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Review

Plant Recruitment and Pathogen Sabotage of Beneficial Rhizosphere Microbiomes: Mechanisms and Future Directions

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Abstract

Plants do not defend themselves in isolation, and over the past decade, a paradigm shift has redefined plant immunity as a community-level process, in which the plant host and its associated microbiome function as a collaborative unit. A key principle of this framework is the "cry for help" hypothesis, which suggests that pathogen-stressed plants modify their root exudate chemistry to attract protective microbial allies from the surrounding soil. Research on pathogen-induced microbiome assembly in soils has identified specific metabolites, such as organic acids, benzoxazinoids, coumarins, and flavonoids, that signal and recruit beneficial soil microbes. Systemic plant signalling pathways link foliar pathogen infections to changes in root metabolic activity, where this microbial recruitment can establish lasting ecological legacies by promoting disease-suppressive soils that benefit future plant generations. At the same time, pathogens are not simply passive targets of this microbiome recruitment but active players that subvert these processes. Using effector proteins with antibacterial properties, interference with recruitment-associated processes, and competitive mechanisms that disrupt plant–microbe communication, pathogens may interfere with the formation of protective microbial communities. This review consolidates recent advances to explore the molecular mechanisms behind microbial recruitment in pathogen-stressed plants, the counter-strategies these infections use to disrupt such interactions, and the ecological memory that allows these processes to continue across plant generations. Additionally, the review discusses future directions such as cross-kingdom synthetic ecosystems, computational modelling for microbiome prediction, and CRISPR-mediated crop engineering, which are becoming key tools for sustainable agriculture and global food security.

Keywords: rhizosphere microbiome; cry for help; disease-suppressive soils; root exudates; pathogen effectors; plant–microbe interactions

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1. Introduction

Over the past fifteen years, the conceptual framework for plant–pathogen interactions has expanded significantly. Traditionally, the "disease triangle" highlighted the interaction among the host, the pathogen, and the environment. Plants now actively shape and are shaped by their microbial communities, redefining the host–microbiome relationship as a co-evolved, functionally integrated unit, or holobiont [1]. In plants, the holobiont includes the plant host and its associated bacteria, fungi, archaea, viruses, and other microorganisms occupying distinct ecological habitats such as the rhizosphere, root endosphere, and phyllosphere. In plant pathology, disease resistance is not determined solely by the plant's

resistance gene repertoire but derives from interactions between the plant host's immunity and the microbiome's defensive capabilities. Functional studies support this view, showing the rhizosphere microbiome can suppress a range of soil-borne pathogens through antibiosis, competition for nutrients and niche space, and induction of systemic resistance in plants [2–4]. The plant microbiome is therefore regarded as an extension of the plant's immune system, with microbiome-mediated resistance providing measurable defence that supplements traditional resistance gene immunity.

The observation that plants can actively recruit specific microbes during distress [5] was articulated as the "cry for help" hypothesis, which proposed that plants actively modulate their rhizosphere to recruit microbes that confer systemic resistance or directly antagonize pathogens [6]. Research has shown that this response is not generic but a tightly coordinated metabolic change in which the plant redirects carbon and energy into specific root exudates to obtain the microbial protection it needs [7]. The focus then shifted from determining which microorganisms were recruited to how they were recruited to help suppress opportunistic pathogens while preferentially enriching beneficial taxa [8,9]. Interestingly, these recruitment events appear to leave a rhizosphere memory that can protect subsequent generations of plants grown in the same soil [10,11]. Although the "cry for help" response was long regarded as an effective defensive strategy, recent advances have unveiled a sophisticated counter-offensive by pathogenic organisms. Some pathogens have developed mechanisms to disrupt these microbial alliances, such as secreting specialized antimicrobial effectors to systematically eliminate the beneficial microbes the plant recruits [12].

Several knowledge gaps prevent us from fully understanding stress-driven microbial recruitment. We know individual metabolites and beneficial taxa linked to plant protection, but the connections between stress signalling, root exudation changes, microbial recruitment, and disease suppression remain unclear. Altered microbial abundance does not necessarily indicate intentional recruitment, and taxon enrichment does not prove it contributes to disease suppression. Translating microbiome research into the field is also a major hurdle. A beneficial microbe that works under controlled conditions may fail to establish, persist, or function in field soil, where microbial competition, environmental variation, and interactions among organisms are common. Synthetic microbial communities, computational approaches to community assembly, and plant engineering are potential routes to improve microbiome-based protection. Whether these approaches will be viable depends on a better understanding of microbial compatibility, community stability, host specificity, and environmental elements that determine whether introduced or engineered traits function in the field.

This review critically evaluates the relationship between stress-induced recruitment of beneficial rhizosphere microbes and pathogen-mediated interference with protective plant–microbiome interactions. It brings together current evidence on the "cry for help" hypothesis, systemic signalling between above- and belowground tissues, and the chemical mechanisms that support microbial community assembly. It then assesses putative pathogen counter-strategies, considers whether the recruitment-associated microbiome could be ecologically persistent, and identifies key evidence gaps. It concludes by considering how synthetic microbial communities, computational prediction, and plant microbiome engineering may overcome these limitations. By considering recruitment and sabotage within a common ecological framework, it seeks to identify the mechanistic and translational questions that must be answered to form more robust microbiome-based approaches to plant disease management.

2. Scope and Literature Search

The relevant literature for this review article was identified via comprehensive searches of different scientific databases, including PubMed, Scopus, SciFinder, Web of Science, ScienceDirect, and Google Scholar. We used a range of keywords and a timeframe of 1996–2026 to narrow the search. Keywords included plant–microbe interactions, rhizosphere microbiome, plant microbial consortia, plant stress signalling, cry for help, root exudates, pathogen effectors, pathogen-mediated microbiome sabotage, rhizosphere pathogen interactions, synthetic microbial communities, rhizosphere microbiome manipulation, and plant microbiome engineering. Of the 116 records initially identified, this review included 103 articles. After removing duplicate articles (9), further screening excluded articles with irrelevant or insufficient data (3) and those outside the timeframe indicated above (1).

3. The "Cry for Help" Hypothesis

The "cry for help" hypothesis proposes that plants under biotic or abiotic stress, such as pathogens or drought, actively modify their root exudates to recruit beneficial soil microorganisms [13]. These microbes colonize the rhizosphere to combat the stressor, effectively acting as a protective, inducible immune system for the plant. Rolfe et al. proposed dividing the hypothesis into four stages: activation of root immune responses due to pathogen attack, release of metabolites from roots, recruitment of beneficial microbes, and pathogen antagonization mediated by the altered microbiome. An attack by an infectious agent therefore induces this pathway, creating a chemical and biological milieu conducive to sustained benefit for both the plant host and microbial partners [11]. A foundational study by Rudrappa et al. demonstrated that pathogen challenge stimulated *Arabidopsis* roots to release malic acid, which attracted beneficial bacteria to the rhizosphere and promoted biofilm formation on roots [5]. This recruitment was associated with enhanced plant resistance, providing an early mechanistic example of how plants can modify root exudation in response to stress to favour protective microbial interactions. The study helped establish a basis for the subsequent "cry-for-help" framework, in which stressed plants influence rhizosphere microbial communities through changes in root-derived signals. Figure 1 illustrates the "cry for help" hypothesis in plants.

While evaluating plant immune regulation of protective rhizosphere microbial communities, Berendsen et al. showed that foliar defence activation of mouse-ear thale cress (*Arabidopsis thaliana*) by the causal agent of downy mildew, *Hyaloperonospora arabidopsidis*, promoted three bacterial species in the rhizosphere, which collectively triggered systemic resistance against this fungal pathogen. The abundance of *Stenotrophomonas*, *Xanthomonas*, and *Microbacterium* species was significantly elevated in *H. arabidopsidis*-infected plants, and in vitro testing showed synergistic cooperation among the three species in biofilm formation [14].

Research on the pathogenic fungus *Fusarium pseudograminearum*, which causes crown rot, showed that wheat infected with this fungus specifically increased the beneficial bacterium *Stenotrophomonas rhizophila* in the rhizosphere and root endosphere, with abundances positively associated with pathogen load and defence gene expression in the plant leaves [15]. Wheat plants infected with *Rhizoctonia solani* progressively altered their rhizosphere microbiome over successive plantings, recruiting distinct bacterial communities linked to reduced disease severity. This selective enrichment favoured antagonistic bacterial genera such as *Pseudomonas*, *Flavobacterium*, *Chitinophaga*, and *Chryseobacterium*, culminating in enhanced natural disease suppression and improved plant robustness [16]. Foliar infection of tea seedlings with *Pseudopestalotiopsis camelliae-sinensis*, the causative agent of tea grey blight, resulted in an altered rhizosphere microbial

community with a significant increase in fungi such as *Gliocladiopsis*, *Penicillium*, and *Trichoderma* and beneficial bacteria including *Bacillus*, *Streptomyces*, and *Pseudomonas*, which could inhibit infection and promote growth of the tea seedlings [17].

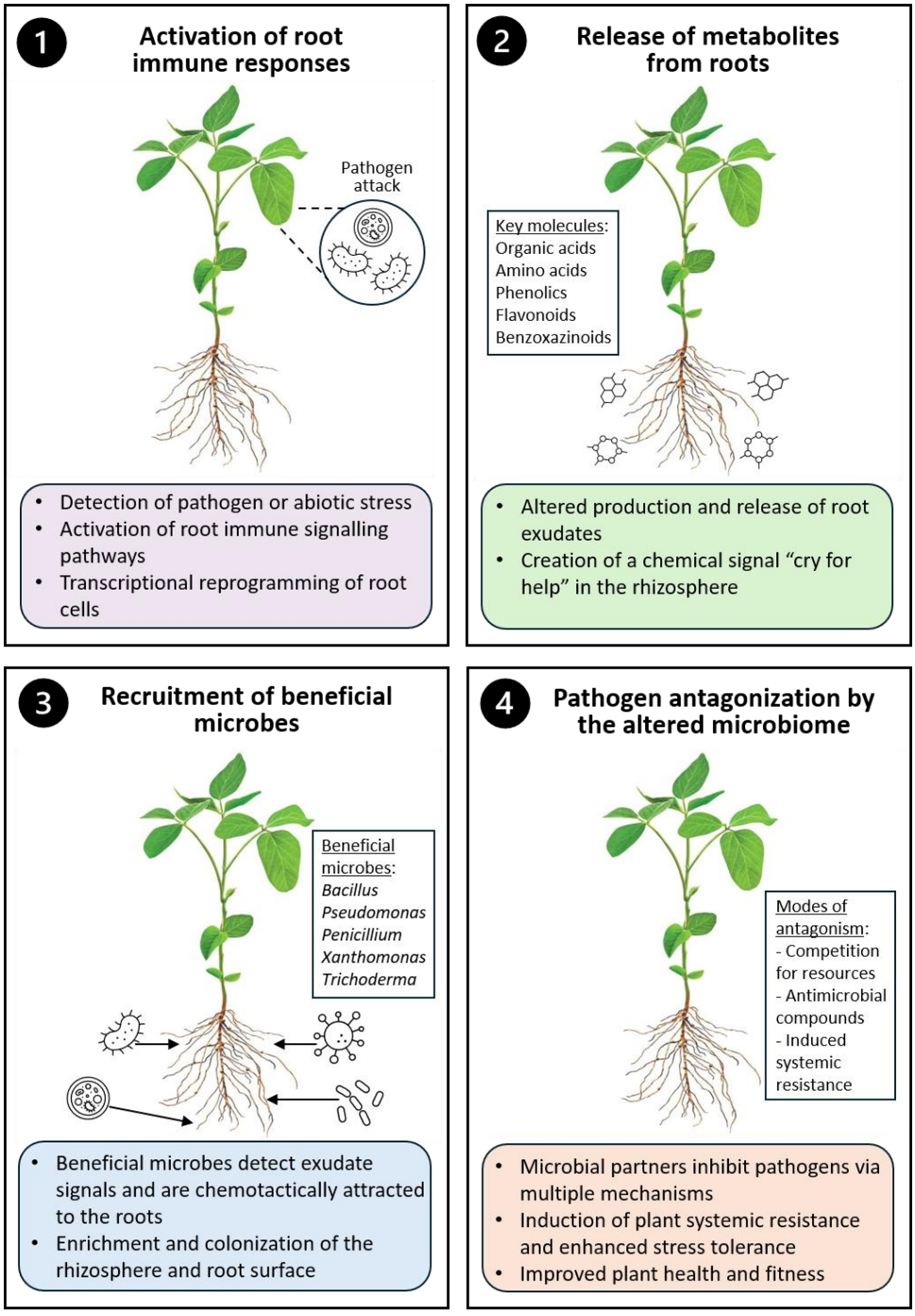

Figure 1. Diagrammatic representation of the "cry for help" hypothesis in plants. Activation of root immune responses after abiotic stress or pathogen attack (**1**) is followed by the release of metabolites from roots (**2**). This recruits beneficial microbes (**3**) and enables pathogen antagonism by the altered microbiome (**4**).

Resistance among banana varieties was associated with their ability to selectively enrich rhizosphere fungal communities that suppress the soil-borne pathogen *Fusarium oxysporum* f. sp. cubense Tropical Race 4, particularly taxa in the genera *Penicillium* and *Trichoderma* [18]. Identification of specific endophytic consortia enriched in sugar beet roots after *R. solani* infection showed that these consortia carried biosynthetic gene clusters

encoding antimicrobial compounds active against the pathogen [3]. More recently, Liu et al. showed that non-pathogenic *Pseudomonas syringae* derivatives and even heat-killed cells could trigger the "cry for help" response in *A. thaliana*. This suggests that the signal is linked to pattern-triggered immunity rather than requiring active infection, highlighting the potential of non-pathogenic bacteria to establish soils with enhanced disease-suppressive properties [19].

Taken together, these studies show that the "cry for help" is not simply metaphorical but a mechanistically defined, experimentally testable process.

4. The Molecular Blueprint of Recruitment

A key question in the "cry for help" hypothesis is how a pathogen attacking a plant's leaves triggers changes in root exudates, sometimes over long distances. The molecular signals that bridge aboveground perception with belowground response occur via a two-step process, beginning with a systemic internal signal and followed by the release of specialized secondary metabolites that modulate rhizosphere microbial communities.

4.1. Systemic Communication: The Foliar-to-Root Signalling Axis

The recruitment process begins long before changes occur in the soil. When the plant senses a foliar pathogen, it initiates a systemic signalling cascade that travels through the phloem to the roots. Research has shown that salicylic acid [20,21] and jasmonic acid [22,23] are not only local defence regulators but also systemic messengers for microbiome assembly in *A. thaliana*. Foliar infection by biotrophic pathogens typically triggers salicylic acid-dependent pathways, while necrotrophs activate jasmonic acid pathways [24]. These signals influence the root's transcriptional profile, specifically upregulating transporters and biosynthetic genes for exudate production [25].

A key molecular switch identified in *A. thaliana* is the transcription factor MYB72, which plays a central role in root immunity, rhizosphere microbiome recruitment, and iron acquisition. Activated in roots after aboveground stimulation, MYB72 is essential for initiating induced systemic resistance (ISR). It regulates the production of iron-mobilising phenolic compounds that also signal beneficial microbes for recruitment [26]. When activated under iron-deficiency conditions and during beneficial rhizobacterial colonization, MYB72 controls the biosynthesis and secretion of scopoletin and other coumarins into the rhizosphere. These coumarins selectively inhibit soil-borne fungal pathogens while promoting beneficial *Pseudomonas* populations [27].

4.2. The Chemistry of Stress-Induced Exudates

Once the systemic signal reaches the roots, the plant actively alters its exudate composition [28]. These exudates perform two key functions: they attract motile microbes via chemotaxis and act as metabolic filters that favour beneficial taxa as well as suppress competitors [29]. The root exudate profile includes compounds such as organic acids, amino acids, phenolics, benzoxazinoids, and flavonoids, which remodel the rhizosphere microbiome to favour plant health [30–33]. Table 1 summarizes the key molecules released in root exudates during the "cry for help" response and their effects.

4.2.1. Organic Acids

One of the earliest identified "cry for help" molecules was malic acid, in which *A. thaliana* infected with *P. syringae* was found to increase malic acid secretion into the rhizosphere, which acted as a potent chemoattractant for the beneficial bacterium *B. subtilis* [5]. Subsequent studies confirmed that malic acid acts as a chemoattractant for multiple *Bacillus* species, with specificity arising from differential chemoreceptor repertoires across bacterial strains [34]. Citric acid and fumaric acid have also been implicated as recruitment

signals, though with lower specificity. The concentration of these organic acids in root exudates increases under pathogen stress, often in a salicylic acid- or jasmonic acid-dependent manner, linking hormonal defence to microbial recruitment [11].

Foliar infection of *Panax notoginseng* by the fungal pathogen *Alternaria panax* significantly upregulated propionic acid, azelaic acid, and palmitic acid [34] and phthalic acid, azelaic acid, and palmitic acid [35] in root exudates, which in turn positively modified the rhizosphere soil microbial community. Roots of *A. thaliana* infected with *P. syringae* showed significantly higher exudation of long-chain organic acids, including octadecanoic acid, palmitoleic acid, and pentadecanoic acid [10]. Additionally, long-chain organic acids and amino acids have been implicated in enriching several *Pseudomonas* strains following foliar *P. syringae* infection, with evidence that these recruited taxa induce systemic resistance in the host. Conversely, in this study, adding short-chain organic acids and sugars significantly increased the proportion of the phylum *Candidatus* Saccharibacteria while reducing Proteobacteria abundance, consequently reducing systemic resistance to pathogen attack [36].

4.2.2. Amino Acids

While evaluating how modified root exudation patterns affect root microbiome assembly in infected plants, Yuan et al. showed that *A. thaliana* plants infected with P. syringae exuded significantly more amino acids (leucine, isoleucine, ornithine, proline, methionine, and tryptophan) than uninfected plants. In this study, exogenous conditioning of soil with the amino acids mentioned above and long-chain organic acids also conferred a higher degree of induced resistance in plants infected with *P. syringae* than in microbiomes from unconditioned control soil [10]. A study evaluating the foliar infection of *P. notoginseng* by the fungal pathogen *A. panax* found enhanced exudation of the amino acids L-aspartic acid, L-serine, alanine, and the amino acid derivative oxoproline, which was associated with the suppression of the soil-borne pathogen *Ilyonectria destructans* and enrichment of beneficial microbes, including *Trichoderma harzianum*, *Trichoderma atroviride*, *Bacillus amyloliquefaciens*, and *Streptomyces coelicolor* in the rhizosphere [35]. Tryptophan-derived metabolites represent another class of recruitment signals; Fusarium oxysporum-infected cucumber roots increase tryptophan exudation, which selectively promotes colonization by the plant growth-promoting rhizobacterium *B. amyloliquefaciens* SQR9 [37]. In contrast, Wang et al. found that amino acid secretion in root exudates of tea seedlings infected with *Pseudopestalotiopsis camelliae-sinensis* was downregulated compared with uninfected controls, which the authors suggested may reflect distinct metabolic profiles across plant species [17].

4.2.3. Phenolic Compounds

Phenolic compounds are vital secondary metabolites that help plants defend against drought, ultraviolet light, and pathogens. Gu et al. showed that infection of tomato plants with *Ralstonia solanacearum* markedly altered root exudation patterns, notably increasing the release of phenolic compounds such as caffeic acid. This changed the soil microbiome composition and directly inhibited pathogen growth [38].

Coumarins are a diverse class of phenolic compounds reported across numerous plant families, including Apiaceae, Rutaceae, Fabaceae, Asteraceae, Rosaceae, Solanaceae, Rubiaceae, and Lamiaceae [39]. These compounds chelate iron, making it available to plants, and act as defence chemicals against stressors and pathogens [40]. Coumarin biosynthesis and secretion by *Arabidopsis* roots, regulated by the MYB72 transcription factor, selectively shape the root-associated microbiome by inhibiting pathogenic microbes while sparing beneficial strains that possess coumarin-tolerance mechanisms. In vitro assays in this study showed that scopoletin selectively inhibited soil-borne fungal pathogens such as *Fusarium*

oxysporum and *Verticillium dahliae*. At the same time, beneficial rhizobacteria, including *Pseudomonas capeferrum* and *Pseudomonas simiae*, remained tolerant to its antimicrobial effects [27]. It was subsequently shown that *Arabidopsis* plants unable to produce coumarins assembled a dysbiotic microbiome with reduced protective capacity, providing genetic evidence that these metabolites are essential for health-promoting microbiome assembly [41]. Coumarins also play a vital role in shaping the rhizosphere microbiome during foliar attack by the downy mildew pathogen *Hyaloperonospora arabidopsidis*, enabling the establishment of a protective soil-borne legacy that improves salicylic acid-dependent systemic resistance against subsequent infections [42].

Flavonoids are polyphenolic secondary metabolites which are well-established chemical mediators of belowground signalling, translating aboveground stress into rhizosphere microbiome assembly. Secondary modifications diversify flavonoids into distinct classes, including chalcones, anthocyanins, isoflavonoids, flavanols, flavones, and flavanones [8,43]. In the "cry for help" framework, flavonoids are not simply passive metabolites but active ecological signals that recruit beneficial partners and reprogram microbial community structure and function [44]. Infection of tea seedling leaves with *Pseudopestalotiopsis camelliae-sinensis* significantly elevated flavonoid and phenolic acid levels in root exudates, altering the rhizosphere microbial community and suppressing grey blight disease in tea plants [17]. A recent study showed that increased flavonoid exudation enhanced chemotaxis, motility, and biofilm formation of *Paraburkholderia xenovorans*, a model bacterial strain for polychlorinated biphenyl degradation, confirming that flavonoids can promote microbial recruitment of beneficial microorganisms in the rhizosphere [45]. Phenolic compounds in root exudates of *Arabidopsis*, exogenously added to soil in the absence of the plant, could enrich taxa typically associated with beneficial functions. Notably, salicylic acid was positively associated with beneficial groups such as Corynebacterineae and Streptomycineae, showing how specific phenolics can recruit distinct, advantageous microbial taxa [46].

4.2.4. Benzoxazinoids

Benzoxazinoids are indole-derived defence compounds produced predominantly by cereal crops, including maize, wheat, and rye [47]. In maize, the principal benzoxazinoids are DIMBOA (2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one) and its breakdown product MBOA (6-methoxy-benzoxazolin-2-one) [48]. Neal et al. demonstrated that DIMBOA, exuded by maize roots, recruits the beneficial rhizobacterium *Pseudomonas putida*, establishing benzoxazinoids as a class of recruitment metabolites [7]. Further evidence that DIMBOA serves as a defence signal in maize immunity comes from a study in which benzoxazinoid-deficient maize was more susceptible to the cereal aphid *Rhopalosiphum padi*. At the same time, plants carrying the mutant alleles also showed significantly greater colonization by the necrotrophic fungus *Setosphaeria turcica* [49]. Hu et al. found that MBOA can shift the composition of root-associated fungal and bacterial communities, selecting for a resistance-inducing soil microbiome [50]. Another benzoxazinoid, HDMBOA (2-hydroxy-4,7-dimethoxybenzoxazin-3-one), has also been shown to inhibit the virulence and host recognition of the soil pathogen *Agrobacterium tumefaciens* [51]. While evaluating the effect of genetic mutations at different steps of the benzoxazinoid pathway using correlation analysis linking bacterial communities with benzoxazinoid-regulated root metabolites, Cotton et al. observed that benzoxazinoid-derived compounds promote the proliferation of methylotrophic bacteria while limiting a range of other soil microbes, thereby positively shaping the maize rhizobiome [52].

Pre-inoculation with arbuscular mycorrhizal fungi has been reported to enhance plant resistance through defence priming. In this case, the beneficial fungus establishes a symbiotic association that can facilitate stronger or faster defence responses following a

subsequent pathogen challenge. Susceptible maize pre-inoculated with *Glomus mosseae* displayed significantly reduced sheath blight severity, coinciding with a marked increase in DIMBOA in roots and leaves. This arbuscular mycorrhizal fungus-induced accumulation of DIMBOA likely contributes directly to disease suppression through its antifungal activity against *R. solani*, alongside the priming of systemic defence responses [53]. In maize knock-out mutants with impaired benzoxazinoid genes, Kudjordjie et al. found significantly reduced fungal diversity in roots, suggesting a possible gatekeeper role for benzoxazinoids in preventing mycological pathogens from entering the root compartment during early-stage maize development [54].

Table 1. Representative root-exuded metabolites involved in rhizosphere microbiome modulation and plant defence.

Molecules Released	Plant Species	Pathogen/Stress Condition	Effect on the Rhizosphere Microbiome	References
Organic acids				
Malic acid	*Arabidopsis thaliana*	*Pseudomonas syringae* pv *tomato*	Chemoattractant for beneficial *Bacillus* bacteria	[5]
Propionic acid, azelaic acid, palmitic acid, phthalic acid	*Panax notoginseng*	*Alternaria panax*	Positive modification of the soil microbial community, including enrichment of beneficial microorganisms	[35]
Octadecanoic acid, palmitoleic acid, pentadecanoic acid	*Arabidopsis thaliana*	*Pseudomonas syringae*	Recruitment of beneficial rhizosphere communities	[10]
Long-chain fatty acids	*Arabidopsis thaliana*	*Pseudomonas syringae*	Enrichment of several beneficial *Pseudomonas* strains	[36]
Amino acids				
Leucine, isoleucine, ornithine, proline, methionine, tryptophan	*Arabidopsis thaliana*	*Pseudomonas syringae*	Confer a higher degree of induced resistance in infected plants	[10]
L-aspartic acid, L-serine, alanine	*Panax notoginseng*	*Alternaria panax*	Suppression of soil-borne pathogens and enrichment of beneficial microbes	[35]
Tryptophan	*Cucumis sativus*	*Fusarium oxysporum*	Promotes colonization by plant growth-promoting rhizobacteria	[37]
Phenolic compounds				
Caffeic acid	*Solanum lycopersicum*	*Ralstonia solanacearum*	Direct inhibition of pathogen growth and improved soil microbiome	[38]
Coumarins	*Arabidopsis thaliana*	*Hyaloperonospora arabidopsidis*	Inhibition of pathogenic microbes and enabling the establishment of a protective soil microbiome	[27,40–42]
Flavonoids	*Camellia sinensis*	*Pseudopestalotiopsis camelliae-sinensis*	Promotes microbial recruitment of beneficial microorganisms, resulting in positive alterations in the microbial community in the rhizosphere	[17,44,45]
Salicylic acid	*Arabidopsis thaliana*	No specific pathogen challenge	Enrichment of taxa typically associated with beneficial functions	[46]
Benzoxazinoids				
DIMBOA	*Zea mays*	*Setosphaeria turcica, Rhopalosiphum padi, Rhizoctonia solani*	Recruitment of beneficial *Pseudomonas* lowers susceptibility to fungal pathogens and primes systemic defence responses	[7,49,52,53]
MBOA	*Zea mays*	No pathogen challenge; soil conditioning	Selection for a resistance-inducing soil microbiome	[50]
HDMBOA	*Zea mays*	*Agrobacterium tumefaciens*	Inhibition of the virulence and host recognition of the soil pathogens	[51]

5. Pathogen Counter-Strategies: The 'Sabotage' Phase

The "cry for help" framework, as initially articulated, casts pathogens as passive agents that plants orchestrate microbial defence against. However, a growing body of evidence reveals that successful pathogens have evolved sophisticated counter-strategies to neutralize or subvert microbiome-mediated defence. These strategies, as shown in Figure 2, can be broadly categorised as direct killing or suppression of recruited beneficial microbes, interference with recruitment-associated processes, and exploitation of microbial metabolites. This Pathogen-Mediated Interference (PMI) ensures that the pathogen can colonize the host without interference from the plant's recruited microbial allies. Although fungal and bacterial pathogens can both interfere with microbiome-mediated plant defence, the mechanisms described in the literature differ in some respects. Fungal pathogens have been shown to secrete antimicrobial effector proteins that directly target beneficial bacteria or competing fungi, thereby disrupting protective microbial interactions [55–57]. In contrast, bacterial pathogens can exploit microbial metabolites such as siderophores [58] and alter microbial chemotaxis and motility [59]. These examples suggest that pathogen-mediated microbiome disruption involves diverse, potentially overlapping strategies rather than a single mechanism shared homogeneously across pathogen groups.

5.1. Pathogen Effectors That Target Beneficial Bacteria

Plant pathogens can accelerate disease development by secreting effector proteins that not only target the host but also directly manipulate host-associated microbiomes that otherwise suppress disease [60,61]. Pathogens appear to have evolved under pressure to target the specific bacterial clades most commonly recruited by the plant's "cry for help", necessitating a co-evolutionary dynamic in which recruitment and counter-recruitment engage in a continuous antagonistic cycle [62].

A striking example of pathogen sabotage comes from work on *V. dahliae*, a fungal vascular wilt pathogen. Snelders et al. discovered that *V. dahliae* secretes the effector proteins VdAve1 and VdAMP2, which possess potent antimicrobial activity. Using a combination of in planta and in vitro experiments, VdAve1 was shown to selectively kill bacteria in the Sphingomonadales taxa, including *Sphingomonas* and *Novosphingobium* species previously identified as components of the plant's recruited protective microbiome. Critically, *V. dahliae* strains carrying VdAve1 showed enhanced virulence in non-sterile soils compared with sterile conditions. In contrast, strains lacking the effector did not show this difference, providing direct evidence that VdAve1's antimicrobial function contributes to pathogen fitness by undermining microbiome-mediated defence [55]. In follow-up studies on *V. dahliae*, the effector VdAMP3, derived from an ancient antimicrobial protein, was deployed to suppress competing fungi during host colonization [56], while the effector VdAve1 and its divergent homolog VdAve1L exhibited antimicrobial activity that suppressed antagonistic microbes, with VdAve1L evolving high sequence variability to evade host recognition while retaining microbiome-modulating functions. Notably, a functional VdAve1L variant selectively targeted beneficial Actinobacteria to promote host colonization, highlighting microbiome manipulation as a key virulence strategy [63]. *V. dahliae* has also been shown to counteract the recruitment of beneficial microbes by secreting the effector Av2, which exhibits antimicrobial activity and contributes to virulence. Av2 specifically suppresses the recruitment of antagonistic *Pseudomonas* species into the rhizosphere, thereby suppressing the "cry for help" and promoting successful host colonization [12].

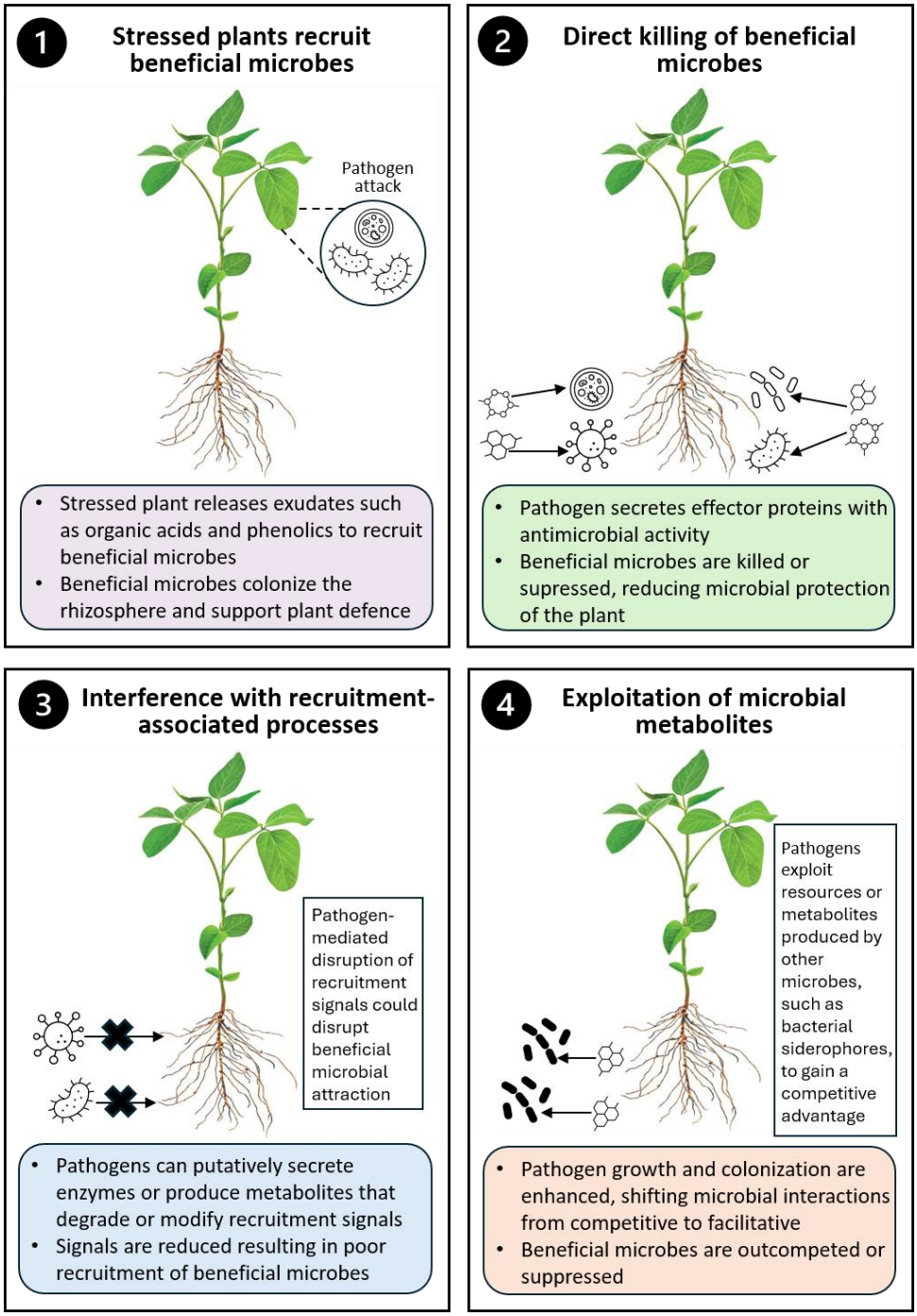

Figure 2. Pathogen-mediated sabotage of plant-protective microbial alliances. After stressed plants recruit beneficial microbes (**1**), these strategies include direct killing of beneficial microbes (**2**), interference with recruitment-associated processes (**3**), and exploitation of microbial metabolites (**4**).

The white root rot pathogen *Rosellinia necatrix* produces antimicrobial effector proteins that may contribute to infection by disrupting plant-associated bacterial communities. Two effectors, FUN_004580 and FUN_011519, were expressed during plant colonization and showed antimicrobial activity against several bacterial taxa, including the antagonistic species *Bacillus licheniformis*, *B. drentensis*, *Cellulosimicrobium cellulans*, and *Sphingobium mellinum* in vitro. These findings suggest that *R. necatrix* may promote disease, at least in part, by suppressing bacteria with potential protective functions [57].

5.2. Interference with Recruitment-Associated Processes

Some pathogens may interfere with plant–microbiome interactions by altering chemical or physiological processes associated with the recruitment of beneficial microorganisms. However, conclusive experimental evidence that pathogens degrade specific plant recruitment signals and thereby disrupt the "cry for help" response remains limited. For example, *Fusarium oxysporum* has pathways for metabolizing plant-derived phenolic compounds, including aromatic acids [64]. Although this indicates that the pathogen can metabolize certain plant phenolics, the cited evidence does not prove that these compounds function as recruitment signals in the relevant interaction or that their degradation directly prevents beneficial microbial recruitment.

Other examples show indirect interference with processes that support microbiome-mediated defence. In citrus affected by Huanglongbing, caused by *Candidatus* Liberibacter asiaticus, the enrichment of microbial taxa from the rhizosphere to the rhizoplane shifts, altering the root-associated microbiome [59]. This demonstrates pathogen-associated disruption of microbiome assembly, although the underlying mechanism has not been shown to involve direct degradation of plant recruitment signals. Similarly, oxalic acid produced by *Sclerotinia sclerotiorum* suppresses the host oxidative burst, facilitating pathogen compatibility [65]. While this represents suppression of plant defence signalling, its direct effects on root-exudate-mediated microbial recruitment remain unclear. Changes in rhizosphere pH can also influence microbial behaviour, including chemotaxis toward root exudates, which organic acids such as oxalic acid can modulate [66].

Taken together, these studies suggest that pathogens can affect plant–microbiome interactions through several potentially indirect routes, including metabolism of plant-derived compounds, altered microbiome assembly, and suppression of host defence responses. Nevertheless, these mechanisms should be distinguished from demonstrated degradation of recruitment signals. More experimental work is needed to identify the relevant plant-derived signals, determine whether pathogens directly modify or degrade them, and establish the consequences for beneficial microbial recruitment and disease outcomes.

5.3. Exploitation of Microbial Metabolites

Pathogens may also benefit from metabolites produced by other members of the rhizosphere microbiome, potentially shifting microbial interactions from pathogen suppression towards pathogen facilitation. *Ralstonia solanacearum*, for example, has been shown to engage in siderophore-mediated interactions with rhizosphere bacteria that influence pathogen growth and disease development. Siderophores are iron-chelating compounds bacteria produce to acquire iron when it is limited. Gu et al. showed that siderophores produced by rhizosphere bacteria can inhibit or promote *R. solanacearum* growth, depending on the siderophore's compatibility with the pathogen's iron-uptake systems [58]. In particular, siderophore-producing bacteria whose metabolites facilitate pathogen growth can unintentionally support pathogen establishment and infection, whereas bacteria producing inhibitory siderophores contribute to pathogen suppression and plant protection. Although this mechanism does not directly demonstrate interference with plant recruitment signalling, it illustrates how microbial metabolites within the rhizosphere can be exploited in ways that undermine microbiome-mediated disease suppression. Such interactions may therefore represent an indirect way pathogens benefit from, rather than simply overcome, the microbial communities associated with plant roots.

5.4. Evolutionary Implications and Prospects for Durable Resistance

The interactions between plants, pathogens, and beneficial rhizosphere microorganisms should also be considered within an evolutionary framework. Pathogen effector repertoires are subject to constant selection imposed by host immune recognition and the need to overcome host defence mechanisms. Consequently, effector genes often show considerable sequence and functional diversity, arising through mechanisms such as mutation, recombination, gene gain and loss, and changes in gene expression [67,68]. Such variation can influence pathogen adaptation to different host genotypes and potentially contribute to differences in host compatibility and virulence. Antimicrobial effectors suggest that pathogen adaptation may go beyond suppressing plant immunity to include manipulating beneficial host-associated microorganisms. However, whether variation in these microbiome-targeting effectors contributes directly to differences in pathogen host range remains largely unexplored.

The evolutionary basis of recruitment signal deterioration is similarly poorly understood. Although some pathogens, including *Fusarium* species, possess enzymatic activities that degrade plant-derived phenolic compounds, it remains unclear whether the ability to interfere with recruitment-associated metabolites is conserved within particular pathogen lineages or has evolved independently in different groups. The diversity of plant-derived recruitment signals and the different chemical strategies used by pathogens suggest that these interactions may depend heavily on the specific host–pathogen combination. Comparative genomic and functional studies are therefore required to determine the evolutionary distribution, substrate specificity, and ecological relevance of these mechanisms.

Such evolutionary considerations have important consequences for developing durable crop resistance. Resistance strategies that depend on a single recognition mechanism, recruitment signal, or beneficial microbial taxon may be vulnerable to pathogen adaptation. In contrast, breeding for plant genotypes that support diverse, functionally complementary protective microbial communities may provide a more robust approach [69]. Ultimately, understanding pathogens' evolutionary responses to plant recruitment strategies will be essential for designing durable resistance systems that remain effective under changing pathogen populations and environmental conditions.

6. Ecological Legacy and Soil Memory

6.1. Disease-Suppressive Soils

Disease-suppressive soils, in which a susceptible crop suffers less disease than expected despite the presence of a virulent pathogen, represent one of the most compelling natural examples of microbiome-mediated plant protection [70,71]. A typical example is the take-all decline (TAD) phenomenon, in which major outbreaks of *Gaeumannomyces tritici* in continuous wheat monoculture are followed by a progressive reduction in disease severity over several years, associated with the enrichment of 2,4-diacetylphloroglucinol (DAPG)-producing *Pseudomonas* spp. in the rhizosphere [72–74]. The impact of a "cry for help" event, therefore, goes beyond the life cycle of the individual plant.

Bakker et al. proposed that each infection episode constitutes a recruitment event that enriches protective microbial taxa and that over successive generations, the cumulative effect of these recruitment events progressively shifts the soil microbiome from pathogen-supportive to disease-limiting [75]. Experimental work directly supported this model, showing that continuously inoculating susceptible plants with soil-borne pathogens over several generations in the same soil transformed disease-conducive soil into disease-suppressive soil and that this change was associated with enrichment of specific beneficial microbial taxa [16,36]. When a plant successfully recruits a protective consortium, these microbes often persist in the soil in a dormant or semi-active state, and subsequent

plantings in the same conditioned soil display significantly higher resistance to the same pathogen, even without an initial foliar trigger [11,14].

6.2. Rhizosphere Memory

A critical advance in rhizosphere microbiology is the recognition that plant-mediated microbial recruitment can go beyond the immediate stress response to generate persistent soil-borne legacies, commonly referred to as "soil memory" [10]. However, it is important to distinguish transient recruitment from long-lasting ecological memory. Transient recruitment refers to short-term changes in microbial abundance or community composition in response to altered root exudation or pathogen stress, which may diminish once the inducing stress is removed. In contrast, soil memory describes persistent changes in the soil microbial community or its chemical properties that influence the growth or disease resistance of subsequent plant generations, even without the original stress stimulus. Such persistence represents an ecological legacy extending beyond the lifetime of the initially affected plant.

Several mechanisms underpin the transition from transient recruitment to durable soil memory. First, recruited beneficial microbes can alter the soil environment through biofilm formation, extracellular polysaccharide production, and modification of soil organic matter in ways that favour their persistence [76]. Infection of *A. thaliana* by *H. arabidopsidis* was shown to trigger the recruitment of a specific consortium of beneficial rhizosphere bacteria that acted synergistically in biofilm formation to enhance plant growth and systemic disease resistance. Critically, these microbiome shifts persisted as a soil-mediated legacy, whereby soil conditioned by infected plants conferred enhanced protection against downy mildew to a subsequent generation grown in the same soil [14]. Although this provides experimental evidence linking microbial recruitment, biofilm-associated interactions, and persistent disease suppression, the relative contribution of biofilm formation itself to the long-term persistence of the protective community remains to be fully established. Liu et al. also demonstrated that "cry for help" responses assemble beneficial microbiomes that generate a persistent, disease-suppressive soil legacy, explicitly linking recruitment to long-term soil effects [19].

Secondly, soil conditioning by compounds such as benzoxazinoids, as shown by Hu et al., can persist across multiple cropping cycles because MBOA and its degradation products are stable in soil organic fractions [50]. This suggests that soil memory may involve not only the persistence of beneficial microorganisms but also the retention of plant-derived chemical compounds that continue to influence subsequent microbial recruitment. Yuan et al. further demonstrated that aboveground infection of Arabidopsis altered root exudation of amino acids and long-chain organic acids, generating soil-borne effects detectable in subsequent plant generations [10]. However, the relative contributions of persistent metabolites and changes in microbial community composition to these legacy effects should be distinguished, as chemical persistence does not necessarily demonstrate the long-term maintenance of a particular protective microbial consortium.

Thirdly, soil memory may be supplemented by the inheritance of seed-associated microbial communities. Kong et al. introduced the concept of "microbiota-induced soil inheritance", highlighting the potential for beneficial microorganisms associated with parental plants to contribute to the microbiome of subsequent generations [77]. Seed-associated microorganisms can be transmitted from parent plants to their offspring via vertical transmission, providing an initial microbial reservoir for seedling development. However, seed microbiome assembly is not exclusively determined by inheritance, as environmental acquisition and horizontal transmission also contribute to the microbial communities established during germination and early plant development [78]. Consequently, seed transmission may provide an additional pathway for maintaining

beneficial plant–microbe associations across successive generations, complementing the recruitment of microorganisms from conditioned soil. Nevertheless, the extent to which vertically transmitted seed microorganisms contribute directly to inherited disease resistance remains dependent on the plant species and microbial associations involved.

Wilkinson et al. introduced the concept of transgenerational stress memory in plants, noting that epigenetic modifications, such as DNA methylation and histone modifications, induced by pathogen stress can alter root exudate profiles in progeny that have never themselves been infected. This raises the possibility that plant-mediated transgenerational stress memory may complement soil-borne ecological legacies through heritable changes in root exudation behaviour, creating a positive feedback loop in which stressed parent plants produce offspring predisposed to maintain a protective microbiome, even without ongoing pathogen pressure [79].

7. Future Directions: Engineering the Holobiont

7.1. Next-Generation Synthetic Communities

Early biocontrol approaches relied on single-strain inoculants, which often failed under field conditions because of poor rhizosphere competence and ecological instability [80]. Synthetic communities (SynComs) enable plant microbiome research to move from correlation to causality by using simplified, gnotobiotic systems to study, manipulate, and quantify specific plant–microbe interactions. These reduced-complexity models let researchers test hypotheses about community assembly, the functional roles of individual microbes, and environmental impacts on plant health, providing a bottom-up approach to understanding complex ecosystem dynamics [81,82]. SynComs are rationally designed, multi-strain consortia assembled based on functional complementarity and ecological compatibility to establish stable microbial networks that enhance plant growth and improve disease resistance [29,83–85]. Unlike traditional single-strain inoculants, SynComs aim to mimic or manipulate native plant microbiomes more precisely and have demonstrated effectiveness in field conditions [86] and greenhouse trials. Effective SynCom construction requires selecting microbial strains with complementary functions to support multiple aspects of plant growth [87]. It also depends on ensuring strain compatibility and choosing microbes adapted to the target environment to maintain resilience and consistent performance [83,88].

Regarding the role of SynComs in strengthening plant defences against pathogenic microbes, these communities can be intentionally engineered to inhibit plant pathogens, improving crop yields while reducing reliance on chemical pesticides [89]. Beneficial microbes in SynComs can contribute to plant disease resistance through various mechanisms, including producing antimicrobial compounds and inducing systemic resistance in plants [83]. A synthetic seven-species community, including species such as *Pseudomonas putida, Chryseobacterium indologenes, Enterobacter cloacae*, and *Stenotrophomonas maltophilia,* was shown to inhibit the pathogenic fungus *Fusarium verticillioides* in maize seedlings [90]. SynComs were shown to activate ISR and rescue *Astragalus mongholicus* from root rot caused by *F. oxysporum* [91], while SynComs containing *Bacillus* and *Trichoderma* species acted cooperatively to trigger defence mechanisms in oilseed rape against *Verticillium longisporum* [92]. The robust suppression of *Fusarium* wilt in tomato by a cross-kingdom SynCom comprising both bacteria and fungi further supports the idea that complementary microbial interactions enhance disease suppression through combined effects on plant immunity [93].

A key consideration in designing next-generation SynComs is their ability to withstand pathogen-mediated interference. As discussed earlier, certain pathogens can selectively suppress beneficial microbial populations through antimicrobial effectors or exploit existing microbial interactions to facilitate their own establishment. Consequently,

developing effective SynComs should go beyond selecting microorganisms with complementary protective functions to include their ecological compatibility, functional redundancy, and resilience to pathogen interference. Incorporating microbial strains with complementary antagonistic mechanisms may provide a more robust approach to maintaining disease-suppressive activity under pathogen pressure.

While SynComs offer significant advantages for plant health and disease resistance, as discussed above, they often fail under field conditions because interactions with native microbes destabilise them, growth dynamics are uneven, and they adapt poorly to complex, fluctuating physicochemical environments and regulatory challenges [88,94,95]. Additionally, unpredictable metabolic interactions, environmental stress responses, and genetic changes such as mutation or plasmid loss can further compromise their functionality and persistence [84]. Future work on SynComs should focus on improving their ecological robustness and functional stability by integrating adaptive strain selection, predictive modelling of microbial interactions, and validation under realistic field conditions.

7.2. Computational Modelling for Microbiome Predictions

Rational microbiome design using SynComs is constrained by the "small-n, large-p" problem, in which limited sample sizes relative to vast microbial diversity hinder the reliable identification of causal taxa and interactions. In addition, strong context dependency and nonlinear, emergent interactions among microbes make it difficult to predict how selected community members will behave across different hosts and environments [96]. Recent advances in computational modelling that simulate the dynamics of biological systems in real time are now being used to explore soil and rhizosphere microbiomes, enabling the rational design of microbial communities and the optimisation of SynCom performance [84,96].

In principle, computational modelling of the rhizosphere could integrate multi-omics data (metagenomics, metatranscriptomics, and metabolomics) with environmental variables (soil type, moisture, and pH) to predict how a given microbiome will respond to pathogen challenge or amendment with specific inoculants [96]. Metagenomic techniques, including 16S rRNA gene and ITS amplicon sequencing and shotgun metagenomics, can be used to characterize microbial community composition and diversity, identify changes associated with plant stress, and investigate the functional potential of rhizosphere communities. While amplicon sequencing provides information on microbial community structure, shotgun metagenomics offers broader insights into the functional genes and metabolic capabilities represented within these communities. Metabolomic approaches, particularly the analysis of root exudates, provide complementary information by identifying chemical signals and metabolites that influence microbial recruitment, community assembly, and pathogen suppression. Integrating metagenomic and metabolomic datasets can therefore help establish relationships between changes in microbial composition and the rhizosphere's chemical environment.

Artificial intelligence, particularly machine learning approaches, can analyse high-dimensional microbiome datasets to identify key taxa, interactions, and predictive patterns that conventional statistics struggle to resolve. These models can uncover nonlinear relationships and reduce dimensionality, improving our ability to distinguish causal drivers of community structure and function. Artificial intelligence can also support the rational design of synthetic communities by predicting how microbial consortia will behave and perform across different hosts and environmental conditions [97–100].

These approaches therefore hold immense promise for moving from empirical trial-and-error to predictive design of microbiome interventions, allowing researchers to

determine which microbial combinations are most likely to withstand pathogen sabotage and enabling accurate projections of SynComs inoculation outcomes.

7.3. Programmable Immunity Using CRISPR

CRISPR-Cas9 is a genome-editing technology derived from a bacterial immune system that uses a guide RNA to direct the Cas9 enzyme to a specific DNA sequence. Cas9 then cuts the DNA at that location, allowing researchers to delete, modify, or insert genes with high precision [101]. This technology could enable precise modifications to traits such as stress tolerance, root colonization efficiency, biosynthesis of antimicrobial compounds, and increased concentrations of recruitment metabolites, potentially improving the plant's ability to recruit beneficial microbial communities and enhancing microbiome-mediated disease resistance [87,102].

Candidate targets include genes encoding metabolite biosynthetic enzymes, transporters, and transcriptional regulators, identified through integrated genetic, transcriptomic, metabolomic, and microbiome analyses. For example, the CRISPR-Cas9-mediated disruption of the tomato gene *SlGAD2*, which contributes to γ-aminobutyric acid (GABA) production, reduced plant GABA levels, altered root and soil microbiome composition, and enhanced tolerance to *Ralstonia solanacearum* [103]. This study illustrates how editing plant metabolic pathways can influence disease outcomes alongside changes in the associated microbiome. Genome editing may also help investigate the molecular basis of root-exudate-mediated microbial recruitment. In melon, cucurbitacin B transport from roots into the soil has been shown to shape the rhizosphere microbiome by enriching *Enterobacter* and *Bacillus*, which contribute to resistance against *Fusarium oxysporum* [104]. Editing genes involved in the biosynthesis or transport of such metabolites could test their contribution to microbial recruitment and disease suppression. Similarly, candidate genes involved in plant recognition of beneficial microorganisms or in the regulation of immune and metabolic signalling could be edited to determine how these pathways influence microbiome assembly. Beyond plant targets, CRISPR-based approaches could also modify pathogen genes involved in virulence or microbiome interference, or beneficial microbial genes associated with colonization and pathogen antagonism. Figure 3 illustrates a conceptual framework for how CRISPR-Cas technology can engineer plant recruitment processes and enhance microbiome-mediated disease resistance.

Although CRISPR-Cas systems have shown strong potential for engineering microbial traits, their application in shaping root microbiomes and exudate-mediated recruitment remains in the early, proof-of-concept stage. Nevertheless, these tools offer significant promise for future precision microbiome design by enabling targeted manipulation of genes [105,106]. Critically, ecological understanding must guide these approaches, as over- or underproduction of compounds could lead to ecological instability, pathogen adaptation, or unintended effects on non-target soil organisms [102].

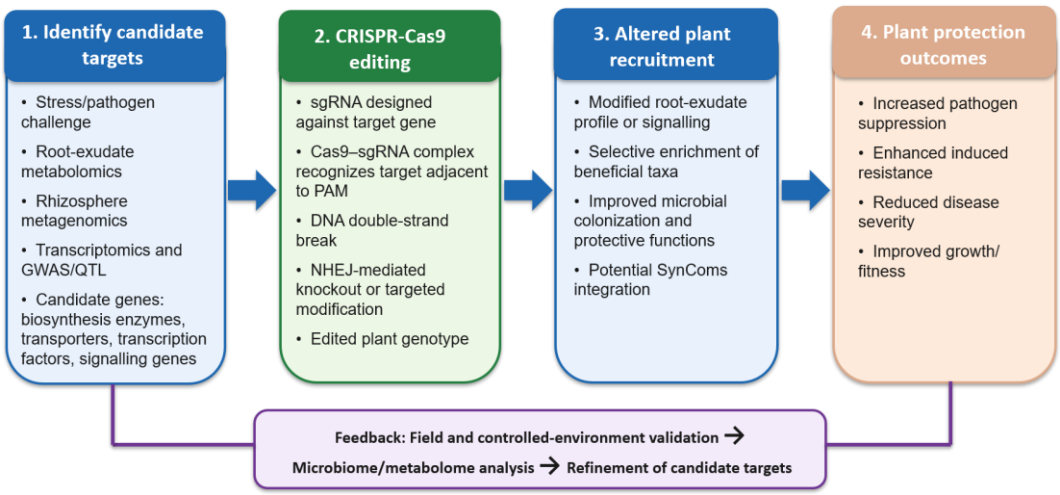

Figure 3. Conceptual framework for CRISPR-Cas-mediated engineering of plant recruitment and microbiome-mediated disease resistance.

8. Conclusions

The past fifteen years have redefined our understanding of plant–pathogen interactions, elevating the microbiome from a passive bystander to a central defensive player. Microbiome-mediated resistance, assembled through the "cry for help", maintained through soil-borne legacy effects, and contested by pathogen counter-strategies, constitutes a quantitative, tuneable, community-level defence that operates alongside, and interacts with, classical innate and acquired immunity [76].

Recognising this complexity requires a holobiont perspective in which resistance is an emergent property of the plant–microbiome system rather than a fixed attribute of the host genotype. Breeding programmes that evaluate disease resistance solely in sterile or pathogen-free conditions risk overlooking the contribution of the soil microbiome. In contrast, agronomic practices that deplete soil microbial diversity (tillage, fumigation, excessive fertilization) may inadvertently disrupt the plant's community-level defences [107].

The United Nations Sustainable Development Goal 2 calls for doubling agricultural productivity and incomes for small-scale food producers by 2030, while ensuring sustainable production systems (https://www.un.org/sustainabledevelopment/hunger/; accessed 4 June 2026). Achieving this goal amid climate change, soil degradation, and emerging pathogen threats will require a diversified approach to crop protection. The rhizosphere diplomacy framework, in which plants, beneficial microbes, and pathogens are engaged in a dynamic, multi-party negotiation, offers actionable opportunities in this regard.

Practically, this translates into three near-term priorities: (i) the development and deployment of rationally designed, cross-kingdom SynCom inoculants informed by "cry for help" research; (ii) the integration of microbiome criteria into crop breeding programmes; and (iii) the adoption of soil management practices (cover cropping, reduced tillage, organic amendments) that preserve and enhance the soil's legacy of disease suppressiveness. Hypothetically, the convergence of computational modelling to assist with microbiome design, CRISPR-based crop engineering, and multi-trophic synthetic ecology promises a new generation of crop protection strategies that work with, rather than against, the ecological complexity of the rhizosphere [108,109]. As pathogen virulence evolves, we must reduce our reliance on chemical pesticides. The future of sustainable agriculture lies in harnessing plants' natural ability to recruit allies while engineering those allies to resist pathogen interference. By integrating molecular biology, microbial ecology, and computational modelling, we can finally treat the plant and its microbiome as a single, formidable unit of defence.

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References

1. Vandenkoornhuyse, P.; Quaiser, A.; Duhamel, M.; Le Van, A.; Dufresne, A. The importance of the microbiome of the plant holobiont. *New Phytol.* **2015**, *206*, 1196–1206. https://doi.org/10.1111/nph.13312.
2. Mendes, R.; Kruijt, M.; de Bruijn, I.; Dekkers, E.; van der Voort, M.; Schneider, J.H.M.; Piceno, Y.M.; DeSantis, T.Z.; Andersen, G.L.; Bakker, P.A.H.M.; et al. Deciphering the rhizosphere microbiome for disease-suppressive bacteria. *Science* **2011**, *332*, 1097–1100. https://doi.org/10.1126/science.1203980.
3. Carrión, V.J.; Perez-Jaramillo, J.; Cordovez, V.; Tracanna, V.; de Hollander, M.; Ruiz-Buck, D.; Mendes, L.W.; van Ijcken, W.F.J.; Gomez-Exposito, R.; Elsayed, S.S.; et al. Pathogen-induced activation of disease-suppressive functions in the endophytic root microbiome. *Science* **2019**, *366*, 606–612. https://doi.org/10.1126/science.aaw9285.
4. Iqbal, S.; Ullah, N.; Janjua, H.A. In vitro evaluation and genome mining of *Bacillus subtilis* strain RS10 reveals its biocontrol and plant growth-promoting potential. *Agriculture* **2021**, *11*, 1273. https://doi.org/10.3390/agriculture11121273.
5. Rudrappa, T.; Czymmek, K.J.; Paré, P.W.; Bais, H.P. Root-secreted malic acid recruits beneficial soil bacteria. *Plant Physiol.* **2008**, *148*, 1547–1556. https://doi.org/10.1104/pp.108.127613.
6. Berendsen, R.L.; Pieterse, C.M.J.; Bakker, P.A.H.M. The rhizosphere microbiome and plant health. *Trends Plant Sci.* **2012**, *17*, 478–486. https://doi.org/10.1016/j.tplants.2012.04.001.
7. Neal, A.L.; Ahmad, S.; Gordon-Weeks, R.; Ton, J. Benzoxazinoids in root exudates of maize attract *Pseudomonas putida* to the rhizosphere. *PLoS ONE* **2012**, *7*, e35498. https://doi.org/10.1371/journal.pone.0035498.
8. Kumar, G.A.; Kumar, S.; Bhardwaj, R.; Swapnil, P.; Meena, M.; Seth, C.S.; Yadav, A. Recent advancements in multifaceted roles of flavonoids in plant–rhizomicrobiome interactions. *Front. Plant Sci.* **2024**, *14*, 1297706. https://doi.org/10.3389/fpls.2023.1297706.
9. Santoyo, G. How plants recruit their microbiome? New insights into beneficial interactions. *J. Adv. Res.* **2022**, *40*, 45–58. https://doi.org/10.1016/j.jare.2021.11.020.
10. Yuan, J.; Zhao, J.; Wen, T.; Zhao, M.; Li, R.; Goossens, P.; Huang, Q.; Bai, Y.; Vivanco, J.M.; Kowalchuk, G.A.; et al. Root exudates drive the soil-borne legacy of aboveground pathogen infection. *Microbiome* **2018**, *6*, 156. https://doi.org/10.1186/s40168-018-0537-x.
11. Rolfe, S.A.; 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.
12. Kraege, A.; Punt, W.; Doddi, A.; Zhu, J.; Schmitz, N.; Snelders, N.C.; Thomma, B.P.H.J. Undermining the cry for help: The phytopathogenic fungus *Verticillium dahliae* secretes an antimicrobial effector protein to undermine host recruitment of antagonistic *Pseudomonas* bacteria. *New Phytol.* **2025**, *249*, 406–417. https://doi.org/10.1111/nph.70686.
13. Rizaludin, M.S.; Stopnisek, N.; Raaijmakers, J.M.; Garbeva, P. The chemistry of stress: Understanding the 'cry for help' of plant roots. *Metabolites* **2021**, *11*, 357. https://doi.org/10.3390/metabo11060357.
14. Berendsen, R.L.; Vismans, G.; Yu, K.; Song, Y.; de Jonge, R.; Burgman, W.P.; Burmølle, M.; Herschend, J.; Bakker, P.A.H.M.; Pieterse, C.M.J. Disease-induced assemblage of a plant-beneficial bacterial consortium. *ISME J.* **2018**, *12*, 1496–1507. https://doi.org/10.1038/s41396-018-0093-1.
15. Liu, H.; Li, J.; Carvalhais, L.C.; Percy, C.D.; Prakash Verma, J.; Schenk, P.M.; Singh, B.K. Evidence for the plant recruitment of beneficial microbes to suppress soil-borne pathogens. *New Phytol.* **2021**, *229*, 2873–2885. https://doi.org/10.1111/nph.17057.
16. Yin, C.; Casa Vargas, J.M.; Schlatter, D.C.; Hagerty, C.H.; Hulbert, S.H.; Paulitz, T.C. Rhizosphere community selection reveals bacteria associated with reduced root disease. *Microbiome* **2021**, *9*, 86. https://doi.org/10.1186/s40168-020-00997-5.

17. Wang, Q.; Yang, R.; Peng, W.; Yang, Y.; Ma, X.; Zhang, W.; Ji, A.; Liu, L.; Liu, P.; Yan, L.; et al. Tea plants with gray blight have altered root exudates that recruit a beneficial rhizosphere microbiome to prime immunity against aboveground pathogen infection. *Front. Microbiol.* **2021**, *12*, 774438. https://doi.org/10.3389/fmicb.2021.774438.
18. Liu, S.; Tao, C.; Zhang, L.; Wang, Z.; Xiong, W.; Xiang, D.; Sheng, O.; Wang, J.; Li, R.; Shen, Z.; et al. Plant pathogen resistance is mediated by recruitment of specific rhizosphere fungi. *ISME J.* **2023**, *17*, 931–942. https://doi.org/10.1038/s41396-023-01406-z.
19. 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*, 1907. https://doi.org/10.1038/s41467-024-46254-3.
20. Vlot, A.C.; Dempsey, D.M.A.; Klessig, D.F. Salicylic Acid, a multifaceted hormone to combat disease. *Annu. Rev. Phytopathol.* **2009**, *47*, 177–206. https://doi.org/10.1146/annurev.phyto.050908.135202.
21. Lebeis, S.L.; Paredes, S.H.; Lundberg, D.S.; Breakfield, N.; Gehring, J.; McDonald, M.; Malfatti, S.; Glavina del Rio, T.; Jones, C.D.; Tringe, S.G.; et al. Salicylic acid modulates colonization of the root microbiome by specific bacterial taxa. *Science* **2015**, *349*, 860–864. https://doi.org/10.1126/science.aaa8764.
22. Wasternack, C.; Hause, B. Jasmonates: Biosynthesis, perception, signal transduction and action in plant stress response, growth and development. An update to the 2007 review in Annals of Botany. *Ann. Bot.* **2013**, *111*, 1021–1058. https://doi.org/10.1093/aob/mct067.
23. Carvalhais, L.C.; Dennis, P.G.; Badri, D.V.; Kidd, B.N.; Vivanco, J.M.; Schenk, P.M. Linking jasmonic acid signaling, root exudates, and rhizosphere microbiomes. *Mol. Plant-Microbe Interact.* **2015**, *28*, 1049–1058. https://doi.org/10.1094/MPMI-01-15-0016-R.
24. Pieterse, C.M.J.; Van der Does, D.; Zamioudis, C.; Leon-Reyes, A.; Van Wees, S.C.M. Hormonal modulation of plant immunity. *Annu. Rev. Cell Dev. Biol.* **2012**, *28*, 489–521. https://doi.org/10.1146/annurev-cellbio-092910-154055.
25. Pieterse, C.M.J.; Zamioudis, C.; Berendsen, R.L.; Weller, D.M.; Van Wees, S.C.M.; Bakker, P.A.H.M. Induced systemic resistance by beneficial microbes. *Annu. Rev. Phytopathol.* **2014**, *52*, 347–375. https://doi.org/10.1146/annurev-phyto-082712-102340.
26. Van der Ent, S.; Verhagen, B.W.M.; Van Doorn, R.; Bakker, D.; Verlaan, M.G.; Pel, M.J.C.; Joosten, R.G.; Proveniers, M.C.G.; Van Loon, L.C.; Ton, J.; et al. MYB72 is required in early signaling steps of rhizobacteria-induced systemic resistance in *Arabidopsis*. *Plant Physiol.* **2008**, *146*, 1293–1304. https://doi.org/10.1104/pp.107.113829.
27. Stringlis, I.A.; Yu, K.; Feussner, K.; de Jonge, R.; Van Bentum, S.; Van Verk, M.C.; Berendsen, R.L.; Bakker, P.A.H.M.; Feussner, I.; Pieterse, C.M.J. MYB72-dependent coumarin exudation shapes root microbiome assembly to promote plant health. *Proc. Natl. Acad. Sci. USA* **2018**, *115*, E5213–E5222. https://doi.org/10.1073/pnas.1722335115.
28. Oldroyd, G.E.D. Speak, friend, and enter: Signalling systems that promote beneficial symbiotic associations in plants. *Nat. Rev. Microbiol.* **2013**, *11*, 252–263. https://doi.org/10.1038/nrmicro2990.
29. Wankhade, A.; Wilkinson, E.; Britt, D.W.; Kaundal, A. A review of plant–microbe interactions in the rhizosphere and the role of root exudates in microbiome engineering. *Appl. Sci.* **2025**, *15*, 7127. https://doi.org/10.3390/app15137127.
30. Sasse, J.; Martinoia, E.; Northen, T. Feed your friends: Do plant exudates shape the root microbiome? *Trends Plant Sci.* **2018**, *23*, 25–41. https://doi.org/10.1016/j.tplants.2017.09.003.
31. Pang, Z.; Chen, J.; Wang, T.; Gao, C.; Li, Z.; Guo, L.; Xu, J.; Cheng, Y. Linking plant secondary metabolites and plant microbiomes: A review. *Front. Plant Sci.* **2021**, *12*, 621276. https://doi.org/10.3389/fpls.2021.621276.
32. Abedini, D.; Jaupitre, S.; Bouwmeester, H.; Dong, L. Metabolic interactions in beneficial microbe recruitment by plants. *Curr. Opin. Biotechnol.* **2021**, *70*, 241–247. https://doi.org/10.1016/j.copbio.2021.06.015.
33. Xu, Z.; Liu, Y.; Zhang, N.; Xun, W.; Feng, H.; Miao, Y.; Shao, J.; Shen, Q.; Zhang, R. Chemical communication in plant-microbe beneficial interactions: A toolbox for precise management of beneficial microbes. *Curr. Opin. Microbiol.* **2023**, *72*, 102269. https://doi.org/10.1016/j.mib.2023.102269.
34. Allard-Massicotte, R.; Tessier, L.; Lécuyer, F.; Lakshmanan, V.; Lucier, J.; Garneau, D.; Caudwell, L.; Vlamakis, H.; Bais, H.P.; Beauregard, P.B. *Bacillus subtilis* early colonization of *Arabidopsis thaliana* roots involves multiple chemotaxis receptors. *mBio* **2016**, *7*, e01664-16. https://doi.org/10.1128/mBio.01664-16.
35. Luo, L.; Zhang, J.; Ye, C.; Li, S.; Duan, S.; Wang, Z.; Huang, H.; Liu, Y.; Deng, W.; Mei, X.; et al. Foliar pathogen infection manipulates soil health through root exudate-modified rhizosphere microbiome. *Microbiol. Spectr.* **2022**, *10*, e0241822. https://doi.org/10.1128/spectrum.02418-22.
36. Wen, T.; Zhao, M.; Yuan, J.; Kowalchuk, G.A.; Shen, Q. Root exudates mediate plant defense against foliar pathogens by recruiting beneficial microbes. *Soil Ecol. Lett.* **2021**, *3*, 42–51. https://doi.org/10.1007/s42832-020-0057-z.

37. Liu, Y.; Chen, L.; Wu, G.; Feng, H.; Zhang, G.; Shen, Q.; Zhang, R. Identification of root-secreted compounds involved in the communication between Cucumber, the beneficial *Bacillus amyloliquefaciens*, and the soil-borne pathogen *Fusarium oxysporum*. *Mol. Plant-Microbe Interact.* **2017**, *30*, 53–62. https://doi.org/10.1094/MPMI-07-16-0131-R.
38. Gu, Y.; Wei, Z.; Wang, X.; Friman, V.P.; Huang, J.; Wang, X.; Mei, X.; Xu, Y.; Shen, Q.; Jousset, A. Pathogen invasion indirectly changes the composition of soil microbiome via shifts in root exudation profile. *Biol. Fertil. Soils* **2016**, *52*, 997–1005. https://doi.org/10.1007/s00374-016-1136-2.
39. Lončar, M.; Jakovljević, M.; Šubarić, D.; Pavlić, M.; Buzjak Služek, V.; Cindrić, I.; Molnar, M. Coumarins in food and methods of their determination. *Foods* **2020**, *9*, 645. https://doi.org/10.3390/foods9050645.
40. Stringlis, I.A.; de Jonge, R.; Pieterse, C.M.J. The age of coumarins in plant–microbe interactions. *Plant Cell Physiol.* **2019**, *60*, 1405–1419. https://doi.org/10.1093/pcp/pcz076.
41. Voges, M.J.E.; Bai, Y.; Schulze-Lefert, P.; Sattely, E.S. Plant-derived coumarins shape the composition of an Arabidopsis synthetic root microbiome. *Proc. Natl. Acad. Sci. USA* **2019**, *116*, 12558–12565. https://doi.org/10.1073/pnas.1820691116.
42. Vismans, G.; van Bentum, S.; Spooren, J.; Song, Y.; Goossens, P.; Valls, J.; Snoek, B.L.; 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*, 22473. https://doi.org/10.1038/s41598-022-26551-x.
43. Yonekura-Sakakibara, K.; Higashi, Y.; Nakabayashi, R. The origin and evolution of plant flavonoid metabolism. *Front. Plant Sci.* **2019**, *10*, 943. https://doi.org/10.3389/fpls.2019.00943.
44. Ghitti, E.; Rolli, E.; Crotti, E.; Borin, S. Flavonoids are intra- and inter-kingdom modulator signals. *Microorganisms* **2022**, *10*, 2479. https://doi.org/10.3390/microorganisms10122479.
45. Ghitti, E.; Rolli, E.; Vergani, L.; Borin, S. Flavonoids influence key rhizocompetence traits for early root colonization and PCB degradation potential of *Paraburkholderia xenovorans* LB400. *Front. Plant Sci.* **2024**, *15*, 1325048. https://doi.org/10.3389/fpls.2024.1325048.
46. Badri, D.V.; Chaparro, J.M.; Zhang, R.; Shen, Q.; Vivanco, J.M. Application of natural blends of phytochemicals derived from the root exudates of Arabidopsis to the soil reveal that phenolic-related compounds predominantly modulate the soil microbiome. *J. Biol. Chem.* **2013**, *288*, 4502–4512. https://doi.org/10.1074/jbc.M112.433300.
47. Li, T.; Liu, X.; Zhang, S.; Lei, J.; Li, R.; Ma, P.; Wu, J.; Xu, Y.; Zhang, H. From defense chemistry to agroecological solutions: The evolving role of benzoxazinoids in plants. *Crop J.* **2025**, *13*, 1333–1349. https://doi.org/10.1016/j.cj.2025.06.023.
48. Zhou, S.; Richter, A.; Jander, G. Beyond defense: Multiple functions of benzoxazinoids in maize metabolism. *Plant Cell Physiol.* **2018**, *59*, 1528–1537. https://doi.org/10.1093/pcp/pcy064.
49. Ahmad, S.; Veyrat, N.; Gordon-Weeks, R.; Zhang, Y.; Martin, J.; Smart, L.; Glauser, G.; Erb, M.; Flors, V.; Frey, M.; et al. Benzoxazinoid metabolites regulate innate immunity against aphids and fungi in maize. *Plant Physiol.* **2011**, *157*, 317–327. https://doi.org/10.1104/pp.111.180224.
50. Hu, L.; Robert, C.A.M.; Cadot, S.; Zhang, X.; Ye, M.; Li, B.; Manzo, D.; Chervet, N.; Steinger, T.; van der Heijden, M.G.A.; et al. Root exudate metabolites drive plant-soil feedbacks on growth and defense by shaping the rhizosphere microbiota. *Nat. Commun.* **2018**, *9*, 2738. https://doi.org/10.1038/s41467-018-05122-7.
51. Maresh, J.; Zhang, J.; Lynn, D.G. The innate immunity of maize and the dynamic chemical strategies regulating two-component signal transduction in *Agrobacterium tumefaciens*. *ACS Chem. Biol.* **2006**, *1*, 165–175. https://doi.org/10.1021/cb600051w.
52. Cotton, T.E.A.; Pétriacq, P.; Cameron, D.D.; Meselmani, M.A.; Schwarzenbacher, R.; Rolfe, S.A.; Ton, J. Metabolic regulation of the maize rhizobiome by benzoxazinoids. *ISME J.* **2019**, *13*, 1647–1658. https://doi.org/10.1038/s41396-019-0375-2.
53. Song, Y.Y.; Cao, M.; Xie, L.J.; Liang, X.T.; Zeng, R.S.; Su, Y.J.; Huang, J.H.; Wang, R.L.; Luo, S.M. Induction of DIMBOA accumulation and systemic defense responses as a mechanism of enhanced resistance of mycorrhizal corn (*Zea mays* L.) to sheath blight. *Mycorrhiza* **2011**, *21*, 721–731. https://doi.org/10.1007/s00572-011-0380-4.
54. Kudjordjie, E.N.; Sapkota, R.; Steffensen, S.K.; Fomsgaard, I.S.; Nicolaisen, M. Maize synthesized benzoxazinoids affect the host associated microbiome. *Microbiome* **2019**, *7*, 59. https://doi.org/10.1186/s40168-019-0677-7.
55. Snelders, N.C.; Rovenich, H.; Petti, G.C.; Rocafort, M.; van den Berg, G.C.M.; Vorholt, J.A.; Mesters, J.R.; Seidl, M.F.; Nijland, R.; Thomma, B.P.H.J. Microbiome manipulation by a soil-borne fungal plant pathogen using effector proteins. *Nat. Plants* **2020**, *6*, 1365–1374. https://doi.org/10.1038/s41477-020-00799-5.
56. Snelders, N.C.; Petti, G.C.; van den Berg, G.C.M.; Seidl, M.F.; Thomma, B.P.H.J. An ancient antimicrobial protein co-opted by a fungal plant pathogen for in planta mycobiome manipulation. *Proc. Natl. Acad. Sci. USA* **2021**, *118*, e2110968118. https://doi.org/10.1073/pnas.2110968118.

57. Chavarro-Carrero, E.A.; Snelders, N.C.; Torres, D.E.; Kraege, A.; López-Moral, A.; Petti, G.C.; Punt, W.; Wieneke, J.; García-Velasco, R.; López-Herrera, C.J.; et al. The soil-borne white root rot pathogen *Rosellinia necatrix* expresses antimicrobial proteins during host colonization. *PLoS Pathog.* **2024**, *20*, e1011866. https://doi.org/10.1371/journal.ppat.1011866.
58. Gu, S.; Wei, Z.; Shao, Z.; Friman, V.; 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*, 1002–1010. https://doi.org/10.1038/s41564-020-0719-8.
59. Zhang, Y.; Xu, J.; Riera, N.; Jin, T.; Li, J.; Wang, N. Huanglongbing impairs the rhizosphere-to-rhizoplane enrichment process of the citrus root-associated microbiome. *Microbiome* **2017**, *5*, 97. https://doi.org/10.1186/s40168-017-0304-4.
60. Rovenich, H.; Boshoven, J.C.; Thomma, B.P. Filamentous pathogen effector functions: Of pathogens, hosts and microbiomes. *Curr. Opin. Plant Biol.* **2014**, *20*, 96–103. https://doi.org/10.1016/j.pbi.2014.05.001.
61. Snelders, N.C.; Rovenich, H.; Thomma, B.P.H.J. Microbiota manipulation through the secretion of effector proteins is fundamental to the wealth of lifestyles in the fungal kingdom. *FEMS Microbiol. Rev.* **2022**, *46*, fuac022. https://doi.org/10.1093/femsre/fuac022.
62. Snelders, N.C.; Kettles, G.J.; Rudd, J.J.; Thomma, B.P.H.J. Plant pathogen effector proteins as manipulators of host microbiomes? *Mol. Plant Pathol.* **2018**, *19*, 257–259. https://doi.org/10.1111/mpp.12628.
63. Snelders, N.C.; Boshoven, J.C.; Song, Y.; Schmitz, N.; Fiorin, G.L.; Rovenich, H.; van den Berg, G.C.M.; Torres, D.E.; Petti, G.C.; Prockl, Z.; et al. A highly polymorphic effector protein promotes fungal virulence through suppression of plant-associated Actinobacteria. *New Phytol.* **2023**, *237*, 944–958. https://doi.org/10.1111/nph.18576.
64. Michielse, C.B.; Rep, M. Pathogen profile update: *Fusarium oxysporum*. *Mol. Plant Pathol.* **2009**, *10*, 311–324. https://doi.org/10.1111/j.1364-3703.2009.00538.x.
65. Cessna, S.G.; Sears, V.E.; Dickman, M.B.; Low, P.S. Oxalic acid, a pathogenicity factor for *Sclerotinia sclerotiorum*, suppresses the oxidative burst of the host plant. *Plant Cell* **2000**, *12*, 2191–2199. https://doi.org/10.1105/tpc.12.11.2191.
66. Liu, X.; Zhang, K.; Liu, Y.; Xie, Z.; Zhang, C. Oxalic acid from Sesbania rostrata seed exudates mediates the chemotactic response of *Azorhizobium caulinodans* ORS571 using multiple strategies. *Front. Microbiol.* **2019**, *10*, 2727. https://doi.org/10.3389/fmicb.2019.02727.
67. Müller, M.C.; Brumm, S.; Hu, Y.; Kemen, E.; Lahaye, T.; Hückelhoven, R. Diversify and conquer: How effector diversity is shaped by host-microbe co-evolution. *PLoS Pathog.* **2026**, *22*, e1013870. https://doi.org/10.1371/journal.ppat.1013870.
68. Sánchez-Vallet, A.; Fouché, S.; Fudal, I.; Hartmann, F.E.; Soyer, J.L.; Tellier, A.; Croll, D. The genome biology of effector gene evolution in filamentous plant pathogens. *Annu. Rev. Phytopathol.* **2018**, *56*, 21–40. https://doi.org/10.1146/annurev-phyto-080516-035303.
69. Feng, Z.; Liang, Q.; Yao, Q.; Bai, Y.; Zhu, H. The role of the rhizobiome recruited by root exudates in plant disease resistance: Current status and future directions. *Environ. Microbiome* **2024**, *19*, 91. https://doi.org/10.1186/s40793-024-00638-6.
70. Jayaraman, S.; Naorem, A.K.; Lal, R.; Dalal, R.C.; Sinha, N.K.; Patra, A.K.; Chaudhari, S.K. Disease-suppressive soils—Beyond food production: A critical review. *J. Soil Sci. Plant Nutr.* **2021**, *21*, 1437–1465. https://doi.org/10.1007/s42729-021-00451-x.
71. Schlatter, D.; Kinkel, L.; Thomashow, L.; Weller, D.; Paulitz, T. Disease suppressive soils: New insights from the soil microbiome. *Phytopathology* **2017**, *107*, 1284–1297. https://doi.org/10.1094/PHYTO-03-17-0111-RVW.
72. Raaijmakers, J.M.; Weller, D.M. Natural plant protection by 2,4-Diacetylphloroglucinol-producing *Pseudomonas* spp. in take-all decline soils. *Mol. Plant-Microbe Interact.* **1998**, *11*, 144–152. https://doi.org/10.1094/MPMI.1998.11.2.144.
73. Yang, M.; Mavrodi, D.V.; Thomashow, L.S.; Weller, D.M. Differential response of wheat cultivars to *Pseudomonas brassicacearum* and take-all decline soil. *Phytopathology* **2018**, *108*, 1363–1372. https://doi.org/10.1094/PHYTO-01-18-0024-R.
74. Biessy, A.; Filion, M. Phloroglucinol derivatives in plant-beneficial *Pseudomonas* spp.: Biosynthesis, regulation, and functions. *Metabolites* **2021**, *11*, 182. https://doi.org/10.3390/metabo11030182.
75. Bakker, P.A.H.M.; Pieterse, C.M.J.; de Jonge, R.; Berendsen, R.L. The soil-borne legacy. *Cell* **2018**, *172*, 1178–1180. https://doi.org/10.1016/j.cell.2018.02.024.
76. Trivedi, P.; Leach, J.E.; Tringe, S.G.; Sa, T.; Singh, B.K. Plant-microbiome interactions: From community assembly to plant health. *Nat. Rev. Microbiol.* **2020**, *18*, 607–621. https://doi.org/10.1038/s41579-020-0412-1. Correction in *Nat. Rev. Microbiol.* **2021**, *19*, 72.
77. Kong, H.G.; Song, G.C.; Ryu, C. Inheritance of seed and rhizosphere microbial communities through plant-soil feedback and soil memory. *Environ. Microbiol. Rep.* **2019**, *11*, 479–486. https://doi.org/10.1111/1758-2229.12760.
78. Shade, A.; Jacques, M.; Barret, M. Ecological patterns of seed microbiome diversity, transmission, and assembly. *Curr. Opin. Microbiol.* **2017**, *37*, 15–22. https://doi.org/10.1016/j.mib.2017.03.010.

79. Wilkinson, S.W.; Magerøy, M.H.; López Sánchez, A.; Smith, L.M.; Furci, L.; Cotton, T.E.A.; Krokene, P.; Ton, J. Surviving in a hostile world: Plant strategies to resist pests and diseases. *Annu. Rev. Phytopathol.* **2019**, *57*, 505–529. https://doi.org/10.1146/annurev-phyto-082718-095959.
80. Lugtenberg, B.; Kamilova, F. Plant-growth-promoting rhizobacteria. *Annu. Rev. Microbiol.* **2009**, *63*, 541–556. https://doi.org/10.1146/annurev.micro.62.081307.162918.
81. Vorholt, J.A.; Vogel, C.; Carlström, C.I.; Müller, D.B. Establishing causality: Opportunities of synthetic communities for plant microbiome research. *Cell Host Microbe* **2017**, *22*, 142–155. https://doi.org/10.1016/j.chom.2017.07.004.
82. Shayanthan, A.; Ordoñez, P.A.C.; Oresnik, I.J. The role of synthetic microbial communities (SynCom) in sustainable agriculture. *Front. Agron.* **2022**, *4*, 896307. https://doi.org/10.3389/fagro.2022.896307.
83. Sharma, A.; Bora, P. Engineering synthetic microbial communities to restructure the phytobiome for plant health and productivity. *World J. Microbiol. Biotechnol.* **2025**, *41*, 228. https://doi.org/10.1007/s11274-025-04460-1.
84. Zhang, Y.; Jing, M.; Lyu, L.; Nie, L.; Xu, X.; Sun, R.; Xu, X.; Chen, S.; He, S.; Zhang, Y.; et al. Principles for rigorous design and application of synthetic microbial communities. *Adv. Sci.* **2026**, *13*, e14750. https://doi.org/10.1002/advs.202514750.
85. Dubey, A.; Malla, M.A.; Vimal, S.R.; Kumar, A.; Prasad, S.M.; Khan, M.L. Plant-microbiome engineering: Synergistic microbial partners for crop health and sustainability. *Plant Growth Regul.* **2025**, *105*, 1825–1839. https://doi.org/10.1007/s10725-025-01385-5.
86. Wang, C.; Li, Y.; Li, M.; Zhang, K.; Ma, W.; Zheng, L.; Xu, H.; Cui, B.; Liu, R.; Yang, Y.; et al. Functional assembly of root-associated microbial consortia improves nutrient efficiency and yield in soybean. *J. Integr. Plant Biol.* **2021**, *63*, 1021–1035. https://doi.org/10.1111/jipb.13073.
87. Adhikary, K.; Selim, S.; Sarkar, R.; Ganguly, K.; Das, J.; Almuhayawi, M.S.; Alruhaili, M.H.; Gattan, H.S.; Karak, P. Synthetic microbiomes in bioengineered rhizospheres: New frontiers for climate-resilient agriculture. *Front. Microbiol.* **2026**, *17*, 1780132. https://doi.org/10.3389/fmicb.2026.1780132.
88. Kong, Z.; Hart, M.; Liu, H. Paving the way from the lab to the field: Using synthetic microbial consortia to produce high-quality crops. *Front. Plant Sci.* **2018**, *9*, 1467. https://doi.org/10.3389/fpls.2018.01467.
89. Teixeira, P.J.P.L.; Colaianni, N.R.; Law, T.F.; Conway, J.M.; Gilbert, S.; Li, H.; Salas-González, I.; Panda, D.; Del Risco, N.M.; Finkel, O.M.; et al. Specific modulation of the root immune system by a community of commensal bacteria. *Proc. Natl. Acad. Sci. USA* **2021**, *118*, e2100678118. https://doi.org/10.1073/pnas.2100678118.
90. Niu, B.; Paulson, J.N.; Zheng, X.; Kolter, R. Simplified and representative bacterial community of maize roots. *Proc. Natl. Acad. Sci. USA* **2017**, *114*, E2450–E2459. https://doi.org/10.1073/pnas.1616148114.
91. Li, Z.; Bai, X.; Jiao, S.; Li, Y.; Li, P.; Yang, Y.; Zhang, H.; Wei, G. A simplified synthetic community rescues *Astragalus mongholicus* from root rot disease by activating plant-induced systemic resistance. *Microbiome* **2021**, *9*, 217. https://doi.org/10.1186/s40168-021-01169-9.
92. Hafiz, F.B.; Moradtalab, N.; Goertz, S.; Rietz, S.; Dietel, K.; Rozhon, W.; Humbeck, K.; Geistlinger, J.; Neumann, G.; Schellenberg, I. Synergistic effects of a root-endophytic *Trichoderma* fungus and *Bacillus* on early root colonization and defense activation against *Verticillium longisporum* in rapeseed. *Mol. Plant-Microbe Interact.* **2022**, *35*, 380–392. https://doi.org/10.1094/MPMI-11-21-0274-R.
93. Zhou, X.; Wang, J.; Liu, F.; Liang, J.; Zhao, P.; Tsui, C.K.M.; Cai, L. Cross-kingdom synthetic microbiota supports tomato suppression of *Fusarium* wilt disease. *Nat. Commun.* **2022**, *13*, 7890. https://doi.org/10.1038/s41467-022-35452-6. Correction in *Nat. Commun.* **2023**, *14*, 6755.
94. Xu, X.; Dinesen, C.; Pioppi, A.; Kovács, Á.T.; Lozano-Andrade, C.N. Composing a microbial symphony: Synthetic communities for promoting plant growth. *Trends Microbiol.* **2025**, *33*, 738–751. https://doi.org/10.1016/j.tim.2025.01.006.
95. Panchal, K.; Sudhir, A.; Prajapati, A.S. Engineering the plant microbiome: Synthetic community approaches to enhance crop protection. *Front. Plant Sci.* **2026**, *16*, 1705289. https://doi.org/10.3389/fpls.2025.1705289.
96. Jing, J.; Garbeva, P.; Raaijmakers, J.M.; Medema, M.H. Strategies for tailoring functional microbial synthetic communities. *ISME J.* **2024**, *18*, wrae049. https://doi.org/10.1093/ismejo/wrae049.
97. Ma, J.; Qiao, J.; Cao, Y.; Cheng, Z. Harnessing artificial intelligence to decode the rhizosphere microbiome. *aBIOTECH* **2026**, *7*, 100005. https://doi.org/10.1016/j.abiote.2025.100005.
98. Portal-Gonzalez, N.; Wang, W.; He, W.; Santos-Bermudez, R. Engineering plant holobionts for climate-resilient agriculture. *ISME J.* **2025**, *19*, wraf158. https://doi.org/10.1093/ismejo/wraf158.

99. Wang, Z.; Wang, S.; He, Q.; Yang, X.; Zhao, B.; Zhang, H.; Deng, Y. Ecological design of high-performance synthetic microbial communities: From theoretical foundations to functional optimization. *ISME Commun.* **2025**, *5*, ycaf133. https://doi.org/10.1093/ismeco/ycaf133.
100. Pace, R.; Monti, M.M.; Cuomo, S.; Affinito, A.; Ruocco, M. Machine learning approaches to assess soil microbiome dynamics and biosustainability. *Physiol. Plant* **2026**, *178*, e70719. https://doi.org/10.1111/ppl.70719.
101. Redman, M.; King, A.; Watson, C.; King, D. What is CRISPR/Cas9? *Arch. Dis. Child Educ. Pract. Ed.* **2016**, *101*, 213–215. https://doi.org/10.1136/archdischild-2016-310459.
102. Singh, S.; Ramakrishna, W. Application of CRISPR-Cas9 in plant-plant growth-promoting rhizobacteria interactions for next Green Revolution. *3 Biotech* **2021**, *11*, 492. https://doi.org/10.1007/s13205-021-03041-x.
103. Zhao, A.; Li, Q.; Meng, P.; Liu, P.; Wu, S.; Lang, Z.; Song, Y.; Macho, A.P. Reduced content of gamma-aminobutyric acid enhances resistance to bacterial wilt disease in tomato. *Plant Biotechnol. J.* **2025**, *23*, 792–806. https://doi.org/10.1111/pbi.14539.
104. 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*, 887–896. https://doi.org/10.1038/s41477-022-01201-2.
105. Ke, J.; Wang, B.; Yoshikuni, Y. Microbiome engineering: Synthetic biology of plant-associated microbiomes in sustainable agriculture. *Trends Biotechnol.* **2021**, *39*, 244–261. https://doi.org/10.1016/j.tibtech.2020.07.008.
106. Shelake, R.M.; Pramanik, D.; Kim, J.-Y. Exploration of plant-microbe interactions for sustainable agriculture in CRISPR era. *Microorganisms* **2019**, *7*, 269. https://doi.org/10.3390/microorganisms7080269.
107. Banerjee, S.; Walder, F.; Büchi, L.; Meyer, M.; Held, A.Y.; Gattinger, A.; Keller, T.; Charles, R.; van der Heijden, M.G.A. Agricultural intensification reduces microbial network complexity and the abundance of keystone taxa in roots. *ISME J.* **2019**, *13*, 1722–1736. https://doi.org/10.1038/s41396-019-0383-2.
108. Upadhyay, S.K. Rhizosphere engineering 2.0: Predictive microbiome design for climate-resilient agriculture, sustainable food production, and global food security. *Plant Sci.* **2026**, *373*, 113469. https://doi.org/10.1016/j.plantsci.2026.113469.
109. Fouad, N.; Elzayat, E.M.; Amr, D.; El-Khishin, D.A.; Radwan, K.H.; Youssef, A.; Khalaf, A.A.; Ahmed, H.A.; Radwan, E.H.; Tawkaz, S.; et al. Rhizosphere microbiome engineering for climate-smart agriculture: From synthetic consortia to precision decision support. *Microorganisms* **2026**, *14*, 1138. https://doi.org/10.3390/microorganisms14051138.

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