

The dynamic interplay of root exudates and rhizosphere microbiome

Ali Yetgin^{1,2} 

¹Toros Agri Industry and Trade Co. Inc., Research and Development Center, Mersin, Türkiye

²Department of Biotechnology, Institute of Nature and Applied Sciences, Cukurova University, 01250 Adana, Türkiye

How to cite

Yetgin A. (2023). The dynamic interplay of root exudates and rhizosphere microbiome. *Soil Studies* 12(2), 111-120.
<http://doi.org/10.21657/soilst.1408089>

Article History

Received 18 April 2023

Accepted 25 July 2023

First Online 21 December 2023

Corresponding Author

Tel.: +90 322 338 60 84

E-mail: ali1992yetgin@gmail.com

Keywords

Rhizosphere microbiome

Root exudates

Plant-microbe interactions

Nutrient cycling

Microbial ecology

Abstract

The rhizosphere microbiome plays a vital role in plant growth, health, and nutrient acquisition. One of the key factors that shape the composition and function of the rhizosphere microbiome is root exudates, the complex mixture of organic compounds released by plant roots. Root exudates serve as a source of energy and nutrients for the rhizosphere microbiome, as well as a means of communication between plants and microbes. The dynamic interplay between root exudates and rhizosphere microbiome is a complex and highly regulated process that involves multiple feedback loops and interactions. Recent studies have revealed that the composition and quantity of root exudates are modulated by a range of biotic and abiotic factors, including plant genotype, soil type, nutrient availability, and microbial community structure. In turn, the rhizosphere microbiome can influence the production and composition of root exudates, through processes such as nutrient cycling, plant hormone synthesis, and modulation of plant defense responses. Understanding the dynamics of root exudates and rhizosphere microbiomes is crucial for developing effective strategies for microbiome engineering, plant-microbe symbiosis, and sustainable agriculture. This review provides an overview of the current state of knowledge on the dynamic interplay between root exudates and rhizosphere microbiomes, highlighting the key factors and mechanisms that govern this complex relationship.

Introduction

The rhizosphere microbiome is a key determinant of plant growth, health, and nutrient acquisition. The rhizosphere, which is the soil surrounding plant roots, harbors a diverse community of microorganisms that interact with plant roots and influence their growth and development ([Garcia and Kao-Kniffin, 2018](#)). These microorganisms include bacteria, fungi, and other microbes that perform a range of functions, such as nutrient cycling, disease suppression, and symbiotic interactions. One of the key functions of the rhizosphere microbiome is to facilitate nutrient uptake by plants. Microorganisms in the rhizosphere can

solubilize nutrients in the soil, such as phosphorus and nitrogen, making them more available to plants. In addition, some microorganisms can fix atmospheric nitrogen, providing a source of nitrogen for plant growth.

The rhizosphere microbiome also plays a key role in plant health and disease resistance. Some microorganisms in the rhizosphere can produce antibiotics and other compounds that protect plants from pathogens and pests. In addition, some microorganisms can induce systemic resistance in plants, priming them to better defend against future

pathogen attacks. The rhizosphere microbiome is a critical component of plant-microbe interactions and plays a key role in plant growth, health, and nutrient acquisition. Understanding the dynamics of the rhizosphere microbiome and its interactions with plants is important for developing sustainable agricultural practices and improving plant health and productivity (Kumawat et al., 2022).

The rhizosphere microbiome also plays a key role in soil health and ecosystem functioning. Microorganisms in the rhizosphere are involved in processes such as nutrient cycling, organic matter decomposition, and carbon sequestration, which are critical for maintaining soil fertility and productivity. Some microbes in the rhizosphere can also detoxify soil pollutants and contaminants, making them valuable for environmental remediation (Khan, 2005). In addition, the composition and diversity of the rhizosphere microbiome can be influenced by a range of factors, including soil type, plant genotype, and environmental conditions. By understanding these factors, we can develop strategies for manipulating the rhizosphere microbiome to promote desirable plant-microbe interactions and improve soil health. The rhizosphere microbiome represents a fascinating and important area of research with significant implications for agriculture, soil science, and environmental management (Mendes et al., 2013).

Root exudates are compounds released by plant roots into the soil, which can have a significant impact on the composition and function of the rhizosphere microbiome. These compounds can provide a source of energy and nutrients for microorganisms in the rhizosphere, shaping their composition and diversity. In addition, root exudates can also influence the behavior and function of microorganisms in the rhizosphere, such as by modulating gene expression or inducing chemotaxis. Root exudates are highly diverse and can include compounds such as sugars, amino acids, organic acids, and secondary metabolites (Carvalhais et al., 2011). The composition of root exudates can vary depending on a range of factors, such as plant genotype, soil type, and nutrient availability. As such, the composition and quantity of root exudates can have a profound impact on the rhizosphere microbiome and the ecosystem processes it supports.

Furthermore, the dynamic interplay between root exudates and the rhizosphere microbiome is a complex and dynamic process. Microorganisms in the rhizosphere can modulate the production and composition of root exudates by influencing plant gene expression or by altering the soil environment. In turn, changes in root exudates can feedback on the composition and function of the rhizosphere microbiome, influencing ecosystem processes such as nutrient cycling and carbon sequestration. Root exudates play a key role in shaping the composition

and function of the rhizosphere microbiome. Understanding the dynamics of this relationship is essential for developing strategies to manipulate plant-microbe interactions for sustainable agriculture and environmental management (Choudhary et al., 2016).

In addition to their role in shaping the rhizosphere microbiome, root exudates can also play a crucial role in plant growth and development. Some root exudates can act as growth promoters, stimulating root elongation and branching, while others can act as signaling molecules, mediating plant-microbe interactions or inducing systemic resistance (Narula et al., 2012). Furthermore, the production and composition of root exudates can be influenced by a range of environmental factors, such as drought, nutrient availability, and soil pH. For example, plants grown under drought stress may produce root exudates that promote water uptake and drought tolerance, while plants grown in nitrogen-limited soils may produce exudates that enhance nitrogen acquisition.

The ability to manipulate root exudates represents an exciting area of research with significant implications for sustainable agriculture and environmental management. By developing strategies to enhance the production of beneficial root exudates or to target specific microorganisms in the rhizosphere, we can improve plant growth and health, enhance nutrient acquisition, and promote ecosystem functioning. The dynamic interplay between root exudates and the rhizosphere microbiome represents a fascinating area of research with broad implications for plant-microbe interactions, soil science, and environmental management.

The Composition and Function of Root Exudates

Root exudates are a complex mixture of organic compounds released by plant roots into the soil. These compounds are secreted by specialized cells in the root and can be actively transported across the plasma membrane and into the rhizosphere. Root exudates can include a wide range of compounds, such as sugars, amino acids, organic acids, enzymes, and secondary metabolites. The production and composition of root exudates can vary depending on a range of factors, such as plant species and genotype, soil type, nutrient availability, and biotic and abiotic stress (Badri and Vivanco, 2009). For example, some plant species may produce specific exudates that are toxic to certain soil pathogens or that attract beneficial microbes, while others may produce exudates that enhance nutrient acquisition or water uptake.

Root exudates are also highly dynamic and can change over time in response to changing environmental conditions or interactions with microbes in the rhizosphere. Microbes in the rhizosphere can

influence the production and composition of root exudates through a range of mechanisms, such as by inducing changes in plant gene expression or by modulating the soil environment ([Vives-Peris et al., 2020](#)). Root exudates are a complex and dynamic mixture of compounds that play a crucial role in shaping the rhizosphere microbiome and mediating plant-microbe interactions. Understanding the production and function of root exudates is essential for developing strategies to promote sustainable agriculture and environmental management.

Root exudates can serve a wide range of functions in the rhizosphere, such as providing a source of energy and nutrients for microbes, mediating plant-microbe interactions, and modulating soil chemistry and structure. For example, some root exudates can promote the growth and activity of beneficial microbes in the rhizosphere, such as nitrogen-fixing bacteria or mycorrhizal fungi, which can enhance nutrient availability and plant growth ([Igiehon and Babalola, 2018](#)). Other exudates can act as signaling molecules, mediating interactions between plants and pathogens or promoting systemic resistance to stress. Root exudates can also influence the physicochemical

properties of the soil, such as by altering soil pH or promoting the formation of soil aggregates, which can impact nutrient cycling, water availability, and soil structure. Some root exudates may also have allelopathic effects, inhibiting the growth of competing plant species or serving as chemical cues for plant defense.

The composition and quantity of root exudates can be influenced by a range of factors, such as plant genetics, nutrient availability, and environmental stressors. Furthermore, the production and function of root exudates can be influenced by the diversity and activity of microorganisms in the rhizosphere. For example, certain microbes can induce changes in root exudate production or composition by modulating plant gene expression or by competing for resources in the rhizosphere ([Berendsen et al., 2012](#)). The dynamic interplay between root exudates and the rhizosphere microbiome is a complex and multifaceted process that plays a crucial role in plant-microbe interactions, soil ecology, and ecosystem functioning. Understanding the production and function of root exudates is essential for developing sustainable agricultural practices, managing soil health, and promoting ecosystem

Table 1. Types of compounds found in root exudates.

Type of Compound	Examples	Function	Reference
Sugars	Glucose, fructose, sucrose	Source of energy for microbes, mediate plant-microbe interactions	Franzino et al., 2022
Amino Acids	Glutamate, aspartate, proline	Source of nitrogen for microbes, mediate plant-microbe interactions	Carvalhais et al., 2013
Organic Acids	Citrate, malate, oxalate	Mobilize nutrients in soil, modulate soil pH	Lopez-Bucio et al., 2000
Enzymes	Phosphatases, cellulases, proteases	Break down complex organic compounds in soil, release nutrients	Pritsch and Garbaye, 2011
Secondary Metabolites	Phenolics, flavonoids, terpenes	Defense against pathogens, allelopathy, signaling molecules	Wang et al., 2018
Hormones	Auxins, cytokinins, gibberellins	Regulation of plant growth and development, mediate plant-microbe interactions	Giron et al., 2013

resilience.

Root exudates play a crucial role in providing energy and nutrients for the rhizosphere microbiome. The exudates released by plant roots contain a diverse range of compounds, including sugars, amino acids, and organic acids, which serve as a primary source of energy and nutrients for microbes in the rhizosphere (Table 1). Microbes in the rhizosphere can use root exudates as a source of carbon and energy for their growth and metabolism. For example, some bacteria can metabolize sugars such as glucose or fructose, while others can break down amino acids or organic acids such as citrate or malate ([Zaunmüller et al., 2006](#)). By utilizing root exudates, microbes in the rhizosphere can increase their population size and activity, which can have a range of positive effects on plant health and growth.

In addition to providing a source of energy, root

exudates can also serve as a source of nutrients such as nitrogen and phosphorus. Some microbes in the rhizosphere, such as nitrogen-fixing bacteria or phosphate-solubilizing bacteria, can utilize root exudates to access these nutrients, which can enhance nutrient availability for plant growth. Furthermore, the release of enzymes by microbes in the rhizosphere can break down complex organic compounds in soil, releasing nutrients such as nitrogen and phosphorus that can be taken up by plant roots. Root exudates play a critical role in shaping the composition and function of the rhizosphere microbiome by providing energy and nutrients for microbial growth and metabolism ([Yue et al., 2023](#)). Understanding the production and function of root exudates is essential for developing strategies to promote sustainable agriculture and soil health.

Root exudates also play a key role in promoting plant-microbe interactions in the rhizosphere. The

release of specific compounds in root exudates can attract beneficial microbes to the rhizosphere, such as those that can promote plant growth or provide protection against pathogens. For example, some plants can release flavonoids in their root exudates, which can attract rhizobial bacteria that can form a symbiotic relationship with the plant, resulting in the formation of nitrogen-fixing nodules on the roots ([Narula et al., 2012](#); [Mahmud et al., 2020](#)). Other plants can release terpenes in their root exudates, which can attract beneficial microbes that can provide protection against pathogens.

Furthermore, the production of root exudates can be regulated by plant hormones, such as auxins, cytokinins, and gibberellins, which can influence plant growth and development ([Kurepin et al., 2014](#)). These hormones can also mediate plant-microbe interactions in the rhizosphere by regulating the production of root exudates and their effects on microbial communities. Root exudates are essential for the functioning of the rhizosphere microbiome and play a vital role in plant growth, health, and nutrient acquisition. By providing a source of energy and nutrients, promoting plant-microbe interactions, and regulating microbial communities, root exudates contribute to sustainable agriculture and soil health.

The Composition and Function of Rhizosphere Microbiome

The rhizosphere microbiome is the complex community of microorganisms that live in the zone of soil surrounding plant roots, known as the rhizosphere. The rhizosphere microbiome is a dynamic and diverse community, consisting of bacteria, fungi, archaea, viruses, and other microorganisms. The characteristics of the rhizosphere microbiome are influenced by a range of factors, including plant species, soil type,

environmental conditions, and microbial interactions. The microbial community in the rhizosphere is distinct from that in bulk soil, as the release of root exudates and other organic compounds from plant roots creates a unique microenvironment that supports the growth and activity of certain microbial taxa ([Hartmann et al., 2009](#)).

The rhizosphere microbiome can have a range of positive effects on plant growth and health. For example, some microbes in the rhizosphere can solubilize nutrients such as phosphorus, making them more available for plant uptake. Other microbes can produce plant growth-promoting hormones or stimulate plant defense mechanisms against pathogens ([Van Loon, 2007](#); [Glick, 2012](#)). The composition and function of the rhizosphere microbiome can be influenced by management practices such as tillage, fertilization, and crop rotation. Understanding the dynamics of the rhizosphere microbiome is essential for developing strategies to promote sustainable agriculture and soil health.

The rhizosphere microbiome is a complex and dynamic community, with microbial populations that can change over time in response to various biotic and abiotic factors. Microbial interactions within the rhizosphere can be competitive, cooperative, or neutral, and can impact the composition and activity of the microbiome ([Hassani et al., 2018](#)). The rhizosphere microbiome is also influenced by the root exudates released by plants. Root exudates can provide a source of energy and nutrients for microbial growth and activity and can also influence the composition and function of the rhizosphere microbiome.

Recent research has shown that the rhizosphere microbiome can have significant effects on plant growth, health, and productivity. For example, certain microbes in the rhizosphere have been shown to promote plant growth by producing hormones or

Table 2. Types of microbes found in rhizosphere microbiome.

Microbe Type	Examples	Function in Rhizosphere	Mode of Interaction	Reference
Bacteria	Pseudomonas, Rhizobium, Bacillus	Nutrient cycling, plant growth promotion, pathogen suppression	Competitive, cooperative, neutral	Hayat et al., 2010
Fungi	Mycorrhizae, Trichoderma, Fusarium	Nutrient cycling, plant growth promotion, pathogen suppression	Mutualistic, parasitic, saprophytic	Azcón-Aguilar and Barea, 1992
Archaea	Methanogens, halophiles, thermophiles	Nitrogen cycling, methane production	Cooperative, neutral	Naitam and Kaushik, 2021
Viruses	Bacteriophages	Regulation of microbial populations, horizontal gene transfer	Parasitic, neutral	Haudiquet et al., 2022
Protozoa	Ciliates, amoebae	Predation on bacteria and fungi, nutrient cycling	Predatory, neutral	Alpei et al., 1996
Nematodes	Root-knot nematodes, predatory nematodes	Pathogenic or beneficial effects on plants and microbes	Parasitic, predatory	Tapia-Vázquez et al., 2022

facilitating nutrient uptake, while others can protect plants from pathogens or other stresses ([Hayat et al., 2010](#)). The study of the rhizosphere microbiome is an important area of research, with significant implications for agriculture and soil health. By understanding the interactions between plants and their associated microbiomes, researchers can develop strategies to promote sustainable agriculture and soil management practices that optimize plant-microbe interactions for enhanced plant growth, health, and productivity.

The rhizosphere microbiome plays a critical role in plant-microbe interactions and soil health (Table 2). One of the primary functions of the rhizosphere microbiome is to facilitate nutrient cycling and uptake by the plant. Microbes in the rhizosphere can solubilize and mineralize nutrients, such as nitrogen and phosphorus, making them available for plant uptake. Additionally, certain microbes can produce plant growth-promoting hormones, such as auxins and cytokinins, which can stimulate root growth and enhance plant growth. The rhizosphere microbiome also plays an important role in plant defense against pathogens. Some microbes in the rhizosphere have been shown to produce antimicrobial compounds that can inhibit the growth of plant pathogens, while others can induce systemic resistance in the plant ([Beneduzi et al., 2012](#)). This can lead to increased plant resistance to a variety of biotic and abiotic stressors.

In addition to their role in plant-microbe interactions, the rhizosphere microbiome can also have a significant impact on soil health. Microbes in the rhizosphere can secrete extracellular enzymes that break down organic matter, releasing nutrients into the soil and improving soil structure ([Frey, 2019](#)). This can lead to increased soil fertility and water-holding capacity, as well as reduced erosion and nutrient leaching. The rhizosphere microbiome is a complex and dynamic ecosystem that plays a vital role in plant health, soil health, and ecosystem function. Understanding the interactions between plants and their associated microbiomes can lead to more sustainable and efficient agricultural practices, as well as improved soil and plant health.

The Dynamic Interplay between Root Exudates and Rhizosphere Microbiome

The production and composition of root exudates are influenced by a variety of factors, including plant genotype, soil type, and nutrient availability ([Singh and Mukerji, 2006](#); [Rengel and Marschner, 2005](#)). These factors can impact the quantity and quality of exudates produced by the plant, as well as the types and abundance of microbes in the rhizosphere. Plant genotype plays a significant role in determining the composition of root exudates. Different plant species

and cultivars produce unique profiles of exudates, which can influence the composition and function of the rhizosphere microbiome ([Tiziani et al., 2022](#)). For example, some plant species produce exudates that are rich in organic acids and sugars, while others produce exudates that are rich in amino acids and proteins. Soil type can also influence the production and composition of root exudates. Soil properties such as texture, pH, and nutrient availability can impact the types and abundance of microbes in the rhizosphere, which in turn can influence the types of exudates produced by the plant. For example, plants grown in nutrient-poor soils may produce exudates that are rich in organic acids and sugars, which can help to solubilize and mobilize nutrients in the soil ([Ström, 1997](#)).

Nutrient availability is another important factor that can influence the production and composition of root exudates. Plants grown under nutrient-rich conditions may produce fewer exudates overall, but those exudates may be of higher quality and contain a greater diversity of compounds ([Oburger et al., 2018](#); [Badri and Vivanco, 2009](#)). Conversely, plants grown under nutrient-poor conditions may produce more exudates overall, but those exudates may be of lower quality and contain a narrower range of compounds. The production and composition of root exudates are complex processes that are influenced by a variety of factors. Understanding the factors that influence exudate production and composition can help optimize plant-microbe interactions and improve soil health and productivity in agricultural systems.

In addition to the factors mentioned above, other environmental factors such as temperature, moisture, and light can also impact root exudate production and composition. For example, plants grown under high temperatures may produce more volatile organic compounds in their exudates, which can influence the types of microbes present in the rhizosphere. Similarly, plants grown under drought conditions may produce exudates that are more concentrated, as a mechanism to conserve water. It is also important to note that the composition of the rhizosphere microbiome can influence the production and composition of root exudates. For example, certain microbial taxa in the rhizosphere have been shown to promote the production of specific compounds in root exudates, which can in turn influence the types of microbes present in the rhizosphere ([Singh and Mukerji, 2006](#); [Berendsen et al., 2012](#)). The complex interplay between plant genotype, soil type, nutrient availability, and environmental factors all contribute to the production and composition of root exudates, which in turn influence the types and abundance of microbes in the rhizosphere. Understanding these complex interactions is essential for developing sustainable agriculture practices that optimize plant-microbe interactions and promote soil health and productivity.

(Mandal et al., 2021; Choudhary et al., 2016).

[Oppenheimer-Shaanan et al., \(2022\)](#) used advanced approaches in microbiology, plant physiology, and organic chemistry to study the dynamic rhizosphere interplay between tree roots and soil bacteria under drought stress. They collected root exudates and analyzed them for metabolites using metabolic profiling. They found that 44 metabolites in exudates were significantly different in concentration between irrigated and drought trees, including phenolic acid compounds and quinate. When adding these metabolites as carbon and nitrogen sources to bacterial cultures of both bacterial species, eight of nine metabolites stimulated bacterial growth. The researchers also found that soil phosphorous bioavailability was maintained only in inoculated trees, mitigating drought-induced decrease in leaf phosphorus and iron.

The rhizosphere microbiome can modulate root exudate production and composition through a variety of mechanisms, including nutrient cycling, hormone synthesis, and modulation of plant defense responses. These interactions can be beneficial for both the plant and the microbes, as they can help to improve nutrient acquisition and promote plant growth and health ([Pettit, 2004](#)). One important mechanism by which the rhizosphere microbiome modulates root exudate production and composition is through nutrient cycling. Many microbes in the rhizosphere are capable of breaking down complex organic compounds in the soil, such as lignin and cellulose, into simpler compounds that can be taken up by plants. This process, known as mineralization, releases nutrients such as nitrogen, phosphorus, and sulfur into the soil, which can then be taken up by the plant and incorporated into its exudates ([Etesami and Adl, 2020](#)). In turn, these exudates can promote the growth of beneficial microbes in the rhizosphere, which can further enhance nutrient cycling and improve plant growth and health.

Another mechanism by which the rhizosphere microbiome can modulate root exudate production and composition is through hormone synthesis. Some microbes in the rhizosphere are capable of synthesizing plant hormones, such as auxins and cytokinins, which can influence the growth and development of the plant ([Hayat et al., 2010; Arshad and Frankenberger, 1991](#)). These hormones can also influence root exudate production and composition, as they can promote the release of specific compounds that are beneficial for the microbes. For example, some microbes have been shown to promote the production of amino acids and organic acids in root exudates, which can provide a source of carbon and nitrogen for the microbes. The rhizosphere microbiome can modulate root exudate production and composition by influencing plant defense responses. Some microbes in the rhizosphere can produce compounds that can stimulate the plant's

immune system, which can in turn influence the types and amounts of exudates produced by the plant. For example, some microbes produce compounds that can trigger the production of phytohormones and other defense-related compounds in the plant, which can help to protect the plant against pathogenic microbes and other stresses ([Zehra et al., 2021](#)). The rhizosphere microbiome can modulate root exudate production and composition through a variety of mechanisms, which can help to improve nutrient cycling, hormone synthesis, and plant defense responses. These interactions are essential for promoting plant growth and health, and for maintaining a healthy and productive soil ecosystem.

In addition to the mechanisms mentioned above, the composition of the rhizosphere microbiome itself can also play a role in modulating root exudate production and composition. For example, studies have shown that the presence of specific microbial taxa in the rhizosphere can influence the types and amounts of exudates produced by the plant ([White et al., 2017](#)). This may be due to the fact that different microbes have different metabolic pathways and nutrient requirements, which can influence the types of compounds they can utilize in root exudates. Furthermore, environmental factors such as soil type and nutrient availability can also play a role in modulating root exudate production and composition. For example, plants growing in nutrient-poor soils may produce more exudates in an effort to attract beneficial microbes that can help to improve nutrient availability. Similarly, plants growing in soils with high levels of pathogens may produce exudates that contain compounds with antimicrobial properties, which can help to protect the plant against infection. The dynamic interplay between root exudates and the rhizosphere microbiome is a complex and multifaceted process that is influenced by a variety of biotic and abiotic factors ([Kotoky et al., 2018](#)). Understanding these interactions is essential for developing strategies to promote plant growth and health, improve soil fertility, and maintain a healthy and productive soil ecosystem.

The relationship between root exudates and the rhizosphere microbiome is bidirectional, meaning that they can both influence each other in a feedback loop. For example, the composition of the rhizosphere microbiome can affect the types and amounts of exudates produced by the plant, which in turn can influence the growth and activity of the microbiome ([Bakker et al., 2012](#)). Similarly, the composition and activity of the microbiome can influence the types and amounts of exudates produced by the plant. One example of this feedback loop is the role of plant hormones in modulating both root exudate production and the composition of the rhizosphere microbiome. Studies have shown that plants can produce hormones such as auxins and cytokinins in response to specific microbial signals, which can then stimulate the

production of specific exudates. These exudates, in turn, can attract specific microbial communities that are capable of metabolizing the exudates and promoting plant growth.

Another example of this feedback loop is the role of nutrient cycling in the rhizosphere. Microbes in the rhizosphere are involved in the cycling of nutrients such as nitrogen, phosphorus, and sulfur, which can then be taken up by the plant ([Osorio Vega, 2007](#)). In turn, the plant can modulate the production of specific exudates that attract microbes capable of mobilizing these nutrients. The feedback loops and interactions between root exudates and the rhizosphere microbiome are complex and dynamic. Understanding these interactions is essential for developing strategies to manipulate the microbiome and promote plant growth and health.

Implications for Microbiome Engineering and Sustainable Agriculture

The manipulation of root exudates and the rhizosphere microbiome has enormous potential for applications in sustainable agriculture and environmental management. By promoting healthy soil microbial communities and optimizing nutrient cycling, these strategies can enhance plant growth and reduce the need for synthetic fertilizers and other inputs. This can lead to improved soil health, reduced greenhouse gas emissions, and increased carbon sequestration in soils. In addition, manipulating root exudates and the rhizosphere microbiome can have important implications for environmental management beyond agriculture ([Bakker et al., 2012](#); [Tiziani et al., 2022](#)). For example, it can help to promote the restoration of degraded soils and ecosystems, enhance carbon sequestration in soils, and improve water quality by reducing nutrient runoff. However, it is important to recognize that any manipulation of the rhizosphere microbiome and root exudates must be carefully evaluated for potential risks and unintended consequences. This includes potential impacts on non-

target species, such as soil organisms and beneficial insects, as well as potential effects on soil and water quality. Therefore, it is essential that these strategies be developed and implemented in a responsible and sustainable manner, with a focus on minimizing negative impacts on the environment and maximizing the benefits for both agriculture and the broader ecosystem.

To achieve the full potential of these strategies, more research is needed to better understand the complex interactions between plants, root exudates, and the rhizosphere microbiome. This includes developing a deeper understanding of the molecular mechanisms that underlie these interactions and how they can be manipulated to achieve specific outcomes. It also involves understanding the role of the broader soil and environmental context in shaping these interactions, including the influence of soil type, climate, and other environmental factors. Furthermore, there is a need for greater collaboration and knowledge-sharing across different scientific disciplines, as well as between scientists, farmers, and other stakeholders in the agriculture and environmental sectors. This will help to ensure that the latest scientific findings are translated into practical and effective strategies that can be implemented on the ground. The manipulation of root exudates and the rhizosphere microbiome represents a promising approach for achieving sustainable agriculture and environmental management ([Bano et al., 2021](#)). By promoting healthy soils and ecosystems, these strategies have the potential to enhance food security, reduce the environmental footprint of agriculture, and contribute to broader efforts to address global environmental challenges such as climate change and biodiversity loss.

Future Directions

Research on the dynamic interplay between root exudates and the rhizosphere microbiome is essential for several reasons. It will help to deepen our

Table 3. Strategies for manipulating root exudates and rhizosphere microbiome.

Strategy	Description	Reference
Plant breeding	Breeding plants with specific exudate profiles that can selectively recruit beneficial microbes, such as nitrogen-fixing bacteria or mycorrhizal fungi	Jacoby et al., 2017
Soil amendments	Adding amendments such as organic matter or biochar can enhance microbial diversity and activity in the rhizosphere, leading to changes in exudate production and composition	Li et al., 2021
Microbial inoculants	Adding specific microbial inoculants to the soil can selectively promote the growth of beneficial microbes, leading to changes in exudate production and composition	Saad et al., 2020
Inter-cropping	Planting two or more crops together can lead to changes in the composition of the rhizosphere microbiome, which can in turn affect exudate production	Bennett et al., 2012
Nutrient management	Managing soil nutrient availability can affect the composition of the rhizosphere microbiome and thus impact exudate production	Kumar and Dubey, 2020
Biostimulants	Biostimulants, such as humic acids or seaweed extracts, can promote plant growth and affect exudate production by stimulating microbial activity	Calvo et al., 2014

understanding of the complex and multifaceted interactions between plants and microbes in the soil, which are essential for the health and productivity of agricultural systems and natural ecosystems. It will enable the development of more effective and sustainable strategies for managing plant-microbe interactions in the soil ([Choudhary et al., 2016](#); [Morgan et al., 2005](#)). By better understanding the mechanisms that underlie these interactions, researchers will be able to develop new approaches for manipulating root exudates and the rhizosphere microbiome to achieve specific outcomes, such as enhancing nutrient acquisition, improving plant health and resilience, and promoting sustainable agriculture and environmental management.

Continued research in this area is necessary to address some of the pressing challenges facing agriculture and the environment today, including climate change, soil degradation, and biodiversity loss. By promoting healthy soils and ecosystems through the manipulation of root exudates and the rhizosphere microbiome, we can contribute to broader efforts to address these global challenges. Continued research on the dynamic interplay between root exudates and the rhizosphere microbiome is crucial for advancing our understanding of plant-microbe interactions in the soil, developing new strategies for managing these interactions, and addressing some of the most pressing challenges facing agriculture and the environment today ([Bakker et al., 2012](#); [Munoz-Ucros et al., 2021](#)).

Additionally, continued research on the dynamic interplay between root exudates and the rhizosphere microbiome can also provide valuable insights into fundamental ecological and evolutionary processes. For example, studying the mechanisms by which plants and microbes co-evolve in the soil can shed light on the origins and maintenance of biodiversity, as well as the mechanisms that underlie the emergence and spread of plant-microbe mutualisms ([Nadarajah et al., 2021](#)). Furthermore, understanding the complex and dynamic nature of root exudates and the rhizosphere microbiome can also have implications for human health. For example, some studies suggest that the composition of the gut microbiome, which plays a critical role in human health, may be influenced by the composition of the rhizosphere microbiome in the foods we eat ([Goulet et al., 2019](#)). Therefore, a better understanding of the interactions between plants and microbes in the soil may have broader implications for human health and wellness. The continued research on the dynamic interplay between root exudates and the rhizosphere microbiome is crucial for advancing our understanding of the ecological and evolutionary processes that shape plant-microbe interactions, developing sustainable strategies for managing these interactions and addressing global challenges such as climate change, soil degradation, and biodiversity loss.

Conclusion

The dynamic interplay between root exudates and the rhizosphere microbiome is a complex and tightly regulated process that is influenced by a range of biotic and abiotic factors. Root exudates serve as a critical source of energy and nutrients for the rhizosphere microbiome, while also shaping the composition and function of microbial communities. Conversely, the rhizosphere microbiome can modulate the production and composition of root exudates, through a range of mechanisms that include nutrient cycling, hormone synthesis, and plant defense modulation. Understanding the complex relationship between root exudates and rhizosphere microbiome is of great importance for agriculture and environmental management. By manipulating root exudates and rhizosphere microbiomes, we can develop strategies for sustainable agriculture, plant-microbe symbiosis, and soil remediation. Further research is needed to fully understand the mechanisms underlying the dynamic interplay between root exudates and rhizosphere microbiome and to develop effective strategies for microbiome engineering and plant-microbe interactions. The dynamic interplay between root exudates and rhizosphere microbiome represents a fascinating and important area of research with significant implications for agriculture, soil science, and environmental management.

References

- Alphei, J., Bonkowski, M., & Scheu, S. (1996). Protozoa, Nematoda, and Lumbricidae in the rhizosphere of *Hordelymus europeus* (Poaceae): faunal interactions, response of microorganisms and effects on plant growth. *Oecologia*, 106(1), 111-126. <https://doi.org/10.1007/BF00334413>
- Arshad, M., & Frankenberger, W. T. (1991). Microbial production of plant hormones. In *The Rhizosphere and Plant Growth: Papers presented at a Symposium held May 8–11, 1989, at the Beltsville Agricultural Research Center (BARC), Beltsville, Maryland* (pp. 327-334). Springer Netherlands. <https://doi.org/10.1007/BF00011893>
- Azcón-Aguilar, C., & Barea, J. M. (1992). Interactions between mycorrhizal fungi and other rhizosphere microorganisms. *Mycorrhizal functioning: an integrative plant-fungal process*. Chapman and Hall, New York, 163-198.
- Badri, D. V., & Vivanco, J. M. (2009). Regulation and function of root exudates. *Plant, cell & environment*, 32(6), 666-681. <https://doi.org/10.1111/j.1365-3040.2009.01926.x>
- Bakker, M. G., Manter, D. K., Sheflin, A. M., Weir, T. L., & Vivanco, J. M. (2012). Harnessing the rhizosphere microbiome through plant breeding and agricultural management. *Plant and Soil*, 360, 1-13.
- Bano, S., Wu, X., & Zhang, X. (2021). Towards sustainable

- agriculture: rhizosphere microbiome engineering. *Applied Microbiology and Biotechnology*, 1-20. <https://doi.org/10.1007/s11104-012-1361-x>
- Beneduzi, A., Ambrosini, A., & Passaglia, L. M. (2012). Plant growth-promoting rhizobacteria (PGPR): their potential as antagonists and biocontrol agents. *Genetics and molecular biology*, 35, 1044-1051. <https://doi.org/10.1590/s1415-47572012000600020>
- Bennett, A. J., Bending, G. D., Chandler, D., Hilton, S., & Mills, P. (2012). Meeting the demand for crop production: the challenge of yield decline in crops grown in short rotations. *Biological reviews*, 87(1), 52-71. <https://doi.org/10.1111/j.1469-185X.2011.00184.x>
- Berendsen, R. L., Pieterse, C. M., & Bakker, P. A. (2012). The rhizosphere microbiome and plant health. *Trends in plant science*, 17(8), 478-486. <https://doi.org/10.1016/j.tplants.2012.04.001>
- Calvo, P., Nelson, L., & Kloepper, J. W. (2014). Agricultural uses of plant biostimulants. *Plant and soil*, 383, 3-41. <https://doi.org/10.1007/s11104-014-2131-8>
- Carvalhais, L. C., Dennis, P. G., Fan, B., Fedoseyenko, D., Kierul, K., Becker, A., ... & Borriss, R. (2013). Linking plant nutritional status to plant-microbe interactions. *PLoS one*, 8(7), e68555. <https://doi.org/10.1371/journal.pone.0068555>
- Carvalhais, L. C., Dennis, P. G., Fedoseyenko, D., Hajirezaei, M. R., Borriss, R., & von Wirén, N. (2011). Root exudation of sugars, amino acids, and organic acids by maize as affected by nitrogen, phosphorus, potassium, and iron deficiency. *Journal of Plant Nutrition and Soil Science*, 174(1), 3-11. <https://doi.org/10.1002/jpln.201000085>
- Choudhary, D. K., Varma, A., & Tuteja, N. (Eds.). (2016). *Plant-microbe interaction: an approach to sustainable agriculture* (pp. 1-509). Singapore: Springer. <https://doi.org/10.1007/978-981-10-2854-0>
- De Mandal, S., Singh, S., Hussain, K., & Hussain, T. (2021). Plant-microbe association for mutual benefits for plant growth and soil health. *Current trends in microbial biotechnology for sustainable agriculture*, 95-121. https://doi.org/10.1007/978-981-15-6949-4_5
- Etesami, H., & Adl, S. M. (2020). Plant growth-promoting rhizobacteria (PGPR) and their action mechanisms in availability of nutrients to plants. *Phyto-microbiome in stress regulation*, 147-203. https://doi.org/10.1007/978-981-15-2576-6_9
- Franzino, T., Boubakri, H., Cernava, T., Abrouk, D., Achouak, W., Reverchon, S., ... & el Zahar Haichar, F. (2022). Implications of carbon catabolite repression for plant-microbe interactions. *Plant Communications*. <https://doi.org/10.1016/j.xplc.2021.100272>
- Frey, S. D. (2019). Mycorrhizal fungi as mediators of soil organic matter dynamics. *Annual review of ecology, evolution, and systematics*, 50, 237-259. <https://doi.org/10.1146/annurev-ecolsys-110617-062331>
- Garcia, J., & Kao-Kniffin, J. (2018). Microbial group dynamics in plant rhizospheres and their implications on nutrient cycling. *Frontiers in microbiology*, 9, 1516. <https://doi.org/10.3389/fmicb.2018.01516>
- Giron, D., Frago, E., Glevarec, G., Pieterse, C. M., & Dicke, M. (2013). Cytokinins as key regulators in plant-microbe-insect interactions: connecting plant growth and defence. *Functional Ecology*, 27(3), 599-609. <https://doi.org/10.1111/1365-2435.12042>
- Glick, B. R. (2012). Plant growth-promoting bacteria: mechanisms and applications. *Scientifica*, 2012. <https://doi.org/10.6064/2012/963401>
- Goulet, O., Hojsak, I., Kolacek, S., Pop, T. L., Cokugras, F. C., Zuccotti, G., ... & Fabiano, V. (2019). Paediatricians play a key role in preventing early harmful events that could permanently influence the development of the gut microbiota in childhood. *Acta Paediatrica*, 108(11), 1942-1954. <https://doi.org/10.1111/apa.14900>
- Hartmann, A., Schmid, M., Tuinen, D. V., & Berg, G. (2009). Plant-driven selection of microbes. *Plant and Soil*, 321, 235-257. <https://doi.org/10.1007/s11104-008-9814-y>
- Hassani, M. A., Durán, P., & Hacquard, S. (2018). Microbial interactions within the plant holobiont. *Microbiome*, 6, 1-17. <https://doi.org/10.1186/s40168-018-0445-0>
- Haudiquet, M., de Sousa, J. M., Touchon, M., & Rocha, E. P. (2022). Selfish, promiscuous and sometimes useful: how mobile genetic elements drive horizontal gene transfer in microbial populations. *Philosophical Transactions of the Royal Society B*, 377(1861), 20210234. <https://doi.org/10.1098/rstb.2021.0234>
- Hayat, R., Ali, S., Amara, U., Khalid, R., & Ahmed, I. (2010). Soil beneficial bacteria and their role in plant growth promotion: a review. *Annals of microbiology*, 60, 579-598. <https://doi.org/10.1007/s13213-010-0117-1>
- Igiehon, N. O., & Babalola, O. O. (2018). Rhizosphere microbiome modulators: contributions of nitrogen fixing bacteria towards sustainable agriculture. *International journal of environmental research and public health*, 15(4), 574. <https://doi.org/10.3390/ijerph15040574>
- Jacoby, R., Peukert, M., Succurro, A., Koprivova, A., & Kopriva, S. (2017). The role of soil microorganisms in plant mineral nutrition—current knowledge and future directions. *Frontiers in plant science*, 8, 1617. <https://doi.org/10.3389/fpls.2017.01617>
- Khan, A. G. (2005). Role of soil microbes in the rhizospheres of plants growing on trace metal contaminated soils in phytoremediation. *Journal of trace Elements in Medicine and Biology*, 18(4), 355-364. <https://doi.org/10.1016/j.jtemb.2005.02.006>
- Kotoky, R., Rajkumari, J., & Pandey, P. (2018). The rhizosphere microbiome: Significance in rhizoremediation of polyaromatic hydrocarbon contaminated soil. *Journal of environmental management*, 217, 858-870. <https://doi.org/10.1016/j.jenvman.2018.04.022>
- Kumar, A., & Dubey, A. (2020). Rhizosphere microbiome: Engineering bacterial competitiveness for enhancing crop production. *Journal of Advanced Research*, 24, 337-352. <https://doi.org/10.1016/j.jare.2020.04.014>
- Kumawat, K. C., Razdan, N., & Saharan, K. (2022). Rhizospheric microbiome: Bio-based emerging strategies for sustainable agriculture development and future perspectives. *Microbiological Research*, 254, 126901. <https://doi.org/10.1016/j.micres.2021.126901>
- Kurepin, L. V., Zaman, M., & Pharis, R. P. (2014). Phytohormonal basis for the plant growth promoting action of naturally occurring biostimulators. *Journal of the Science of Food and Agriculture*, 94(9), 1715-1722. <https://doi.org/10.1002/jsfa.6545>
- Li, Y., Gong, X., Xiong, J., Sun, Y., Shu, Y., Niu, D., ... & Zhang, R. (2021). Different dissolved organic matters regulate the bioavailability of heavy metals and rhizosphere microbial activity in a plant-wetland soil system. *Journal*

- of *Environmental Chemical Engineering*, 9(6), 106823. <https://doi.org/10.1016/j.iece.2021.106823>
- Lopez-Bucio, J., Nieto-Jacobo, M. F., Ramirez-Rodriguez, V., & Herrera-Estrella, L. (2000). Organic acid metabolism in plants: from adaptive physiology to transgenic varieties for cultivation in extreme soils. *Plant Science*, 160(1), 1-13. [https://doi.org/10.1016/S0168-9452\(00\)00347-2](https://doi.org/10.1016/S0168-9452(00)00347-2)
- Mahmud, K., Makaju, S., Ibrahim, R., & Missaoui, A. (2020). Current progress in nitrogen fixing plants and microbiome research. *Plants*, 9(1), 97. <https://doi.org/10.3390/plants9010097>
- Mendes, R., Garbeva, P., & Raaijmakers, J. M. (2013). The rhizosphere microbiome: significance of plant beneficial, plant pathogenic, and human pathogenic microorganisms. *FEMS microbiology reviews*, 37(5), 634-663. <https://doi.org/10.1111/1574-6976.12028>
- Morgan, J. A. W., Bending, G. D., & White, P. J. (2005). Biological costs and benefits to plant-microbe interactions in the rhizosphere. *Journal of experimental botany*, 56(417), 1729-1739. <https://doi.org/10.1093/jxb/eri205>
- Munoz-Ucros, J., Zwetsloot, M. J., Cuellar-Gempeler, C., & Bauerle, T. L. (2021). Spatiotemporal patterns of rhizosphere microbiome assembly: From ecological theory to agricultural application. *Journal of Applied Ecology*, 58(5), 894-904. <https://doi.org/10.1111/1365-2664.13850>
- Nadarajah, K., & Abdul Rahman, N. S. N. (2021). Plant-microbe interaction: aboveground to belowground, from the good to the bad. *International Journal of Molecular Sciences*, 22(19), 10388. <https://doi.org/10.3390/ijms221910388>
- Narula, N., Kothe, E., & Behl, R. K. (2012). Role of root exudates in plant-microbe interactions. *Journal of Applied Botany and Food Quality*, 82(2), 122-130. <https://doi.org/10.1002/9781119246329.ch10>
- Oburger, E., & Jones, D. L. (2018). Sampling root exudates—mission impossible? *Rhizosphere*, 6, 116-133. <https://doi.org/10.1016/j.rhisph.2018.06.004>
- Oppenheimer-Shaanan, Y., Jakoby, G., Starr, M. L., Karliner, R., Eilon, G., Itkin, M., ... & Klein, T. (2022). A dynamic rhizosphere interplay between tree roots and soil bacteria under drought stress. *Elife*, 11, e79679. <https://doi.org/10.7554/eLife.79679>
- Osorio Vega, N. W. (2007). A review on beneficial effects of rhizosphere bacteria on soil nutrient availability and plant nutrient uptake. *Revista Facultad Nacional de Agronomía Medellín*, 60(1), 3621-3643.
- Pettit, R. E. (2004). Organic matter, humus, humate, humic acid, fulvic acid and humin: their importance in soil fertility and plant health. *CTI Research*, 10, 1-7.
- Pritsch, K., & Garbaye, J. (2011). Enzyme secretion by ECM fungi and exploitation of mineral nutrients from soil organic matter. *Annals of Forest Science*, 68, 25-32. <https://doi.org/10.1007/s13595-010-0004-8>
- Rengel, Z., & Marschner, P. (2005). Nutrient availability and management in the rhizosphere: exploiting genotypic differences. *New Phytologist*, 168(2), 305-312. <https://doi.org/10.1111/j.1469-8137.2005.01558.x>
- Saad, M. M., Eida, A. A., & Hirt, H. (2020). Tailoring plant-associated microbial inoculants in agriculture: a roadmap for successful application. *Journal of Experimental Botany*, 71(13), 3878-3901. <https://doi.org/10.1093/jxb/eraa111>
- Singh, G., & Mukerji, K. G. (2006). Root exudates as determinant of rhizospheric microbial biodiversity. *Microbial activity in the rhizosphere*, 39-53. https://doi.org/10.1007/3-540-29420-1_3
- Ström, L. (1997). Root exudation of organic acids: importance to nutrient availability and the calcifuge and calcicole behaviour of plants. *Oikos*, 459-466. <https://doi.org/10.2307/3546618>
- Tapia-Vázquez, I., Montoya-Martínez, A. C., De los Santos-Villalobos, S., Ek-Ramos, M. J., Montesinos-Matías, R., & Martínez-Anaya, C. (2022). Root-knot nematodes (*Meloidogyne* spp.) a threat to agriculture in Mexico: Biology, current control strategies, and perspectives. *World Journal of Microbiology and Biotechnology*, 38(2), 26. <https://doi.org/10.1007/s11274-021-03211-2>
- Tiziani, R., Miras-Moreno, B., Malacrino, A., Vescio, R., Lucini, L., Mimmo, T., ... & Soragonà, A. (2022). Drought, heat, and their combination impact the root exudation patterns and rhizosphere microbiome in maize roots. *Environmental and Experimental Botany*, 203, 105071. <https://doi.org/10.1016/j.envexpbot.2022.105071>
- Van Loon, L. C. (2007). Plant responses to plant growth-promoting rhizobacteria. *Eur J Plant Pathol*, 119, 243-254. <https://doi.org/10.1007/s10658-007-9165-1>
- Vives-Peris, V., De Ollas, C., Gómez-Cadenas, A., & Pérez-Clemente, R. M. (2020). Root exudates: from plant to rhizosphere and beyond. *Plant cell reports*, 39, 3-17. <https://doi.org/10.1007/s00299-019-02447-5>
- Wang, W., Li, Y., Dang, P., Zhao, S., Lai, D., & Zhou, L. (2018). Rice secondary metabolites: structures, roles, biosynthesis, and metabolic regulation. *Molecules*, 23(12), 3098. <https://doi.org/10.3390/molecules23123098>
- White, L. J., Ge, X., Brözel, V. S., & Subramanian, S. (2017). Root isoflavonoids and hairy root transformation influence key bacterial taxa in the soybean rhizosphere. *Environmental Microbiology*, 19(4), 1391-1406. <https://doi.org/10.1111/1462-2920.13602>
- Yue, H., Yue, W., Jiao, S., Kim, H., Lee, Y. H., Wei, G., ... & Shu, D. (2023). Plant domestication shapes rhizosphere microbiome assembly and metabolic functions. *Microbiome*, 11(1), 1-19. <https://doi.org/10.1186/s40168-023-01513-1>
- Zaunmüller, T., Eichert, M., Richter, H., & Uden, G. (2006). Variations in the energy metabolism of biotechnologically relevant heterofermentative lactic acid bacteria during growth on sugars and organic acids. *Applied microbiology and biotechnology*, 72, 421-429. <https://doi.org/10.1007/s00253-006-0514-3>
- Zehra, A., Raytekar, N. A., Meena, M., & Swapnil, P. (2021). Efficiency of microbial bio-agents as elicitors in plant defense mechanism under biotic stress: A review. *Current Research in Microbial Sciences*, 2, 100054. <https://doi.org/10.1016/j.crmicr.2021.100054>