

# Plant exudates-driven microbiome recruitment and assembly facilitates plant health management

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Editor: [Guo Hui-Shan]

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## Abstract

Plant-microbiome symbiotic interactions play a crucial role in regulating plant health and productivity. To establish symbiotic relationships, the plant secretes a variety of substances to facilitate microbial community recruitment and assembly. In recent years, important progress has been made in studying how plant exudates attract beneficial microorganisms and regulate plant health. However, the mechanisms of plant exudates-mediated microbial community recruitment and assembly and their effects on plant health are no comprehensive review. Here, we summarize the interaction mechanisms among plant exudates, microbial community recruitment and assembly, and plant health. First, we systematically evaluate the type and distribution of plant exudates, as well as their role in microbiome recruitment and assembly. Second, we summarize the mechanisms of plant exudates in terms of microbiome recruitment, diversity regulation and chemotaxis. Finally, we list some typical examples for elucidating the importance of plant exudates in promoting plant health and development. This review contributes to utilizing plant exudate or beneficial microbiome resources to manage plant health and productivity.

**Keywords:** plant exudate; plant-microbiome interaction; microbial community recruitment; plant health

## Introduction

Plant-microbiome interactions are critical for plant health, growth, and development. Plant diseases and pests can cause up to 30% of global harvest losses, utilizing beneficial microorganisms enhancing plant immunity by 40%, thereby reducing harvest losses by 5%–20% (Savary et al. 2019, Paasch et al. 2023). Plants-microbiome interactions boosts plant quality by mobilizing soil nutrients, resulting in a 30%–50% increase in macronutrient levels (Vilchez et al. 2020, Wang et al. 2020). In addition, the diversity, community richness, and compositions of plants and microbes were positively correlated that is beneficial for the evolution of phytocommunity (Seabloom et al. 2023). Therefore, analysis of the interaction models between plants and microorganisms is essential for enhancing plant immunity, productivity, and species diversity.

Among the various interaction models between plants and microorganisms, symbiotic relationships play the most important role (Santoyo 2022). Studies have shown that the establishment of 10%–50% symbiotic relationships is relied on plant exudates owing to they can serve as medium for information exchange, material exchange, and energy transfer between plants and microbes (Delaux and Schornack 2021). Plants secrete specific compounds

that act as signaling molecules, selectively recruitment of beneficial microorganisms and enhancing their colonization and proliferation by up to 50% (Palmieri et al. 2020). Coumarin biosynthesis in root reorganizes the microbiota at the amplicon sequence variant level and is critical for plant growth and root microbiota composition to encounter the iron-limited soils (Harbort et al. 2020). Therefore, plant exudate-mediated microbial recruitment and assembly is essential for maintaining plant-microbe symbioses.

In recent years, important progress has been made in studying how plants attract beneficial microbiomes through exudates and regulate microbial communities. The OsPAL02 controls 4-hydroxycinnamic acid synthesis, promoting enrichment in the rice leaves, thereby enhancing rice's resistance to diseases (Su et al. 2024). Nonpathogenic bacteria and their elicitors can trigger the “cry for help” mechanism in plants, facilitating the assembly of beneficial microbial communities, thereby suppressing pathogen invasion and promoting plant growth (Liu et al. 2024). *Trichoderma* can activate transcriptional ability, thereby acting as a plant growth promoter and improving the plant's ability to respond to local and systemic defenses against biotic and abiotic organisms (Woo et al. 2023). Therefore, utilization of the plant exudates-mediated microbial recruitment and assembly is

Received 31 October 2024; revised 10 February 2025; accepted 28 March 2025

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of great significance to improve plant health and productivity. However, there is lack of summative and critical review for establishing the relationship among plant exudates-mediated microbial recruitment and assembly and plant health.

Here, we systematically review the mechanism of plant exudates in facilitating microbiome recruitment and assembly for promoting plant health. First, we explored the types and distribution of plant exudates, as well as their multifaceted roles in microbiome recruitment and assembly. Second, we summarize how plant exudates drive microbiome recruitment and assembly by affecting microbial perception, balance species diversity, and influence regulating chemotaxis. Finally, we list some successful cases for proving the significance of plant exudate-mediated microbiome recruitment and assembly in promoting plant health and productivity. This comprehensive review can provide guidance for utilization plant exudates and microbial resources to manage plant growth and development.

## Plant exudates-mediated microbiome recruitment and assembly

Plant exudates play a crucial role in the recruitment and assembly of microorganisms. These exudates include organic acids, sugars, amino acids, phenolic compounds, volatile organic compounds (VOCs), and phytohormones, which are distributed in various plant organs such as roots, leaves, flowers, and fruits (Trivedi et al. 2020, Saurav et al. 2021). They mediate microbiome recruitment and assembly primarily through various measures such as nutrient provision, chemical signaling, environmental regulation, and competitive inhibition (Tripathi et al. 2022). This process contributes to enhance plant disease resistance, improved nutrient absorption, increased plant quality and yield, and the regulation of plant growth and development (Vives-Peris et al. 2020). Environmental stressors such as drought, salinity, and temperature extremes significantly influence exudate composition, which in turn affects microbiome recruitment. For example, drought stress leads to the release of soluble sugars, amino acids, and organic acids, creating favorable conditions for drought-tolerant microbes. Similarly, salinity alters metabolic pathways, promoting the release of amino acids and organic acids that recruit halophilic microbes to help mitigate salt stress. Extreme temperatures can modify exudates, enhancing the recruitment of thermotolerant or psychrophilic microbes, depending on the temperature. In addition to these stress-induced changes, microbial community stability is critical for plant health. Factors such as soil pH, organic matter content, and seasonal fluctuations affect the long-term stability of microbial communities. Soil pH can shift microbial growth conditions, while organic matter supports microbial diversity. Seasonal changes in temperature and moisture further influence microbial dynamics, and understanding these factors is essential for maintaining a resilient microbiome in agricultural systems. In the following section, we will explore in detail the type and distribution of plant exudates and analyze their specific roles in microbiome recruitment and assembly.

### Types and distribution of plant exudates

Plant exudates mainly include amino acids, sugars, growth factors, vitamins, fatty acids, organic acids, sterols, enzymes, flavonoids, and nucleotides/purines, which can be secreted by different plant tissues (Afridi et al. 2024) (Table 1). These exudates play various roles in plant growth and development owing to their distinct functions and chemical composition. Root exudates are

primarily found in the root tip and root sheath (Canarini et al. 2019). Root tip exudates are rich in organic acids (such as citric acid and malic acid), plant hormones, and proteins, facilitating the regulation of rhizosphere environments and interactions with soil microorganisms (Gargallo-Garriga et al. 2018). The rhizosphere is the main functional area for root exudates, which are key drivers of microbial community dynamics. Root exudates influence the structure and function of microbial communities, shaping the rhizosphere environment by attracting beneficial microbes, such as nitrogen-fixing bacteria and mycorrhizal fungi, while inhibiting the growth of pathogens. For example, certain root exudates may modulate quorum sensing in bacteria, promoting the colonization of beneficial microbes and suppressing pathogenic species. This complex chemical signaling mechanism underscores the critical role of the rhizosphere in plant health, nutrient acquisition, and disease resistance. Root sheath exudates consist of mucilage and glycoproteins, enhancing soil adhesion and root stability (Galloway et al. 2020, Xu et al. 2023). Leaf exudates include leaf surface exudates and leaf interior exudates. The former is rich in antimicrobial substances, resins, and VOCs, serving to defend against pathogenic microorganisms and predatory insects (Chaudhry et al. 2021). The latter contain enzymes and odorants, regulating plant metabolism and environmental responses (Shiade et al. 2024). Stem exudates, although less studied, are known to include resins and flavonoids, which can improve plant immunity against herbivores and pathogens, as well as regulate plant growth and wound healing (Van Deynze et al. 2018, Galloway et al. 2020). Among these, root exudates are particularly important due to their crucial role in shaping soil microbial communities and influencing nutrient uptake, making them a focal point in understanding plant-soil interactions (Vives-Peris et al. 2020, Afridi et al. 2024).

### Role of plant exudates in microbiome recruitment and assembly

Plant exudates mediate microbial recruitment and assembly through nutrient supply, signal transduction, inhibition of pathogens, and environmental regulation (Solomon et al. 2024). First, as nutrient sources such as sugars, organic acids, and amino acids, they provide essential growth substrates and energy for microorganisms in the surrounding soil, is a dynamic preparation for the aggregation of the plant-associated microbiota (Sasse et al. 2018). For instance, citric acid secreted by maize roots facilitates iron solubilization, making iron nutrition available as a resource for bacterial utilization, thus recruiting siderophilic bacteria to achieve the effect of inhibiting pathogenic bacteria (Wei et al. 2020, Mayneris-Perxachs et al. 2022, Wang et al. 2024) (Fig. 1A). Second, chemical compounds in plant exudates act as signaling molecules, influencing microbial behavior and community structure (Sasse et al. 2018, Santoyo 2022, Guerrieri and Rasmann 2024). These signaling molecules attract specific microbial species (e.g. *Sinorhizobium*, *Azorhizobium*, and *Pseudomonas*), promoting their colonization in the rhizosphere (Hayat et al. 2017). For example, isoflavonoids secreted by leguminous plants induce symbiotic nitrogen-fixing relationships with rhizobia (Santoyo 2022) (Fig. 1B). Third, certain plant exudates contain antimicrobial substances that inhibit the growth of pathogenic microorganisms, thereby safeguarding beneficial microbial communities around plant roots (Sasse et al. 2018, Ahlawat et al. 2024). For instance, isoflavonoids from soybean roots suppress fungal pathogens in soil, contributing to the maintenance of a healthy rhizospheric microbial community (Qiu et al. 2024) (Fig. 1C). Lastly, this modu-

**Table 1.** Types and distribution of plant exudates.

Type	Compounds	Distribution
Amino acids	$\alpha$ -alanine, $\beta$ -alanine, $\gamma$ -aminobutyric, $\alpha$ -aminoadipic, arginine, asparagine, aspartic, citrulline, cystathionine, cysteine, cystine, deoxymugineic, 3-epihydroxymugineic, glutamine, glutamic, glycine, histidine, homoserine, isoleucine, leucine, lysine, methionine, mugineic, ornithine, phenylalanine, praline, proline, serine, threonine, tryptophan, tyrosine, and valine	Root, leaf
Sugars	Arabinose, fructose, galactose, glucose, maltose, mannose, mucilages of various compositions, oligosaccharides, raffinose, rhamnose, ribose, sucrose, xylose, deoxyribose	Root
Growth factors and vitamins	<i>p</i> -amino benzoic acid, biotin, choline, <i>N</i> -methyl nicotinic acid, niacin, pathothenic, thiamine, riboflavin, pyridoxine, pantothenate, and inositol	Root, leaf
Fatty acids	Linoleic, linolenic, oleic, palmitic, and stearic	Root, leaf
Organic acids	Acetic, aconitic, ascorbic, aldonic, benzoic, butyric, caffeic, citric, pcoumaric, erythronic, ferulic, formic, fumaric, glutaric, glycolic, lactic, glyoxilic, malic, malonic, oxalacetic, oxalic, <i>p</i> -hydroxybenzoic, piscidic, propionic, pyruvic, succinic, syringic, tartaric, tetrionic, valeric, and vanillic	Root, leaf, Flower, stem
Sterols	Campesterol, cholesterol, sitosterol, and stigmasterol	Root
Enzymes	Amylase, invertase, peroxidase, phenolase, acid/alkaline phosphatase, polygalacturonase, and protease	Root
Flavonoids	Chalcone, coumarine, flavones, flavonols, flavanones, flavonones, isoflavones, luteolin, apigenin, quercetin, chrysin, naringenin, genistein	Root
Nucleotides/purines	Adenine, guanine, and uridine/cytidine	Root
Others	Al-induced polypeptides, alcohols, alkyl sulphides, auxins, camalexin, dihydroquinone, ethanol, glucosides, glucosinolates, glycinebetaine, hydrocyanic acid, inorganic ions and gaseous molecules (e.g. CO <sub>2</sub> , H <sup>+</sup> , OH <sup>-</sup> , and H <sub>2</sub> CO <sub>3</sub> ), isothiocyanates, unidentified ninhydrin positive compounds, unidentifiable soluble proteins, reducing compounds, scopoletin, sorgoleone, strigolactones, citrate, malate, oxalate coumarins, camalexin, benzoxazinoids, ethylene, methyl jasmonate, flavonoids, and malic acid	Root, leaf, Flower, fruit

lation includes alterations in soil pH or reduction of harmful substance accumulation, promoting the establishment and growth of beneficial microbes (Vives-Peris et al. 2020) (Fig. 1D). Besides, under certain conditions of environmental stress, such as phosphate or iron limitation, some plants tend to enhance the secretion of citrate, malate, or oxalate to enrich the rhizosphere with organic carbon, which attracts beneficial microorganisms (Santoyo 2022). In conclusion, plant exudates have multiple effects on microbiota dynamics. Mutual selection between plants and microbes ultimately results in microbial community structures that are critical to plant health and ecosystem function.

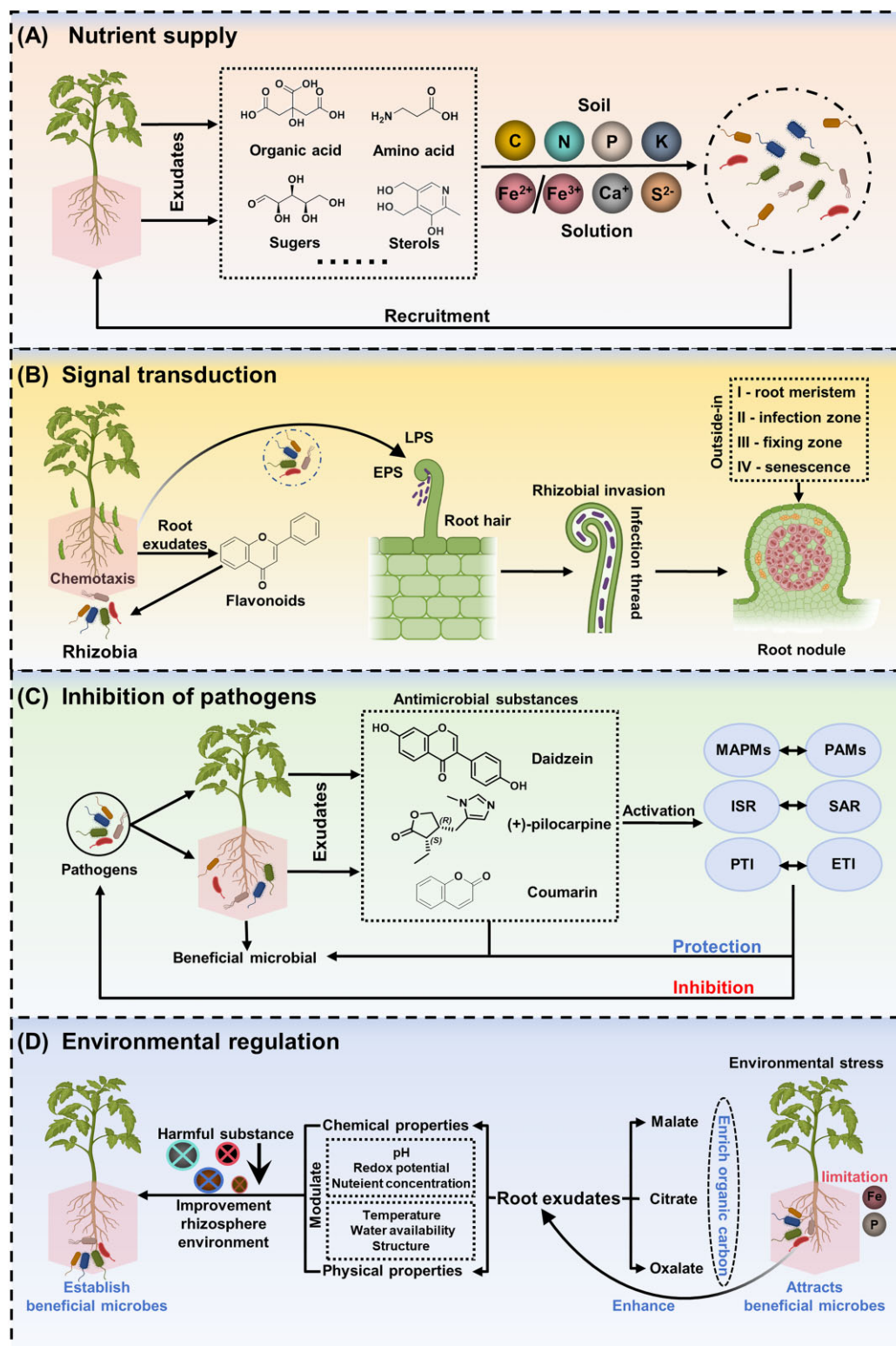
## Mechanisms of microbiome recruitment and assembly driven by plant exudates

Plant exudates create a dynamic environment that mediates interactions between plants and microbes. The mechanisms of plant exudates influence microbiome recruitment and assembly mainly including microbial perception, species selection, diversity, chemotaxis, motility, and community migration. Plant exudates influence microbial perception, population diversity, movement, and migration by modulating several pathways such as signal transduction, selective cultivation, chemotaxis signaling, and adhesion mechanisms, resulting in a dynamic interroot microbial

community. Understanding these mechanisms is crucial for exploring gene resources to regulate plant-microbe interactions.

## Regulating microbes perception and recognition

Plant rhizosphere exudates regulate microbial perception and recognition through three main mechanisms: masking microbe-associated molecular patterns (MAMPs), suppressing reactive oxygen species (ROS) bursts, targeting mitogen-activated protein kinase (MAPK) signaling, and JA/SA-mediated signaling pathway. Additionally, environmental stressors can significantly alter the plant's root exudate profile, thereby influencing microbial recognition and perception mechanisms. For example, under salinity stress, plants may increase the secretion of particular ions, such as calcium and magnesium, which are involved in signaling pathways that help microbes sense the salt-stressed environment. Similarly, temperature extremes can lead to the production of heat shock proteins and secondary metabolites, such as flavonoids, which may signal heat- or cold-adapted microbes to associate with the plant roots. The presence of specific mechanisms in plant-associated microbes allows them to evade host immune recognition, which facilitates their colonization and symbiotic relationships with plants. First, certain microbes secrete proteases like AprA to degrade flagellin or produce chitin-binding effectors, which strengthen the cell wall and help evade recognition by plant pattern recognition receptors, such as CERK1 (Yu et al.



**Figure 1.** Various ways of microbial recruitment and assembly mediated by plant exudates. (A) Plants attract surrounding beneficial microorganisms to colonize them by secreting organic acids, amino acids, sugars, and sterols. (B) All stages of legume symbiosis with *Rhizobium* are regulated by signals from themselves: (i) the preinfection stage, when both parties produce chemical signals of mutual recognition, leading to bacterial attachment to the cell walls of the root hairs; (ii) the infection process leading to curling of the root hairs and the formation of infection threads within the hairs, which transport the bacteria to the nodule cells; (iii) the formation of the rhizobium—the specialized root organ; and (iv) differentiation of the bacteria into nitrogen-fixing bacilli in the root nodule. (C) When plants are stressed by pathogens, they secrete some antimicrobial substances (e.g. soybean glycosides, (+)-pilocarpine, coumarins) to activate the immune system and inhibit the pathogenic bacteria. (D) When the soil is stressed by iron and phosphorus, plants will secrete exudates such as malate, citrate, and oxalate to enrich organic carbon and attract beneficial microorganisms to gather, and at the same time regulate soil temperature, pH value, redox potential, and other properties. Abbreviations meaning: pathogen-associated molecular patterns (PAMPs); microbe-associated molecular patterns (MAMPs); systemic acquired resistance (SAR); induced systemic resistance (ISR); exopolysaccharide (EPS); and lipopolysaccharide (LPS).

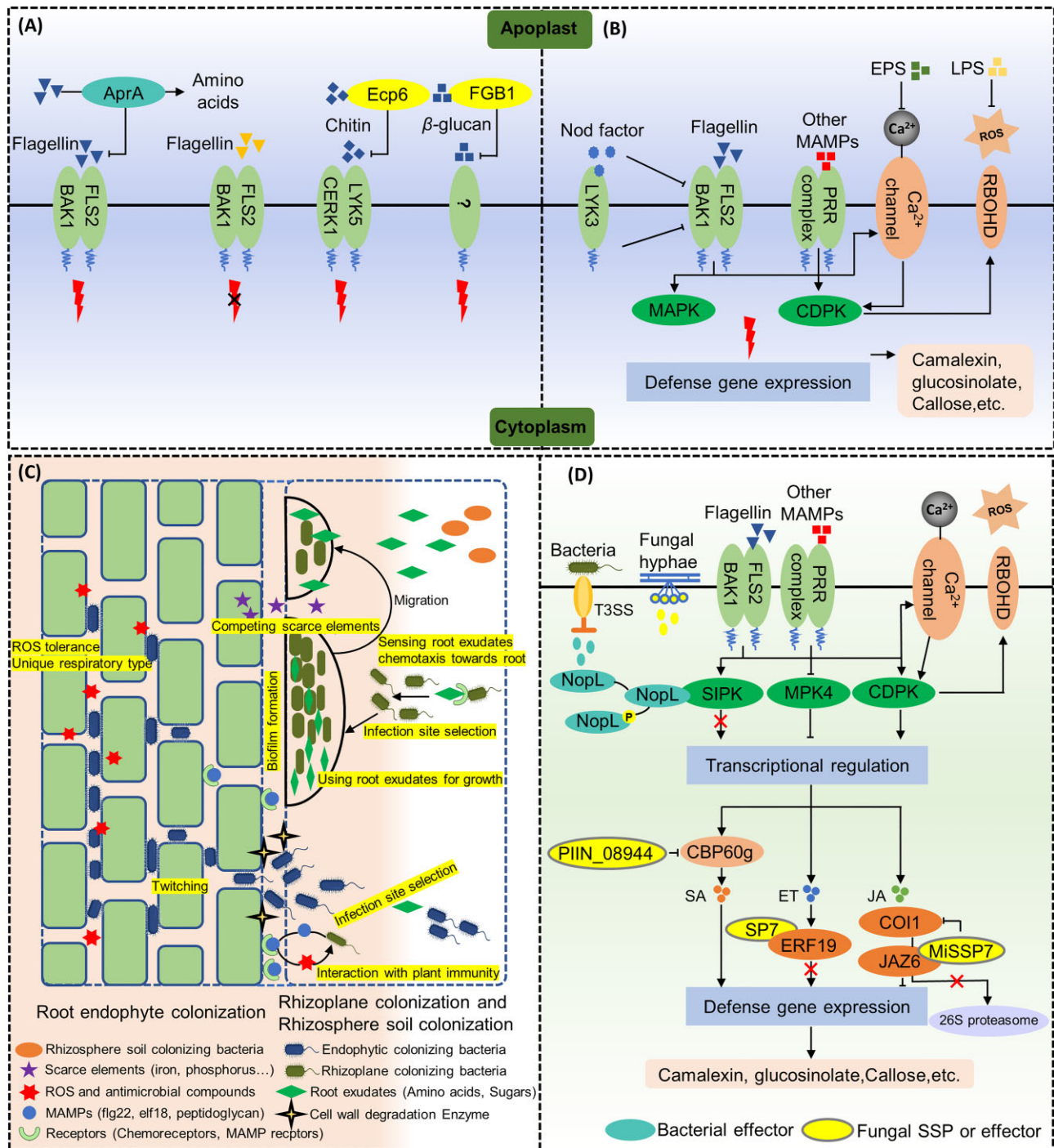


2019). This mechanism of MAMP concealment is also observed in beneficial microbes, suggesting an adaptive strategy to minimize host immune responses. Additionally, beneficial microbes can suppress ROS bursts, which are rapid immune responses triggered by MAMP detection. For instance, rhizobial effectors, such as specific E3 ubiquitin ligases, can inhibit ROS production to mitigate oxidative stress and support microbial establishment (Xin et al. 2012) (Fig. 2A). To further enhance the understanding, specific beneficial microbes, such as *Pseudomonas fluorescens*, produce antibiotics (e.g. 2,4-diacetylphloroglucinol) to suppress pathogenic microbes in the rhizosphere, thereby providing a competitive advantage. These microbes also release siderophores to outcompete pathogenic bacteria for iron, thus limiting pathogen growth and helping protect the plant from infection.

The MAPK cascade is a key pathway in plant immune signaling, and it is also a target of microbial effectors. Bacteria such as *Pseudomonas aeruginosa* and *Pseudomonas syringae* secrete AprA protease to degrade flagellin and evade immune detection. Similarly, fungal pathogens produce chitin-binding effectors like Avr4 and Ecp6 to reinforce the cell wall and evade recognition. Fungal effectors such as PIIN\_08 944 can reduce flg22/chitin-induced ROS in barley roots, promoting fungal establishment. Additionally, the effector NopL mimics MAPK substrates, inhibiting phosphorylation and interfering with the expression of defense-related genes, thereby preventing immune-triggered cell death in tobacco (Bartsev et al. 2004). In soybeans, the MAPK GmMPK4, which is regulated during colonization by *Sinorhizobium fredii*, is suppressed to facilitate symbiosis (Jiménez-Guerrero et al. 2015) (Fig. 2B). Through these mechanisms, beneficial microbes effectively mask their presence, attenuate direct immune responses, and disrupt downstream signaling to achieve coexistence with plant hosts. Moreover, the salicylic acid (SA)-dependent pathway plays a pivotal role in microbial perception and recognition, especially in response to biotrophic pathogens. Upon detection of MAMPs like bacterial flagellin or fungal chitin by leaf surface PRRs, this pathway is activated. Once detected, PRRs trigger downstream signaling, including a rapid ROS burst as an early defense. SA synthesis is subsequently induced via two main pathways: the isochorismate pathway in chloroplasts and the phenylalanine ammonia-lyase (PAL) pathway in the cytoplasm. The ICS1 (isochorismate synthase 1) gene is essential for chloroplast-derived SA biosynthesis, converting chorismate to isochorismate, a direct precursor of SA (Bari and Jones 2009). Meanwhile, the PAL pathway, regulated by the PAL gene family, converts phenylalanine to trans-cinnamic acid, contributing to SA synthesis. Accumulated SA is transported to surrounding leaf cells, where it initiates systemic acquired resistance (SAR) as a signal molecule. SA binds to NPR1 (nonexpressor of PR genes 1) in the cytoplasm, inducing a conformational change that releases NPR1 from an inhibitory complex with thioredoxin (Mishra et al. 2024). Active NPR1 then translocates to the nucleus and interacts with TGA transcription factors, leading to the expression of pathogenesis-related (PR) genes such as PR1, PR2, and PR5. These PR genes encode proteins with various defense functions. Notably, PR1 and PR5 proteins enhance lignification to strengthen the cell wall, forming a physical barrier against microbial invasion. Additionally, PR2, a  $\beta$ -1,3-glucanase, degrades the cell walls of invading fungal pathogens, preventing infection on the leaf surface. SA's systemic distribution within the plant body promotes SAR, establishing a long-term defense state in uninfected leaves and increasing resilience to subsequent microbial attacks. Interestingly, some beneficial microbes on the leaf surface have evolved mechanisms to evade this SA-induced immune response (Zhang et al. 2020). For instance, specific strains of

*P. fluorescens* produce SA-degrading enzymes, which neutralize the surrounding SA to avoid immune detection (Chaudhry et al. 2021). This selective adaptation allows beneficial microbes to establish themselves on the leaf surface without triggering plant defenses (Fig. 2D). Thus, SA and its downstream signaling play a dual role in microbial perception and recognition, either activating immunity to repel pathogens or allowing symbiosis with SA-neutralizing beneficial microbes. Through the SA-dependent pathway, plants finely regulate the leaf surface microbial community, balancing immune activation and symbiotic tolerance (Mishra et al. 2024). It is important to note that the ability of beneficial microbes like *P. fluorescens* to neutralize SA suggests a sophisticated immune evasion strategy that can be linked to their capacity to produce antimicrobial peptides (AMPs) or other chemical signals that disrupt pathogen colonization.

The jasmonic acid (JA)-mediated signaling pathway is crucial for controlling microbial perception and immune responses, particularly in defense against necrotrophic pathogens. JA is synthesized upon wounding, pathogen attack, or herbivore grazing, coordinating defense responses throughout the plant, especially within vascular tissues (Roychowdhury et al. 2024). JA biosynthesis begins in the chloroplast, where linolenic acid is converted to 12-oxo-phytodienoic acid (OPDA) via enzymes such as LOX2 (lipoxygenase 2) and allene oxide synthase. OPDA is then transported to the peroxisome, where it undergoes a series of  $\beta$ -oxidation reactions to produce JA. In response to microbial attack, JA conjugates with isoleucine via the JAR1 (JA resistant 1) enzyme, forming the active signaling compound JA-Ile. This JA-Ile binds with its receptor complex COI1-JAZ (coronatine-insensitive 1-JA ZIM-domain protein), leading to the ubiquitination and degradation of JAZ repressor proteins (Fig. 2D). Without JAZ proteins, MYC transcription factors can freely enter the nucleus, activating JA-responsive genes. These genes include those encoding PR proteins such as PDF1.2 and protease inhibitors, which inhibit microbial growth and prevent pathogen invasion. Protease inhibitors disrupt the activity of pathogen-derived proteases necessary for nutrient acquisition and tissue invasion. Additionally, JA induces the synthesis of AMPs targeting microbial membranes, providing an additional layer of direct defense within the vascular tissue. Certain symbiotic microbes, such as nitrogen-fixing rhizobia, can manipulate JA signaling to their advantage. Rhizobia secrete specific nodulation (Nod) factors, which indirectly reduce JA levels, minimizing immune resistance upon entry into plant tissues. By degrading ethylene, a signaling molecule that cross-communicates with the JA pathway, rhizobia can further suppress JA signaling in the stem, promoting colonization within vascular tissues. Under multiple stresses, such as wounding and pathogen attack, JA signaling interacts with other pathways, particularly the ethylene (ET) pathway. This JA-ET crosstalk enhances the expression of defense-related genes, modulating the intensity of the immune response (Bari and Jones 2009). However, some pathogens, like *P. syringae*, produce coronatine, a molecular mimic of JA-Ile, which hijacks the JA pathway by binding to COI1, inappropriately activating JA-responsive genes in favor of the pathogen rather than the plant. This highlights the complexity of microbial perception and JA signaling within stem tissues, emphasizing the balance plants maintain between initiating defense and allowing symbiosis. Through JA-mediated signaling, stems can dynamically regulate microbial perception and recognition, deploying specific defense strategies against pathogen attacks while selectively permitting beneficial microbes. This intricate regulation underscores JA's role as a key mediator in the immune environment of stem tissues.



**Figure 2.** This figure illustrates the complex interactions between plant roots and beneficial microbes in the rhizosphere, focusing on microbial evasion of plant immune responses and the steps of rhizosphere colonization. The image is divided into four panels (A–D) that highlight different aspects of microbial colonization and immune modulation mechanisms. (A) Microbial recognition and evasion: this panel demonstrates how beneficial microbes evade plant immune recognition. Pathogen-associated molecular patterns (PAMPs), such as flagellin and chitin, are detected by plant receptors (e.g. FLS2, EFR, and LYK5). Certain microbial proteins (e.g. Ecp6) can mask or evade these responses, helping microbes avoid immune activation. (B) Immune signaling modulation: beneficial microbes can alter plant immune signaling. Nod factors, flagellin, and other MAMPs are detected by receptors, activating signaling cascades like MAPK and CDPK. This leads to the expression of defense genes, such as those for camalexin and glucosinolate, and the production of ROS via calcium ( $\text{Ca}^{2+}$ ) channels and respiratory burst oxidase homolog (RBOHD). (C) Colonization process: this panel outlines the colonization stages for nonsymbiotic bacteria, including chemotaxis, root attachment, biofilm formation, and endophytic penetration. Key steps involve sensing root exudates, selecting infection sites, and overcoming plant immunity, with microbial competition for scarce elements like iron and phosphorus also shown. (D) Effector-mediated immune suppression: this panel illustrates how bacterial and fungal effectors suppress plant immune responses. Bacterial effectors (e.g. NopL) and fungal small secreted proteins (SSPs, such as MiSSP7) interfere with host signaling pathways, such as SIPK, MPK4, and CDPK. This leads to changes in transcriptional regulation, influencing defense-related gene expression and promoting root colonization.

## Balancing microbes species selection and diversity

The mechanisms by which plant exudates influence microbial species selection and diversity involve a complex interplay of biochemical signaling and resource-driven dynamics. These dynamics are essential for determining the recruitment, competition, and cooperation among microorganisms in the rhizosphere, thus optimizing microbial communities and sustaining ecosystem functions (Yin et al. 2021). Moreover, the recruitment of microbial species is tightly regulated by plant exudates, which serve as selective cues for microbial communities. Environmental stress, such as salt stress or drought, triggers the plant to release exudates that favor specific microbial species capable of thriving under such conditions. This selective recruitment process is crucial for maintaining microbial diversity in the rhizosphere. For instance, during salt stress, the increased secretion of certain organic acids like citric acid and malic acid can attract halotolerant bacteria, fungi, and actinobacteria, which can mitigate the effects of salt by producing enzymes that break down toxic compounds. At the same time, drought stress may lead to a greater abundance of drought-tolerant microbes, such as *Bacillus* and *Pseudomonas* species, which help to retain soil moisture and promote plant survival. These selective processes are critical in determining the balance between microbial species in the rhizosphere, ensuring that beneficial microbes are selected to enhance plant stress tolerance. Additionally, the interactions between plant exudates and microbial communities are not only dependent on environmental conditions but also influenced by plant genotype, as different genotypes may release distinct exudate profiles. This can lead to variation in microbial community composition, further enhancing ecological flexibility and resilience. As chemical signals, plant exudates attract specific microbial species based on their metabolic preferences, recruiting those that possess specific receptors or metabolic pathways to detect and utilize compounds in the exudates (Bahar et al. 2010). This recruitment process is not random but rather targeted, guided by microbial capacities to recognize and metabolize the chemical composition of exudates, thus facilitating selective attraction (Berendsen et al. 2012). Additionally, certain exudates regulate microbial behavior through quorum sensing, a cell-density-dependent mechanism that microbes use to coordinate gene expression (Hartmann and Schikora 2012, Venturi and Keel 2016). Quorum sensing (QS) is mediated by small diffusible signal molecules such as *N*-acyl homoserine lactones in Gram-negative bacteria and autoinducing peptides in Gram-positive bacteria. As microbial populations increase, these QS signals accumulate in the environment until they reach a threshold concentration that triggers coordinated changes in gene expression, regulating behaviors like biofilm formation, virulence, and secondary metabolite production. Importantly, plant exudates contain a variety of chemical compounds—such as phenolic acids, flavonoids, and organic acids—that can either mimic or interfere with QS signal molecules. By binding to QS receptors or altering the stability of these signals, exudate components modulate QS-regulated gene expression, allowing plants to influence microbial functional behaviors within the rhizosphere. While selective recruitment favors certain beneficial microbes, the heterogeneity of root exudates also supports microbial diversity through niche differentiation (Kiers et al. 2011, Shi et al. 2011). Temporal and spatial variations in exudate composition create diverse niches within the rhizosphere, enabling the coexistence of different microbial species, each adapted to utilize different exudate components (Bulgarelli et al. 2012). This resource-driven

separation minimizes direct competition for the same substrates, promoting the coexistence of varied microbial communities. The presence of multiple niches enhances the functional diversity of the microbial community, as different species contribute to ecosystem services such as nutrient cycling and pathogen suppression (Philippot et al. 2013).

Research has shown that plants can also modulate the availability of certain exudate compounds in response to the presence of specific microbial species, thereby further refining the microbial composition in the rhizosphere. This feedback loop plays a significant role in sustaining both microbial diversity and the stability of the plant–microbe symbiosis. Plant exudates also mediate competitive and cooperative interactions among microbes, further shaping microbial diversity and community composition. Within the rhizosphere, microbial species such as *Pseudomonas*, *Bacillus*, and arbuscular mycorrhizal fungi (AMF) engage in both competitive and cooperative interactions, shaping community structure and function. These interactions are influenced by nutrient availability, environmental conditions, and microbial metabolic capabilities. In soybean, *Bradyrhizobium* spp. interact with AMF to enhance nitrogen-fixation efficiency, while competition with *Bacillus* spp. can limit their nodulation efficiency under nitrogen-rich conditions. Furthermore, in tomato (*Solanum lycopersicum*), *Bacillus subtilis*-produced exopolysaccharides facilitate AMF colonization, improving drought resistance by enhancing water uptake. These findings suggest that microbial interactions are highly crop-specific, emphasizing the need to tailor microbial inoculants (MIs) based on host plant species. Furthermore, research has highlighted that cooperative microbial interactions can result in synergistic effects, where the combined action of different species leads to greater plant benefits, such as enhanced nutrient uptake and stress resilience. This cooperation is often driven by the exchange of metabolic by-products, reinforcing the necessity of considering microbial consortia in inoculant design. In some cases, exudates trigger competitive mechanisms, such as the production of antibiotics or siderophores (Wang et al. 2021, Wu et al. 2023). Certain microbes produce antibiotics to inhibit competitor growth, while others produce siderophores that sequester iron, restricting its availability to competing microbes and giving siderophore producers an advantage (Kiers et al. 2011). This selective inhibition prevents any single microbial species from dominating the rhizosphere, fostering community diversity. In terms of cooperation, specific exudates promote positive interactions like cross-feeding, where one microbial species utilizes the metabolic by-products of another. This metabolic interdependence supports microbial coexistence, thereby enhancing community stability. Such division of labor within the microbial community allows multiple species to thrive and contributes to the ecosystem's overall functionality. Plant exudates create feedback loops, influencing microbial recruitment and diversity (Chaparro et al. 2014). This dynamic interaction between plants and microbes ensures that microbial community structures continuously adapt to environmental changes, promoting rhizosphere stability and resilience.

Flavonoids, organic acids, and sugars in exudates can selectively attract beneficial microbes, such as nitrogen-fixing bacteria (e.g. *Rhizobia* and *Azospirillum*) or plant growth-promoting rhizobacteria (PGPR) like *Pseudomonas* and *Bacillus* (Badri et al. 2009). For instance, phenolic compounds in exudates can regulate quorum sensing pathways in PGPR, influencing biofilm formation and antimicrobial production (Venturi and Keel 2016). These phenolic compounds may act by interfering with the binding of QS signal molecules to their receptors or by mimicking QS signals, thereby fine-tuning the transcription of genes associated with collective



microbial behaviors. Fast-growing bacteria such as Proteobacteria are drawn to easily degradable sugars, whereas stress-resistant groups like Actinobacteria thrive on phenolic compounds due to their complex structure and slower degradation rate (Afridi et al. 2024, Tong et al. 2024). Certain bacteria can degrade complex organic compounds into simpler forms, making them available to other microbes (Zhalnina et al. 2018). Furthermore, as specific microbes metabolize exudates, they may alter the chemical environment of the rhizosphere, influencing the type and quantity of exudates released by the plant. Depending on the plant's metabolic response, these changes can either reinforce the presence of the initial microbial community or create opportunities for recruiting new microbial groups (Sasse et al. 2018).

### Impacting microbes chemotaxis and motility

Chemotaxis signaling pathways are highly conserved across various bacterial species. When bacteria move toward root exudates, this process is initiated by transmembrane chemotaxis receptors, known as methyl-accepting chemotaxis proteins (MCPs), which detect chemoeffectors in root exudates (Feng et al. 2021). MCPs typically form a ternary complex with the CheA histidine kinase and the coupling protein CheW. Structurally, MCPs consist of an extracellular ligand-binding domain responsible for signal detection and an intracellular methyl-accepting (MA) domain for adaptation—a key feature of MCPs (Sampedro et al. 2015). Upon binding to ligands such as sugars and amino acids, MCPs initiate a signaling cascade across the cell membrane, which regulates CheA autophosphorylation through CheW (Lacal et al. 2010).

Within the two-component system, phosphorylated CheA interacts with CheY, promoting the transphosphorylation of CheY, which subsequently modulates motor proteins to direct bacterial movement. The accumulation of phosphorylated CheY propels bacterial motility toward the signal source, while dephosphorylation reduces chemotactic behavior. The methylation state of the MA domain is critical for this adaptation mechanism, with methylation enhancing CheA activity and demethylation reducing it (Sampedro et al. 2015). This dynamic regulation allows bacteria to continuously sense and respond to chemoattractant gradients within the rhizosphere.

The concentration of root exudates decreases with increasing distance from the root. Recent studies have introduced the concept of chemotactic signal relays, suggesting that bacteria may release secondary chemotactic signals to compensate for the diminishing exudate concentration (Cremer et al. 2019, Insall et al. 2022). Although specific bacterial signaling molecules have yet to be identified, this mechanism indicates that bacterially generated signals may reinforce the chemical gradient, promoting bacterial migration toward the root zone. Additionally, chemotaxis is influenced by interspecies microbial interactions (Tian et al. 2021), including bacterial attraction to root-associated fungal exudates (Jiang et al. 2021, Mesny et al. 2023) (Fig. 2C).

Numerous studies have provided insights into the chemotactic behaviors of various bacterial species in the rhizosphere. For example, multiple MCPs and their corresponding ligands have been identified in *Pseudomonas*, *Bacillus*, and *Sinorhizobium* species. *Bacillus subtilis* utilizes multiple chemotaxis receptors to colonize root surfaces, while the colonization of *P. putida* KT2440 and *B. velezensis* SQR9 is driven by various root exudate compounds (Ortega et al. 2017, Feng et al. 2019). Notably, *Pseudomonas* species exhibit chemotactic responses to over 140 compounds, establish-

ing them as models for studying MCP structure–function relationships (Sampedro et al. 2015). In *P. putida* KT2440, 27 MCPs have been identified, each responsive to a range of signaling molecules such as amino acids, fatty acids, sugars, and secondary metabolites. Likewise, *B. velezensis* SQR9 contains eight MCPs, including McpA, McpB, and others, indicating its capacity for diverse chemoeffector recognition (Corral-Lugo et al. 2016, Liu et al. 2020). Root exudates also enhance bacterial motility; for instance, root-secreted sucrose promotes the synthesis of the extracellular polymeric substance levan in *B. subtilis*, which regulates flagellar synthesis, and *Arabidopsis* mutants lacking sucrose secretion exhibit reduced root colonization by *B. subtilis* (Tian et al. 2021). Additionally, polysaccharides in root exudates stimulate surfactin production, essential for bacterial motility (Debois et al. 2015, Hoff et al. 2021), while inositol enhances swimming motility in *Pseudomonas* by repressing the transcriptional regulator DksA, an inhibitor of motility (Vilchez et al. 2020, O'Banion et al. 2023, Sánchez-Gil et al. 2023).

### Promoting microbial community migration

Bacterial chemotaxis and motility are critical for determining bacterial colonization sites and migration patterns along plant roots (Fan et al. 2012, Gao et al. 2013, Tovi et al. 2019, O'Neal et al. 2020). This process is mediated by signaling pathways that guide bacteria toward specific regions based on chemical cues present in root exudates. MCPs are pivotal in these pathways, as they sense the chemical composition of exudates and initiate signal transduction cascades. This signaling leads to changes in bacterial motility and spatial organization, enabling bacteria to move toward areas rich in exudates. Root zones with higher exudation, such as the elongation zone located just behind the root tip, release a diverse array of signaling molecules that attract bacteria, thereby creating colonization hotspots for microbial communities (Darrah 1991, Marschner et al. 2011).

Furthermore, chemotaxis and motility facilitate dynamic colonization, allowing bacteria to relocate in response to shifts in root exudation patterns over time. Initially, chemotactic signals direct bacteria to specific root zones; however, as root development progresses and the distribution of exudates changes, bacterial migration adjusts accordingly. This adaptability allows bacteria to follow root growth and maintain optimal access to nutrient-rich zones. Influenced by root-derived chemoattractants and repellents, chemotactic pathways regulate not only the site of initial attachment but also subsequent migration to new exudate-rich regions as the root matures (Zboralski and Filion 2020). Additionally, bacterial relocation may serve to evade immune-activating zones along the root, where certain root cells produce antimicrobial compounds that deter colonization (Fröschel et al. 2021, Verbon et al. 2023).

Evidence for these chemotactic and migratory processes is observed across various bacterial species and plant systems. For instance, *Bacillus megaterium* NCT-2 is initially found in the elongation zone of maize roots but subsequently colonizes the meristematic and root hair zones over time (Chu et al. 2018). In another example, *Azospirillum brasilense* mutants lacking essential chemoreceptors for root exudate-directed chemotaxis exhibit impaired accumulation on the rhizoplane, highlighting the critical role of chemotactic perception in root colonization (O'Neal et al. 2020). Moreover, root-secreted ROS function as repellents, guiding bacterial migration away from root tips and into more favorable zones (Fig. 2C). In *Pseudomonas*, the  $\Delta$ morA mutant's inability to migrate away from immune-activated sites severely limits



its capacity for rhizosphere colonization, underscoring the importance of motility in successful colonization (Liu et al. 2018). Despite these insights, challenges remain in accurately measuring bacterial colonization across different root zones. Traditional microscopy-based methods often capture only partial root areas and may introduce observational biases, complicating a comprehensive understanding of colonization dynamics (Cao et al. 2023).

## Application of microbiome recruitment and assembly for regulating plant health

Microbiome recruitment and assembly strategies play a vital role in enhancing plant health by optimizing microbial communities. For instance, the recruitment of beneficial microbes can mask pathogenic bacteria and boost plant disease resistance. Additionally, increasing rhizosphere microbial diversity has been shown to improve plant productivity and stress tolerance. Allelopathic recruitment, where plants release specific compounds to attract beneficial microorganisms, also plays a critical role in stress mitigation. Furthermore, coordinating microbial communities to enhance nutrient utilization represents a sustainable approach to improving crop yields. In the subsequent section, we delineate several illustrative cases demonstrating microbiome recruitment and assembly strategies hold significant promise for advancing plant health management (Table 2, Supplementary Table 1).

### “Masking pathogenic bacteria” to reduce their infection

In recent years, plant infection diseases are globally on the rise (Yang et al. 2023), causing up to 30% of global harvest losses (Savary et al. 2019). The health status of plants is closely related to their microbial communities in microhabitats, such as interroots and leaves. A variety of microorganisms, including beneficial microorganisms and pathogenic bacteria, exist inside and outside the plant body, among which pathogenic bacteria are able to cause diseases by invading plant tissues, which can seriously affect plant growth and yield. However, studies have shown that beneficial microorganisms are able to inhibit the invasion of pathogenic bacteria in a variety of ways, such as competing for resources, producing antimicrobial substances, and inducing plant immunity. Additionally, beneficial microbes can also enhance plant immunity by activating systemic resistance mechanisms. This includes inducing SAR or induced systemic resistance (ISR), which can improve the plant's ability to respond to pathogen challenges. For instance, certain strains of *Bacillus* and *Pseudomonas* can trigger the production of ROS and other defense-related molecules, bolstering the plant's natural immune response to pathogens (Dimkić et al. 2022). Therefore, the recruitment and assembly of microbial communities is gradually being considered as a potential strategy to regulate plant health by optimizing the microbial environment around plants to mask the colonization and spread of pathogenic bacteria (Fig. 3A).

The RIPENING-INHIBITOR (RIN) in tomatoes is a key transcription factor that regulates fruit ripening and also plays an important role in plant disease resistance. Yang Keming et al. (2023) investigated how RIN mediates the recruitment and assembly of rhizosphere microbiomes to enhance plant resistance to soil-borne pathogens. The study investigated the role of the RIN gene in the regulation of plant microbial communities, especially its effect in microbial-mediated disease resistance, using wild-type (WT) tomato and its homozygous RIN mutant (*rin*). It was found

that RIN not only promoted fruit ripening, but also slightly improved plant disease resistance under aseptic conditions, with WT tomato exhibiting lower disease severity and pathogen counts than the *rin* mutant. This disease resistance effect was further enhanced under conditions where natural microbial communities were present, with WT plants showing a significant reduction in disease severity and pathogen numbers. These results suggest that the effect of RIN on disease resistance is not only directly related to plant genotypes, but also enhanced through interactions with the interroot microbial community. Further macrogenomic analyses revealed significant differences in the composition and function of the interroot microbial communities of the WT and *rin* mutants. The microbial communities of the WT plants showed higher  $\alpha$ -diversity, and in particular, the relative abundance of the phylum *Actinomycetes* was higher in the WT plants. It was also found that the abundance of *Actinomycetes* was negatively correlated with the abundance of *R. solanacearum*, suggesting that *Actinomycetes* may mitigate the disease by inhibiting the growth of pathogenic bacteria. In addition, the interroot microbial communities of WT plants demonstrated more complex cooccurrence networks, suggesting that these microbial communities may inhibit the spread of pathogens through stronger competitive pressures. *Actinomycetes* played an important role in the microbial network of WT plants, which gradually increased with advancing stages of plant development, especially during fruit ripening. Root secretion analyses revealed a significant change in the composition of secretions in the *rin* mutant, which secreted a reduced amount of metabolites compared with WT plants, especially some organic acids, sugars, and alkaloids (e.g. riboflavin and 3-hydroxyflavonoids) that are associated with disease suppression. Further experiments showed that root secretions of WT plants could significantly affect the composition of soil microbial communities and increase the relative abundance of *Actinomycetes*. These results suggest that WT plants drive the recruitment of disease-inhibiting microorganisms through root secretions, thereby enhancing their disease resistance. Finally, the role of riboflavin and 3-hydroxyflavone in disease suppression was verified by greenhouse experiments. Disease severity was significantly reduced in *rin* mutants administered with both compounds, approaching the level of WT plants. It was also found that 3-hydroxyflavonoids and riboflavinoids could indirectly reduce the abundance of pathogenic bacteria by impacting the composition of the microbial community. In summary, the RIN gene significantly affected tomato disease resistance by regulating root secretions and the assembly of interroot microbial communities, especially by enhancing the recruitment of disease-suppressive microbes such as *Actinomycetes*. These results provide new ideas and theoretical basis for strategies to enhance crop disease resistance by regulating plant microbial communities (Fig. 3B).

The application of RIN-mediated root exudates to recruit disease-suppressive microbiota presents significant potential for enhancing plant disease resistance. However, several critical considerations emerge: (i) optimizing exudate concentrations is crucial to avoid imbalances that affect microbial recruitment and stability. (ii) The mechanisms of how specific microbes, such as *Streptococcus lysimachiae*, are recruited and interact with pathogens remain unclear and require further research. (iii) Soil type, microbial diversity, and environmental conditions may impact the stability and adaptability of this strategy. (iv) Maintaining the long-term stability of disease-suppressive microbes is challenged by factors such as crop rotation and seasonal changes, which could alter microbial community dynamics.

Table 2. Research studies performed to promote plant health by using microbiome recruitment and assembly.

Application	Plant	Condition	Microbial species	Main effects	Action mechanisms	References
Reduce pathogenic bacteria infection	Tomato ( <i>Solanum lycopersicum</i> )	<i>Fusarium oxysporum</i> f. sp. <i>lycopersici</i> (FOL)	<i>Sphingomonas</i> sp., <i>Sphingobium</i> sp., <i>Lysobacter</i> sp. et al.	Inhibition of pathogens. Promoted plant growth and health.	Enhanced expression of defense-related genes in tomato roots and promoted pathogen inhibition by inducing systemic resistance.	Jin et al. (2024)
Affect plant productivity	Tomato ( <i>Solanum lycopersicum</i> )	Chitosan-encapsulated microbial biofertilizer ( <i>Pseudomonas fluorescens</i> ).	<i>Pseudomonas</i> sp., <i>Bacillus</i> sp., <i>Lysobacter</i> sp. et al.	Improved crop productivity. Improved soil fertility. Promoted plant health.	Dissolved phosphate in the soil, promoted plant uptake of phosphorus, facilitated root elongation, crop maturity, and proliferation.	Beula Isabel et al. (2024)
Enhance plant stress	Maize ( <i>Zea mays</i> )	Hg stress (20 mg/kg Hg, 25 days)	<i>Fusarium</i> sp., <i>Exophiala</i> sp., <i>Meyerozyma</i> sp. et al.	Promoted plant growth and alleviated the effects of mercury-induced phytotoxicity and biological stress.	Promoted IAA production and phosphate dissolution.	Feng et al. (2024)
	Vetiveria zizanioides ( <i>V. zizanioides</i> )	Sb and As stress (30 mg/kg Sb and As, 120 days)	<i>Sphingomonas</i> sp., <i>Rhodospirillum</i> sp., <i>Streptomyces</i> sp. et al.	Effectively reduced toxicity through microbial oxidation. Promoted plant growth and photosynthesis. Enhanced the accumulation of flavonoids and alleviated soil borne diseases such as root rot. Promoted plant growth.	The key genes encoding arsenate reductase is responsible for the reduction of As and Sb.	Yu et al. (2024)
	<i>Panax notoginseng</i>	Light stress (correspond to 5%, 15%, and 30% of full sunlight (~100000 lux), 60 days)	<i>Pseudomonas</i> sp., <i>Arthrobacter</i> sp., <i>Paenibacillus</i> sp. et al.	Enhanced the accumulation of flavonoids and alleviated soil borne diseases such as root rot. Promoted plant growth.	It is related to the mechanism by which receptor like kinases interact with transcription factors and phosphorylate and regulate flavonoids.	Fang et al. (2024)
	Rice ( <i>Oryza sativa</i> )	Cold stress (15°C, 14 days)	<i>Pseudomonas</i> sp., <i>Enterobacter</i> sp., <i>Bacillus</i> sp. et al.	Promoted plant growth. Improved survival, yield, and quality.	Increased soil nitrogen content and arginine secretion capacity	Zhang et al. (2024)

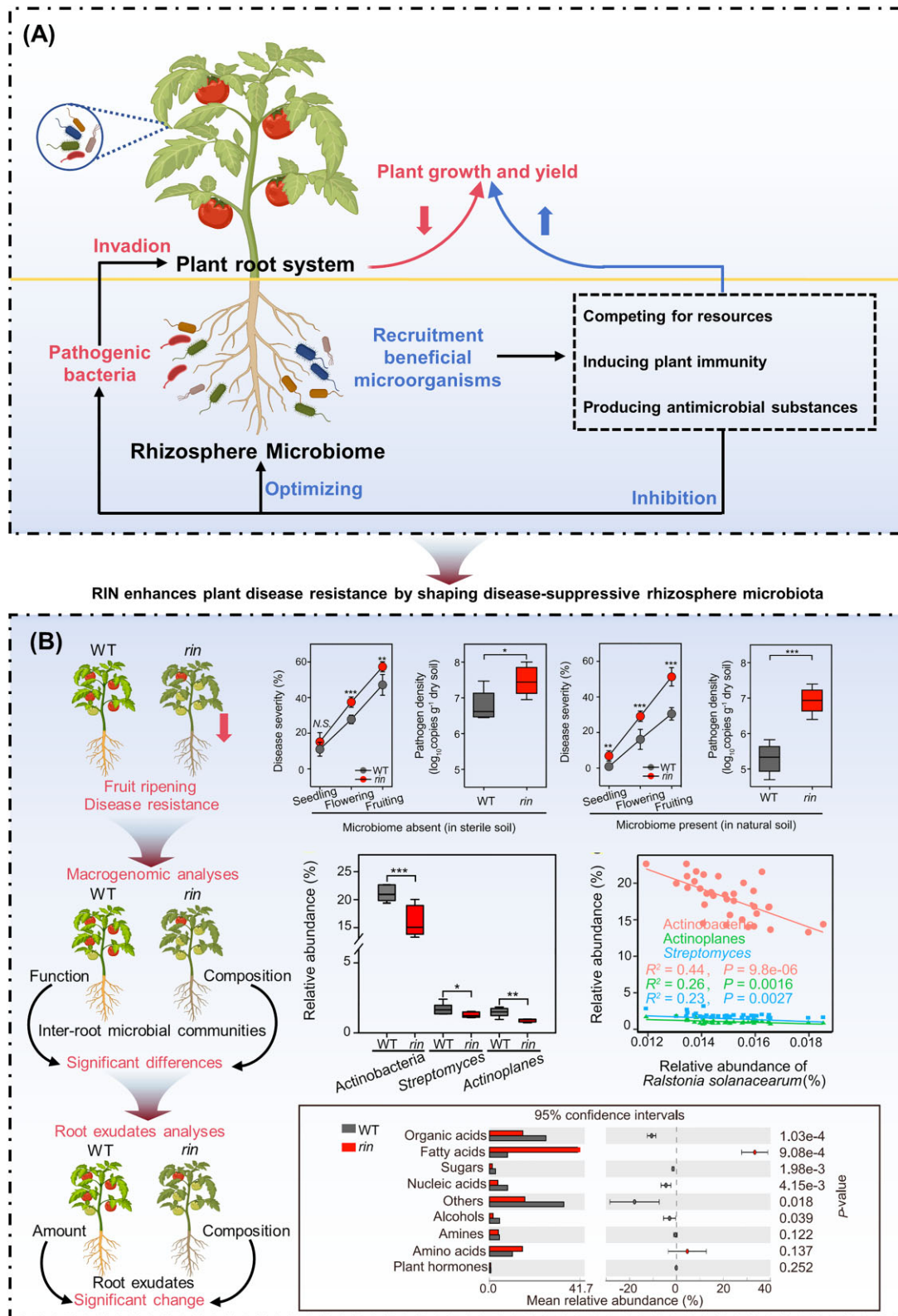
Table 2. Continued

Application	Plant	Condition	Microbial species	Main effects	Action mechanisms	References
Improve plant nutrient utilization	<i>Mimosa pudica</i>	Salt stress (100 and 200 mM NaCl, twice a week, plus once a week with tap water, 65 days), Water stress (watered only once a week with tap water, 65 days)	<i>Pseudomonas</i> sp., <i>Paenibacillus</i> sp., <i>Bacillus</i> sp. et al.	Promoted plant growth and photosynthesis. Accelerated the occurrence of inflorescences.	Exhibited higher superoxide dismutase, glutathione reductase and ascorbate peroxidase activities, proline concentration and root/shoot ratios	Sapiña-Solano et al. (2024)
	Strawberry ( <i>Fragaria × ananassa</i> Duch.)	Cold stress (Grow in cold weather of late fall, from 7 September 2022 to 27 October 2022)	<i>Glomus</i> sp., <i>Pseudomonas</i> sp., <i>Staphylococcus</i> sp. et al.	Alleviated the damage of cold stress and stimulated plant growth.	The perturbation titer of tryptophan metabolism was increased and the expression of related genes was downregulated.	Ayyanath et al. (2024)
	Soybean ( <i>Glycine max</i> )	Introduction of <i>Pseudomonas chlororaphis</i> IRHB3 to aggregate beneficial microbes.	<i>Geobacter</i> sp., <i>Geomonas</i> sp., <i>Agrobacterium</i> sp. et al.	Stimulated root development. Promoted full utilization of nitrogen and phosphorus. Promoted plant growth and development.	IRHB3 activated rhizoma-associated gene expression and rapidly awakened the JA signaling pathway to induce resistance.	Wei et al. (2024)
	Rice ( <i>Oryza sativa</i> )	Introduced beneficial bacteria (Arbuscular mycorrhizal fungi).	<i>Pseudomonas</i> sp., <i>Sphingomonas</i> sp., <i>Bacillus</i> sp. et al.	Increased nutrient use efficiency. Increased plant growth and yields. Reduced agrochemical inputs.	Facilitated plant uptake of nitrogen and phosphorus and increased photosynthetic efficiency. Improved microbial community structure.	Yang et al. (2024)
	Wheat ( <i>Triticum aestivum</i> )	Nanoparticle-mediated modulation of plant performance and microbiome dynamics	<i>Bacteroides</i> sp., <i>Nitrosomonas</i> sp., <i>Pseudomonas</i> sp. et al.	Reduced pathogenic infections. Increased nutrient use efficiency. Promoted plant growth and health.	Increased photosynthetic efficiency and antioxidant enzyme activity. Improved soil pH and nutrient content. Regulated the plant microbiome.	Li et al. (2024)



Table 2. Continued

Application	Plant	Condition	Microbial species	Main effects	Action mechanisms	References
	Pea ( <i>Pisum sativum</i> )	Inoculated with Bioinoculants (Arbuscular mycorrhizal fungi).	<i>Pseudomonas</i> sp., <i>Cytophaga</i> sp., <i>Rhizobium</i> sp., <i>Bacillus</i> sp. et al.	Accelerated soil nutrient cycling. Improved nutrient utilization by plants. Promoted plant growth and health.	Microbial inoculation indirectly affected carbon and other nutrient acquisition by increasing soil microbial diversity and enriching the microbiota involved in nutrient cycling.	Calderon and Dangi (2024)
	Rice ( <i>Oryza sativa</i> )	Used OSCIPK2-overexpressing transgenic rice plants	<i>Phenyllobacterium</i> sp., <i>Sphingomonas</i> sp., <i>Pleomorphomonas</i> sp. et al.	Improved nutrient utilization by plants. Reduced salt stress. Promoted plant growth and health.	Overexpression of OSCIPK2 in the root system promotes citric acid production by uptake of rhizosphere nitrogen-fixing bacteria in rice under low nitrogen stress.	
	Wheat ( <i>Triticum aestivum</i> )	Introduced beneficial bacteria (Phosphate-solubilizing Microorganisms, PSMs).	<i>Pseudomonas</i> sp., <i>Lysinibacillus</i> sp., <i>Streptomyces</i> sp., <i>Bacillus</i> sp. et al.	Increased phosphorus uptake and utilization by plants. Promoted plant growth and health.	PSMs secreted organic acids and phosphatases and promoted plants to increase root weight and root length to accelerate phosphorus uptake and utilization.	Pang et al. (2024)



**Figure 3.** Rhizosphere microbiome dynamics and their impact on plant health and productivity. (A) Interroot microbial communities enhance plant disease resistance through mechanisms, such as recruitment of beneficial microorganisms, inhibition of pathogen invasion, competition for resources, production of antimicrobial substances, and induction of plant immunity. This optimization fosters disease-inhibiting microbial communities, increasing plant resistance. (B) The RIN gene influences disease resistance by shaping the rhizosphere microbiome. A comparison of wild-type (WT) and RIN (ripening inhibitor) mutant plants revealed that WT plants had greater rhizobial microbiota diversity, which correlated with reduced disease severity and improved health. In contrast, *rin* mutants exhibited altered microbial composition and root exudates, negatively affecting microbial function. Macrogenomic analyses indicated that WT plants recruited more diverse and active microbial communities, effectively suppressing pathogens and supporting growth. Meanwhile, *rin* mutants showed reduced microbial diversity and disease resistance, leading to lower crop yields. RIN enhances disease resistance by optimizing interroot microbial composition, increasing beneficial microorganisms, and decreasing pathogens. (Yang et al. 2023) Copyright © 2023, Elsevier. Some elements in this figure are created with BioRender (BioRender.com) .

## Diversity of rhizosphere microorganisms affects plant productivity

The diversity of rhizosphere microorganisms plays a crucial role in determining plant productivity and health. In this section, “high microbial diversity” refers to an increase in both bacterial and fungal community richness and evenness, while “low-diversity soils” indicate reduced species richness and an uneven distribution of microbial taxa. To quantify these aspects, we utilized the Shannon index, which accounts for both species richness and evenness, and the Chao1 index, which estimates species richness based on the presence of rare taxa. For example, research conducted on wheat fields demonstrated that fields with high microbial diversity had up to 15% higher yields compared to those with low microbial diversity (Ren et al. 2023). A study on tomato plants found that introducing a diverse MI reduced disease severity by 30%, significantly improving plant yield (Guo et al. 2024). During the remodeling of the interroot microbial community, the effect of AMF inoculation on microbial diversity is mainly reflected in regulating the microbial community structure rather than simply increasing the overall diversity index. AMF influences microbial community interactions and ecological functions by altering the inter-root nutrient availability, the composition of root secretions, and microbial competitive relationships, which in turn affects microbial community interactions. Although AMF mainly forms a reciprocal symbiotic relationship with plants, its colonization also affects interroot bacterial and fungal dynamics, which further influences nutrient uptake and tolerance to environmental stresses. In maize, inoculation with AMF increased phosphorus uptake by 40%, resulting in a 10% increase in biomass under phosphorus-limited conditions (de Souza Buzo et al. 2023). Thus, AMF not only enhances productivity by directly promoting plant nutrient uptake, but also enhances crop health by indirectly affecting microbial community structure. Quantitatively, microbial diversity has been linked to improvements in plant productivity across multiple crop species. A meta-analysis of 57 field studies found that, on average, crops grown in soils with high microbial diversity had a 21% increase in yield compared to those grown in low-diversity soils (Hooper et al. 2012). In this context, selection and modification of the rhizosphere microbiome represent an important strategy to improve crop health (Pretty and Bharucha 2014). Therefore, increasing rhizosphere microorganisms diversity is key to achieve high productivity (Fig. 4A).

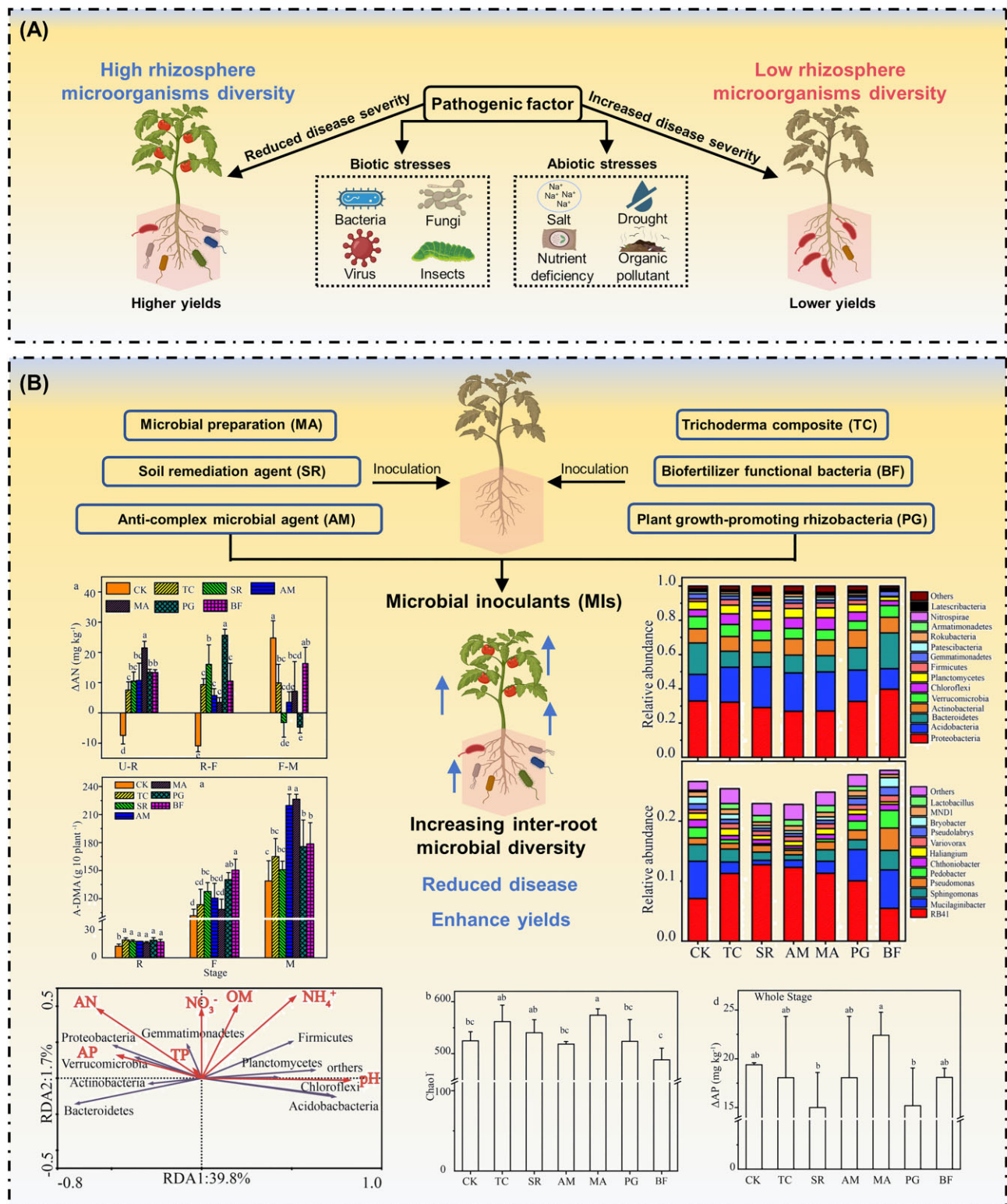
MIIs are a key approach to enhancing microbial diversity in the plant rhizosphere. Chen et al. (2021) investigated the effects of six different MIIs on the growth, nutrient uptake, yield, and soil properties of winter wheat in a farmland located in Jining, Shandong Province, China. A randomized block design was used, with six treatments: *Trichoderma* composite (TC), soil remediation agent (SR), anticomplex microbial agent (AM), microbial preparation (MA), plant growth-promoting rhizobacteria (PG), and biofertilizer functional bacteria (BF). The study measured dry matter accumulation (DMA), nutrient uptake, and yield at various growth stages, including the regreening, flowering, and harvest stages. The results showed that the application of MIIs significantly increased both aboveground and belowground biomass of wheat. Particularly, at the flowering stage, the BF, PG, and MA treatments improved DMA by 48.0%, 37.9%, and 25.5% compared to the control. By the harvest stage, the aboveground dry matter of wheat in the BF, PG, AM, and MA treatments was 26.5%–63.1% higher than the control. Regarding nitrogen uptake, BF and AM significantly enhanced nitrogen absorption, increasing it by 6.0% and 1.1%, respectively, compared to the control. In terms of yield, MIIs

boosted wheat production by 15.2%–33.4%, with the PG, MA, and TC treatments achieving the highest yields of 9.38–10.38 t/ha. In terms of soil nutrients, the application of MIIs significantly increased available nitrogen (AN) and available phosphorus (AP) in the soil. Specifically, during the regreening and flowering stages, the AN content in the PG and MA treatments reached 21.5 g/kg and 25.67 g/kg, respectively. AP levels followed a trend of rising and then declining throughout the growth cycle, with all MI-treated groups showing significant differences from the control at various stages.

Analysis of the soil bacterial community revealed that, although the Shannon index—which accounts for both species richness and evenness—did not show significant differences among treatments, the Chao1 index, an estimator of species richness, was significantly higher in the MA, TC, and SR treatments. This suggests that while the overall diversity (richness plus evenness) of the bacterial community remained relatively constant, there was a notable increase in the number of bacterial species (richness) in these treatments. In other words, MI application may have introduced or stimulated the growth of rare or previously underrepresented bacterial taxa, which was captured by the Chao1 index but not by the Shannon index. The dominant bacterial phyla identified included Proteobacteria, Acidobacteria, and Bacteroidetes; notably, the MA treatment significantly increased the relative abundance of Variovorax. Redundancy analysis further indicated that soil pH had a significant impact on the abundance and composition of the bacterial community. Heatmap analysis demonstrated that AN and AP were positively correlated with Proteobacteria and Bacteroidetes, while showing a negative correlation with pH. These findings imply that MI treatments not only improved soil nutrient content but also modulated the structure of the bacterial community, likely contributing to enhanced wheat growth and yield. In summary, while MI treatments promoted plant growth at different developmental stages, the significant increase observed in the Chao1 index (but not in the Shannon index) underscores that the primary effect of these treatments was an increase in bacterial species richness rather than a marked shift in overall community evenness. This differential response of diversity indices suggests that the functional benefits observed may be closely associated with the enrichment of specific bacterial taxa, highlighting the importance of considering multiple diversity metrics when evaluating the impact of MIIs on soil health and crop productivity. Future studies should also explore fungal and other microbial community responses to provide a more comprehensive understanding of soil microbial diversity and its role in agricultural systems (Fig. 4B).

While current studies demonstrate the short-term efficacy of MIIs, their long-term effects on soil ecological networks warrant deeper examination. Repeated inoculation may cause significant shifts in microbial community composition over time, with some introduced microbes facing competitive exclusion by native populations. For example, a 5-year maize monoculture trial showed that AMF inoculation initially increased phosphorus uptake by 38%–42%, but this benefit diminished to 15%–18% by year four, alongside a reduction in saprotrophic fungal diversity (Yang et al. 2022). This suggests that, over time, introduced microbes may face competitive exclusion by native microbes, highlighting the need for monitoring these dynamics for sustainable inoculant use. Moreover, pulse inoculation strategies (e.g. every three seasons) have been shown to maintain up to 89% of yield benefits compared to annual inoculation, while preserving higher native microbial richness. Furthermore, crop rotation modulates inoculation outcomes: legume-based rotations enhanced MI survival





**Figure 4.** Rhizosphere microbial diversity and its influence on plant productivity. (A) Rhizosphere microbial diversity significantly impacts plant health and productivity. A decline in microbial diversity increases plant vulnerability to biotic stressors (bacteria, viruses, insects, and fungi) and reduces resilience against abiotic stresses (nutrient deficiency, drought, salinity, and organic pollutants), leading to decreased yields. Conversely, high microbial diversity can mitigate these stress effects, enhancing productivity. (B) Strategies to enhance rhizosphere microbial diversity and their benefits include the use of microbial inoculants such as Trichoderma composites (TC), biofertilizer functional bacteria (BF), plant growth-promoting rhizobia (PGPR), antagonistic microbial formulations (AM), and soil remediators (SR). TC and BF suppress diseases by competing with pathogens or producing antimicrobial compounds. PGPR enhance growth via nutrient solubilization and hormone secretion, improving yields and reducing disease severity. AM and SR address soil issues, fostering beneficial microbial communities. Collectively, these strategies increase microbial diversity, promoting resilient communities that resist pathogens, mitigate nutrient deficiencies, and alleviate abiotic stresses. The benefits include reduced disease severity, enhanced crop yields, and improved plant health, highlighting the importance of microbial diversity in sustainable agriculture. (Chen et al. 2021) Copyright © 2021, Springer Nature. Some elements in this figure are created with BioRender (BioRender.com).

by 40% compared to cereal monocultures through root exudate complementarity. Critical knowledge gaps persist regarding ecological succession in inoculated systems. Meta-genomic analyses reveal that 15%–20% of inoculated strains develop CRISPR-associated antimicrobial resistance genes within five generations, raising concerns about horizontal gene transfer. From an agronomic perspective, the “microbial legacy effect”—where prior inoculants alter subsequent crop responses—creates both opportunities and risks. For example, soybeans planted after MI-treated wheat showed 12% yield gains without reinoculation, whereas canola experienced 8% yield penalties due to residual *Pseudomonas* dominance (Fig. 4B).

The study involving the application of various MIs to enhance wheat growth and soil health reveals several key challenges: (i) balancing microbial and chemical treatments: ensuring that the amount and type of MIs do not disrupt the nutrient balance or soil conditions is crucial to maximize their effectiveness. (ii) Understanding microbial interactions: the specific mechanisms by which different microbial agents (e.g. TC versus PGPR) affect soil microbial communities and crop performance remain underexplored, necessitating further investigation. (iii) Impact of soil and environmental variability: soil properties, such as pH and nutrient levels, as well as environmental factors, including seasonal changes, can influence the efficacy and stability of microbial treatments. Seasonal fluctuations in temperature, moisture, and nutrient availability can alter microbial community composition, which in turn may affect the effectiveness of MIs. Therefore, it is essential to account for these variables in the experimental design to ensure that microbial treatments remain stable across different seasons. (iv) Sustainability and long-term effects: the long-term effectiveness of MIs can be influenced by factors such as soil management practices, crop rotation, and tillage. For instance, crop rotation helps maintain microbial diversity and stability by alternating plant species with varying root exudates and nutrient demands, which can prevent the dominance of a single microbial group. Tillage practices, on the other hand, may disrupt soil structure, reduce organic matter, and alter microbial habitats, potentially affecting the long-term success of MIs. These factors need to be addressed to ensure ongoing benefits for crop productivity and soil health.

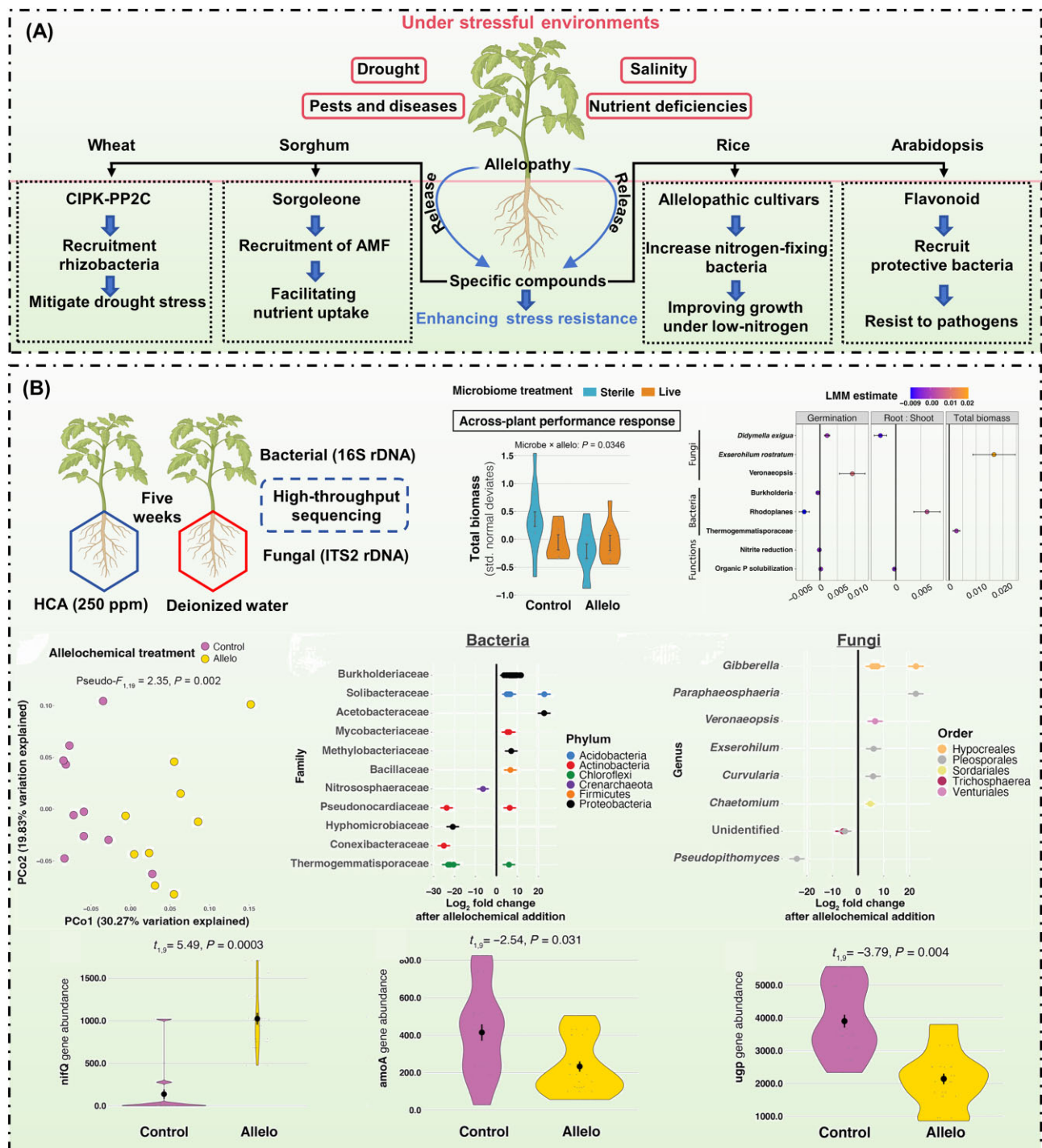
### Allelopathic recruitment of microorganisms to enhance plant stress tolerance

Allelopathy enables plants to release specific compounds that modify the rhizosphere microbiome, thereby attracting beneficial microorganisms that bolster stress tolerance. In saline soils, plants under salt stress may increase the secretion of particular exudates, such as certain amino acids and organic acids, which selectively recruit salt-tolerant microbes. These microbes can reduce the toxic effects of excessive salt and enhance plant salt tolerance by facilitating the breakdown of excess salt or by enhancing the plant's ability to uptake water. In drought conditions, plants may recruit microorganisms capable of synthesizing osmoprotectants or producing phytohormones, such as abscisic acid or cytokinins, which promote drought tolerance. The recruited microbes may also contribute to enhanced nutrient uptake, improved root development, and increased water retention in the soil. For instance, sorghum secretes sorgoleone, which fosters the recruitment of AMF, facilitating nutrient uptake under stress (de Oliveira et al. 2021). Similarly, wheat root exudates enhance the prevalence of beneficial rhizobacteria, which helps mitigate drought stress (Kong et al. 2018). In rice, allelopathic culti-

vars have been shown to increase nitrogen-fixing bacteria in the rhizosphere, improving growth under low-nitrogen conditions (Liu et al. 2021). In response to pathogen attack, *Arabidopsis* release specific root exudates, such as flavonoid, that help recruit protective bacteria to resist pathogens, enhancing biotic stress resistance (Berendsen et al. 2012). Polyak and Sukharevich reviewed the role of allelopathy in recruiting beneficial microorganisms and reported that plants employing this strategy could experience significant stress mitigation. Some species demonstrated a 20%–30% increase in drought tolerance compared to plants lacking such microbial associations. Thus, allelopathic recruitment of microorganisms represents a crucial strategy for enhancing plant tolerance to environmental stresses, offering a pathway to more resilient agricultural practices (Fig. 5A).

Recent studies in Florida scrub ecosystems have further elucidated the relationship between soil microbial communities and plant growth performance. Daniel Revillini et al. (2023) investigated the effects of chemical compounds released by Florida rosemary, such as ceratiolin and its derivative hydrocinnamic acid (HCA), on soil microbial communities. They collected soil samples from ten distinct rosemary scrub patches and applied two treatments: HCA (250 ppm) and a control (deionized water). After 5 weeks, the soil samples were analyzed for microbial community changes using high-throughput sequencing of bacterial (16S rRNA) and fungal (ITS2 rRNA) communities, focusing on shifts in community structure. HCA treatment significantly altered bacterial community composition, whereas fungal community changes were not significant. Within the bacterial community, *Burkholderia tuberum* and *Burkholderia bryophila* became core species with significantly increased relative abundance following HCA treatment. Among fungi, the genera *Gibberella* and *Chaetomium* showed significant increases in abundance. The treatment also impacted bacterial functional genes, increasing the abundance of nitrogen cycle-related genes (e.g. *nifQ*) while decreasing the abundance of ammonia-oxidizing (*amoA*) and phosphate transport (*ugp*) genes. The effects of microbial communities on plant performance were notable. Although HCA treatment reduced plant biomass, this effect was significantly mitigated in the presence of microbial communities ( $P = .034$ ). Specifically, for *Balduina angustifolia*, the microbial community significantly enhanced total biomass ( $P = .0001$ ). The effect of HCA on root ratio varied significantly among plant species ( $P = .016$ ). The study identified significant relationships between specific microbial taxa and plant performance. For instance, the fungal species *Exserohilum rostratum* was positively correlated with total plant biomass, while bacterial genera *Rhodoplanes* and *Bacillus* were negatively correlated with plant biomass and root biomass, respectively. Changes in *nir* and *ugp* functional genes also affected plant performance. Analysis of HCA concentrations in soil samples indicated that active microbial communities had limited effects on HCA degradation ( $t_4 = -0.643$ ,  $P = .55$ ), suggesting a limited role of soil microbes in HCA degradation. This study highlights the complex interactions between HCA, soil microbial communities, and plant growth, revealing that while HCA treatment negatively impacts plant growth, soil microbial communities can partially mitigate these effects. Various microbial taxa and functional genes play key roles in this process, offering new insights into plant mechanisms for coping with environmental stress (Fig. 5B).

The impact of allelopathy on soil microbiome and plant performance presents several challenges: (i) the shift in microbial composition and function under allelopathic influence, particularly the increase in beneficial bacteria and pathogenic fungi, complicates the understanding of plant–microbe interactions. (ii)



**Figure 5.** Plant allelopathy and its role in enhancing plant stress resistance. (A) Plants (such as sorghum, wheat, rice, and *Arabidopsis*) release specific compounds through allelopathy to cope with environmental stress, enhancing plant stress resistance and defense mechanisms. These secondary metabolites (e.g. sorghum ketone Sorgoleone) increase plant stress resistance under adverse conditions such as nutrient deficiency, drought, salinity, and pest damage. For example, allelochemicals enhance stress responses via the CIPK-PP2C signaling pathway and recruit beneficial microorganisms (e.g. arbuscular mycorrhizal fungi) to improve nutrient uptake and drought tolerance. (B) Allelopathy alters the rhizosphere microbial community structure, promoting the enrichment of beneficial microorganisms, thereby further enhancing plant stress resistance. The study employed high-throughput sequencing to analyze the changes in rhizosphere microbial communities under HCA 250 ppm treatment compared to controls, revealing that allelochemical treatment significantly increased microbial diversity, selectively promoting the growth of nitrogen-fixing and protective bacteria while suppressing harmful microbes. The enrichment of these stress-resistant microorganisms effectively improved the overall stress resistance of the plants. (Revillini et al. 2023) Copyright © 2023, John Wiley and Sons. Some elements in this figure are created with BioRender (BioRender.com).



The weak overall effect of allelochemical-altered microbiomes on plant productivity, with significant effects observed only in a single species, suggests limitations in the broader applicability of these findings. (iii) Predictions based on functional gene shifts using algorithms like PICRUSt2 may be imprecise, necessitating more targeted experimental methods. (iv) The long-term adaptation of plants and microbes to persistent allelopathy, which weakens microbial mediation of plant responses, poses challenges for predicting the ecological impact of such stressors.

### Microbial community coordination improves plant nutrient utilization

Recent studies highlight the role of microbial community coordination in enhancing plant nutrient utilization. The interactions between *Pseudomonas*, *Bacillus*, and AMF not only influence microbial community dynamics but also have significant implications for nutrient cycling and plant health. In wheat fields, long-term inoculation with *B. subtilis* improved nitrogen-use efficiency and increased grain yield by 15% over three growing seasons, demonstrating sustained benefits for soil fertility. In perennial cropping systems, AMF communities evolve over multiple years, shifting from *Glomus* spp. dominance to *Rhizophagus* spp. depending on soil nutrient availability and plant age, highlighting the dynamic nature of microbial interactions. These results underscore the importance of considering long-term microbial adaptation when implementing microbiome-based agricultural strategies. Beneficial bacteria such as *Pseudomonas* and *Bacillus* contribute to nutrient mobilization. For instance, a study on wheat showed that *P. putida* improved phosphorus solubilization by 20%, leading to a 12% increase in biomass under phosphorus-limited conditions (Elhaisoufi et al. 2022). Similarly, *Bacillus amyloliquefaciens* was found to enhance potassium uptake in tomato plants, boosting growth by 18% (Egamberdieva et al. 2017). In rice, inoculation with *A. brasilense*, a well-known nitrogen-fixing bacterium, increased nitrogen uptake by 25%, resulting in a 15% rise in grain yield under nitrogen-limited conditions (García de Salamone et al. 2012). Moreover, the interaction between phosphate-solubilizing bacteria and nitrogen-fixers in maize improved nutrient use efficiency by 22%, reducing dependency on chemical fertilizers (Cheng et al. 2023). Thus, harmonizing microbial communities to improve nutrient utilization by plants provides a sustainable way to increase crop yields and reduce environmental impacts (Fig. 6A).

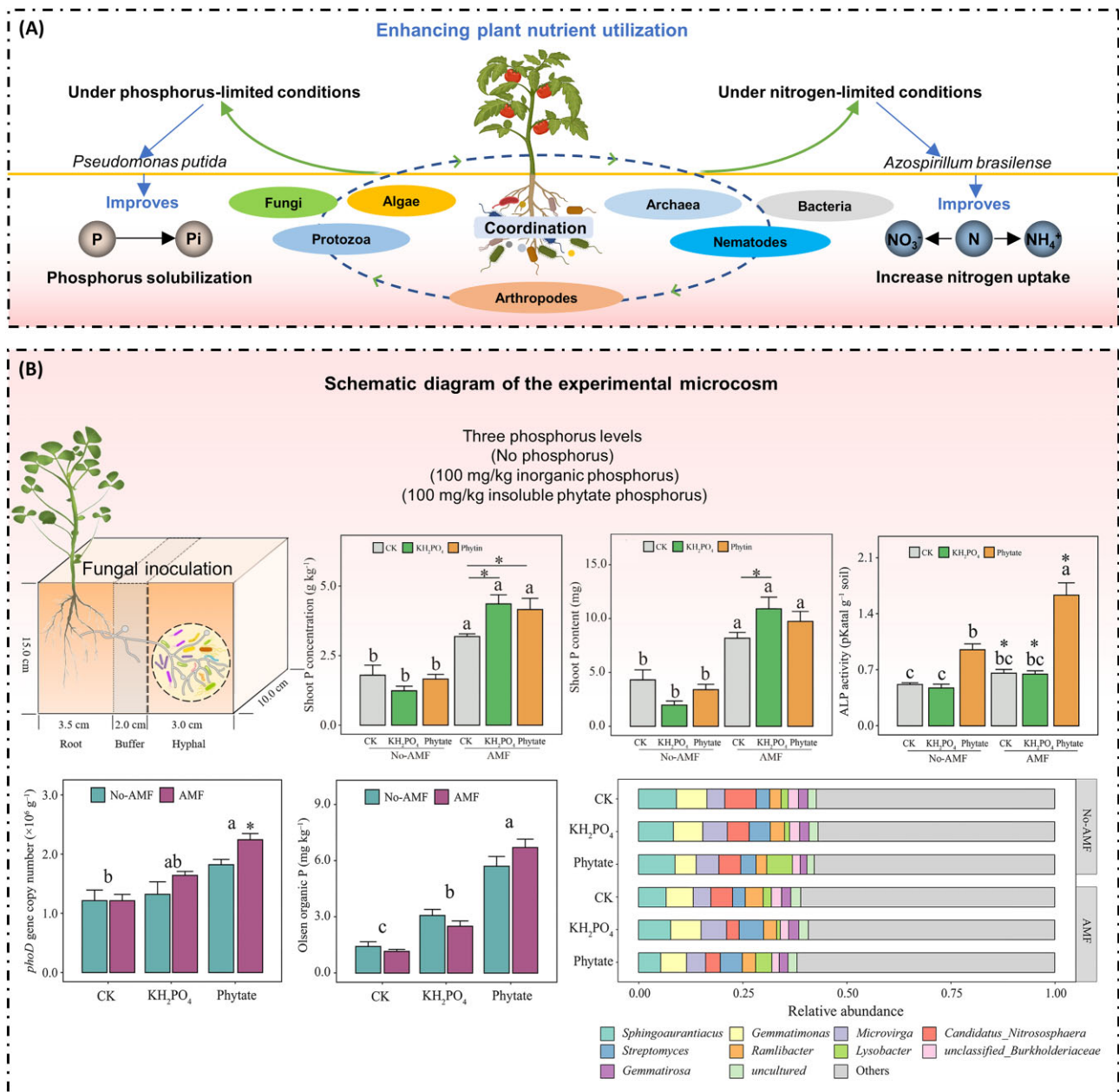
Guiwei Wang et al. (2023) used *Medicago truncatula* (cv Paragio) inoculated with *Rhizophagus irregularis* (spores from Quebec, Canada) to investigate the impact of AMF and different phosphorus levels on plant phosphorus uptake and soil microbial communities. The soil used in the experiment was collected from a maize field in Taian, Shandong, China, characterized by a pH of 6.85 and nutrient levels of 0.26 g/kg total nitrogen, 4.05 g/kg organic matter, 17.43 mg/kg mineral nitrogen, 3.87 mg/kg Olsen phosphorus, and 82.0 mg/kg exchangeable potassium. This soil was sieved and sterilized with gamma radiation to eliminate indigenous microbes. Nutrients were added to the soil, and bacterial filtrates were prepared to stabilize the microbial community before planting. A dual-compartment microcosm system was employed, with a nylon mesh separating the root compartment and a compartment only accessible to fungal hyphae (HC). The design considered two factors: fungal inoculation and three phosphorus levels (no phosphorus, 100 mg/kg inorganic phosphorus, and 100 mg/kg insoluble phytate phosphorus). The experiment lasted about 3 months in a climate-controlled chamber at the Institute of Genetics and Developmental Biology, Chinese Academy

of Sciences, with soil moisture maintained at approximately 70% of field capacity. At the end of the experiment, soil samples from HC were collected, and plant roots and shoots were separated. Shoots were dried to constant weight, and phosphorus content was determined using the method of Thomas et al. (1967). Mycorrhizal phosphorus concentration response and mycorrhizal phosphorus content response were calculated using Janos' (2007) formula. Alkaline phosphatase (ALP) activity, Olsen phosphorus content, mycorrhizal colonization rates, and hyphal length density were measured using standard methods, including Tabatabai and Bremner (1969) and Schoenau and Huang (1991). Statistical analysis included two-way ANOVA for treatment comparison ( $P \leq .05$ ), Kolmogorov-Smirnov normality tests, and Levene's test for homogeneity of variance. Quantitative polymerase chain reaction (q-PCR) for 16S rRNA and *phoD* genes was performed to study microbial community shifts, and principal component analysis (PCA) was used to visualize these changes. Results showed that inoculation with *R. irregularis* significantly enhanced phosphorus uptake, particularly with inorganic phosphorus addition. However, phytate phosphorus addition showed minimal effects on phosphorus absorption. Phytate significantly increased soil ALP activity, while inorganic phosphorus had less impact. Although phytate increased soil organic phosphorus, fungal inoculation did not significantly influence this result. In terms of microbial communities, fungal inoculation caused significant changes in the abundance of bacterial genera, notably *Lysobacter* and *Streptomyces*, under phytate treatment. Additionally, inoculation significantly affected the abundance of phosphorus-cycling genes in the microbial network, particularly increasing the abundance of the *phoD* gene encoding ALP. In conclusion, *R. irregularis* inoculation significantly enhanced phosphorus uptake, especially under inorganic phosphorus conditions, and altered the soil microbial community structure and gene abundance related to phosphorus cycling. These findings contribute to a deeper understanding of the role of mycorrhizal fungi in promoting plant nutrient uptake through microbial interactions (Fig. 6B).

The study of *R. irregularis* and phosphorus levels on plant phosphorus uptake and soil microbial communities presents several key challenges: (i) ensuring effective sterilization of soil without compromising its nutrient content, which can be challenging to balance. (ii) Maintaining consistent soil moisture and replicating field conditions in a climate-controlled environment is critical to avoid variability in plant and microbial responses. (iii) Accurately measuring shifts in microbial communities and gene abundance using complex techniques such as quantitative PCR and PCA can be technically demanding and susceptible to variability, necessitating rigorous quality control.

### Conclusion and prospect

The evidence presented in this review underscores the significance of plant root exudates in attracting beneficial microorganisms, regulating microbial diversity, and enhancing stress resistance. Plant exudates play a crucial role in microbiome recruitment and plant health management, offering new possibilities for sustainable agriculture through their mechanisms: (i) role of plant exudates in microbiome recruitment: plant root exudates act as chemical signals, playing a key role in attracting beneficial microorganisms. These exudates regulate microbial diversity and enhance plant resilience by influencing nutrient solubilization, pathogen suppression, and overall stress tolerance. (ii) Exudate-driven microbial community coordination: exudate-driven microbial recruitment mechanisms form microbial consortia, which



**Figure 6.** Coordination of microbial communities enhancing plant nutrient use efficiency. (A) Various microbial groups (archaea, bacteria, fungi, algae, nematodes, protozoa, and arthropods) contribute to plant nutrient uptake under phosphorus and nitrogen limitations. For example, fungi enhance phosphorus solubility, while nitrogen-fixing bacteria (e.g. *Azospirillum brasilense*) thrive in low-nitrogen conditions, improving the uptake of phosphorus (Pi), ammonium (NH<sub>4</sub><sup>+</sup>), and nitrate (NO<sub>3</sub><sup>-</sup>), thus promoting overall plant growth. (B) This study assessed the impact of fungal inoculation on plant nutrient use efficiency under varying phosphorus concentrations (no phosphorus, 100 mg/kg inorganic phosphorus, and 100 mg/kg insoluble phytic phosphorus). Under phosphorus deficiency, plant growth was significantly inhibited. Growth improved with increasing phosphorus availability, but not optimally, indicating low utilization of insoluble phosphorus. Fungal inoculation enhanced plant growth at all phosphorus levels, especially under insoluble phytic phosphorus conditions, suggesting fungi improve phosphorus bioavailability. Fungal treatment significantly increased soluble phosphorus concentrations in the soil, particularly in soils with insoluble phytic phosphorus, confirming fungi's role in phosphorus transformation and uptake. Compared to controls, fungal inoculation markedly improved phosphorus uptake efficiency, especially under low-phosphorus conditions, highlighting its importance for plant resilience and growth under stress. (Wang et al. 2023) Copyright © 2023, John Wiley and Sons. Some elements in this figure are created with BioRender (BioRender.com).

hold great potential for improving crop resilience and nutrient use efficiency. By targeting exudates, it is possible to foster microbial communities that promote plant growth, reduce disease, and improve stress tolerance. (iii) Allelopathic recruitment and microbial inoculation: allelopathic recruitment and microbial inoculation strategies have been successful in enhancing nutrient uptake and increasing crop productivity across various systems.

(iv) Environmental and economic viability: the cost of producing MIs and allelopathic compounds varies widely, potentially limiting their widespread adoption, particularly for smallholder farmers. Despite the promise of MIs, large-scale production and distribution come with significant costs. (v) Ecological risks and non-target effects: careful management of allelopathic compounds is necessary to prevent negative impacts on nontarget species.

and ecosystem services, adding complexity to their application. (vi) Long-term stability of microbial communities: microbial community stability may decline over time, especially under fluctuating environmental conditions. Soil composition, crop rotation, and local climate must be optimized to ensure the sustainability of microbiome-based strategies. (vii) Reduction in synthetic inputs: microbiome-based strategies can reduce the need for synthetic fertilizers and pesticides, lowering input costs and promoting more sustainable agricultural practices. (viii) Improved soil health and crop resilience: these strategies enhance soil health, improve crop resilience to stresses like drought and nutrient deficiencies, and can lead to higher crop yields. (ix) Knowledge gaps and future research: a deeper understanding of the molecular mechanisms by which exudates influence microbiome assembly is needed, especially regarding plant immune responses and environmental factors. Additionally, more research is needed to understand how environmental stressors (e.g. drought and nutrient limitations) affect exudate composition and microbial dynamics. Future research should also focus on optimizing soil management practices, crop rotation, and other factors that affect the long-term stability of microbial communities. In conclusion, the study of plant exudates and microbiome recruitment offers significant potential to enhance plant health management, and harnessing the power of microbial communities could lead to more resilient, sustainable, and productive agricultural systems. In conclusion, the continued study of plant exudates and microbiome recruitment holds the potential to revolutionize plant health management. By harnessing the power of microbial communities, future agricultural practices can become more resilient, sustainable, and productive.

## Author contributions

C.-X.Y., Y.-Y.G., and G.-F.H. designed and outlined the manuscript. C.-X.Y. performed the literature search, generated the figures, and prepared the initial draft of the manuscript. S.-J.C., X.-Y.H., H.-M.W., L.-Z.W., and Y.-Y.T. contributed to the data curation and figure beautification. Y.-Y.G., and G.-F.H. critically reviewed and revised the manuscript.

## Supplementary data

Supplementary data are available at [FEMSRE Journal](#) online.

Conflict of interest: None declared.

## Funding

This work was supported by the National Natural Science Foundation of China (32125033, 32260687) and the Central Government Guides Local Science and Technology Development Fund Projects (Qiankehezhongyindi (2023) 001). Science and Technology Planning Project of Guizhou Province (Qiankehejichu-ZK[2024] Key project 028). China Postdoctoral Science Foundation (2024T170200).

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