

Review Article

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## Unravelling the Zone of Rhizosphere and its Biotic Interaction over Plant-Soil Relationship

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### ABSTRACT

Intensive agriculture, while increasing food production, has caused second generation problems in respect of nutrient imbalance including greater mining of soil nutrients to the extent of 10 million tons every year depleting soil fertility, emerging deficiencies of secondary and micronutrients, decline of water table and its quality of water, decreasing organic carbon content, and overall deterioration in soil health. Indian soils not only show deficiency in both primary nutrients (Nitrogen, Phosphorous and Potassium) but also of secondary nutrients (Sulphur, Calcium and Magnesium) and micronutrients (Boron, Zinc, Copper, and Iron etc.) (Ministry of Agriculture, 2015). Improved grain production to meet the food demand of an increasing population has been highly dependent on chemical fertilizer input based on the traditionally assumed notion of 'high input, high output', However, crop yield has not increased proportionally with growing fertiliser inputs in recent decades, resulting in low nutrient use efficiency and increased environmental concerns which results in overuse of fertilizers ignores the biological potential of roots or rhizosphere for efficient mobilization and acquisition of soil nutrient. The plant roots and rhizosphere interaction in the Rhizosphere region where plant releases exudates from roots which act as chemical signals. This involves in Nutrient cycling and nutrient transformation. The rhizosphere offers a potential solution to combat these deficiencies and improve soil fertility. Also signalling between plant and rhizosphere is very rich and complex micro biome diversity which they undergoes both interspecies and intraspecies signalling.

#### Keywords

Soil fertility, rhizosphere, nutrient, nutrient cycles, signalling

#### Article Info

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### Introduction

It has been a big challenges in field of food related approaches (Pischetsrieder, 2018; Gao *et al.*, 2021). To

get in adequate level of food production in future, it is necessary to make preliminary assessment over the agriculture system. This agriculture system is fond of running beyond three functional unit. Land, air and

water. And one among the important is land i.e. soil, which is the base for cultivating crops and allied activities. Hence to progress better future, we are responsible for making soil suitable for cultivation. The crop development is directly proportion to the development of the soil ecosystem.

The traditional way of approaching farming system is unadequate and currently imbalance in present state due to production of less yield, climate change, drought occurrence, and most important is extreme weather change pattern (Singh *et al.*, 2020). The rhizosphere is the narrow dynamic zone of soil that surrounds and is influenced by plants in which complex interactions occur between root exudates and soil micro biome (Coskun *et al.*, 2017). The simple root – soil interface is depicted in Fig. 1.

### Concept of Rhizosphere

The rhizosphere is a thin layer of soil that surrounds plant roots and is a central place for microbial activity. It's made up of soil particles, organic matter, plant roots, and a diverse community of microbes. The rhizosphere is a micro ecosystem where complex interactions take place between the plant roots and the microorganisms.

### Plant – microbe interaction

On the basis of our current knowledge, plant–microbial interactions can be classified into three basic groups: (i) negative (pathogenic) interactions; (ii) positive interactions, in which either both partners derive benefits from close association (symbiosis), both partners derive benefits from loose association or only one partner derives benefits without harming the other (associative); and (iii) neutral interactions, where none of the partners derives a direct benefit from interaction and in which neither is harmed. Symbiotic and pathogenic interactions have attracted the most scientific attention (Hirsch *et al.*, 2003).

### Rhizosphere and nutrient cycling

Next to water and temperature, nutrients are the environmental factor that most strongly constrains terrestrial plant growth. Rhizosphere generally acts as a biodiversity hotspot area since it was abundant with numerous microorganisms. The zone of root exudation has clearly shown in progress with increase the mass and activity of soil microbes and fauna found in the

rhizosphere (Butler *et al.*, 2003). Most of the studies in which plants were grown in pots as a monoculture revealed that specific groups of microorganisms were associated with the rhizosphere (Baudoin *et al.*, 2003).

Soil microorganisms depend upon plant C and, in turn, provide plants with nitrogen (N), phosphorus (P) and other minerals through decomposition of soil organic matter.

The species of different plants differ in their capacity for acquiring the available nutrients from the soil. Some of the plants were capable of acquiring Iron, Phosphorus or other ions from the calcareous soils, wherein others cannot able to extract enough nutrients to persist as such soils (Lambers *et al.*, 2008b). In case of phosphorus pattern, the acquisition from soils with low level of P concentrations in solution as well as plant growth can be enhanced by mycorrhizal symbioses (Bolan, 1991; Richardson *et al.*, 2009).

At every function level, these microorganism will colonize, e.g. the presence of arbuscular mycorrhiza can extend its hyphae and in turn mobilize insoluble phosphorus and make available to plant uptake, and some will enhance N uptake from the soil by their effect on root morphology and physiology (Tolove *et al.*, 2003; Cocking, 2003).

Approximately 80% of all higher plant species can form a mycorrhizal symbiosis; of these, the arbuscular mycorrhizal (AM) association is the most common (Brundrett, 2009).

Some ericoid mycorrhizas and ectomycorrhizas (ECM) belonging to groups that are incapable of symbiotic N<sub>2</sub> fixation may access complex organic N, including peptides and proteins (Högberg, 1990). The pure AMF inoculum is composed of colonized roots, spores and mycelium. Using a photomicroscope, it was possible to observe the pure inoculum of AM fungi and its effect on root morphology in rhizosphere. The systematic observation involving colonization of root in soybean crop is represented in Fig. 4.

Normally, at different ecosystem pattern the range for microorganism gets Vary at different ecosystem. For example, at marine type, there may be less relative abundance of the microorganisms and in case of soil, the diversified microorganism were seen at different proportion.

For this to get into brief, a study conducted by [Parmar et al., in 2018](#) and [Raval, nirmal in 2021](#) elucidated the abundance of microorganisms in different ecosystem and their varying pattern. The pie diagram was given in Fig. 5 & Fig. 6 respectively.

The rhizophagy cycle is a process where plants actively take in bacteria from the soil into their root cells, use them to get nutrients, and then release them back into the soil. The key importance are given below.

1. Nutrient uptake: Beneficial bacteria in the soil are attracted to plant roots by root exudates. Plant roots then absorb those beneficial bacteria from the soil.
2. Nutrient extraction: Inside the plant root cells, the roots extract nutrient from the bacteria by encasing the bacteria in vesicles. These vesicles are part of the plant cell's internal transport and storage system. The roots weaken bacterial cell walls to extract the nutrients from the bacteria by releasing chemically reactive molecules containing oxygen (ROS).
3. Release pattern: The plant carefully manages the levels of ROS to ensure that the bacteria are weakened enough to release nutrients, but not completely destroyed. This allows the bacteria to survive and be safely released back into the soil, continuing the cycle.
4. Nutrient recycling: The cycle repeats as new, "nutrient full" bacteria are taken up by the roots again after replenishing their nutrient reserve. The discovery of the rhizophagy cycle challenges our entire understanding of how plants uptake nutrients from the soil.

### Root exudates in rhizosphere region

The rhizosphere, is a complex environment where interaction between plants and soil microbes occurs, and it may have up to  $10^{11}$  cells/g of root, with greater than 30,000 bacterial species present in rhizosphere ([Mendes et al., 2011](#)).

A mixture of organic compounds released by plant roots is root exudates, plants alter the soil environment, shape the rhizosphere microbiome, and improve their growth conditions through root exudates. Root exudates helps in communication with soil microorganisms and leads to improve plant health by enriching beneficial microbes, productivity, and fitness.

Plant growth-promoting rhizobacteria (PGPRs), is a beneficial rhizobacteria, which can promote plant growth and health by providing numerous benefits and are

widely used in agricultural production, such as *Bacillus* spp. and *Pseudomonas* spp ([Liu et al., 2024](#)). PGPR can facilitate nutrient uptake by fixing atmospheric nitrogen, mobilizing soil phosphorus, solubilizing minerals and also produce growth-promoting substances, such as phytohormones and enzymes that enhance plant growth and development ([Han et al., 2023](#)).

Plant diseases can also suppress by beneficial rhizobacteria which produces antimicrobial compounds, inducing systemic resistance, competing with pathogens for resources and induce abiotic stress tolerance ([Peng et al., 2023](#)). Non-symbiotic beneficial rhizobacteria colonization consist of several steps, including chemotaxis, root surface attachment, and biofilm formation ([Liu et al., 2024](#)).

Root exudates play a major role in promoting colonization with soil rhizobacteria. Plants conduct selective recruitment of specific microbes to the rhizosphere. In root exudates certain compounds act as signaling molecules that mediate motility, chemotaxis, biofilm formation, the "cry-for-help" response, and symbiotic relationships ([Sasse et al., 2018](#)).

### Composition of root exudates

Plants release 11–40% of their photosynthetic yield as root exudates into the rhizosphere ([Zhalnina et al., 2018](#)) which can be identified as low- or high-molecular-weight compounds. Low-molecular-weight compounds (LMWC), consist of diverse molecules, such as sugars, organic acids, amino acids, alcohols, volatile compounds, and other secondary metabolites. High-molecular-weight compounds (HLWC), including mucilage (polysaccharides) and proteins, constitute a larger fraction of exudates ([Chagas et al., 2018](#)).

### Root colonization with molecular compounds of root exudates

#### Organic Acids

Organic acids such as malic acid, citric acid, fumaric acid, tartaric acid, and succinic acid, are investigated to be nutrients for microbes and signals during the process of colonization by diverse beneficial soil rhizobacteria ([Korenblem et al., 2020](#)). Through organic acid treatment soil physicochemical conditions is improved and microbial load is altered in soil, especially by inducing the growth, chemotactic response, motility, and biofilm

formation of rhizobacteria by some beneficial bacteria (Wang *et al.*, 2023).

### Amino Acids

Amino acids play a main role in root exudates, it is the primary source of nitrogen for many soil microbes and promote the growth and proliferation of beneficial microbes. These amino acids can be utilized by microbial communities directly to build their own proteins or can be degraded for energy (Moe, 2013). Specific amino acids in exudates can act as attractants for beneficial soil rhizobacteria and selectively improves the growth of beneficial rhizobacteria over pathogenic rhizobacteria.

### Sugars

Sugars is important carbon source and for colonization signals of rhizobacteria (Sasse *et al.*, 2018). Sucrose, a disaccharide which is widely present and secreted abundantly by roots, selectively shapes the soil microbial community, particularly that of bacilli and pseudomonas (Tian *et al.*, 2021). In *Arabidopsis* plant the roots cannot effectively colonized by *B. subtilis* when deficient in soluble sucrose. Sucrose which present in *Arabidopsis* plant root exudates triggers a signaling cascade that activates the solid surface motility (SSM) of *Bacillus subtilis*.

### Sugar Alcohols

Polyols is a sugar alcohols which are imported by secondary active proteins in plants with broad substrate specificity. Important eukaryotic structural and signaling molecule is known as inositol, that is a sugar alcohol. Myo-inositol is the most abundant inositol isomer present in root exudates (Zhalnina *et al.*, 2018). A major carbon source to promote bacterial growth and as a signaling molecule to enhance various processes, including chemotaxis, biofilm formation, siderophore production, and colonization by beneficial plant-associated bacteria is inositol (Vilchez *et al.*, 2020).

### Phenolics

Phenolic compounds mediate defense mechanisms against pathogens and attract some microbes by serving as signaling molecules and carbon sources (Lattanzio *et al.*, 2006). The exudation of phenolic compounds like vanillin, syringic acid, vanillic acid, and ferulic acid, into the rhizosphere of *Avena fatua* was believed to have

allelopathy effects in roots (Iannucci *et al.*, 2013). Plant-associated beneficial bacteria produce coumarins in root exudates that enhance plant growth under iron starvation.

### Root Volatiles and secondary metabolites

The long-distance interactions (millimeter scale and up to 12 cm away from the roots) in the soil rhizosphere and serve as energy sources or signaling molecules that regulate bacterial growth, chemotaxis, and competition is root volatile which including volatile organic compounds (VOCs) and inorganic molecules (Sharifi *et al.*, 2022). Root volatiles can easily diffuse throughout the soil due to their physicochemical properties, also affecting a broad area and impacting microbial communities. VOCs produced by plants such as terpenes and terpenoids increase upon pathogen infection, inhibit pathogen growth through antimicrobial effects and attract and promote the growth of specific beneficial bacteria through signals and act as a carbon sources (Chagas *et al.*, 2018). Benzoxazinoids and camalexin are indole-derived specialized secondary metabolites that are important for interactions between rhizobacteria and plants which also involved in plant defenses against pathogens. Root exudates, like benzoxazinoids, also play a role in regulating the interactions among rhizosphere signaling molecules. An important antimicrobial compounds in many grass species is benzoxazinoids and it produced in response to pathogen infection or insect damage. The exudation of camalexin from *Arabidopsis* roots can improve the growth-promoting effects of some beneficial strains, such as *Pseudomonas* sp.

### Mechanism of Root exudates

Root exudates consist of two types of release mechanisms based on the mode of transportation: Active and passive transport (Bertin *et al.*, 2003). Specific membrane-bound transport proteins such as ATP-binding cassette (ABC) transporters, aquaporins, and the major facilitator superfamily (MFS) are involved in the utilization of active secretion process (Badri *et al.*, 2009). Hydrolysis of adenosine triphosphate (ATP) in order to power the transport of a wide range of compounds the ABC transporters are used while water and solute movement, are facilitated by aquaporins and a wide spectrum of compounds across cell membranes, particularly in root cells is transported by MFS proteins and vesicular transport, enabling the release of low-molecular weight compounds such as sugars, amino acids, carboxylic acids, and phenolics (Canarini *et al.*, 2019).

**Table.1** Composition of root exudates

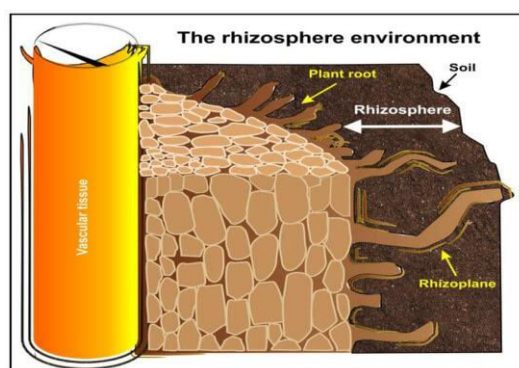
Root composition	Organic compounds (examples)	Functions
<b>Sugars (LMWC)</b>	glucose, maltose, sucrose, galactose, fructose	Carbon sources that increase soil microbial biomass
<b>Enzymes (LMWC)</b>	Protease, Amylase, Invertase, Phosphatase	Biocatalyst for the transformation of organic matter and the release of nutrients from organic molecules, resulting in soil microorganism nutrition sources
<b>Organic acids (LMWC)</b>	lactic, malic, oxalic, and citric acids	Soil microbial carbon and energy sources
<b>Amino acids (LMWC)</b>	$\alpha$ -Alanine, $\beta$ -alanine, arginine, asparagine, aspartic acid	Attract soil microorganisms Nutrient source for soil microorganisms
<b>Phenolic acids and coumarins (LMWC)</b>	Cinnamic acid, ferulic acid, syringic acid, salicylic acid, caffeic acid	Attracts plant–microbe symbiosis, Impact rhizobial growth, Induce plant–microbe symbiosis Results in quorum quenching in pathogenic soil bacteria, Activates virulence genes in phytopathogen <i>Agrobacterium</i>
<b>Proteins (HMWC)</b>	polysaccharides or long chains of sugar molecules	Responsible for effective pathogen defense
<b>Mucilage (HMWC)</b>	chitinases, glucanases, myrosinases	Develops a symbiotic relationship with the soil-dwelling fungi

**Table.2** Root metabolites and its function as in rhizosphere

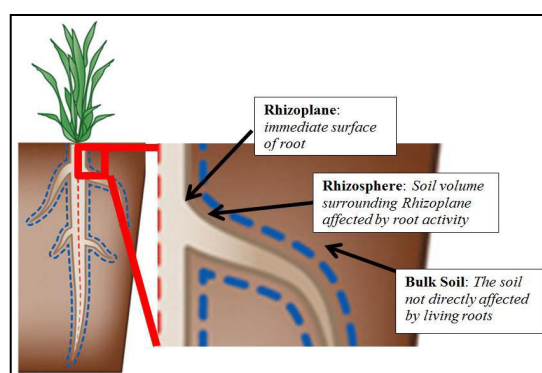
Root metabolites	Functions	Reference
<b>Malic acid</b>	Recruits <i>Bacillus subtilis</i> FB17 and activates the plant immune system	(Yuan <i>et al.</i> , 2018)
<b>Salicylic acid</b>	Immune signal or carbon source, mainly inhibits Actinobacteria and enrich Proteobacteria	(Sarah <i>et al.</i> , 2015)
<b>Jasmonic acid</b>	Enriches bacteria for biological control	(Ruan <i>et al.</i> , 2019)
<b>Benzoxazinoids</b>	Alter the root microbiome, decrease plant growth, increase jasmonate signaling and plant defenses, and inhibit herbivore in the next generation of plant	(Hu <i>et al.</i> , 2018)
<b>Triterpene</b>	Plant defense and antimicrobial activities, regulate the growth of root bacteria of <i>Arabidopsis thaliana</i>	(Huang <i>et al.</i> , 2019)
<b>Coumarin</b>	Inhibits the soil-borne fungal pathogens <i>Fusarium oxysporum</i> and <i>Verticillium dahliae</i> by affecting assemble of rhizosphere microbiome	(Stringlis <i>et al.</i> , 2018)



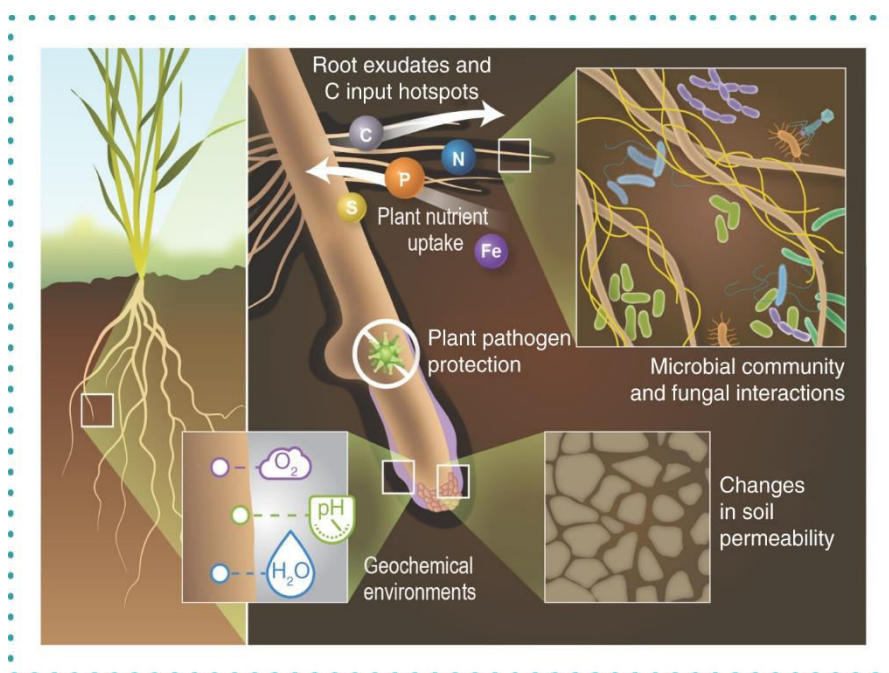
**Figure.1** The general representation of rhizosphere environment and interaction between root and soil system.



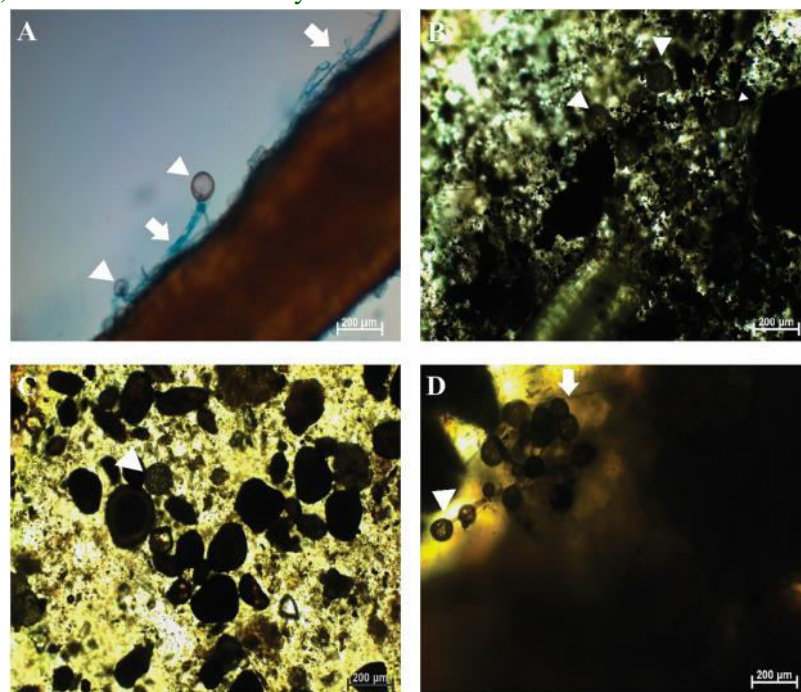
**Figure.2** Zone of Rhizosphere



**Figure.3** The rhizosphere is a physically constrained area surrounding the roots that has a great impact on overall plant and soil health and represents an area of major inter kingdom biological interaction as well as a localized nexus of geochemical reaction.

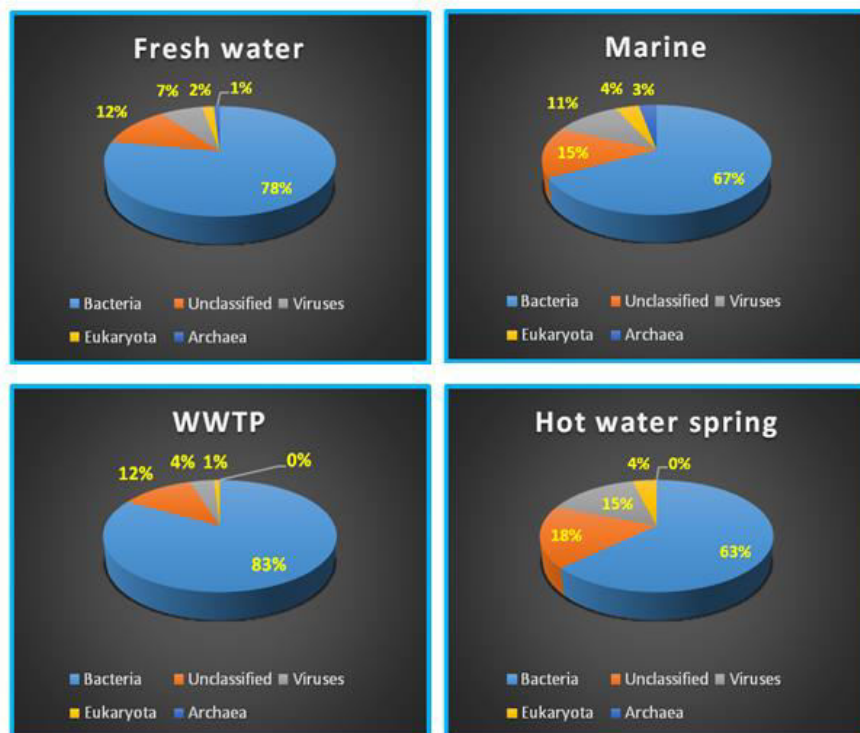


**Figure.4** Distribution of arbuscular mycorrhizal fungi *Rhizophagus clarus* inocula produced in vitro, added to different vehicles. Pure inoculum (a), inoculum+peat (b), inoculum+rock phosphate (c), inoculum+vermiculite. Arrow heads indicate a spore, and arrows indicate a mycelium.



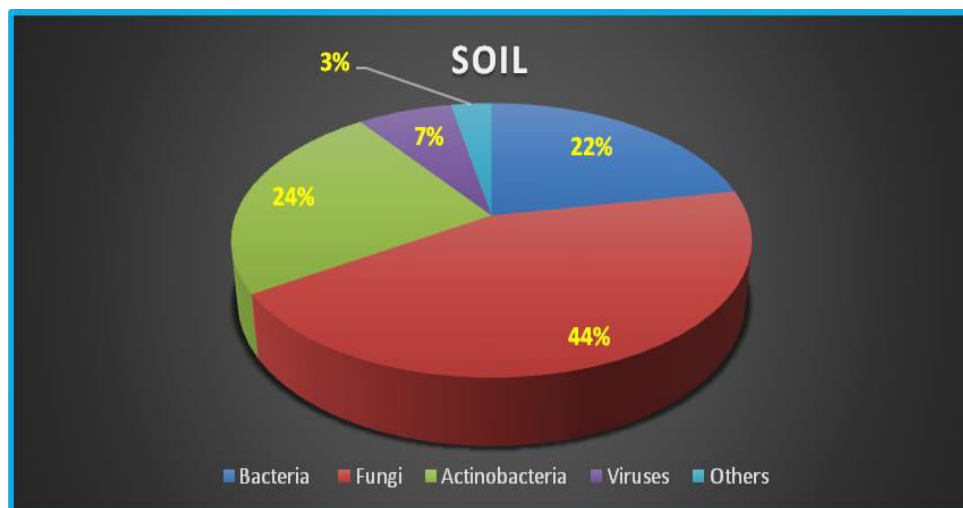
(Lambers *et al.*, 2009)

**Figure.5** Comparative microbial diversity at different habitats. Pie chart was generated using microbial abundance data. Each chart represents the percentage abundance of microbial group in a specific habitat. Abundance values are generated from normalized and statistical analysis carried on data retrieved from MG-RAST



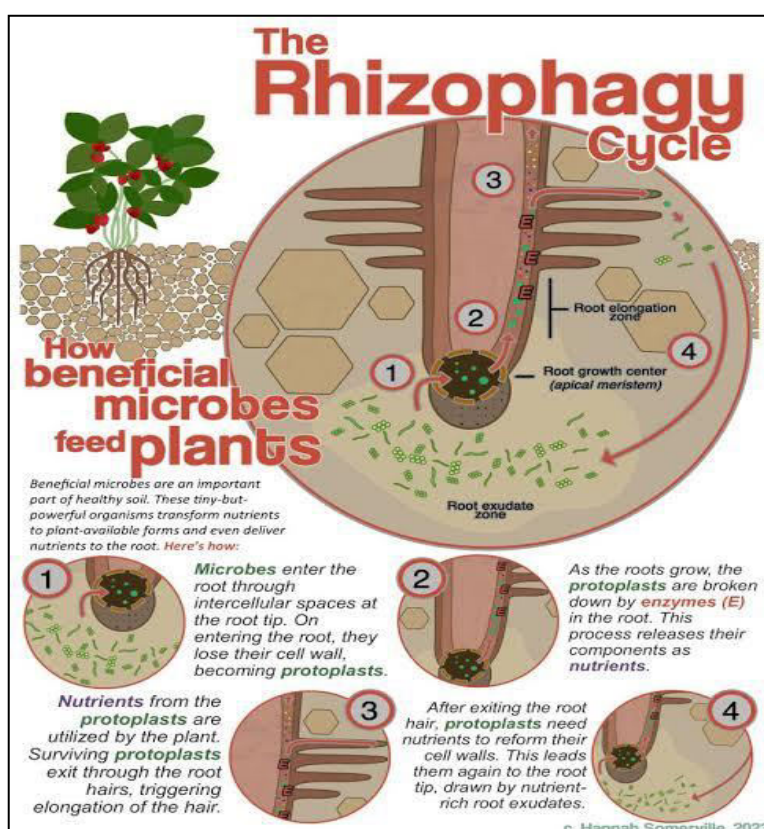
(Parmar *et al.*, 2018)

**Figure.6** Comparative microbial diversity at soil ecosystem and its abundance.



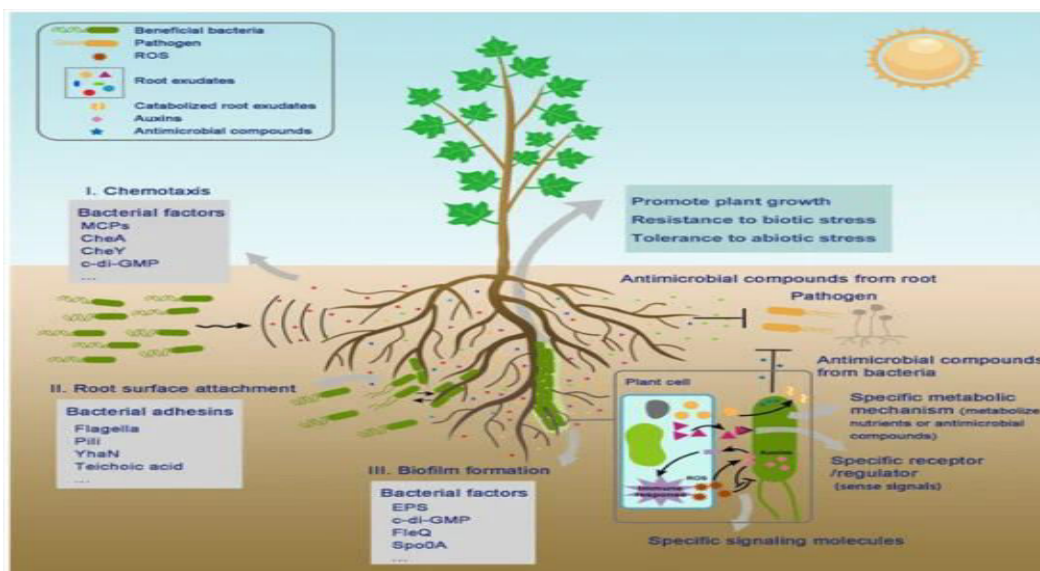
(Raval and Nirmal, 2021)

**Figure.7** The Rhizophagy cycle





**Figure.8** Colonization of rhizosphere beneficial bacteria



**Figure.9** Mechanism of root exudates

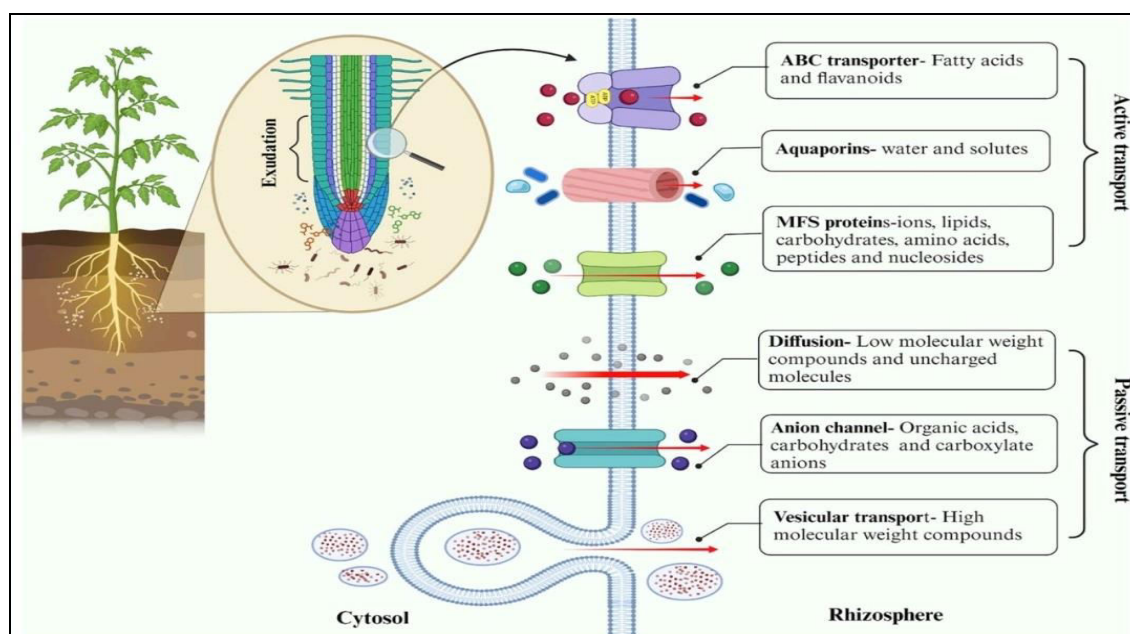


Figure.10 Overview of flavonoid functions in the rhizosphere

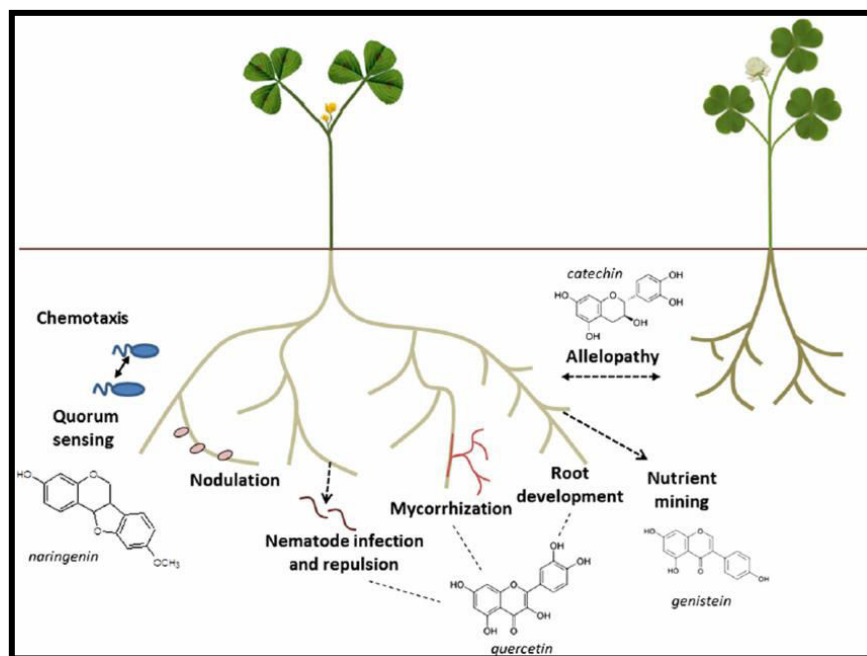
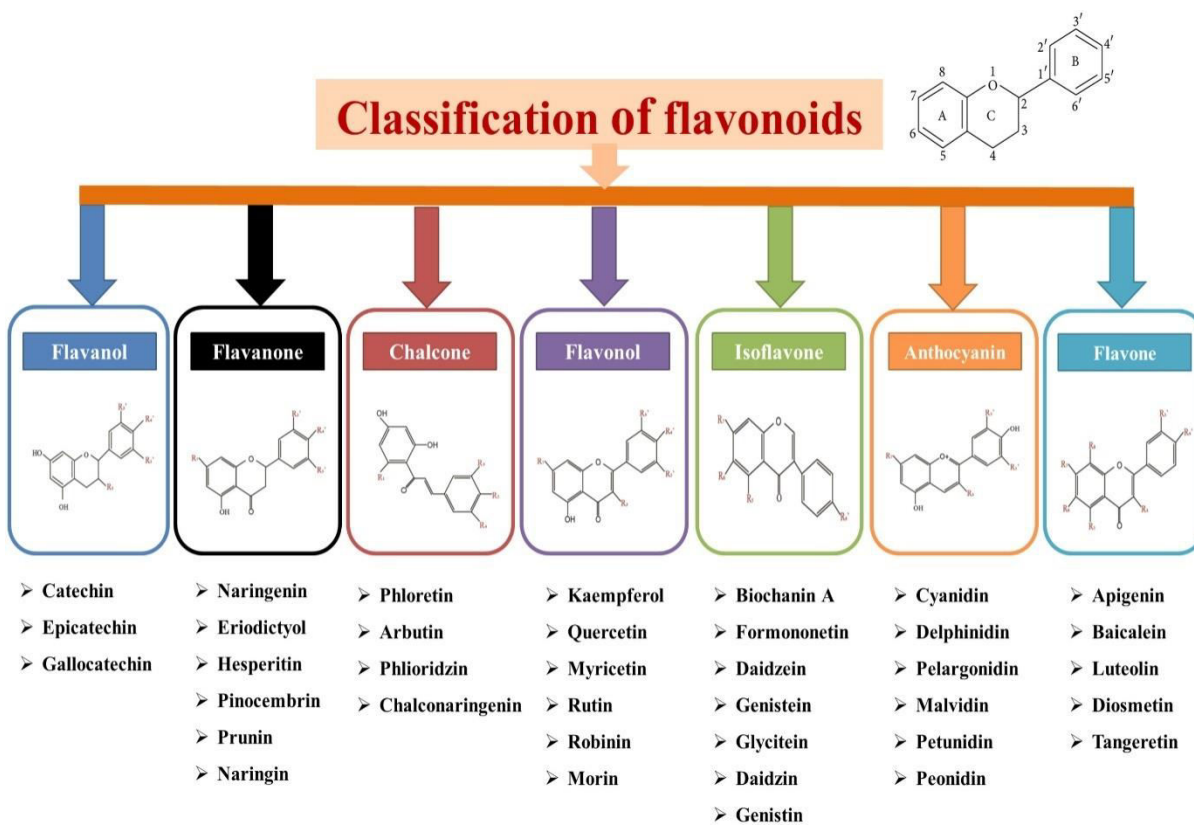


Figure.11 Classification of flavonoids compounds



## **Role of flavonoids in root– rhizosphere signalling**

And the most important root phenomenon is flavonoids compound. This pathway of flavonoid will produces a difference group of plant compound with a main key function as UV protection, as antioxidants, pigments, and auxin transport regulators, defense compounds against pathogens and during signalling in symbiosis. Flavonoids are not only found within the plant system but also a major constitute a large part of root exudates (Cesco *et al.*, 2010). The function of flavonoids is illustrated in Fig. 10.

The roots of the plants secrete root exudates, containing various chemical signals, one of which is our compound of interest, flavonoids. Flavonoid exudation in the rhizosphere is not well clearly understood, although some of the progress has been made towards the identification of transporters. Flavonoids are likely to be actively exuded from roots, often in response to elicitors (Schmidt *et al.*, 1994; Armero *et al.*, 2001).

Flavonoid functions in the rhizosphere are usually ranges from nod gene inducers and chemoattractants in rhizobia, stimulators of mycorrhizal spore germination and hyphal branching, possible quorum-sensing regulators in bacteria, repellents for parasitic nematodes, nutrient mining, and as allelochemicals in plant–plant interactions.

## **Flavonoids secretion in rhizosphere**

Flavonoids are one of the most prominent classes of polyphenolic compounds synthesized by the various biosynthetic pathways such as shikimic acid pathway, phenylpropanoid pathway and flavonoids pathways (Cesco *et al.*, 2012). Flavonoids are a group of phenylpropanoid metabolites synthesized via the p-coumaroyl-CoA and malonyl-CoA pathways (Ferrer *et al.*, 2008). In major plants, almost all the flavonoids which accumulate in vacuoles as glycosides, whereas some are released by the roots into the rhizospheres.

The released flavonoids in the rhizosphere can play an important multifunctional roles, such as protecting plants from both biotic and abiotic threats (Wang *et al.*, 2022). And it is known that ABC transporters are important compound and will facilitate the easy release of flavonoids compound in the rhizosphere. They are actively exuded from the root zone with response to various elicitors. Generally two important transportation

occur here. One is Active transport mechanism and other is passive transport mechanism. A number of research studies have unequivocally proved that secondary metabolites such as flavonoids play a key role in mediating the communication between plants and beneficial microbes. However, various biotic and abiotic factors affecting the parameters of soil such as mineral concentration, since calcium is seen to protect the flavonoids from degrading (Sugiyama and Yazaki, 2014).

## **Classification of flavonoid compound**

Flavonoids are included in a diverse group of low-molecular-weight phenolic compounds or polyphenols that are mainly found in the ubiquitous plant kingdom (Samanta *et al.*, 2011; Roy *et al.*, 2022).

## **Reduce fertilization by modulating the root micro biome for improving plant nutrient acquisition**

The traditional agricultural systems depend on large-scale application of fertilizers, which causes a series of environmental problems (Coskun *et al.*, 2017). Improving low N fertilizer use efficiencies and decreasing the N losses is vital for development of sustainable agriculture. Root exudates can recruit beneficial microbes helping the plants to take up more N via enriching diazotroph for biological N fixation (BNF), increasing N bioavailability, or promoting N conservation in soil by inhibiting microbial processes responsible for N losses. In addition to N, root exudates can also increase the availability of phosphorus and iron in the rhizosphere.

Biotic interactions in the rhizosphere drive biogeochemical processes and modulate plant nutrient availability in agroecosystems. However, in order to improve our knowledge on the role of the rhizosphere in C, N and P biogeochemical processes a more holistic and functional approaches is required.

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## Author Contributions

G. Muhilan: Investigation, formal analysis, writing—original draft. V. G. Venkatesan: Validation, methodology, writing—reviewing. A. Kalaiselvi:—Formal analysis, writing—review and editing. K. P. Lenin Babu: Investigation, writing—reviewing. S. Harini: Resources, investigation writing—reviewing. M. Karthikeyan: Validation, formal analysis, writing—reviewing.

## Data Availability

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

## Declarations

**Ethical Approval** Not applicable.

**Consent to Participate** Not applicable.

**Consent to Publish** Not applicable.

**Conflict of Interest** The authors declare no competing interests.

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