

## REVIEW ARTICLE

# The rhizosphere microbiome: Plant–microbial interactions for resource acquisition

Hugo A. Pantigoso  | Derek Newberger | Jorge M. Vivanco

Center for Root and Rhizosphere  
Biology, Department of Horticulture  
and Landscape Architecture, Colorado  
State University, Fort Collins, Colorado  
80523-1173, United States

**Correspondence**

Hugo Pantigoso and Jorge Vivanco,  
Center for Root and Rhizosphere  
Biology, Department of Horticulture  
and Landscape Architecture, Colorado  
State University, Fort Collins, CO  
80523-1173, USA.  
Email: [hugopg@colostate.edu](mailto:hugopg@colostate.edu);  
[j.vivanco@colostate.edu](mailto:j.vivanco@colostate.edu)

**Abstract**

While horticulture tools and methods have been extensively developed to improve the management of crops, systems to harness the rhizosphere microbiome to benefit plant crops are still in development. Plants and microbes have been coevolving for several millennia, conferring fitness advantages that expand the plant's own genetic potential. These beneficial associations allow the plants to cope with abiotic stresses such as nutrient deficiency across a wide range of soils and growing conditions. Plants achieve these benefits by selectively recruiting microbes using root exudates, positively impacting their nutrition, health and overall productivity. Advanced knowledge of the interplay between root exudates and microbiome alteration in response to plant nutrient status, and the underlying mechanisms there of, will allow the development of technologies to increase crop yield. This review summarizes current knowledge and perspectives on plant–microbial interactions for resource acquisition and discusses promising advances for manipulating rhizosphere microbiomes and root exudation.

**KEYWORDS**

microbiome, nutrient, plant growth promoting rhizobacteria, rhizosphere, root exudates, signalling, soil

**INTRODUCTION**

Diverse microbes (archaea, bacteria, fungi and protists) cohabiting with plants are collectively known as the plant microbiota (Bulgarelli et al., 2013; Compant et al., 2019). The plant microbiota, its inhabitants, habitats, genomes and surrounding environmental conditions are termed collectively the plant microbiome (Berg et al., 2020; Marchesi & Ravel, 2015), which is presently considered an extended plant trait with functional capabilities that contribute to plant host nutrition, development and immunity (Lemanceau et al., 2017; Teixeira et al., 2019; Vandenkoornhuysen et al., 2015). The highly diverse

plant-associated microbial communities are shaped by biotic and abiotic constraints varying on time, and space (Hassani et al., 2018; Xiong et al., 2021). Plants gradually enrich microbes in specific plant compartments creating microbial habitats that typically start from the bulk soil and can move into above-ground internal plant tissues. Thus, the composition of the plant microbiome is compartment specific and is divided into rhizosphere (soil surrounding the plant roots; Zhang et al., 2017), the endosphere (interior of the above and below plant organs; Compant et al., 2021), and the phyllosphere (above-ground portion of the plant; Koskella, 2020). The deeper these soil bacteria, fungi and other micro-organisms move into these different plant

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compartments, the more they are filtered out or selectively recruited by the plant's signaling molecules and immune system (Xiong et al., 2021). The rhizosphere is dominated by prokaryotic phyla including Proteobacteria, Actinobacteria, Bacteroidetes, Firmicutes and Acidobacteria. In terms of the fungal phyla, the rhizosphere is dominated by Ascomycota and Basidiomycota, which are also the most common taxonomical phyla in soils (Mohanram & Kumar, 2019). Deciphering plant and microbial interaction is a multi-disciplinary research endeavor that integrates different branches of biology including ecology, microbial, plant and molecular biology applying informatics, statistics and modelling as well as biotechnology (Berg et al., 2020). Efforts to link specific microbial processes to specific microbial taxa have been accelerated with genomic data (i.e. marker gene, genomic and metagenomic) by grouping taxa according to similarity in strategies and functional attributes (Carrión et al., 2019; Song et al., 2020). These methodological and conceptual advances have accelerated our understanding of the plant microbiome (Fierer, 2017). By describing and understanding the plant-associated microbial communities and their functional features, we can manipulate the plant rhizosphere microbiome to enhance plant health and productivity (Xun et al., 2021).

## PLANT-MICROBIAL INTERACTIONS IN THE RHIZOSPHERE

Healthy and asymptomatic plants maintain a complex relationships with their rhizosphere microbiota that support plant performance (Hassani et al., 2018). Plants locally influence the composition and activity of their rhizosphere microbiome by altering soil pH, soil structure, oxygen availability and by providing an energy source of carbon-rich exudates (Dennis et al., 2010; Jacoby et al., 2021). Plant root exudates are chemically diverse primary and secondary metabolites, many of which exert bioactive effects on micro-organisms affecting their composition and function (Pascale et al., 2020). Plant root exudation, which represents up to one-third of photosynthesized carbon, plays a major role in determining the outcome of individual- and community-level chemical interactions (Pausch & Kuzyakov, 2018; O'Banion et al., 2020). Plants use their root exudates as a primary form of communication with their biotic surroundings, facilitating a number of responses such as nutrient absorption, resource competition, same species signaling, attraction of micro-organisms, along with many other interactions (Rizaludin et al., 2021; Sasse et al., 2018). A brief list of major exudate-derived organic compounds include sugars, amino acids, organic acids, phenolic compounds and secondary metabolites which comprise

coumarins, glucosinolates, benzoxazinoids, camalexin and triterpenes (Jacoby et al., 2020). By providing a diverse carbon-rich environment, plant species harbor a distinctive microbial community in their rhizosphere which, in turn, confers several fitness advantages to the plant host, shaping their assemblage and modulating their beneficial traits (Badri & Vivanco, 2009; Mönchgesang et al., 2016; Trivedi et al., 2020). In addition, root exudate-derived metabolites act as important mediators structuring a stress-resistant microbiota to alleviate plant abiotic stresses including nutrient deprivation, disease and drought stress (Ab Rahman et al., 2018; Monohon et al., 2021; Olanrewaju et al., 2017; Pieterse et al., 2014; Venturi & Keel, 2016; Vessey, 2003). Identification of stress-derived metabolome and microbiota constitutes a feasible strategy to deal with abiotic and biotic constraints, however, the beneficial effects of root-enriched microbial taxa driven by specialized root exudate derived metabolites remain understudied (Hong et al., 2021; Pantigoso, Manter, & Vivanco, 2020; Pantigoso, Yuan, et al., 2020). In this review, we highlight current research on the plant rhizosphere microbiome and root exudate-derived metabolites for nutrient acquisition.

## FACTORS DRIVING ASSEMBLY OF RHIZOSPHERE MICROBIOME

Host plants influence the composition of their respective rhizosphere microbiome from proximal soils, in which some microbiome members are specifically recruited by the host, while other microbial members assemble opportunistically (Lennon & Jones, 2011; Stopnisek & Shade, 2021). Soil physicochemical properties are the primary determinant of root-associated bacterial community composition followed by environmental conditions, host genotype and nutrient availability (Lundberg et al., 2012; Ren et al., 2020; Stopnisek & Shade, 2021; Yeoh et al., 2017). Temporal patterns and evolution over long timescales also shape the root microbiome assembly, which in turn influences how hosts respond to biotic and abiotic environmental stressors (Fitzpatrick et al., 2018). Several recent comprehensive reviews have addressed the assembly, and macroecological patterns of root microbiome (Brunel et al., 2020; Cordovez et al., 2019; Fitzpatrick et al., 2020; Munoz-Ucros et al., 2021).

## PLANT AND MICROBE COMMUNICATION IN THE RHIZOSPHERE

Rhizosphere-associated micro-organisms perceived and interpret signals produced by themselves, other microbes

and plants, and are capable of influencing their plant host by the release of signaling molecules. The major outcomes from this communication are related to inductions of plant immunity, stress tolerance, overall growth, health, nutrition and the maintenance of associated rhizosphere microbiome. Examples of these signaling molecules are N/acyl homoserine lactones (AHLAs), diffusible signal factors, diketopiperazines, phytohormone-like molecules and volatile organic compounds (Bailly & Weisskopf, 2012; Kakkar et al., 2015; Oldroyd, 2013; Ortiz-Castro et al., 2011; Xu et al., 2015). This interaction with the plant can happen at the single-strain or at the microbiome level. Individual microbes and their communities can form beneficial, neutral or detrimental interactions. Plant and microbe communication has been investigated predominantly for soil bacteria and fungi, and more recently communication in nematodes and protists are being revealed (Geisen et al., 2018; Manosalva et al., 2015). The main type of signaling mechanisms known to occur in the rhizosphere can be divided into three categories according to the pathway of the communication and players involved:

1. Microbe-to-microbe: microbial intraspecies and interspecies signaling are primarily performed by the synthesis and detection of autoinducers through a mechanism that is also known as Quorum sensing (QS). These autoinducers activate or deactivate the transcription of numerous QS-regulated genes that include biofilm formation, chemotaxis and virulence factors. This allows micro-organisms within microbial communities to monitor cell density and to coordinate collective changes in behavior (Fuqua et al., 2001; Venturi & Keel, 2016). N-acyl homoserine lactones (AHL) autoinducer is one better-documented class of QS molecules acting on gram-negative bacteria, including well-known soil bacteria genera such as *Pseudomonas* spp., *Burkholderia* spp. and *Serratia* spp. Gram-positive rhizobacteria use other means of intra and interspecies level communication such as peptides (Monnet et al., 2016). QS appears to be also important for interkingdom communication between bacteria and plant-associated fungi, however specific mechanisms have not yet been described (Deveau et al., 2018; Jarosz et al., 2011). QS communication of diffusible autoinducers is typically executed in short cell-cell distances and at high concentration of signaling molecules. In contrast, Volatile Inorganic and Organic Compounds (VICs and VOCs) have important roles as signals intra-kingdom and inter-kingdom interaction at low concentration and over long distances (Farag et al., 2017; Schulz-Bohm et al., 2017; Weisskopf et al., 2021). However, there is very limited
2. Plant-to-microbe: several root exudates ubiquitous in most plants have been identified as signals towards soil microbes. To recognize associated rhizosphere microbes plants use dedicated pattern recognition receptors (PRRs; Venturi & Keel, 2016). Signaling from plant to micro-organisms via plant-secreted molecules has been shown to participate in several plant beneficial interactions (Mathesius et al., 2003; Mhlongo et al., 2018). Signaling between plants and rhizosphere micro-organism has been mainly studied in intimate symbiotic associations, in particular those involving mycorrhizal fungi and rhizobial bacteria (Hassan & Mathesius, 2012; Kiers et al., 2011). For example, under nutrient-deficient conditions, the host plant increases synthesis of strigolactones to promote mycorrhizal fungal development and symbiosis establishment as mechanism for nutrient acquisition (Aliche et al., 2020). Similarly, flavonoids have been shown to stimulate bacterial root infection that results in formation of nodules allowing nitrogen fixation in legumes (Cooper, 2004; Hassan & Mathesius, 2012). Flavonoids can indirectly affect biological cycling of C, P and N in soils, and their synthesis is also affected by soil phosphorus and nitrogen soil content and supply (Coronado et al., 1995; Juszczuk et al., 2004). Phosphorus solubility for plant uptake can be increased by flavonoids which desorb phosphates from soil-mineral surfaces or dissolution of mineral-phosphate complexes (Cesco et al., 2012). It is well documented that several chemical groups exuded by the plant and present in the rhizosphere can serve as food sources and signaling for a variety of micro-organisms. For instance Hida et al. (2020) showed that the plant growth promoting rhizobacteria *Pseudomonas protegens* CHA0 possesses four putative chemoreceptors for amino acids, enhancing chemotaxis towards amino acids. Many other unidentified molecules are involved in stress-induced

belowground chemical interactions in addition to the well-described low molecular weight organic acids, phenolics, flavonoids, strigolactones, cutin and monomers (Rizaludin et al., 2021; Rolfe et al., 2019).

3. Microbe-to-plant: Micro-organisms produce signaling molecules which can be detected by plants and affect their development, gene expression and immune and stress responses (Badri & Vivanco, 2009; Venturi & Keel, 2016). Rhizosphere micro-organisms trigger plant response via microbial elicitors known as microbe-associated molecular patterns (MAMPs), such as lipopolysaccharide, peptidoglycans, flagellin and chitin (Millet et al., 2010). MAMPs trigger systemic defense responses (also known as induced systemic resistance [ISR]) and priming by rhizosphere beneficial bacteria. MAMPs can also trigger systemic acquired resistance (SAR) which is induced mostly by pathogens (Conrath et al., 2015; Fu & Dong, 2013; Pieterse et al., 2014). Other well-described molecules, such as Nod and Myc factors released by rhizobia and mycorrhiza, are utilized to initiate symbiosis with plants (Oldroyd, 2013). Similar to microbe–microbe signaling, AHL-type QS molecules are also reported to affect plant gene expression and functions related to plant development, stress response and immunity (Palmer et al., 2014). Root-associated microbes, free-living, symbiotic or endophytic, can produce various types of molecules. Rhizosphere microbes mitigate stress responses by regulating the nutritional and hormonal balance in plants and inducing systemic tolerance to biotic and abiotic stresses and plant growth. Rhizosphere microbes have the ability to synthesize phytohormones such as abscisic acid, indole acetic acid, cytokinins, gibberellic acid, salicylic acid, auxins, cytokinins, gibberellins, among others (Egamberdieva et al., 2017). Another class of molecule emitted by rhizosphere microbes, VOCs, can lead to drastic plant growth promotion (Bailly et al., 2014; Ryu et al., 2003; Sánchez-López et al., 2016). VOCs can also influence the uptake of specific nutrients such as iron and sulfur by plants (del Carmen Orozco-Mosqueda et al., 2013; Meldau et al., 2013; Zhang et al., 2009) suggesting that VOCs originating from bacterial metabolic activity could be used by plants in conditions of nutrient deficiency. However, the mechanisms underlying growth promotion and nutrient acquisition by microbial volatiles are still poorly understood.

Recent research has proposed that a unique bacterial root microbiota is stimulated by specific chemical compounds (e.g. coumarins) produced by plants under nutrient-limiting soils (Harbort et al., 2020; Stringlis

et al., 2018; Voges et al., 2019). These studies have shown that root-secreted coumarins are inducible under iron starvation and mediate an interaction between the host and microbial commensals that improve host iron nutrition (Fourcroy et al., 2014; Jin et al., 2007). This interaction suggests that the root microbiota is an integral component of plant edaphic adaptation to growth in iron-limiting soils. Similarly, a study from Koprivova et al. (2019) using a loss of function mutant showed that root-specific camalexin biosynthesis controls the plant growth promoting effects of multiple bacterial strains; however, no nutritional component was shown in this study. Brisson et al. (2022) showed that amino acids, shikimic and quinic acid, increased under phosphate stress are preferentially absorbed by micro-organisms that were positively correlated with root growth (Zhalnina et al., 2018). Other studies have demonstrated the direct integration between plant phosphate status, associated root microbiota and soil phosphorus content (Castrillo et al., 2017; Finkel et al., 2019). This may suggest that plants modulate their root exudation profiles to stimulate the proliferation of groups of micro-organisms that aid with nutrient acquisition or are involved in plant–microbe signaling (Table 1). Despite the advances in our understanding of variability and functional roles of root exudates in soil phosphorus, nitrogen, iron acquisition among plant species (as shown in Figure 1), this topic remains understudied compared to research on root morphology and microbial symbiosis for plant nutrient acquisition. Wen et al. (2021) proposed that incorporation of root exudation, root morphology and microbial symbiosis is key for a holistic understanding of belowground interactions.

## MANIPULATING RHIZOSPHERE MICROBES AND PLANT ROOT EXUDATES FOR NUTRIENT ACQUISITION

Plants recruit the majority of their microbes within proximal soils and can be heavily influenced by keystone microbial strains (Sánchez-Cañizares et al., 2017). Several strategies to manage and manipulate the rhizosphere microbiome for plant health have been proposed; however, their ability to be successfully applied on a broader scale is limited (Chaparro et al., 2012; Wallenstein, 2017). Currently, several approaches are available and applicable. One approach is to alter the rhizosphere by directly inoculating bacterial or fungal strains in soils near plant roots (He et al., 2019).

Although this is becoming a widely used strategy, drawbacks include difficulty in fine-tuning microbial

**TABLE 1** Root-derived metabolites acting as substrates or signals of plant rhizosphere beneficial bacteria participating in mobilization of nutrients in substrates or plant nutrient acquisition

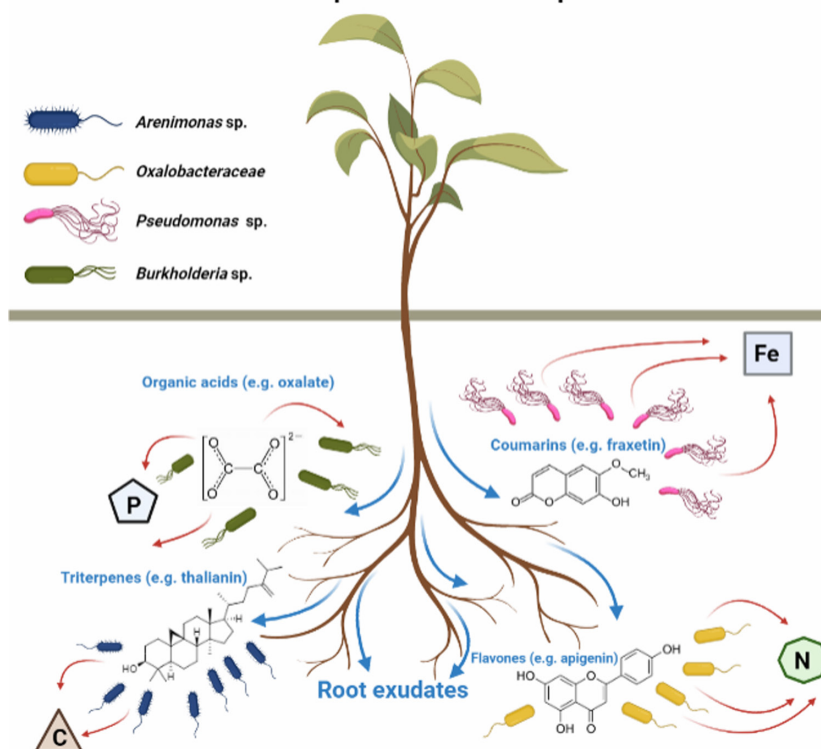
Root-derived metabolites	Signalling or substrate-associated function	Reference
Isoflavonoids (Daidsein, genistein)	Regulation of nodule factors	White et al. (2017)
Benzoxazinoids (indol-3-glycerol-phosphate)	Trigger colonizarion of plant growth promoting rhizobacteria	Neal et al. (2012)
Coumarin (scopoletin)	Iron deficiency	Stringlis et al. (2018)
Coumarins (scopoletin,fraxetin)	Recruitment of iron (III) reducing bacteria for iron acquisition	Harbort et al. (2020)
Coumarin	Semiochemicals in the communication between the roots and <i>Pseudomonas simiae</i>	Yu, He, et al. (2021); Yu, Stringlis, et al. (2021)
Phytoalexin (camalexin)	Stimulate activity of plant growth-promoting rhizobacteria	Koprivova et al. (2019)
Flavones (apigenin and luteolin)	Enrich Oxalabacteraceae under nitrogen deprivation	Yu, He, et al. (2021); Yu, Stringlis, et al. (2021)
Triterpenes (thalianin, thalianyl fatty acid sters, arabidin)	Carbon source for bacteria proliferation	Huang et al. (2019)
Phenazines	Key-stone metabolites with growth-promoting properties	Dahlstrom et al. (2020)
Organic acids (malate)	P,K,Mn,Zn and Cu increase soil availability	Tesfaye et al. (2003)
Organic acids (oxalate, citrate)	Siderophore producing Burkholderia species	Weisskopf et al. (2011)
Fatty acid (2-Methylbutyric acid, palmitic acid)	Enhancing bacterial recruitment to enhance plant growth under salinity stress	Xiong et al. (2020)
Galactoside	Supporting growth of nitrogen-fixing <i>Ensifer meliloti</i>	Bringhurst et al., 2001
Organic acids (fumaric acid)	Colonization of <i>Bacillus amyloliquefaciens</i> SQR9	Zhang et al. (2014)
Flavonoids (2-phenyl-1,4-benzopyrone)	Plant–fungal symbiotic signal	Maillet et al. (2011)
Amino acids	Chemotaxis to plant growth-promoting bacteria <i>Pseudomonas protegens</i> CHA0	Hida et al. (2020)

root colonization, competition with native microbiota and maintaining functionality under highly managed agricultural settings (Kaminsky et al., 2019; Salomon et al., 2022). This can be partially explained by the spatial and temporal variability that microbes experience in the field after application due to differences in management, and the technical challenges encountered in the selection, formulation and production process (Kaminsky et al., 2019). The identification of key genes involved in microbial association with roots can substantially help to better understand how bacteria colonize roots (Bible et al., 2021). In support of this, Cole et al. (2017) identified a comprehensive set of microbial genes that control or influence competitive root colonization in the model plant *Arabidopsis*. Mavrodi et al. (2021) demonstrated how root exudates alter the expression of diverse metabolic, transport, regulatory and stress response genes of *Pseudomonas* in the rhizosphere of *Brachypodium distachyons*. These findings stress the potential for manipulation and improvement of the colonization capabilities of plant beneficial microbes. Studies have used metagenomic analysis of endophytic bacterial

communities to determine protein-encoding gene fragments that can be used to predict key traits for the microbe's survival (Sessitsch et al., 2012). In order to deploy a soil inoculant's full functional potential, microbial colonization and survival mechanisms need to be fully elucidated.

Structure and activity of microbial communities are strongly influenced by the bioavailability and composition of organic materials in soils. Different organic materials with an undefined biochemical composition, such as organic amendments (e.g. manure, compost, compost teas, plant extracts, humic and fulvic acids, etc.), are used to increase diversity under the expectation that this would lead to enhanced microbial functionality (Griffiths & Philippot, 2013). A more targeted approach proposes the use of identified and known organic amendments to steer desired outputs in an advantageous direction, stimulating functional groups of bacteria via management practices (Chaparro et al., 2012; van Agtmaal et al., 2015). Adding organic materials containing precursors for metabolic pathways could lead to the production of biocontrol,

## Role of Root Exudates on the Recruitment of Rhizosphere Bacteria To Improve Nutrient Acquisition



**FIGURE 1** Overview of specialized root-derived metabolites mediating nutrient acquisition for plants. Nutrient deprivation induces the release of specialized primary and secondary metabolites from the plant roots to the soil. In turn, specialized metabolites serve as resource or signals for rhizosphere micro-organisms that are enriched under nutrient stress. These micro-organisms can mediate nutrient availability or display other plant growth-promoting traits. Thus, root exudates can modulate the rhizosphere microbiome or individual microbial taxa capable to solubilize or mineralize plant nutrients such as nitrogen, phosphorus and iron increasing nutrient procurement for plants. Depicted in the picture are identified metabolites and associated bacteria taxa. Lastly, most metabolites mediating similar interactions with other plant essential nutrients are not yet identified.

nutritional and anti-stress from indigenous soil bacteria (Garbeva & Weiskopf, 2020). For instance, volatiles emitted belowground by bacteria differentially impacted plant nutrient content indicating that these volatiles can affect the nutritional status of plants (Martín-Sánchez et al., 2020). Similarly, Tsolakidou et al. (2019) proposed that microbial synthetic communities can be used as compost inoculants to produce compost with desired characteristics such as biocontrol of targeted pathogens and plant growth promotion. The development of targeted inoculation methods and synthetic communities offer a venue to disentangle the inherent complexity of interactions in situ enabling tractable testing of hypotheses by manipulation in gnotobiotic systems. Challenges, limitations and opportunities of synthetic communities for plant research are further reviewed by Vorholt et al. (2017).

Research in synthetic biology has begun to explore the optimization of engineered plant growth-promoting rhizobacteria to develop strains which do not suffer the ecological shortfalls of their natural progenitors. Transfer of plant growth-promoting bacteria traits on mobile genetic

elements into selected bacterial ‘chassis’ or whole communities can be used to customize effective rhizosphere bacteria with desirable traits for specific purposes (Haskett et al., 2021). Many mechanisms of nutrient mobilizing bacteria including nitrogen, phosphorus solubilization and phytohormone biosynthesis, have been elucidated in a fine detail to be genetically engineered. For example, a recent study used a combinatorial synthetic biology-based approach to generate 82 biochemically diverse phytase enzymes which were integrated into the genomes of three bacterial strains. In this study, a fraction of the enzymes was able to mineralize phytate and promoted *Arabidopsis* growth (Shulse et al., 2019). Similarly, other important advances have been made recently towards developing application to N-fixing rhizobacteria that are associated with cereals (Ryu et al., 2020), which use phytohormones to enhance biomass, tolerance to abiotic stressors and improve resident bacteria colonization (Zúñiga-Feest et al., 2018; Guo et al., 2019). However, an important prevalent challenge is to engineer rhizobacteria with important qualities for plant assimilation (e.g. N-fixing, P-solubilizing)

without impacting the energetic balance in the plant (Haskett et al., 2021).

Root exudates have been proposed as a plausible mechanism for fine tuning the plant microbiome because of their chemically diverse composition with signaling properties and their capacity to influence the composition and function of the root microbial community (Jacoby et al., 2020). Earlier research explored genetic variation to induce traits that increase the exudation of organic acids or positive associations with symbiotic or nonsymbiotic soil organisms that favor plant nutrition. For example, P-efficient crop lines used natural and induced genetic variations for carboxylate (Pearse et al., 2007) and phosphatase exudation (George & Richardson, 2008). Although carboxylate and phosphatase exudation were evident under controlled conditions, the strategy showed variable success when evaluated in soils.

More recently, research on root exudate traits from wild relatives of modern crops has offered opportunities to reduce the use of fertilizers and pesticides (Iannucci et al., 2017; Preece & Penuelas, 2020). Because wild plant species are often able to successfully grow, reproduce and maintain adequate nutrition in nutrient-poor soils, it has been hypothesized that wild types may produce different extracellular enzymes and higher proportion of organic anions release resulting in more efficient solubilization of phosphorus (Preece & Peñuelas, 2020). Differential microbial composition patterns in the rhizosphere of modern crops relative to their wild progenitors have been reported in potato and maize (Pantigoso, Manter, & Vivanco, 2020; Pantigoso, et al., 2020; Schmidt et al., 2020). For instance the rhizosphere microbiome of wild potatoes was shown to be correlated with the higher capacity to uptake and utilize phosphorus when compared to modern potato cultivars. Other important studies deciphering differences in cultivated crops' rhizosphere microbiomes relative to their wild ancestors' have expanded our understanding on rhizobacterial community shifts during domestication (Mendes et al., 2018; Pérez-Jaramillo et al., 2017; 2019). The tight association between root exudates and rhizosphere microbiome and the latest discoveries on the heritability component of the plant microbiome support the efforts of harnessing root exudates from wild relatives to improve functional features of modern crops (Peiffer et al., 2013; Rügger et al., 2021). Recent evidence shows that the manipulation of root exudate composition from root apices enriching certain bacterial communities throughout the root system is feasible (Kawasaki et al., 2021). The advantage of this approach is that exudates are deposited at the root-soil interface, where they are most likely impacting microbial growth. Additionally, the release of substrates along host life cycle can maintain selection pressure on a given established community. Alternative approaches

encourage the identification, selection and use of certain root exudates to directly mobilize nutrients in the soils and use them in combination with elicitors to encourage inoculant proliferation (Garbeva & Weisskopf, 2020; Rizaludin et al., 2021).

## FUTURE RESEARCH AND PERSPECTIVES

Due to its multifunctional properties, root exudates are key to manipulate plant-microbial interactions to improve nutrient acquisition. Future research should focus on: (1) Identifying specialized molecules with elicitation of microbial activity, (2) Identifying microbes which help plants to alleviate nutrient scarcity efficiently, (3) Investigating the molecular mechanisms underlying the composition of root exudates under nutrient scarcity and (4) Developing protocols to discover and test root exudate derived compounds that could increase the nutrient acquisition ability of PGPR. To achieve the discovery of these specialized metabolites, we still need to develop optimal and universally standardized methods of root exudate collection and analysis that resemble environmental soil conditions (Pantigoso et al., 2021). In addition, identifying patterns in root exudate profiles and rhizosphere microbiomes under a wide range of environmental conditions, nutrient status and plant developmental stages will increase our understanding of plant-microbial interactions in the rhizosphere.

As soil environment and nutrient status changes, tradeoffs occur among the three plant functional traits for nutrient procurement: root exudation, root morphology and root-microbial symbiosis. However, often only the two latter strategies are considered, limiting our holistic understanding of plant acquisition strategies. A deeper understanding of integrated strategies of resource acquisition used by plants is needed in order to by combining knowledge on the roles of root exudates with the other two better-studied strategies (Galindo-Castañeda et al., 2022; Wen et al., 2021). The frontiers of an integrative functional strategy for resource acquisition include the identification of root exudate compounds, prevalent across plant species, that are enriched under macro and micronutrient limited environments as well as identifying novel molecules that correlate with high nutrient uptake efficiency, enrichment of PGPR species in the rhizosphere or colonization and activity of symbiotic microbes. In addition, advances in the development of improved methods in analytical chemistry and bioinformatics that allow the detection of novel metabolic signals, in chromatography-mass spectrometry profiling, would remain critical to better understand which parts of whole biochemical networks

respond to genetic perturbation or environmental stress (Obata & Fernie, 2012; Wang et al., 2016).

Second, the effects of root exudated compounds, from sufficient versus nutrient-deficient conditions, on the activity of either individual beneficial micro-organism or synthetic communities, need to be further investigated under various soils with and without the influence of the plant. Before that, protocols need to be developed to test the functional potentially of newly identified single compounds or blends, on nutrient content availability, microbial community composition and function and its potential positive effect on plant health and yield (Badri et al., 2013; Zhalnina et al., 2018). Although metabolic composition of root exudates is under the genetic control of the plant, external factors such as soil type and environmental stresses affect root exudation (Badri & Vivanco, 2009; Pantigoso et al., 2021). Revealing molecular mechanisms underlying the composition of the root exudates under nutrient-limiting conditions for plants, soil types and rhizosphere microbial communities will be valuable information to use microbes and root exudate derived compounds to help plant alleviate plant nutritional stress (Hong et al., 2021). However, the identification of genes associated with root exudation profiles require multidisciplinary approaches incorporating plant genetics, nutrient stress biology, molecular biology, soil microbiology and bioinformatics. Successful integration of these disciplines can greatly improve our understanding of the mechanistic processes controlling root exudate, under abiotic conditions and different soil types, further allowing development of applications that can be incorporated to targeted plant breeding and formulation of customized chemical blends to ultimately customize compound-microbe-crop combinations that enhance efficiency of resource acquisition for plants (Hong et al., 2021; Song et al., 2020). Likewise, the development of plant-controlled symbiosis in which rhizosphere bacteria are able to display nitrogen fixation or phosphorus solubilization only when in contact with an engineering compound-producing plant (e.g. rhizopine; Haskett et al., 2021). Similarly, the development of plant-controlled symbiosis in which the bacteria display its functionality (e.g. nitrogen fixation) only when in contact with the desired host plant; thus, preventing their interaction with non-targeted plant species (Haskett et al., 2022).

Third, the exploitation of root exudate traits in wild relatives of crops offers opportunities to reduce the use of fertilizers and pesticides by providing a large course of genetic material with desirable traits (Preece & Peñuelas, 2020). Investigating root exudate composition, for instance, the abundance and number of compounds involved in mobilizing and chelating nutrient in wild relatives compared to their domesticated counterparts may reveal missed molecules lost in the process of conventional breeding and

domestication. This is in parallel to the recently revealed changes on wild and domesticated rhizosphere microbiomes (Pérez-Jaramillo et al., 2018). Speculating further, observed changes in structure and function of rhizosphere microbiomes may be a consequence of the shifted chemical composition of root exudate profiles from wild relatives, since rhizosphere microbes utilized these diverse molecules blends as source of nutrient and signals (Lannucci et al., 2017; Preece & Peñuelas, 2020).

## CONFLICT OF INTEREST

The authors declare no conflict of interests.

## ORCID

Hugo A. Pantigoso  <https://orcid.org/0000-0002-7121-7253>

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**How to cite this article:** Pantigoso, H.A., Newberger, D. & Vivanco, J.M. (2022) The rhizosphere microbiome: Plant-microbial interactions for resource acquisition. *Journal of Applied Microbiology*, 133, 2864–2876. Available from: <https://doi.org/10.1111/jam.15686>