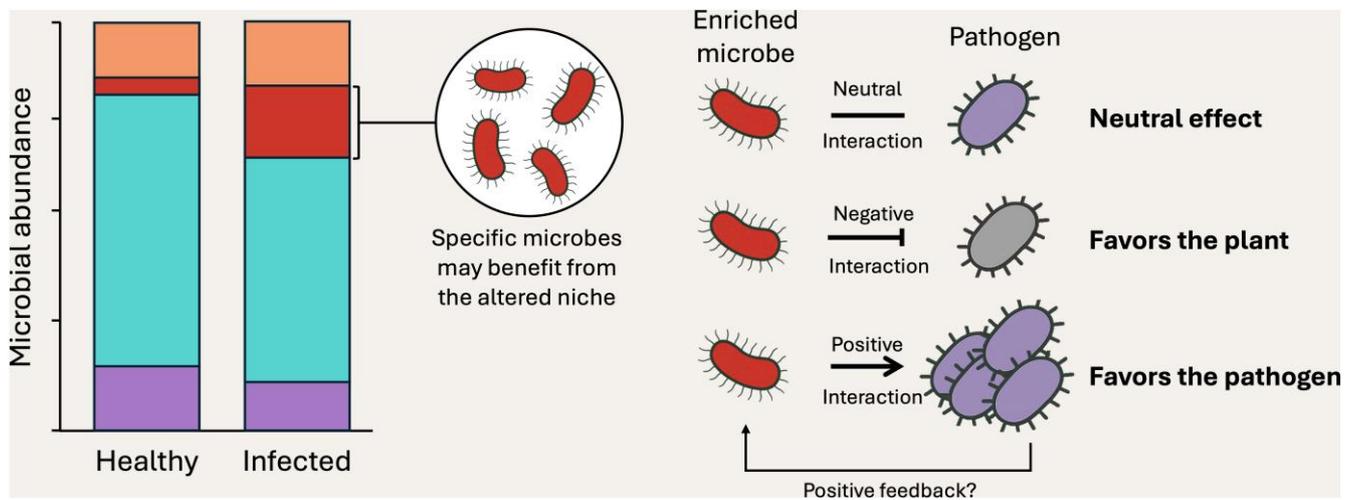
Figure 3. Disease-induced microbiome shifts may influence pathogen infection and affect plant health. Infection can alter the plant-associated microbiome, leading to the enrichment of specific microbial strains, such as the red-colored microbe shown in the image. These microbes may benefit from the new niche created by the infection. Depending on their interaction with the pathogen, enriched microbes can have different consequences for disease progression. Some may have a neutral interaction, with no impact on the pathogen or the plant. Others may inhibit pathogen growth or virulence by competing for resources or producing antimicrobials, ultimately favoring the plant and helping mitigate disease. In contrast, some enriched microbes may positively interact with the pathogen, enhancing its growth or activity and thereby worsening disease outcomes. In such cases, we can expect pathogens to even promote the proliferation of specific partners as a virulence strategy, creating a potential positive feedback loop.

recruiting *B. subtilis* FB17, a bacterium known to induce ISR and enhance resistance against this tomato pathogen (Rudrappa et al. 2008). Similarly, foliar attack of Arabidopsis by *H. arabidopsidis* results in the recruitment of 3 rhizospheric bacteria that contribute to plant protection (Berendsen et al. 2018). Interestingly, the recruitment of beneficial microbes is also triggered by herbivorous insects (Lee et al. 2012; Friman et al. 2021) and even by other beneficial microorganisms (Sommer et al. 2024). In addition, systemic recruitment of beneficial microbes is not limited to leaf–root communication. In barley, split-root experiments have demonstrated that infection by *Fusarium graminearum* leads to systemic alterations in the exudate profile of noninfected parts of the root, rendering them more attractive to the beneficial bacterium *Pseudomonas protegens* CHA0 (Dudenhöffer et al. 2016). Likewise, studies with cucumber and tomato in split-root systems have shown that exudates enriched in peroxidases and oxylipins serve as chemical signals that attract the biocontrol fungus *Trichoderma harzianum* during *Botrytis cinerea* infection (Lombardi et al. 2018).

Although systemic alterations have received considerable attention, local modifications at the infection site have also been associated with the enrichment of protective microbes. For example, localized accumulation of antimicrobial compounds and ROS in infected tissues can create microenvironments that favor the establishment of beneficial microbial populations (Stringlis et al. 2018; Tzipilevich et al. 2021; Thoenen et al. 2023). A study by Li et al. (2022) demonstrated that infection of citrus leaves with the fungus *Diaporthe citri* alters the local bacterial community, leading to an enrichment of strains with potential antifungal properties (Li et al. 2022). In rice, infection with *X. oryzae* pv. *oryzae* caused significant alterations in the phyllosphere microbiome and promoted the enrichment of antagonist microbes (Yang et al. 2020). Similarly, rice panicles infected with the pathogen *Ustilaginoidea virens* show enrichment of beneficial bacteria capable of suppressing disease via modulation of the host's branched-chain amino acid metabolism (Liu et al. 2023). These observations suggest that, in addition to systemic signals, plants may orchestrate spatially confined microbiome shifts to counteract pathogen invasion at the local level.

However, the precise molecular signals and regulatory mechanisms underlying these local recruitment processes remain poorly understood.

Repeated pathogen exposure over multiple plant generations, coupled with the recruitment of beneficial microbes, can lead to the development of "disease-suppressive soils," in which the occurrence of specific diseases remains low, even in the presence of a virulent pathogen and a susceptible host plant (Gómez Expósito et al. 2017; Schlatter et al. 2017). Suppressive soils are typically enriched with antimicrobial-producing microbes (Cha et al. 2016; Mendes et al. 2018; Carrión et al. 2019; Tracanna et al. 2021), which accumulate in the soil and form a self-perpetuating "soil-borne legacy" that transcends individual plant generations (Bakker et al. 2018; Berendsen et al. 2018). The development of disease-suppressive soils is a direct consequence of plant-driven microbiome shifts triggered by disease. Importantly, the legacy effect is not merely a transient response but a stable, heritable restructuring of soil communities, offering a blueprint for sustainable disease management.

Negative impacts of microbiome shifts

Microbiome shifts during pathogen exposure can have detrimental effects on plant health, often resulting in dysbiosis—a condition marked by reduced microbial diversity, loss of protective taxa, and altered microbial functions (Paasch and He 2021; Arnault et al. 2023). In Arabidopsis, for example, the proliferation of specific groups of bacteria in immunocompromised plants has been shown to cause leaf damage under high humidity (Chen et al. 2020). Similarly, the Arabidopsis mutant *rbohD*, with impaired pattern-triggered immunity, supports the overgrowth of an opportunistic *Xanthomonas* pathogen. This leads to significant shifts in the phyllosphere microbiota, culminating in dysbiosis and reduced plant fitness (Pfeilmeier et al. 2021, 2024; Entila et al. 2024). In tomato, infection by *R. solanacearum* reduces the abundance of beneficial microbes, further facilitating pathogen colonization and increasing disease incidence (Lee et al. 2021). Together, these studies highlight how microbiome imbalances can exacerbate plant vulnerability to pathogens and opportunistic microbes.

In some cases, immune activation itself can unintentionally disrupt beneficial interactions. For instance, while the symbiotic fungus *T. harzianum* T-78 enhances Arabidopsis resistance against the nematode *Meloidogyne incognita*, the activation of SA-regulated defenses can reduce fungal colonization, suggesting that plant immune responses may limit beneficial symbionts (Martínez-Medina et al. 2017). Similarly, infection by the nematode *Pratylenchus penetrans* interferes with soybean–*Bradyrhizobium japonicum* symbiosis through plant-mediated mechanisms, resulting in fewer nodules and lower bacterial density (Elhady et al. 2020). Interestingly, defense signals in aboveground tissues, triggered by chemical elicitors or pathogens, can also cause systemic responses that will negatively affect belowground mutualisms, including arbuscular mycorrhizal fungi and rhizobia colonization (De Román et al. 2011; Ballhorn et al. 2014). These examples illustrate the trade-offs that plants may face: activating defense pathways to suppress pathogens can inadvertently compromise beneficial interactions (Fig. 3).

Microbiome shifts inform engineering strategies for sustainable disease management

Microbiome engineering holds significant potential to enhance plant health and productivity by shaping plant-associated microbial communities (Jurburg et al. 2022). However, despite encouraging laboratory results, translating these findings into consistent field applications has proven challenging. The widespread adoption of microbial interventions in agriculture is largely hindered by our incomplete knowledge of plant–microbe interactions and the complex molecular mechanisms governing them. In this context, advancing microbiome-based strategies for pathogen control requires deeper insights into the causes and consequences of microbial shifts and dynamics that occur during disease development.

Manipulation of the plant microbiome can be achieved through various methods: agricultural practices (e.g. intercropping and crop rotation), soil amendments, soil transplantations, selective breeding for microbiome-associated (M) genes, and microbial inoculants (Arif et al. 2020; Cernava 2024; Su et al. 2024). Each of these approaches aims to modulate the composition or function of microbial communities to enhance plant health, productivity, or resilience to stress. In modern agriculture, microbial inoculants, such as biological control agents, are increasingly recognized as a promising and sustainable strategy for disease management (De Cal et al. 2020; Galli et al. 2024). Traditionally, biological control has relied on introducing individual microbial strains to promote plant health. However, their inconsistent performance across diverse agricultural environments remains a major limitation (Albright et al. 2022). Factors such as competition with native microbiomes, low colonization rates, and environmental variability often reduce their effectiveness (Compant et al. 2025). Addressing these issues requires innovative approaches grounded in a mechanistic understanding of microbial establishment and persistence under field conditions.

Advancements in microbiome research have enabled the development of microbial consortia-based strategies. By combining multiple strains with complementary or synergistic functions, consortia can enhance colonization, persistence, and pathogen suppression across a wider range of environments. One approach to designing microbial consortia involves assembling strains with distinct pathogen-suppression mechanisms, such as competition for nutrients and space, antibiosis, and ISR. This functional redundancy increases the chances of successful establishment and function, even if some strains are compromised under specific field conditions (Russ et al. 2023). Another approach focuses on combining pathogen-suppressing strains that can tolerate a range of temperatures, pH levels, and soil conditions, thereby improving their ecologic robustness across diverse agricultural settings (Russ et al. 2023). A better understanding of how plant microbiomes are naturally modulated under diverse and changing environmental conditions may guide the rational assembly of synthetic consortia with desirable properties.

Interestingly, the effectiveness of microbial consortia depends not only on the traits of individual strains but also on their collective interactions. Some consortia require helper strains that do not directly combat pathogens but instead create favorable conditions for biological control agents, improving their establishment and persistence (Li et al. 2025). Moreover, a high genetic diversity in the introduced microbial communities can improve their survival and efficacy. For instance, Hu et al. (2016) demonstrated that more diverse *Pseudomonas* consortia exhibited enhanced survival and stronger suppression of *R. solanacearum* in the tomato rhizosphere. Stochastic factors, such as the timing and order of microbial colonization, can further influence community composition and functional outcomes under natural settings. While promising, microbial consortia (especially those composed of multiple diverse species) still face challenges related to microbial compatibility, ecologic stability, and regulatory approval (Mitter et al. 2019; Russ et al. 2023).

Beyond artificially assembled consortia, an alternative involves engineering single microbial strains with multiple beneficial traits (Russ et al. 2023). Advances in gene editing and synthetic biology now enable the consolidation of several pathogen-suppressing functions into a single strain, reducing the complexity of multi-strain formulations while maintaining high efficacy. Engineered microbes can be tailored to enhance pathogen suppression through antimicrobial compound production, ISR activation, and niche competition, offering robust disease control. In addition to pathogen inhibition, they can deliver broader agronomic benefits, such as improved nutrient uptake, drought tolerance, and plant growth promotion. By integrating multiple traits and functions into a single microbe, this approach simplifies application and formulation, reducing microbial compatibility issues that can affect the efficiency of consortia-based products (Prigigallo et al. 2022). Microbes that are well adapted to the target host plant and resilient to fluctuating environmental conditions make promising chassis for engineering these multibeneficial strains.

While these scientific advances are promising, microbiome engineering must address issues of public acceptance and regulatory frameworks, particularly regarding the deployment of genetically engineered microorganisms (GEMs; Ke et al. 2021). Environmental regulation represents a major barrier to the release of GEMs, which may persist and spread beyond release sites, potentially altering microbial networks and ecosystem functions (Chemla et al. 2025). Horizontal gene transfer of synthetic DNA represents an additional concern, as it could enable engineered sequences to move into native bacteria (George et al. 2024). Furthermore, the use of selectable markers, particularly antibiotic-resistance genes, can contribute to resistance dissemination in agroecosystems, highlighting the importance of alternative selection methods (Mahdi et al. 2022). To mitigate such unintended impacts, rigorous environmental risk assessment and robust biocontainment strategies are required to prevent the uncontrolled spread of GEMs in natural environments (Ke et al. 2021; George et al. 2024).

Ongoing research in microbiome continues to drive significant progress in developing effective solutions for plant disease management. A notable example is the study by Liu et al. (2024), which presents a promising approach for disease control based on the

cry-for-help mechanism. Their findings demonstrate that nonpathogenic *Pseudomonas* strains and their MAMPs/metabolites can function as safe elicitors of the plant's cry-for-help response and induce the formation of a disease-suppressive soil legacy. These results offer a promising strategy for sustainable disease management without the risks associated with using virulent pathogens to trigger plant immunity. By decoding the specific signals that lead to the recruitment of disease-suppressive bacteria, these interactions can be leveraged to design targeted interventions, whether through microbial inoculants or elicitors, to fortify plant defenses.

Given the complexity of interactions and factors that shape the plant microbiome, defining the significance of microbial shifts during pathogen attack is essential for developing reliable and robust microbiome-based strategies. Moreover, the temporal dynamics of these shifts throughout the course of infection must be considered. Certain microbial groups are likely to emerge early, playing a role in plant defense or signaling the onset of disease, while others may become dominant only as the plant condition deteriorates. Equally important is identifying the specific molecular mechanisms driving microbial recruitment and community restructuring in response to infection. Also, not all microbial shifts are directly associated with disease resistance, adding another layer of complexity to plant–microbiome–pathogen interactions. Although our understanding of microbiome shifts and dynamics during disease is still in its infancy, addressing the existing knowledge gaps will allow for the optimization of microbial interventions. With continued progress, microbiome engineering offers a compelling solution to transform agriculture by reducing reliance on chemical pesticides and enhancing crop resilience in an environmentally sustainable manner.

Concluding remarks and future directions

Over the past 3 decades, major advances in plant biology have uncovered the molecular underpinnings of plant immunity and revealed general principles that govern plant–pathogen interactions. More recently, a parallel revolution has unfolded: the recognition that the plant microbiome is not a passive bystander but an active and dynamic extension of the plant immune system. Although individual microbes were noted for their disease-protective properties as early as a century ago, it is only within the last decade that plant microbiomes have been widely accepted as major modulators of disease outcomes.

Microbiome shifts are increasingly recognized as a hallmark of plant responses to pathogen infection, yet their underlying causes and functional consequences remain incompletely understood. Emerging evidence indicates that these shifts are not random but arise from a complex interplay among plant immunity, pathogen activity, and microbial traits. Immune activation reconfigures the chemical landscape of plant tissues, imposing selective pressure on resident microbes. Simultaneously, pathogens may actively manipulate microbiome composition via effector proteins or metabolic alterations. In turn, plants can selectively recruit beneficial microbes through targeted exudation, a strategic cry-for-help response that reshapes microbial communities to enhance resistance.

Despite this progress, major knowledge gaps persist, which requires mechanistic, time-resolved studies that move beyond correlative descriptions. Many microbial shifts observed during infection are interpreted as adaptive or beneficial, yet few studies establish causality. Some alterations may be neutral by-products of infection, while others may inadvertently compromise host defenses or facilitate pathogen colonization. To advance the field, future research must unravel the relative influence of plant immune responses,

pathogen interference, and microbial traits in driving microbiome restructuring. Dissecting these contributions will require mechanistic studies using synthetic microbial communities, trait-based screening, and temporally resolved experiments that capture microbiome dynamics over the course of infection. Understanding why certain microbes are enriched while others decline will be important for predicting and directing microbiome trajectories. Such insights will inform the development of microbiome-based strategies aimed at enhancing disease suppression, maintaining microbial balance, and blocking pathogen-facilitating interactions. Ultimately, deepening our understanding of microbiome shifts during disease will not only advance basic plant pathology but also enable the rational design of microbiome-informed tools. Whether through microbial inoculants, engineered consortia, or metabolite-based cues, these tools will play a role in achieving consistent and sustainable disease control across agricultural systems.

Advances Box

- The microbiome is now recognized as an extension of the plant immune system, shaping disease outcomes through dynamic shifts during infection.
- Not all microbial shifts are protective—some may be neutral or even detrimental—highlighting the complexity of plant–microbe–pathogen interactions.
- Plant–pathogen interactions induce structural and functional microbiome changes locally at infection sites and systemically in distant tissues.
- Plants use stress-induced exudates, including primary and specialized metabolites, to recruit beneficial microbes during infection.
- Pathogens can interfere with host microbiomes via effector proteins, highlighting microbiome manipulation as a virulence strategy.

Outstanding Questions Box

Growing recognition of the microbiome as an active player in plant defense raises new molecular and functional questions. Despite recent advances, many aspects of microbiome–pathogen–plant interactions remain unresolved. The following questions highlight areas where further research could advance the field. Given the context-specific nature of microbiome dynamics, answers will likely vary with host, pathogen, and environment.

- What molecules mediate microbiome reorganization during infection?
- Which plant/microbial metabolites maintain microbiome balance and prevent disease?
- Do pathogens foster the growth of specific microbes to aid infection?
- How do pathogens with different lifestyles (biotrophic vs. necrotrophic) modulate microbiomes across environments?
- How have plant–pathogen coevolutionary dynamics shaped microbiome shifts?
- What role do rare microbial taxa play in pathogen-induced microbiome shifts?
- Can we engineer microbiomes to mimic beneficial natural shifts, such as those promoting stress resistance?

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References

Aggarwal N, Kitano S, Puah GRY, Kittelmann S, Hwang IY, Chang MW. Microbiome and human health: current understanding, engineering, and enabling technologies. *Chem Rev*. 2023:123(1):31–72. https://doi.org/10.1021/acs.chemrev.2c00431

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(1):e1002352. https://doi.org/10.1371/journal.pbio.1002352

Albright MBN, Louca S, Winkler DE, Feeser KL, Haig S-J, Whiteson KL, Emerson JB, Dunbar J. Solutions in microbiome engineering: prioritizing barriers to organism establishment. *ISME J*. 2022:16(2):331–338. https://doi.org/10.1038/s41396-021-01088-5

Andargie YE, Lee G, Jeong M, Tagele SB, Shin J-H. Deciphering key factors in pathogen-suppressive microbiome assembly in the rhizosphere. *Front Plant Sci*. 2023:14:1301698. https://doi.org/10.3389/fpls.2023.1301698

Aragón W, Formey D, Aviles-Baltazar NY, Torres M, Serrano M. Arabidopsis thaliana cuticle composition contributes to differential defense response to *Botrytis cinerea*. *Front Plant Sci*. 2021:12:738949. https://doi.org/10.3389/fpls.2021.738949

Arif I, Batool M, Schenk PM. Plant microbiome engineering: expected benefits for improved crop growth and resilience. *Trends Biotechnol*. 2020:38(12):1385–1396. https://doi.org/10.1016/j.tibtech.2020.04.015

Arnault G, Mony C, Vandenkoornhuyse P. Plant microbiota dysbiosis and the Anna Karenina principle. *Trends Plant Sci*. 2023:28(1):18–30. https://doi.org/10.1016/j.tplants.2022.08.012

Bakker PAHM, Pieterse CMJ, De Jonge R, Berendsen RL. The soil-borne legacy. *Cell*. 2018:172(6):1178–1180. https://doi.org/10.1016/j.cell.2018.02.024

Ballhorn DJ, Younginger BS, Kautz S. An aboveground pathogen inhibits belowground rhizobia and arbuscular mycorrhizal fungi in *Phaseolus vulgaris*. *BMC Plant Biol*. 2014:14(1):321. https://doi.org/10.1186/s12870-014-0321-4

Basak AK, Piasecka A, Hucklenbroich J, Türksoy GM, Guan R, Zhang P, Getzke F, Garrido-Oter R, Hacquard S, Strzałka K, *et al*. ER body-resident myrosinases and tryptophan specialized metabolism

modulate root microbiota assembly. *New Phytol*. 2024:241(1):329–342. https://doi.org/10.1111/nph.19289

Bass E. Getting to the root of divergent outcomes in the modulation of plant–soil feedbacks by benzoxazinoids. *New Phytol*. 2024:241(6):2316–2319. https://doi.org/10.1111/nph.19545

Berendsen RL, Pieterse CMJ, Bakker PAHM. The rhizosphere microbiome and plant health. *Trends Plant Sci*. 2012:17(8):478–486. https://doi.org/10.1016/j.tplants.2012.04.001

Berendsen RL, Vismans G, Yu K, Song Y, De Jonge R, Burgman WP, Burmølle M, Herschend J, Bakker PAHM, Pieterse CMJ. Disease-induced assemblage of a plant-beneficial bacterial consortium. *ISME J*. 2018:12(6):1496–1507. https://doi.org/10.1038/s41396-018-0093-1

Bourdenx B, Bernard A, Domergue F, Pascal S, Léger A, Roby D, Pervent M, Vile D, Haslam RP, Napier JA, *et al*. Overexpression of Arabidopsis *ECERIFERUM1* promotes wax very-long-chain alkane biosynthesis and influences plant response to biotic and abiotic stresses. *Plant Physiol*. 2011:156(1):29–45. https://doi.org/10.1104/pp.111.172320

Bulgarelli D, Schlaeppi K, Spaepen S, Ver Loren van Themaat E, Schulze-Lefert P. Structure and functions of the bacterial microbiota of plants. *Annu Rev Plant Biol*. 2013:64(1):807–838. https://doi.org/10.1146/annurev-arplant-050312-120106

Buscaill P, van der Hoorn RAL. Defeated by the nines: nine extracellular strategies to avoid microbe-associated molecular patterns recognition in plants. *Plant Cell*. 2021:33(7):2116–2130. https://doi.org/10.1093/plcell/koab109

Caballero-Flores G, Pickard JM, Núñez G. Microbiota-mediated colonization resistance: mechanisms and regulation. *Nat Rev Microbiol*. 2023:21(6):347–360. https://doi.org/10.1038/s41579-022-00833-7

Cai Q, Qiao L, Wang M, He B, Lin F-M, Palmquist J, Huang S-D, Jin H. Plants send small RNAs in extracellular vesicles to fungal pathogen to silence virulence genes. *Science*. 2018:360(6393):1126–1129. https://doi.org/10.1126/science.aar4142

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(6465):606–612. https://doi.org/10.1126/science.aaw9285

Cernava T. Coming of age for microbiome gene breeding in plants. *Nat Commun*. 2024:15(1):6623. https://doi.org/10.1038/s41467-024-50700-7

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(1):119–129. https://doi.org/10.1038/ismej.2015.95

Chaparro JM, Badri DV, Vivanco JM. Rhizosphere microbiome assemblage is affected by plant development. *ISME J*. 2014:8(4):790–803. https://doi.org/10.1038/ismej.2013.196

Chavarro-Carrero EA, Snelders NC, Torres DE, Kraege A, López-Moral A, Petti GC, Punt W, Wieneke J, García-Velasco R, López-Herrera CJ, *et al*. The soil-borne white root rot pathogen *Rosellinia necatrix* expresses antimicrobial proteins during host colonization. *PLoS Pathog*. 2024:20(1):e1011866. https://doi.org/10.1371/journal.ppat.1011866

Chemla Y, Sweeney CJ, Wozniak CA, Voigt CA. Design and regulation of engineered bacteria for environmental release. *Nat Microbiol*. 2025:10(2):281–300. https://doi.org/10.1038/s41564-024-01918-0

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(7805):653–657. https://doi.org/10.1038/s41586-020-2185-0

Chen Y, Cui W, Li X, Yang H. Interaction between commensal bacteria, immune response and the intestinal barrier in inflammatory

bowel disease. *Front Immunol.* 2021:12:761981. https://doi.org/10.3389/fimmu.2021.761981

Cheng YT, Zhang L, He SY. Plant–microbe interactions facing environmental challenge. *Cell Host Microbe.* 2019:26(2):183–192. https://doi.org/10.1016/j.chom.2019.07.009

Chepsergon J, Moleleki LN. Rhizosphere bacterial interactions and impact on plant health. *Curr Opin Microbiol.* 2023:73:102297. https://doi.org/10.1016/j.mib.2023.102297

Chhajed S, Mostafa I, He Y, Abou-Hashem M, El-Domiaty M, Chen S. Glucosinolate biosynthesis and the glucosinolate–myrosinase system in plant defense. *Agronomy.* 2020:10(11):1786. https://doi.org/10.3390/agronomy10111786

Chialva M, di Fossalunga AS, Daghino S, Ghignone S, Bagnaresi P, Chiapello M, Novero M, Spadaro D, Perotto S, Bonfante P. Native soils with their microbiotas elicit a state of alert in tomato plants. *New Phytol.* 2018:220:1296–1308. https://doi.org/10.1111/nph.15014

Chroston ECM, Bziuk N, Stauber EJ, Ravindran BM, Hielscher A, Smalla K, Wittstock U. Plant glucosinolate biosynthesis and breakdown pathways shape the rhizosphere bacterial/archaeal community. *Plant Cell Environ.* 2024:47(6):2127–2145. https://doi.org/10.1111/pce.14870

Cole BJ, Feltcher ME, Waters RJ, Wetmore KM, Mucyn TS, Ryan EM, Wang G, Ul-Hasan S, McDonald M, Yoshikuni Y, *et al.* Genome-wide identification of bacterial plant colonization genes. *PLoS Biol.* 2017:15(9):e2002860. https://doi.org/10.1371/journal.pbio.2002860

Compant S, Cassan F, Kostić T, Johnson L, Brader G, Trognitz F, Sessitsch A. Harnessing the plant microbiome for sustainable crop production. *Nat Rev Microbiol.* 2025:23(1):9–23. https://doi.org/10.1038/s41579-024-01079-1

Contreras MP, Lüdke D, Pai H, Toghani A, Kamoun S. NLR receptors in plant immunity: making sense of the alphabet soup. *EMBO Rep.* 2023:24(10):e57495. https://doi.org/10.15252/embr.202357495

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(7):1647–1658. https://doi.org/10.1038/s41396-019-0375-2

De Bruijn WJC, Gruppen H, Vincken J-P. Structure and biosynthesis of benzoxazinoids: plant defence metabolites with potential as antimicrobial scaffolds. *Phytochemistry.* 2018:155:233–243. https://doi.org/10.1016/j.phytochem.2018.07.005

De Cal A, Melgarejo P, Magan N, editors. *How research can stimulate the development of commercial biological control against plant diseases.* Berlin, Germany: Springer Nature; 2020. https://doi.org/10.1007/978-3-030-53238-3

De Román M, Fernández I, Wyatt T, Sahrawy M, Heil M, Pozo MJ. Elicitation of foliar resistance mechanisms transiently impairs root association with arbuscular mycorrhizal fungi. *J Ecol.* 2011:99(1):36–45. https://doi.org/10.1111/j.1365-2745.2010.01752.x

Drumo R, Pesciaroli M, Ruggeri J, Tarantino M, Chirullo B, Pistoia C, Petrucci P, Martinelli N, Moscati L, Manuali E, *et al. Salmonella enterica* serovar typhimurium exploits inflammation to modify swine intestinal microbiota. *Front Cell Infect Microbiol.* 2015:5:106. https://doi.org/10.3389/fcimb.2015.00106

Dudenhöffer J, Scheu S, Jousset A. Systemic enrichment of antifungal traits in the rhizosphere microbiome after pathogen attack. *J Ecol.* 2016:104(6):1566–1575. https://doi.org/10.1111/1365-2745.12626

Elhady A, Hallmann J, Heuer H. Symbiosis of soybean with nitrogen fixing bacteria affected by root lesion nematodes in a density-dependent manner. *Sci Rep.* 2020:10(1):1619. https://doi.org/10.1038/s41598-020-58546-x

El-Sawy ER, Abdel-Aziz MS, Abdelmegeed H, Kirsch G. Coumarins: quorum sensing and biofilm formation inhibition. *Molecules.* 2024:29(19):4534. https://doi.org/10.3390/molecules29194534

Entila F, Han X, Mine A, Schulze-Lefert P, Tsuda K. Commensal lifestyle regulated by a negative feedback loop between Arabidopsis ROS and the bacterial T2SS. *Nat Commun.* 2024:15(1):456. https://doi.org/10.1038/s41467-024-44724-2

Fitzpatrick CR, Salas-González I, Conway JM, Finkel OM, Gilbert S, Russ D, Teixeira PJPL, Dangl JL. The plant microbiome: from ecology to reductionism and beyond. *Annu Rev Microbiol.* 2020:74(1):81–100. https://doi.org/10.1146/annurev-micro-022620-014327

Fitzpatrick CR, Smith RA, Hige J, Law TF, Russ D, Eida AA, Jacob P, Jowers M, Kumar N, Lai CTU, *et al. Streptomyces* enrichment in roots during drought is uncoupled from plant benefit and is driven by host suppression of iron uptake and immunity. In press.

Fonseca-Garcia C, Pettinga D, Caddell D, Ploemacher H, Louie K, Bowen BP, Park J, Sanchez J, Zimic-Sheen A, Traxler MF, *et al.* Uncovering the hidden diversity and functional roles of root endophytic Streptomyces under drought stress. Northen, Devin Coleman-Derr. bioRxiv 2025.06.25.661566. https://doi.org/10.1101/2025.06.25.661566

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(6):2475–2490. https://doi.org/10.1111/nph.17746

Galli M, Feldmann F, Vogler UK, Kogel K-H. Can biocontrol be the game-changer in integrated pest management? A review of definitions, methods and strategies. *J Plant Dis Prot.* 2024:131(2):265–291. https://doi.org/10.1007/s41348-024-00878-1

Gao M, Xiong C, Gao C, Tsui CKM, Wang M-M, Zhou X, Zhang A-M, Cai L. Disease-induced changes in plant microbiome assembly and functional adaptation. *Microbiome.* 2021:9(1):187. https://doi.org/10.1186/s40168-021-01138-2

George DR, Danciu M, Davenport PW, Lakin MR, Chappell J, Frow EK. A bumpy road ahead for genetic biocontainment. *Nat Commun.* 2024:15(1):650. https://doi.org/10.1038/s41467-023-44531-1

Getzke F, Hassani MA, Crüsemann M, Malisic M, Zhang P, Ishigaki Y, Böhringer N, Jiménez Fernández A, Wang L, Ordon J, *et al.* Cofunctioning of bacterial exometabolites drives root microbiota establishment. *Proc Natl Acad Sci U S A.* 2023:120(15):e2221508120. https://doi.org/10.1073/pnas.2221508120

Glawischnig E. Camalexin. *Phytochemistry.* 2007:68(4):401–406. https://doi.org/10.1016/j.phytochem.2006.12.005

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. https://doi.org/10.3389/fmicb.2017.02529

Gómez-Pérez D, Schmid M, Chaudhry V, Hu Y, Velic A, Maček B, Ruhe J, Kemen A, Kemen E. Proteins released into the plant apoplast by the obligate parasitic protist *Albugo* selectively repress phyllosphere-associated bacteria. *New Phytol.* 2023:239(6):2320–2334. https://doi.org/10.1111/nph.18995

González JE, Marketon MM. Quorum sensing in nitrogen-fixing rhizobia. *Microbiol Mol Biol Rev.* 2003:67(4):574–592. https://doi.org/10.1128/MMBR.67.4.574-592.2003

Goossens P, Spooren J, Baremans KCM, Andel A, Lapin D, Echobardo N, Pieterse CMJ, Van den Ackerveken G, Berendsen RL. Obligate biotroph downy mildew consistently induces near-identical protective microbiomes in *Arabidopsis thaliana.* *Nat Microbiol.* 2023:8(12):2349–2364. https://doi.org/10.1038/s41564-023-01502-y

Gu S, Wei Z, Shao Z, Friman V-P, Cao K, Yang T, Kramer J, Wang X, Li M, Mei X, *et al.* Competition for iron drives phytopathogen control

by natural rhizosphere microbiomes. *Nat Microbiol*. 2020:5(8): 1002–1010. https://doi.org/10.1038/s41564-020-0719-8

Gupta U, Dey P. Rise of the guardians: gut microbial maneuvers in bacterial infections. *Life Sci*. 2023:330:121993. https://doi.org/10.1016/j.lfs.2023.121993

Haas D, Défago G. Biological control of soil-borne pathogens by fluorescent pseudomonads. *Nat Rev Microbiol*. 2005:3(4):307–319. https://doi.org/10.1038/nrmicro1129

Hacquard S, Spaepen S, Garrido-Oter R, Schulze-Lefert P. Interplay between innate immunity and the plant microbiota. *Annu Rev Phytopathol*. 2017:55(1):565–589. https://doi.org/10.1146/annurev-phyto-080516-035623

Hartmann A, Klink S, Rothballer M. Plant growth promotion and induction of systemic tolerance to drought and salt stress of plants by quorum sensing auto-inducers of the N-acyl-homoserine lactone type: recent developments. *Front Plant Sci*. 2021:12:683546. https://doi.org/10.3389/fpls.2021.683546

Helman Y, Chernin L. Silencing the mob: disrupting quorum sensing as a means to fight plant disease. *Mol Plant Pathol*. 2015:16(3): 316–329. https://doi.org/10.1111/mpp.12180

Hiruma K, Gerlach N, Sacristán S, Nakano RT, Hacquard S, Kracher B, Neumann U, Ramírez D, Bucher M, O'Connell RJ, *et al*. Root endophyte *Colletotrichum tofieldiae* confers plant fitness benefits that are phosphate status dependent. *Cell*. 2016:165(2):464–474. https://doi.org/10.1016/j.cell.2016.02.028

Hönig M, Roeber VM, Schmülling T, Cortleven A. Chemical priming of plant defense responses to pathogen attacks. *Front Plant Sci*. 2023:14:1146577. https://doi.org/10.3389/fpls.2023.1146577

Hu J, Wei Z, Friman V-P, Gu S-H, Wang X-F, Eisenhauer N, Yang T-J, Ma J, Shen Q-R, Xu Y-C, *et al*. Probiotic diversity enhances rhizosphere microbiome function and plant disease suppression. *mBio*. 2016:7(6):e01790-16. https://doi.org/10.1128/mBio.01790-16

Hu L, Mateo P, Ye M, Zhang X, Berset JD, Handrick V, Radisch D, Grabe V, Köllner TG, Gershenzon J, *et al*. Plant iron acquisition strategy exploited by an insect herbivore. *Science*. 2018a:361(6403): 694–697. https://doi.org/10.1126/science.aat4082

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*. 2018b:9(1):2738. https://doi.org/10.1038/s41467-018-05122-7

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(6440):eaau6389. https://doi.org/10.1126/science.aau6389

Huang C-Y, Araujo K, Sánchez JN, Kund G, Trumble J, Roper C, Godfrey KE, Jin H. A stable antimicrobial peptide with dual functions of treating and preventing citrus Huanglongbing. *Proc Natl Acad Sci U S A*. 2021:118(6):e2019628118. https://doi.org/10.1073/pnas.2019628118

Ilyaskina D, Altveş S, Dong L, Bouwmeester H, El Aidy S. Adaptive and metabolic convergence in rhizosphere and gut microbiomes. *Microbiome*. 2025:13(1):173. https://doi.org/10.1186/s40168-025-02179-7

Jin X, Jia H, Ran L, Wu F, Liu J, Schlaeppi K, Dini-Andreote F, Wei Z, Zhou X. Fusaric acid mediates the assembly of disease-suppressive rhizosphere microbiota via induced shifts in plant root exudates. *Nat Commun*. 2024:15:5125. https://doi.org/10.1038/s41467-024-49218-9

Jones JDG, Dangl JL. The plant immune system. *Nature*. 2006:444(7117):323–329. https://doi.org/10.1038/nature05286

Joshi JR, Khazanov N, Senderowitz H, Burdman S, Lipsky A, Yedidia I. Plant phenolic volatiles inhibit quorum sensing in pectobacteria

and reduce their virulence by potential binding to ExpI and ExpR proteins. *Sci Rep*. 2016:6:38126. https://doi.org/10.1038/srep38126

Jurburg SD, Eisenhauer N, Buscot F, Chatzinotas A, Chaudhari NM, Heintz-Buschart A, Kallies R, Küsel K, Litchman E, Macdonald CA, *et al*. Potential of microbiome-based solutions for agrifood systems. *Nat Food*. 2022:3(8):557–560. https://doi.org/10.1038/s43016-022-00576-x

Ke J, Wang B, Yoshikuni Y. Microbiome engineering: synthetic biology of plant-associated microbiomes in sustainable agriculture. *Trends Biotechnol*. 2021:39(3):244–261. https://doi.org/10.1016/j.tibtech.2020.07.008

Khare D, Choi H, Huh SU, Bassin B, Kim J, Martinoia E, Sohn KH, Paek K-H, Lee Y. Arabidopsis ABCG34 contributes to defense against necrotrophic pathogens by mediating the secretion of camalexin. *Proc Natl Acad Sci U S A*. 2017:114(28):E5712–E5720. https://doi.org/10.1073/pnas.1702259114

Kim JH, Jander G. *Myzus persicae* (green peach aphid) feeding on Arabidopsis induces the formation of a deterrent indole glucosinolate. *Plant J*. 2007:49(6):1008–1019. https://doi.org/10.1111/j.1365-313X.2006.03019.x

Knights HE, Ramachandran VK, Jorrin B, Ledermann R, Parsons JD, Aroney STN, Poole PS. Rhizobium determinants of rhizosphere persistence and root colonization. *ISME J*. 2024:18(1):wrae072. https://doi.org/10.1093/ismejo/wrae072

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(31):15735–15744. https://doi.org/10.1073/pnas.1818604116

Kudjordjie EN, Sapkota R, Steffensen SK, Fomsgaard IS, Nicolaisen M. Maize synthesized benzoxazinoids affect the host associated microbiome. *Microbiome*. 2019:7(1):59. https://doi.org/10.1186/s40168-019-0677-7

Kulkarni OS, Mazumder M, Kini S, Hill ED, Aow JSB, Phua SML, Elejalde U, Kjelleberg S, Swarup S. Volatile methyl jasmonate from roots triggers host-beneficial soil microbiome biofilms. *Nat Chem Biol*. 2024:20(4):473–483. https://doi.org/10.1038/s41589-023-01462-8

Lebeis SL, Paredes SH, Lundberg DS, Breakfield N, Gehring J, McDonald M, Malfatti S, Glavina Del Rio T, Jones CD, Tringe SG, *et al*. Salicylic acid modulates colonization of the root microbiome by specific bacterial taxa. *Science*. 2015:349(6250):860–864. https://doi.org/10.1126/science.aaa8764

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(2):281–290. https://doi.org/10.1093/aob/mcs055

Lee S-M, Kong HG, Song GC, Ryu C-M. Disruption of Firmicutes and Actinobacteria abundance in tomato rhizosphere causes the incidence of bacterial wilt disease. *ISME J*. 2021:15(1):330–347. https://doi.org/10.1038/s41396-020-00785-x

Lemarié S, Robert-Seilaniantz A, Lariagon C, Lemoine J, Marnet N, Levrel A, Jubault M, Manzanares-Dauleux MJ, Gravot A. Camalexin contributes to the partial resistance of *Arabidopsis thaliana* to the biotrophic soilborne protist *Plasmodiophora brassicae*. *Front Plant Sci*. 2015:6:539. https://doi.org/10.3389/fpls.2015.00539

Lerenard T, Aligon S, Berruyer R, Poupard P, Le Corff J. Plant defense compounds can enhance antagonistic effects against *Alternaria brassicicola* of seed-associated fungi isolated from wild

Brassicaceae. *Front Plant Sci*. 2024:15:1466043. https://doi.org/10.3389/fpls.2024.1466043

Levy A, Salas Gonzalez I, Mittelviefhaus M, Clingenpeel S, Herrera Paredes S, Miao J, Wang K, Devescovi G, Stillman K, Monteiro F, *et al*. Genomic features of bacterial adaptation to plants. *Nat Genet*. 2018:50(1):138–150. https://doi.org/10.1038/s41588-017-0012-9

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(1):56. https://doi.org/10.1186/s40168-022-01234-x

Li X, Chen D, Carrión VJ, Revillini D, Yin S, Dong Y, Zhang T, Wang X, Delgado-Baquerizo M. Acidification suppresses the natural capacity of soil microbiome to fight pathogenic *Fusarium* infections. *Nat Commun*. 2023:14(1):5090. https://doi.org/10.1038/s41467-023-40810-z

Li Y, Li R, Liu R, Shi J, Qiu X, Lei J, Xu Z, Wang C, Ge M, Xu H, *et al*. A simplified SynCom based on core–helper strain interactions enhances symbiotic nitrogen fixation in soybean. *J Integr Plant Biol*. 2025:67(6):1582–1598. https://doi.org/10.1111/jipb.13881

Liu H, Brettell LE, Qiu Z, Singh BK. Microbiome-mediated stress resistance in plants. *Trends Plant Sci*. 2020:25(8):733–743. https://doi.org/10.1016/j.tplants.2020.03.014

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*. 2021a:229(5):2873–2885. https://doi.org/10.1111/nph.17057

Liu X, Matsumoto H, Lv T, Zhan C, Fang H, Pan Q, Xu H, Fan X, Chu T, Chen S, *et al*. Phyllosphere microbiome induces host metabolic defence against rice false-smut disease. *Nat Microbiol*. 2023:8(8):1419–1433. https://doi.org/10.1038/s41564-023-01379-x

Liu Y, Kong D, Wu H-L, Ling H-Q. Iron in plant–pathogen interactions. *J Exp Bot*. 2021b:72(6):2114–2124. https://doi.org/10.1093/jxb/eraa516

Liu Y, Zhang H, Wang J, Gao W, Sun X, Xiong Q, Shu X, Miao Y, Shen Q, Xun W, *et al*. Nonpathogenic Pseudomonas syringae derivatives and its metabolites trigger the plant "cry for help" response to assemble disease suppressing and growth promoting rhizomicrobiome. *Nat Commun*. 2024:15(1):1907. https://doi.org/10.1038/s41467-024-46254-3

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(10):982–994. https://doi.org/10.1094/MPMI-12-17-0310-R

Lv S, Yang Y, Yu G, Peng L, Zheng S, Singh SK, Vílchez JI, Kaushal R, Zi H, Yi D, *et al*. Dysfunction of histone demethylase IBM1 in *Arabidopsis* causes autoimmunity and reshapes the root microbiome. *ISME J*. 2022:16(11):2513–2524. https://doi.org/10.1038/s41396-022-01297-6

Mahdi I, Fahsi N, Hijri M, Sobeh M. Antibiotic resistance in plant growth promoting bacteria: a comprehensive review and future perspectives to mitigate potential gene invasion risks. *Front Microbiol*. 2022:13:999988. https://doi.org/10.3389/fmicb.2022.999988

Martínez-Medina A, Appels FVW, Van Wees SCM. Impact of salicylic acid– and jasmonic acid–regulated defences on root colonization by *Trichoderma harzianum* T-78. *Plant Signal Behav*. 2017:12(8):e1345404. https://doi.org/10.1080/15592324.2017.1345404

Mazzola M. Mechanisms of natural soil suppressiveness to soilborne diseases. *Antonie Van Leeuwenhoek*. 2002:81(1-4):557–564. https://doi.org/10.1023/A:1020557523557

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(1):212–224. https://doi.org/10.1038/ismej.2017.158

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(6033):1097–1100. https://doi.org/10.1126/science.1203980

Mesny F. Co-evolution within the plant holobiont drives host performance. *EMBO Rep*. 2023:24(9):e57455. https://doi.org/10.15252/embr.202357455

Mesny F, Bauer M, Zhu J, Thomma BPHJ. Meddling with the microbiota: fungal tricks to infect plant hosts. *Curr Opin Plant Biol*. 2024:82:102622. https://doi.org/10.1016/j.pbi.2024.102622

Mitter B, Brader G, Pfaffenbichler N, Sessitsch A. Next generation microbiome applications for crop production—limitations and the need of knowledge-based solutions. *Curr Opin Microbiol*. 2019:49:59–65. https://doi.org/10.1016/j.mib.2019.10.006

Mo Y, Bier R, Li X, Daniels M, Smith A, Yu L, Kan J. Agricultural practices influence soil microbiome assembly and interactions at different depths identified by machine learning. *Commun Biol*. 2024:7(1):1349. https://doi.org/10.1038/s42003-024-07059-8

Nemergut DR, Schmidt SK, Fukami T, O'Neill SP, Bilinski TM, Stanish LF, Knelman JE, Darcy JL, Lynch RC, Wickey P, *et al*. Patterns and processes of microbial community assembly. *Microbiol Mol Biol Rev*. 2013:77(3):342–356. https://doi.org/10.1128/MMBR.00051-12

Ngou BPM, Ding P, Jones JDG. Thirty years of resistance: zig-zag through the plant immune system. *Plant Cell*. 2022a:34(5):1447–1478. https://doi.org/10.1093/plcell/koac041

Ngou BPM, Jones JDG, Ding P. Plant immune networks. *Trends Plant Sci*. 2022b:27(3):255–273. https://doi.org/10.1016/j.tplants.2021.08.012

Nguyen NH, Trotel-Aziz P, Clément C, Jeandet P, Baillieul F, Aziz A. Camalexin accumulation as a component of plant immunity during interactions with pathogens and beneficial microbes. *Planta*. 2022:255(6):116. https://doi.org/10.1007/s00425-022-03907-1

Paasch BC, He SY. Toward understanding microbiota homeostasis in the plant kingdom. *PLoS Pathog*. 2021:17(4):e1009472. https://doi.org/10.1371/journal.ppat.1009472

Pereira LB, Thomazella DPT, Teixeira PJPL. Plant–microbiome crosstalk and disease development. *Curr Opin Plant Biol*. 2023:72:102351. https://doi.org/10.1016/j.pbi.2023.102351

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(7):852–864. https://doi.org/10.1038/s41564-021-00929-5

Pfeilmeier S, Werz A, Ote M, Bortfeld-Miller M, Kirner P, Keppler A, Hemmerle L, Gäbelein CG, Petti GC, Wolf S, *et al*. Leaf microbiome dysbiosis triggered by T2SS-dependent enzyme secretion from opportunistic *Xanthomonas* pathogens. *Nat Microbiol*. 2024:9(1):136–149. https://doi.org/10.1038/s41564-023-01555-z

Piasecka A, Jedrzejczak-Rey N, Bednarek P. Secondary metabolites in plant innate immunity: conserved function of divergent chemicals. *New Phytol*. 2015:206(3):948–964. https://doi.org/10.1111/nph.13325

Pieterse CMJ, Berendsen RL, De Jonge R, Stringlis IA, Van Dijken AJH, Van Pelt JA, Van Wees SCM, Yu K, Zamioudis C, Bakker PAHM. Pseudomonas simiae WCS417: star track of a model beneficial rhizobacterium. *Plant Soil*. 2021:461(1-2):245–263. https://doi.org/10.1007/s11104-020-04786-9

Pieterse CMJ, Van Der Does D, Zamioudis C, Leon-Reyes A, Van Wees SCM. Hormonal modulation of plant immunity. *Annu Rev Cell Dev Biol*. 2012:28(1):489–521. https://doi.org/10.1146/annurev-cellbio-092910-154055

Polturak G, Dippe M, Stephenson MJ, Chandra Misra R, Owen C, Ramirez-Gonzalez RH, Haidoulis JF, Schoonbeek H-J, Chartrain L, Borrill P, et al. Pathogen-induced biosynthetic pathways encode defense-related molecules in bread wheat. *Proc Natl Acad Sci U S A*. 2022:119(16):e2123299119. https://doi.org/10.1073/pnas.2123299119

Prigigallo MI, Gómez-Lama Cabanás C, Mercado-Blanco J, Bubici G. Designing a synthetic microbial community devoted to biological control: the case study of Fusarium wilt of banana. *Front Microbiol*. 2022:13:967885. https://doi.org/10.3389/fmicb.2022.967885

Pun M, Khazanov N, Galsurker O, Weitman M, Kerem Z, Senderowitz H, Yedidia I. Phloretin, an Apple phytoalexin, affects the virulence and fitness of *Pectobacterium brasiliense* by interfering with quorum-sensing. *Front Plant Sci*. 2021:12:671807. https://doi.org/10.3389/fpls.2021.671807

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(8):1957–1969. https://doi.org/10.1038/s41396-022-01245-4

Raaijmakers JM, Paulitz TC, Steinberg C, Alabouvette C, Moënne-Loccoz Y. The rhizosphere: a playground and battlefield for soil-borne pathogens and beneficial microorganisms. *Plant Soil*. 2009:321(1-2):341–361. https://doi.org/10.1007/s11104-008-9568-6

Ristaino JB, Anderson PK, Bebber DP, Brauman KA, Cunniffe NJ, Fedoroff NV, Finegold C, Garrett KA, Gilligan CA, Jones CM, et al. The persistent threat of emerging plant disease pandemics to global food security. *Proc Natl Acad Sci U S A*. 2021:118(23):e2022239118. https://doi.org/10.1073/pnas.2022239118

Robe K, Izquierdo E, Vignols F, Rouached H, Dubos C. The coumarins: secondary metabolites playing a primary role in plant nutrition and health. *Trends Plant Sci*. 2021:26(3):248–259. https://doi.org/10.1016/j.tplants.2020.10.008

Rogers EE. Mode of action of the *Arabidopsis thaliana* phytoalexin camalexin and its role in *Arabidopsis*–pathogen interactions. *Mol Plant Microbe Interact*. 1996:9(8):748. https://doi.org/10.1094/MPMI-9-0748

Rolfe SA, Griffiths J, Ton J. Crying out for help with root exudates: adaptive mechanisms by which stressed plants assemble health-promoting soil microbiomes. *Curr Opin Microbiol*. 2019:49:73–82. https://doi.org/10.1016/j.mib.2019.10.003

Rudrappa T, Czymmek KJ, Paré PW, Bais HP. Root-secreted malic acid recruits beneficial soil bacteria. *Plant Physiol*. 2008:148(3):1547–1556. https://doi.org/10.1104/pp.108.127613

Russ D, Fitzpatrick CR, Saha C, Law TF, Jones CD, Kliebenstein DJ, Dangl JL. An effluent pump family distributed across plant commensal bacteria conditions host- and organ-specific glucosinolate detoxification. *Nat Commun*. 2025:16(1):5699. https://doi.org/10.1038/s41467-025-61266-3

Russ D, Fitzpatrick CR, Teixeira PJPL, Dangl JL. Deep discovery informs difficult deployment in plant microbiome science. *Cell*. 2023:186(21):4496–4513. https://doi.org/10.1016/j.cell.2023.08.035

Savary S, Willocquet L, Pethybridge SJ, Esker P, McRoberts N, Nelson A. The global burden of pathogens and pests on major food crops. *Nat Ecol Evol*. 2019:3(3):430–439. https://doi.org/10.1038/s41559-018-0793-y

Schlaeppi K, Abou-Mansour E, Buchala A, Mauch F. Disease resistance of Arabidopsis to *Phytophthora brassicae* is established by the sequential action of indole glucosinolates and camalexin: glucosinolates and camalexin in disease resistance. *Plant J*. 2010:62(5):840–851. https://doi.org/10.1111/j.1365-313X.2010.04197.x

Schlaeppi K, Gross JJ, Hapfelmeier S, Erb M. Plant chemistry and food web health. *New Phytol*. 2021:231(3):957–962. https://doi.org/10.1111/nph.17385

Schlatter D, Kinkel L, Thomashow L, Weller D, Paulitz T. Disease suppressive soils: new insights from the soil microbiome. *Phytopathology*. 2017:107(11):1284–1297. https://doi.org/10.1094/PHYTO-03-17-0111-RVW

Seybold H, Demetrowitsch TJ, Hassani MA, Szymczak S, Reim E, Haueisen J, Lübbers L, Rühlemann M, Franke A, Schwarz K, et al. A fungal pathogen induces systemic susceptibility and systemic shifts in wheat metabolome and microbiome composition. *Nat Commun*. 2020:11(1):1910. https://doi.org/10.1038/s41467-020-15633-x

Siebers M, Rohr T, Ventura M, Schütz V, Thies S, Kovacic F, Jaeger K-E, Berg M, Dörmann P, Schulz M. Disruption of microbial community composition and identification of plant growth promoting microorganisms after exposure of soil to rapeseed-derived glucosinolates. *PLoS One*. 2018:13(7):e0200160. https://doi.org/10.1371/journal.pone.0200160

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*. 2023:237(3):944–958. https://doi.org/10.1111/nph.18576

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(49):e2110968118. https://doi.org/10.1073/pnas.2110968118

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. *Nat Plants*. 2020:6(11):1365–1374. https://doi.org/10.1038/s41477-020-00799-5

Snoeck S, Johanndrees O, Nürnberger T, Zipfel C. Plant pattern recognition receptors: from evolutionary insight to engineering. *Nat Rev Genet*. 2025:26(4):268–278. https://doi.org/10.1038/s41576-024-00793-z

Sommer A, Wenig M, Knappe C, Kublik S, Foesel BU, Schloter M, Vlot AC. A salicylic acid-associated plant–microbe interaction attracts beneficial *Flavobacterium* sp. to the *Arabidopsis thaliana* phyllosphere. *Physiol Plant*. 2024:176(4):e14483. https://doi.org/10.1111/ppl.14483

Song S, Morales Moreira Z, Briggs AL, Zhang X-C, Diener AC, Haney CH. PSKR1 balances the plant growth–defence trade-off in the rhizosphere microbiome. *Nat Plants*. 2023:9(12):2071–2084. https://doi.org/10.1038/s41477-023-01539-1

Song Y, Wilson AJ, Zhang X-C, Thoms D, Sohrabi R, Song S, Geissmann Q, Liu Y, Walgren L, He SY, et al. FERONIA restricts *Pseudomonas* in the rhizosphere microbiome via regulation of reactive oxygen species. *Nat Plants*. 2021:7(5):644–654. https://doi.org/10.1038/s41477-021-00914-0

Spooren J, van Bentum S, Thomashow LS, Pieterse CMJ, Weller DM, Berendsen RL. Plant-driven assembly of disease-suppressive soil microbiomes. *Annu Rev Phytopathol*. 2024:62(1):1–30. https://doi.org/10.1146/annurev-phyto-021622-100127

Stolpe C, Giehren F, Krämer U, Müller C. Both heavy metal-amendment of soil and aphid-infestation increase cd and zn concentrations in phloem exudates of a metal-hyperaccumulating plant. *Phytochemistry*. 2017:139:109–117. https://doi.org/10.1016/j.phytochem.2017.04.010

Stotz HU, Sawada Y, Shimada Y, Hirai MY, Sasaki E, Krischke M, Brown PD, Saito K, Kamiya Y. Role of camalexin, indole glucosinolates, and side chain modification of glucosinolate-derived

isothiocyanates in defense of Arabidopsis against *Sclerotinia sclerotiorum*. *Plant J*. 2011:67(1):81–93. https://doi.org/10.1111/j.1365-313X.2011.04578.x

Stringlis IA, De Jonge R, Pieterse CMJ. The age of coumarins in plant–microbe interactions. *Plant Cell Physiol*. 2019:60(7):1405–1419. https://doi.org/10.1093/pcp/pcz076

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 U S A*. 2018:115(22): E5213–E5222. https://doi.org/10.1073/pnas.1722335115

Su P, Kang H, Peng Q, Wicaksono WA, Berg G, Liu Z, Ma J, Zhang D, Cernava T, Liu Y. Microbiome homeostasis on rice leaves is regulated by a precursor molecule of lignin biosynthesis. *Nat Commun*. 2024:15(1):23. https://doi.org/10.1038/s41467-023-44335-3

Teixeira PJP, Colaianni NR, Fitzpatrick CR, Dangl JL. Beyond pathogens: microbiota interactions with the plant immune system. *Curr Opin Microbiol*. 2019:49:7–17. https://doi.org/10.1016/j.mib.2019.08.003

Thimmappa R, Geisler K, Louveau T, O'Maille P, Osbourn A. Triterpene biosynthesis in plants. *Annu Rev Plant Biol*. 2014:65(1): 225–257. https://doi.org/10.1146/annurev-arplant-050312-120229

Thoenen L, Giroud C, Kreuzer M, Waelchli J, Gfeller V, Deslandes-Hérold G, Mateo P, Robert CAM, Ahrens CH, Rubio-Somoza I, *et al*. Bacterial tolerance to host-exuded specialized metabolites structures the maize root microbiome. *Proc Natl Acad Sci U S A*. 2023:120(44):e2310134120. https://doi.org/10.1073/pnas.2310134120

Thoenen L, Kreuzer M, Pestalozzi C, Florean M, Mateo P, Züst T, Wei A, Giroud C, Rouyer L, Gfeller V, *et al*. The lactonase BxdA mediates metabolic specialisation of maize root bacteria to benzoxazinoids. *Nat Commun*. 2024:15(1):6535. https://doi.org/10.1038/s41467-024-49643-w

Tian D, Chen Z, Lin Y, Liang T, Chen Z, Guo X, Wang F, Wang Z. The interaction between rice genotype and *Magnaporthe oryzae* regulates the assembly of rice root-associated microbiota. *Rice*. 2021:14(1):40. https://doi.org/10.1186/s12284-021-00486-9

Tong Y, Zheng X, Hu Y, Wu J, Liu H, Deng Y, Lv W, Yao H, Chen J, Ge T. Root exudate-mediated plant–microbiome interactions determine plant health during disease infection. *Agric Ecosyst Environ*. 2024:370:109056. https://doi.org/10.1016/j.agee.2024.109056

Torres MA, Jones JDG, Dangl JL. Reactive oxygen species signaling in response to pathogens. *Plant Physiol*. 2006:141(2):373–378. https://doi.org/10.1104/pp.106.079467

Toruño TY, Stergiopoulos I, Coaker G. Plant–pathogen effectors: cellular probes interfering with plant defenses in spatial and temporal manners. *Annu Rev Phytopathol*. 2016:54(1):419–441. https://doi.org/10.1146/annurev-phyto-080615-100204

Tracanna V, Ossowicki A, Petrus MLC, Overduin S, Terlouw BR, Lund G, Robinson SL, Warris S, Schijlen EGWM, Van Wezel GP, *et al*. Dissecting disease-suppressive rhizosphere microbiomes by functional amplicon sequencing and 10× metagenomics. *mSystems*. 2021:6(3):e01116-20. https://doi.org/10.1128/mSystems.01116-20

Tripathy BC, Oelmüller R. Reactive oxygen species generation and signaling in plants. *Plant Signal Behav*. 2012:7(12):1621–1633. https://doi.org/10.4161/psb.22455

Trivedi P, Leach JE, Tringe SG, Sa T, Singh BK. Plant–microbiome interactions: from community assembly to plant health. *Nat Rev Microbiol*. 2020:18(11):607–621. https://doi.org/10.1038/s41579-020-0412-1

Tzipilevich E, Russ D, Dangl JL, Benfey PN. Plant immune system activation is necessary for efficient root colonization by auxin-secreting beneficial bacteria. *Cell Host Microbe*. 2021:29(10):1507–1520.e4. https://doi.org/10.1016/j.chom.2021.09.005

Van De Mortel JE, De Vos RCH, Dekkers E, Pineda A, Guillod L, Bouwmeester K, Van Loon JJA, Dicke M, Raaijmakers JM. Metabolic and transcriptomic changes induced in Arabidopsis by the rhizobacterium *Pseudomonas fluorescens* SS101. *Plant Physiol*. 2012:160(4):2173–2188. https://doi.org/10.1104/pp.112.207324

Vannier N, Agler M, Hacquard S. Microbiota-mediated disease resistance in plants. *PLoS Pathog*. 2019:15(6):e1007740. https://doi.org/10.1371/journal.ppat.1007740

Venturi V, Fuqua C. Chemical signaling between plants and plant–pathogenic bacteria. *Annu Rev Phytopathol*. 2013:51(1):17–37. https://doi.org/10.1146/annurev-phyto-082712-102239

Verhagen BWM, Van Loon LC, Pieterse CMJ. Induced disease resistance signaling in plants. In: da Silva JAT, editors. *Floriculture, Ornamental and Plant Biotechnology*. Vol III. Ikenobe, Kagawa, Japan: Global Science Books; 2006. p. 334–343.

Vincent SA, Ebertz A, Spanu PD, Devlin PF. Salicylic acid-mediated disturbance increases bacterial diversity in the phyllosphere but is overcome by a dominant core community. *Front Microbiol*. 2022:13:809940. https://doi.org/10.3389/fmicb.2022.809940

Vishwanathan K, Zienkiewicz K, Liu Y, Janz D, Feussner I, Polle A, Haney CH. Ectomycorrhizal fungi induce systemic resistance against insects on a nonmycorrhizal plant in a CERK1-dependent manner. *New Phytol*. 2020:228(2):728–740. https://doi.org/10.1111/nph.16715

Vismans G, van Bentum S, Spooren J, Song Y, Goossens P, Valls J, Snoek BL, Thiombiano B, Schilder M, Dong L, *et al*. Coumarin biosynthesis genes are required after foliar pathogen infection for the creation of a microbial soil-borne legacy that primes plants for SA-dependent defenses. *Sci Rep*. 2022:12(1):22473. https://doi.org/10.1038/s41598-022-26551-x

Vogel C, Bodenhausen N, Gruissem W, Vorholt JA. The Arabidopsis leaf transcriptome reveals distinct but also overlapping responses to colonization by phyllosphere commensals and pathogen infection with impact on plant health. *New Phytol*. 2016:212(1):192–207. https://doi.org/10.1111/nph.14036

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(12):1537–1548. https://doi.org/10.1038/s41564-021-00997-7

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 U S A*. 2019:116(25):12558–12565. https://doi.org/10.1073/pnas.1820691116

Vorholt JA. Microbial life in the phyllosphere. *Nat Rev Microbiol*. 2012:10(12):828–840. https://doi.org/10.1038/nrmicro2910

Wagner MR, Lundberg DS, Del Rio TG, Tringe SG, Dangl JL, Mitchell-Olds T. Host genotype and age shape the leaf and root microbiomes of a wild perennial plant. *Nat Commun*. 2016:7(1): 12151. https://doi.org/10.1038/ncomms12151

Wan J, He M, Hou Q, Zou L, Yang Y, Wei Y, Chen X. Cell wall associated immunity in plants. *Stress Biol*. 2021:1(1):3. https://doi.org/10.1007/s44154-021-00003-4

Wang M, Weiberg A, Lin F-M, Thomma BPHJ, Huang H-D, Jin H. Bidirectional cross-kingdom RNAi and fungal uptake of external RNAs confer plant protection. *Nat Plants*. 2016:2(10):16151. https://doi.org/10.1038/nplants.2016.151

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(14):5052–5066. https://doi.org/10.1093/jxb/erac202

Wei Z, Hu J, Gu Y, Yin S, Xu Y, Jousset A, Shen Q, Friman V-P. *Ralstonia solanacearum* pathogen disrupts bacterial rhizosphere microbiome during an invasion. *Soil Biol Biochem*. 2018:118:8–17. https://doi.org/10.1016/j.soilbio.2017.11.012

Weller DM, Raaijmakers JM, Gardener BBM, Thomashow LS. Microbial populations responsible for specific soil suppressiveness to plant pathogens. *Annu Rev Phytopathol*. 2002:40(1):309–348. https://doi.org/10.1146/annurev.phyto.40.030402.110010

Wolinska KW, Vannier N, Thiergart T, Pickel B, Gremmen S, Piasecka A, Piślewska-Bednarek M, Nakano RT, Belkhadir Y, Bednarek P, *et al*. Tryptophan metabolism and bacterial commensals prevent fungal dysbiosis in *Arabidopsis* roots. *Proc Natl Acad Sci U S A*. 2021:118(49): e2111521118. https://doi.org/10.1073/pnas.2111521118

Xia X, Wei Q, Wu H, Chen X, Xiao C, Ye Y, Liu C, Yu H, Guo Y, Sun W, *et al*. Bacillus species are core microbiota of resistant maize cultivars that induce host metabolic defense against corn stalk rot. *Microbiome*. 2024:12(1):156. https://doi.org/10.1186/s40168-024-01887-w

Yang C-X, Chen S-J, Hong X-Y, Wang L-Z, Wu H-M, Tang Y-Y, Gao Y-Y, Hao G-F. Plant exudates-driven microbiome recruitment and assembly facilitates plant health management. *FEMS Microbiol Rev*. 2025:49:fuaf008. https://doi.org/10.1093/femsre/fuaf008

Yang F, Zhang J, Zhang H, Ji G, Zeng L, Li Y, Yu C, Fernando WGD, Chen W. Bacterial blight induced shifts in endophytic microbiome of rice leaves and the enrichment of specific bacterial strains with pathogen antagonism. *Front Plant Sci*. 2020:11:963. https://doi.org/10.3389/fpls.2020.00963

Yang K, Fu R, Feng H, Jiang G, Finkel O, Sun T, Liu M, Huang B, Li S, Wang X, *et al*. RIN enhances plant disease resistance via root exudate-mediated assembly of disease-suppressive rhizosphere microbiota. *Mol Plant*. 2023:16(9):1379–1395. https://doi.org/10.1016/j.molp.2023.08.004

Yang W, Zhang L, Yang Y, Xiang H, Yang P. Plant secondary metabolites-mediated plant defense against bacteria and fungi pathogens. *Plant Physiol Biochem*. 2024:217:109224. https://doi.org/10.1016/j.plaphy.2024.109224

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(1):156. https://doi.org/10.1186/s40168-018-0537-x

Zamioudis C, Korteland J, Van Pelt JA, Van Hamersveld M, Dombrowski N, Bai Y, Hanson J, Van Verk MC, Ling H, Schulze-Lefert P, *et al*. Rhizobacterial volatiles and photosynthesis-related signals coordinate *MYB 72* expression in Arabidopsis roots during onset of induced systemic resistance and iron-deficiency responses. *Plant J*. 2015:84(2):309–322. https://doi.org/10.1111/tpj.12995

Zaynab M, Khan J, Al-Yahyai R, Sadder M, Li S. Toxicity of coumarins in plant defense against pathogens. *Toxicon*. 2024:250:108118. https://doi.org/10.1016/j.toxicon.2024.108118

Zhang Y, Cao B, Pan Y, Tao S, Zhang N. Metabolite-mediated responses of phyllosphere microbiota to rust infection in two *Malus* species. *Microbiol Spectr*. 2023:11(2):e03831-22. https://doi.org/10.1128/spectrum.03831-22

Zhong Y, Xun W, Wang X, Tian S, Zhang Y, Li D, Zhou Y, Qin Y, Zhang B, Zhao G, *et al*. Root-secreted bitter triterpene modulates the rhizosphere microbiota to improve plant fitness. *Nat Plants*. 2022:8(8):887–896. https://doi.org/10.1038/s41477-022-01201-2

Zhou J, Ning D. Stochastic community assembly: does it matter in microbial ecology? *Microbiol Mol Biol Rev*. 2017:81(4):e00002-17. https://doi.org/10.1128/MMBR.00002-17

Zhou J-M, Zhang Y. Plant immunity: danger perception and signaling. *Cell*. 2020:181(5):978–989. https://doi.org/10.1016/j.cell.2020.04.028

Zhou Y, Yang Z, Liu J, Li X, Wang X, Dai C, Zhang T, Carrión VJ, Wei Z, Cao F, *et al*. Crop rotation and native microbiome inoculation restore soil capacity to suppress a root disease. *Nat Commun*. 2023:14(1):8126. https://doi.org/10.1038/s41467-023-43926-4

Zhu L, Wang S, Duan H, Lu X. Foliar pathogen-induced assemblage of beneficial rhizosphere consortia increases plant defense against *Setosphaeria turcica*. *Front Biosci (Landmark Ed)*. 2021:26(9):543. https://doi.org/10.52586/4966