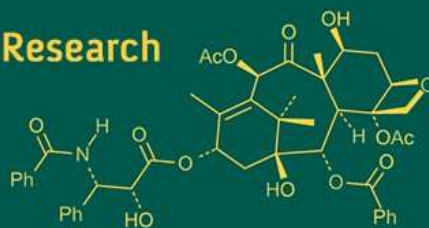
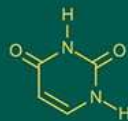
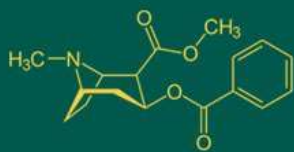


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Mechanistic insights into rhizosphere colonization by beneficial rhizobacteria

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Abstract

Plant-associated microbiomes are essential for host growth, health, and environmental adaptation. Among them, rhizosphere microorganisms play pivotal roles in promoting plant growth through nutrient mobilization, phytohormone production, pathogen suppression, and induction of systemic resistance, making them valuable biofertilizers and biocontrol agents for sustainable agriculture. The effectiveness of these beneficial microorganisms, however, depends largely on their ability to successfully colonize plant roots. Rhizosphere colonization is a dynamic, multi-step process involving root exudate-mediated microbial recruitment, chemotaxis, attachment, biofilm formation, and persistence, all of which are regulated by intricate plant-microbe signaling networks. Recent studies have also revealed that plants actively recruit beneficial microorganisms under stress through the "cry-for-help" mechanism, thereby enhancing resilience against pathogens and environmental stresses. This review summarizes the physiological, molecular, and genetic mechanisms underlying rhizosphere colonization, highlights recent advances in the "cry-for-help" concept, and discusses emerging strategies to improve root colonization for the development of more effective microbial inoculants and sustainable crop production.

Keywords: Rhizosphere colonization, root exudates, Chemotaxis, biofilm, plant growth-promoting rhizobacteria (PGPR), cry-for-help, sustainable agriculture

Introduction

Plant-associated microbiomes are increasingly recognized as essential determinants of plant growth, development, health, and environmental adaptation ^[56]. Among these, the rhizosphere microbiome constitutes one of the most diverse and metabolically active microbial communities, contributing significantly to nutrient acquisition, phytohormone production, pathogen suppression, and induction of systemic resistance against biotic and abiotic stresses ^[65]. Owing to these multifunctional benefits, beneficial rhizobacteria are widely exploited as biofertilizers and biocontrol agents, offering sustainable alternatives to chemical inputs in modern agriculture.

The effectiveness of these microbial inoculants, however, depends largely on their ability to successfully colonize plant roots. Stable rhizosphere colonization enables beneficial bacteria to survive, proliferate, compete with native microbial communities, and maintain long-term associations with the host, thereby ensuring consistent expression of plant growth-promoting and disease-suppressive traits ^[56].

The rhizosphere is a specialized soil region directly influenced by root exudates, mucilage, and other plant-derived compounds that selectively recruit and shape microbial communities ^[19]. Successful colonizers detect these chemical cues, migrate toward the root through chemotaxis, attach to the rhizoplane, form biofilms, and in some cases colonize internal root tissues. Colonization is spatially heterogeneous, with bacterial populations preferentially inhabiting root hairs, elongation zones, and lateral root junctions, where microcolonies typically occupy only 10-40% of the root surface ^[17].

While the molecular mechanisms underlying obligate symbioses, such as rhizobial and mycorrhizal interactions, have been extensively investigated ^[70, 78, 99, 25, 30, 66, 97], the mechanisms governing colonization by non-symbiotic plant growth-promoting rhizobacteria (PGPR) remain comparatively less integrated.

Recent studies have shown that successful colonization is a sequential process involving chemotaxis, root attachment, biofilm formation, efficient utilization of root exudates, adaptation to rhizosphere conditions, and modulation of plant immune responses. Moreover, plants actively recruit beneficial microorganisms under stress through alterations in root exudation, a phenomenon described by the "cry-for-help" hypothesis. These dynamic plant-microbe interactions play a crucial role in determining the persistence and functional efficacy of beneficial bacteria in the rhizosphere.

Although considerable progress has been made in understanding individual aspects of rhizosphere colonization, knowledge remains fragmented across multiple disciplines. This review summarizes the current understanding of the molecular, physiological, and ecological mechanisms underlying root colonization by beneficial non-symbiotic bacteria, discusses recent advances in the "cry-for-help" concept, and highlights emerging strategies to enhance microbial establishment for sustainable agricultural applications.

Root Exudates: Drivers of Rhizosphere Assembly

Root exudates are the primary determinants of rhizosphere microbial assembly, serving as major sources of carbon, energy, and signaling molecules for soil microorganisms. Plants allocate approximately 11-40% of their net photoassimilates to the rhizosphere through root exudation, creating a metabolically active niche that supports significantly higher microbial abundance and activity than the surrounding bulk soil^[104]. These chemically diverse exudates, released in solid, liquid, or gaseous forms, include a wide range of primary and secondary metabolites that regulate microbial recruitment, colonization, and plant-microbe interactions.

Root exudates are broadly classified into low- and high-molecular-weight compounds based on their chemical composition and molecular size. Low-molecular-weight exudates include sugars, amino acids, organic acids, alcohols, volatile compounds, and phenolics. These metabolites are primarily released through passive diffusion across the plasma membrane and serve as major carbon sources and signaling molecules that influence microbial recruitment and activity in the rhizosphere^[4]. In contrast, high-molecular-weight exudates, mainly polysaccharides and proteins, are secreted through vesicle-mediated exocytosis involving the endoplasmic reticulum and Golgi apparatus. These compounds contribute to root lubrication, soil aggregation, microbial attachment, and protection against soil-borne pathogens^[4, 13, 94].

Plants allocate a substantial proportion of their photosynthetically fixed carbon below ground, with approximately 11% of net fixed carbon released as root exudates. The quantity and composition of these exudates vary with plant genotype, developmental stage, and nutrient status^[6, 31, 60]. Although root exudate composition has been extensively characterized in herbaceous species such as

Arabidopsis, soybean, rice, and common bean^[79, 82, 83], studies in woody plants remain comparatively limited, with most reports restricted to species such as apple (*Malus pumila*), peach (*Prunus persica*), and jujube (*Ziziphus jujuba*)^[107, 87].

Genetic Regulation of Root Exudation

Root exudation is regulated by coordinated genetic networks and membrane transport systems that control the release of metabolites into the rhizosphere^[9]. While many low-molecular-weight compounds are released through passive diffusion, the secretion of organic acid anions such as malate and oxalate is mediated by specialized membrane transport proteins, including slow-activating (SLAC/S-type) and rapid-activating (QUAC/R-type) anion channels^[18]. Among these transporters, the Aluminium-Activated Malate Transporter (ALMT) family plays a central role in root exudation and plant adaptation to acidic soils. ALMT proteins facilitate the efflux of malate in response to aluminum toxicity, enabling the chelation of Al³⁺ ions and protecting root tissues from damage^[75]. In addition to aluminum detoxification, ALMT transporters participate in nutrient stress responses. For example, AtALMT3 promotes malate exudation under phosphorus deficiency, whereas AtALMT1 enhances malate secretion that not only alleviates aluminum toxicity but also recruits beneficial rhizobacteria capable of stimulating plant immune responses^[36, 54]. These findings demonstrate that genetically regulated root exudation integrates environmental stress adaptation with the selective recruitment of beneficial microorganisms.

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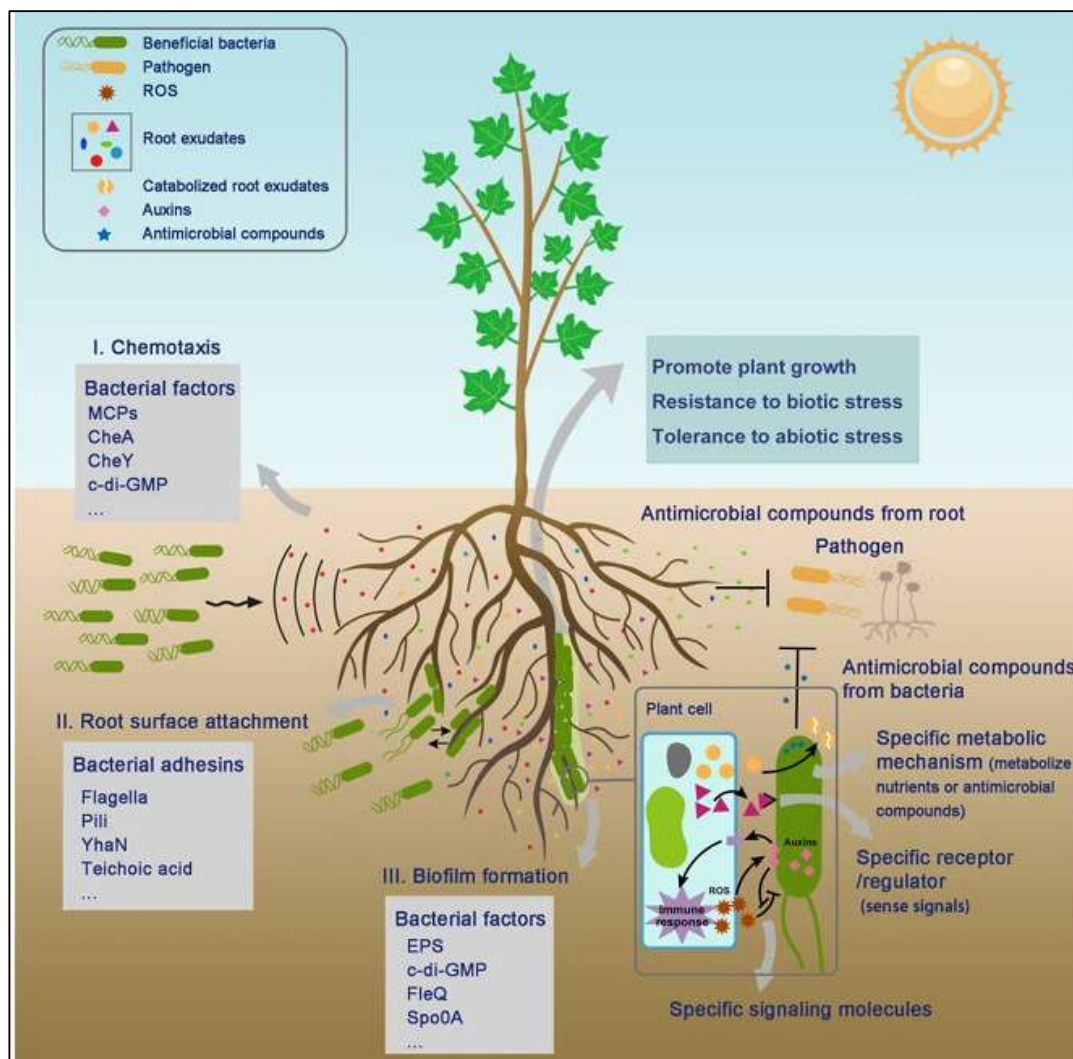


Fig 1: Root colonization process [49]

Active Transporter Superfamilies

Active root exudation is mediated by energy-dependent membrane transporters that regulate the export of metabolites into the rhizosphere [9]. Two major transporter superfamilies play central roles in this process: ATP-Binding Cassette (ABC) transporters and Multidrug and Toxic Compound Extrusion (MATE) transporters [32].

ABC transporters use ATP hydrolysis to transport a wide range of metabolites across the plasma membrane [30, 63]. Genetic studies in *Arabidopsis thaliana* have demonstrated that mutations in several ABC transporter genes alter root exudate composition and reshape rhizosphere microbial communities. For example, disruption of AtABCG30 changes the secretion of sugars and phenolic compounds, leading to significant shifts in microbial community structure, highlighting the role of ABC transporters in regulating plant-microbe interactions [3, 5, 49].

MATE transporters function as secondary active transporters that utilize electrochemical gradients to export organic acids and other metabolites [94]. Several MATE proteins, including SbMATE1 in sorghum, OsFRDL4 in rice, HvAACT1 in barley, and AtMATE1 in *Arabidopsis*, mediate citrate secretion to chelate toxic Al^{3+} ions under acidic soil conditions [51, 45, 103, 100]. In rice, OsPEZ1 and OsPEZ2 regulate the secretion of phenolic compounds that influence rhizosphere chemistry and microbial interactions [81]. Together, ABC and MATE transporters play pivotal roles in controlling root exudation, enabling plants to adapt

to environmental stresses while selectively shaping the rhizosphere microbiome.

Bacterial Chemotaxis and Motility

Chemotaxis is a motility-dependent process that enables bacteria to detect and respond to chemical gradients, allowing movement toward root-derived attractants and away from harmful compounds. Root exudates serve as the primary chemical signals guiding beneficial rhizobacteria to the rhizosphere, making chemotaxis a critical first step in root colonization [21]. Rhizobacteria employ several forms of motility to navigate the soil environment, including swimming (flagella-driven movement in liquid), swarming (coordinated surface migration), twitching (type IV pili-mediated movement), and gliding (surface translocation independent of flagella or pili) [34, 58, 72]. These motility mechanisms facilitate bacterial migration through soil pores, enhance root exploration, and promote efficient attachment to the root surface. Mutations affecting chemotactic receptors or flagellar biosynthesis markedly reduce root colonization, highlighting the essential role of bacterial motility in successful rhizosphere establishment [22, 88].

Colonization Site Selection and Dynamic Migration

Following chemotactic attraction, bacteria selectively colonize root regions with high exudation rates, particularly the root tip, elongation zone, lateral root junctions, and root hair regions, where carbon availability is greatest [18, 53, 27].

Colonization patterns are highly dynamic and vary among bacterial species and throughout plant development [24, 84, 61, 85]. For example, *Bacillus megaterium* NCT-2 initially colonizes the maize root elongation zone before spreading to other root regions during plant growth, whereas chemotaxis-deficient mutants of *Azospirillum brasilense* exhibit poor root localization and reduced colonization efficiency [15, 61]. These observations demonstrate that chemotaxis and motility not only facilitate root recognition but also determine the spatial and temporal patterns of bacterial colonization.

Chemotactic site selection is influenced by local variations in root exudate composition, root immune responses, and the production of antimicrobial compounds [23, 89]. For example, reactive oxygen species (ROS) released by root tissues can repel bacteria from the root tip during early colonization, shaping their spatial distribution along the root axis [61]. As roots continue to grow, chemotaxis and motility enable bacteria to migrate toward newly emerging exudation sites while avoiding immune-active regions, thereby enhancing long-term colonization [103, 86]. This dynamic behavior is exemplified by the *morA* mutant of *Pseudomonas*, which exhibits reduced rhizosphere competence due to its inability to relocate after triggering localized plant immune responses [51].

Although advances in fluorescence microscopy, GUS reporters, and fluorescence in situ hybridization (FISH) have improved visualization of bacterial colonization patterns, accurately quantifying bacterial populations within specific root micro-niches remains technically challenging [12].

Following chemotactic migration, successful root colonization depends on bacterial attachment to the rhizoplane. During this transition, bacteria shift from a motile to a sessile lifestyle by suppressing flagellar activity and activating signaling pathways that regulate adhesion. Studies in *Pseudomonas*, *Bacillus*, *Agrobacterium*, *Azospirillum*, *Bradyrhizobium*, and *Salmonella* indicate that

attachment follows a biphasic process consisting of an initial reversible physicochemical interaction, followed by irreversible adhesion mediated by extracellular polymeric substances (EPS) [95, 35]. Stable attachment provides the foundation for biofilm formation, endophytic colonization, and persistence within the rhizosphere while facilitating the evasion of host immune responses [88].

Multi-Organismal Interactions in the Rhizosphere

Root exudation is a dynamic process influenced by plant genotype, developmental stage, and interactions with surrounding organisms, all of which shape rhizosphere microbial communities. Genetic variation among plant species and cultivars results in distinct exudate profiles that influence microbial recruitment and community composition, as demonstrated in *Arabidopsis thaliana*, potato, maize, and sorghum [16, 57, 1, 29]. Root exudate composition also changes during plant development, with young plants releasing higher levels of simple sugars and mature plants producing greater amounts of amino acids and phenolic compounds, thereby driving microbial succession in the rhizosphere [14]. In addition, neighboring plants, insect herbivores, nematodes, fungi, and resident bacterial communities continuously modify the rhizosphere environment and influence plant-microbe interactions [74, 19]. Rhizosphere assembly is further shaped by interactions between plants and beneficial microorganisms. Arbuscular mycorrhizal fungi (AMF) enhance nutrient acquisition, modify root architecture, and improve plant tolerance to environmental stresses through physiological and molecular changes [11, 59]. Likewise, plant growth-promoting rhizobacteria (PGPR) enhance plant growth through nutrient mobilization, phytohormone production, pathogen suppression, and induction of systemic resistance. Together, these multi-organismal interactions determine the composition, stability, and functional capacity of the rhizosphere microbiome.

Table 1: Comparative analysis of mycorrhizal symbioses and plant growth-promoting rhizobacteria (PGPR) interactions within the host rhizosphere.

Interaction Type	Target Genera/Organisms	Core Physiological Mechanisms	Primary Agricultural Benefits
Mycorrhizal Symbiosis	Glomeromycota (AMF), Ectomycorrhizal (ECM) Fungi	Differential expression of >500 protein-coding genes; upregulation of ammonium and phosphate transporters; metabolic and phytohormone reprogramming (ABA, SA, JA).	Enhanced nitrogen and phosphorus uptake; osmotic potential maintenance; improved photosynthetic efficiency; stress and allelochemical tolerance.
Plant Growth Promoting Rhizobacteria (PGPR)	<i>Agrobacterium</i> , <i>Alcaligenes</i> , <i>Arthrobacter</i> , <i>Azospirillum</i> , <i>Azotobacter</i> , <i>Bacillus</i> , <i>Burkholderia</i> , <i>Enterobacter</i> , <i>Klebsiella</i> , <i>Pseudomonas</i> , <i>Serratia</i> , <i>Streptomyces</i>	Direct: Nitrogen fixation, phosphate solubilization, ACC deaminase production, siderophore synthesis, auxin/gibberellin production. Indirect: Antibiotic secretion, lytic enzyme production, pathogen niche competition.	Direct growth and root development stimulation; reduction of drought- and salinity-induced ethylene stress; active suppression of soil-borne pathogens.

Biotic Stress-Induced "Cry for Help" Responses

Plants respond to pathogen attack by actively reshaping their root exudation patterns to recruit beneficial microorganisms, a phenomenon known as the "cry-for-help" response [8, 102, 73, 96, 93]. This adaptive strategy involves three sequential events: activation of plant immune responses, stress-induced changes in root exudate composition, and selective recruitment of protective rhizosphere microbes that enhance plant defense and contribute to the establishment of disease-suppressive soils [68, 92].

One of the best-characterized examples is the infection of *Arabidopsis thaliana* by *Pseudomonas syringae* pv. *tomato*

DC3000, which stimulates the secretion of L-malic acid from roots. This organic acid acts as a chemoattractant for *Bacillus subtilis* FB17, promoting rhizosphere colonization and systemic resistance [71]. This recruitment is mediated by pathogen-associated signals such as flg22 and coronatine, highlighting the coordinated role of phytohormone signaling and root exudates in microbiome assembly [38, 45, 55, 100].

Similar recruitment mechanisms occur during fungal infections. Pathogen challenge alters root exudation to attract beneficial bacteria, including *Bacillus*, *Sphingomonas* and *Stenotrophomonas* which suppress pathogens through enhanced chemotaxis, biofilm formation, and induction of

systemic resistance [49, 75, 46, 96, 93]. Secondary metabolites such as coumarins also play important roles by selectively promoting beneficial microbes while inhibiting soil-borne pathogens. In *Arabidopsis*, coumarin biosynthesis, regulated by *MYB72* and *F6'H1*, is essential for recruiting protective microbial consortia and establishing long-lasting disease-suppressive rhizosphere communities [80, 37, 91].

Collectively, these findings demonstrate that plants actively engineer their rhizosphere microbiome during pathogen attack by modifying root exudation, thereby enhancing the recruitment of beneficial microorganisms that improve disease resistance and plant resilience.

Strategies for Artificial Enhancement of Root Colonization

Improving rhizobacterial colonization is essential for maximizing the field performance of biofertilizers and biocontrol agents. Three major strategies have been explored to enhance colonization efficiency.

Substrate supplementation involves the application of organic compounds such as malic, citric, and fumaric acids that stimulate chemotaxis, biofilm formation, and root colonization by beneficial bacteria, thereby improving plant growth and disease suppression [108, 22, 26].

Genetic engineering enhances bacterial responsiveness to plant-derived signals by modifying genes involved in chemotaxis, metabolism, and biofilm formation. For example, engineered *Bacillus velezensis* SQR9 with a xylose-inducible *degQ* system and metabolically enhanced *Azospirillum brasilense* have shown improved root colonization and biocontrol efficacy [98, 77].

Adaptive evolution and targeted domestication employ repeated cycles of plant inoculation and bacterial selection to enrich strains with superior rhizosphere competence. This approach has successfully generated *Bacillus subtilis* variants with enhanced colonization ability, although adaptation under controlled conditions may compromise fitness under variable field environments [10, 28, 40].

Conclusions

Root colonization by beneficial non-symbiotic bacteria is a dynamic, multi-step process governed by coordinated plant-microbe interactions. Root exudates play a central role by providing nutrients and signaling molecules that regulate microbial recruitment, chemotaxis, attachment, biofilm formation, and persistence in the rhizosphere. Plants further reshape their rhizosphere microbiome under stress through the "cry-for-help" mechanism, selectively recruiting beneficial microorganisms that enhance disease resistance and stress tolerance. Recent advances in substrate supplementation, genetic engineering, and adaptive evolution provide promising strategies to improve rhizobacterial establishment and the consistency of microbial inoculants under field conditions. A deeper understanding of these molecular and ecological interactions will facilitate the development of next-generation bioinoculants for sustainable and climate-resilient agriculture.

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