

Plant-microbe Cross-talk in the Rhizosphere: Insight and Biotechnological Potential

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Abstract: Rhizosphere, the interface between soil and plant roots, is a chemically complex environment which supports the development and growth of diverse microbial communities. The composition of the rhizosphere microbiome is dynamic and controlled by multiple biotic and abiotic factors that include environmental parameters, physiochemical properties of the soil, biological activities of the plants and chemical signals from the plants and bacteria which inhabit the soil adherent to root-system. Recent advancement in molecular and microbiological techniques has unravelled the interactions among rhizosphere residents at different levels. In this review, we elaborate on various factors that determine plant-microbe and microbe-microbe interactions in the rhizosphere, with an emphasis on the impact of host genotype and developmental stages which together play pivotal role in shaping the nature and diversity of root exudations. We also discuss about the coherent functional groups of microorganisms that colonize rhizosphere and enhance plant growth and development by several direct and indirect mechanisms. Insights into the underlying structural principles of indigenous microbial population and the key determinants governing rhizosphere ecology will provide directions for developing techniques for profitable applicability of beneficial microorganisms in sustainable agriculture and nature restoration.

Keywords: Agriculture, ecology, microbe-microbe interaction, plant-microbe interaction, rhizosphere, root exudates.

INTRODUCTION

Rhizosphere, the soil adjacent to plant-roots, is a unique niche for microbial colonization. The term, rhizosphere, was first coined by Lorenz Hiltner [1]. It is a complex chemical matrix replete with diverse microbial species. Rhizosphere microbial community is recruited from the surrounding soil which acts as a microbial seed bank, while the plants determine which members of this bulk soil reservoir of microorganisms will flourish and thrive in the rhizosphere [2]. The present review is organized mainly into three sections. In the first section, we define rhizosphere effect and discuss the role of different factors such as plant genotype, plant age and environmental interferences that affect rhizodeposition processes. In the second section, we elaborate how the chemistry at the root-soil interface influences the microbial community with a highlight on plant-microbe and microbe-microbe interactions. Finally, few studies have been cited which exploit the mechanistic and ecological knowledge of rhizosphere into the programs linked to bio-based agriculture and economy.

RHIZOSPHERE-EFFECT

'Rhizosphere effect', a term coined by Starkey (1938), is defined by collective processes occurring at the root-soil

interface of a plant and includes root exudation, microbial activity, genetic exchange, nutrient transformation and gradient diffusion [3]. In living plants, organic carbon released by plant roots is decomposed to CO₂ in a mechanism known as rhizosphere priming effect (RPE) [4]. Although the estimate of plant carbon economy is still controversial, approximately one-third to half of total assimilated carbon is allocated to below-ground, of which 15-25% is exuded from the roots into the soil to induce fast carbon-turnover in the rhizosphere [4]. Due to intensive carbon uptake by the roots, other nutrients in the rhizosphere are strongly limited [5]. In contrast, in a root-free soil, all the nutrients except carbon are unlimited [6]. The surplus of easily available carbon and strong nutrient limitation, together, make the rhizosphere milieu strongly different from that of the root-free zones. The increased microbial number and activity in the rhizosphere compared to those in bulk soil are mainly due to the release of organic carbon by the plant roots [7].

The substances released by plant roots are collectively termed as "rhizodeposits." These compounds include (i) water-soluble ions and low-molecular-mass compounds such as mono-saccharides, amino acids and organic acids which are lost passively along a concentration gradient, (ii) high-molecular-mass compounds such as carbohydrates, proteins and lipids which are actively transported along an electrochemical gradient, (iii) insoluble mucilage composed of polysaccharides and polygalacturonic acid, (iv) an array of secondary metabolites such as antimicrobial compounds, nematicides and flavonoids and (v) remnants of the dead and

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lysed root-cap and border cells [8-11]. Of these, sugars and amino acids are thought to be released in the greatest quantities.

FACTORS AFFECTING ROOT-EXUDATION

The quantity and composition of rhizodeposits are influenced by a variety of biotic and abiotic factors and vary in time and space with respect to the position on the root [12]. The host-dependent factors include genotype and age of the plant while the abiotic components include different environmental factors, grazing activities and anthropometric habits [13]. The wide quantitative and qualitative variation in root exudation of different plant species suggests that it is determined by plant genetic makeup. In a study with eight accessions of *Arabidopsis thaliana*, a unique combination of exudates was found to be secreted from the plants of different cultivars grown simultaneously under uniform conditions. This gave rise to genotype-specific rhizobacterial communities at six weeks post-germination [14]. The cultivar-specific variation in root exudation is mainly regulated by the root system architecture (RSA) [15]. The zone immediately behind the root tip is considered to be the major site of exudation although different sites have been recorded to be active in different plant species [16, 17]. Furthermore, different parts of the root system exude different compounds. For example, asparagine and threonine are exuded from meristem and root elongation zone; glutamic acid, valine, leucine and phenylalanine are secreted from root hair zone; while aspartic acid is exuded from the whole root [18]. Use of ^{14}C to identify the sites of exudation from wheat roots has shown that non-diffusible materials are released from both primary and lateral root tips and diffusible materials are released from the whole length of roots [19].

In general, apical meristem of plant roots is covered by root cap which sloughs off as the root tip wends its way through the soil. These sloughed-off cap cells, known as 'border cells,' play a significant role in determining the rhizosphere chemical environment [20]. Border cells produce polysaccharide mucilages accounting for 2–12% of the total rhizodeposition and 10% of total carbon released by roots. The number of border cells varies between plant species and this variability appears to be related to the organization of the root apical meristem (RAM) in monocotyledons and dicotyledons [21]. Border cells regulate microbial interaction by avoiding pathogens and favoring association with beneficial microbes. They also protect against heavy metal toxicity [22]. The root cap and hair cells are also involved in secretion of compounds. Root hairs are the extensions of single epidermal cells and comprise as much as 77% of the total root surface area of cultivated crops, developing a connection between the plant and the rhizosphere [23]. They play an important role in rhizosphere processes including uptake of water, nutrients and exudation of different compounds [24]. In addition to the root cap and hair cells, other cells are also involved in secretion. For example, citrate secretion from maize roots in response to aluminum toxicity predominantly involves cortex and stellar cells located 5 cm above the root cap [25].

Plant age vis-a-vis developmental stages plays a pivotal role in characterizing root-exudation pattern by its impact on RSA. Garcia *et al.* (2001) has shown that exudation is positively correlated with root growth [26]. Seedlings produce the lowest amounts of root exudates which gradually increases until flowering and decreases again at maturity [27]. Plant developmental windows seem to influence the chemistry of root-exudates as well. Secretion of phenolic compounds and defense-related proteins by *Arabidopsis* roots at flowering stage has been correlated with the age-related resistance of the plant [28]. Accumulation of pathogenesis-related1 (PR1) in the apoplast of tobacco plant during its transition to flowering stage in response to infection by *Phytophthora parasitica* and interaction of Xa-21 resistance gene product with the *X. oryzae* Ax21 effector molecule during the vegetative growth of rice in response to infection by *Xanthomonas oryzae* *pv.* *oryzae* are other well studied examples of developmentally regulated plant defense mechanisms against fungal pathogens [29, 30].

The environmental factors affecting root exudation include soil characteristics such as soil texture, pH, and moisture content in addition to climate, temperature, light and humidity. High soil moisture leads to hypoxia which may cause an increased anaerobic respiration rate, accumulation of ethanol, lactic acid and alanine in the rhizosphere [31]. The presence or absence of particular minerals or toxic metals in the soil affects the composition of root-exudation. For example, citric, malic and oxalic acids are secreted to detoxify aluminum; secretion of phenolic compounds is increased in phosphorus deficient soils [32, 33]. Secretion of signaling molecules like flavanones and flavones is enhanced in nitrogen limiting conditions [34]. Mineral-deficiency enhances the production of elicitors that influence root-exudation. Potassium deficiency increases jasmonic acid mediated defense responses [35]. Lower temperatures and light reduce the secretion of root exudates. For example, the exudation of tannins and phenolic compounds in *Vicia faba* was greatly reduced at 4 °C [36]. The root exudation process follows diurnal rhythms [37]. Flavonoid content in the root exudates from *Alnus glutinosa* (L.) is elevated under light conditions [38]. The presence of neighboring plant species and the rhizosphere microflora also affect the root exudation. Outcome of glucosinolates activation in *Arabidopsis* was regulated by the presence of neighboring plants. Production of glucosinolates is increased in a high-density environment having large number of *Arabidopsis* plants grown together compared with a low-density range [39].

ROOT EXUDATES AND MICROBIAL COLONIZATION

The structural and functional diversities of rhizosphere microbial communities of a wide variety of plants including *Arabidopsis*, *Medicago*, maize, pea, wheat and sugar beet are shaped by plant developmental stages. For example, rhizosphere microbial communities in early development of *Arabidopsis* were different from that observed in the bulk soil and this difference decreased with plant age [14]. In an elegant study by Chaparro *et al.* (2013) a strong correlation has been documented between compounds released from the roots at different stages of plant development and the

expression of microbial genes involved in metabolism of specific compounds [29]. Metatranscriptomic analysis of the rhizosphere microbiome of *Arabidopsis thaliana* (genotype Pna-10) revealed that eighty-one unique transcripts were significantly expressed at different stages of plant development. It was surmised from these studies that the blend of compounds and phytochemicals in the root-exudates were differentially produced at distinct stages of plant development and orchestrated the rhizobiota.

Components of root exudates are diverse and the researchers have only begun to dissect the role on individual compound. Carbohydrates, organic acids and amino acids stimulate positive chemotactic responses in bacteria [40]. The capacities of different microbial species to compete for these substrates and utilize vary. In the rhizosphere of maize, exudation of the benzoxazinone DIMBOA (2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one) resulted in an increase of population density of *Pseudomonas putida* strain with plant beneficial characteristics [41]. In *A. thaliana*, active exudation of phytochemicals mediated by ABC (ATP-binding cassette) transporters was demonstrated [42]. Phenolic compounds in the root exudates were suggested to send specific signals for soil bacteria [43]. Besides chemoattraction, root exudates regulate the adherence, colonization and formation of biofilm in the rhizosphere among the bacterial isolates [44]. Many soil-borne organisms follow the concentration gradients of sugars and amino acids towards the root. This leads to differential proliferation of microorganisms along different compartments of rhizosphere [44]. Since quantity and composition of root exudates respond rapidly to subtle environmental changes, the

selective pressure exerted on microbial communities varies spatiotemporally [45]. Rhizosphere pH also shapes microbial ecology in the root environment [46]. Root-induced pH changes have a dramatic impact on key biogeochemical processes such as (i) dissolution/precipitation of soil minerals and (ii) adsorption/desorption of ions, and hence bioavailability of either anions (e.g. phosphate) or cations (e.g. copper). Further understanding of rhizosphere biogeochemistry is required to quantify the driving role of higher plants in ecosystem services such as soil formation and nutrient cycling.

PLANT-MICROBE AND MICROBE-MICROBE INTERACTIONS

The plant-microbe interaction in the rhizosphere may be categorized as associative, symbiotic, neutralistic, or parasitic. The positive interactions include symbiotic and associative interactions with beneficial microbes, such as endo- and ecto-mycorrhizal fungi, nitrogen-fixing bacteria and plant growth-promoting rhizobacteria (PGPR) whereas negative interactions include association with parasitic plants, pathogenic bacteria, fungi, oomycetes, nematodes and invertebrate herbivores.

Symbiosis between legume plants and *Rhizobia* in the soil is of particular importance in agriculture and much research has been focused on characterization of the molecular mechanisms that establishes species-specific collaboration [47]. Legume-*Rhizobia* interactions are mediated by host-specific flavonoids secreted in the root-exudates (Table 1). These molecules belong to a diverse

Table 1. List of compounds attracting *Rhizobia* from the root exudates of legumes.

Host Species	Compounds released	Reference
Alfalfa (<i>Medicago sativa</i>)	Luteolin	[92]
	7,40-Dihydroxyflavone, 7,40-Dihydroxyflavanone, 4,40-Dihydroxy-20-methoxychalcone	[93]
	Chrysoeriol	[94]
	Trigonelline and Stachydrine	[95]
Barrel Medic (<i>Medicago truncatula</i>)	7,40-Dihydroxyflavone	[96]
Black Locust (<i>Robinia pseudoacacia</i>)	Apigenin, Naringenin, Chrysoeriol, and Isoliquiritigenin	[97]
Common bean (<i>Phaseolus vulgaris</i>)	Eriodictyol Naringenin, Genistein 7-O-glycoside, Delphinidin Petunidin, Malvidin, Myricetin and Quercetin	[98]
Common vetch (<i>Vicia sativa</i>)	7,30-Dihydroxy-40-methoxyflavanone	[99]
Cowpea (<i>Vigna unguiculata</i>)	Daidzein, Genistein and Coumestrol	[100]
Pea (<i>Pisum sativum</i>)	Apigenin and Eriodictyol	[101]
Rostrate sesbania (<i>Sesbania rostrata</i>)	7,40-Dihydroxyflavanone	[102]
Soybean (<i>Glycine max</i>)	Daidzein and Genistein	[103]
	Coumestrol	[104]
White clover (<i>Trifolium repens</i>)	7,40-Dihydroxyflavone and Geraldone	[105]

family of aromatic compounds derived from plant's secondary metabolism. Depending on the host and the bacterium, flavonoids activate a series of transcriptional events culminating in the production of main rhizobial nodulation signals called Nod factors (NF) or lipo-chito oligosaccharides (LCOs) [48]. Nod factors induce diverse developmental processes in the plant partner leading to morphological changes in legume root hairs, infection thread formation, nodule development and symbiotic nitrogen fixation [49]. *Rhizobium sp.* is a vast group of soil-borne rhizobia with other plant growth promoting activities such as siderophore production and disease suppression [50, 51].

The arbuscular mycorrhiza fungi (AMF) symbiotically interact with more than 80% of plant species [52]. AMF forms hyphal branching to establish its contact with the roots and the "branching factor" at play has been recognized to be strigolactone [53]. Strigolactone is exuded from the roots and considered to be the plant signal molecule for AMF symbiosis [53]. The fragility of these compounds results in a steep concentration gradient which determines these obligate biotrophs to reach living plant roots. It is hypothesized that AMF may use the ancestral receptor to perceive signals of strigolactones in the rhizosphere [54]. Hence, the identification of the receptors for strigolactones in fungi might be a fascinating topic for future research.

Rhizosphere microbial populations are not simple spectators. They too communicate among themselves in addition to interacting with the plant root system. Based on their primary effects, the beneficial rhizosphere organisms are generally classified into two broad groups (i) biological control agents (BCA) that indirectly assist with plant productivity through the control of plant pathogens and (ii) plant growth promoting microorganisms (PGPM) with direct effects on plant growth promotion.

BCA adversely affect the population density, spatio-temporal dynamics and metabolic activities of soil borne pathogens *via* three types of interactions. These include competition, antagonism by producing secondary antimicrobial metabolites [55, 56], lytic enzymes [57] and effectors [58, 59] and hyperparasitism [60]. *Trichoderma sp.* is the most studied fungal BCA which has been proved to reduce plant diseases by multifarious modes of action. *Bacillus amyloliquefaciens* SQR9, isolated from cucumber rhizosphere, could protect the host from invasion by *Fusarium oxysporum f.sp. cucumerinum* J. H. Owen (FOC) through competition for nutrients and space [61]. Hyperparasitism among BCA involves the secretion of chitinases and cellulases which degrade pathogen's cell-wall [62]. This has been documented for *Trichoderma* [63, 64], *Gliocladium* [65] and *Pasteuria penetrans* [66]. The pathogens in the rhizosphere also exert diverse array of mechanisms to counteract antagonism. These include active efflux and degradation of antimicrobial compounds detoxification of oxygen radicals resulting from the oxidative stress generated by the antimicrobial compounds, conversion of antimicrobial metabolite into less toxic derivatives [67] and interference with the regulation and biosynthesis of enzymes and antimicrobial metabolites produced by antagonistic microorganisms [68]. BCAs have been shown to

interfere with quorum sensing among plant pathogens as a mean to control plant diseases and promote plant health. Converse to quorum sensing, many pathogenic microorganisms execute "quorum quenching" by repression of the production or inactivation of quorum signaling molecules, or interference with the signal perception of rhizospheric colonizing bacteria [69, 70].

Studies on bacteria in the legume rhizosphere have shown that indigenous *Rhizobia* compete *via* either antagonism or synergism not only with diazotrophs such as *Azotobacter* and *Azospirillum* but with *Pseudomonas* and *Bacillus* species for nodulation and nitrogen fixation [71-73]. The diazotrophs manage important biological functions by symbiotically interacting with *Rhizobium* populations within the rhizosphere to form a beneficiary region where interacting microorganisms benefit from nutrient resources [72]. Synergistic effects of PGPR and *Rhizobium* enhance nodulation, rate of nitrogen fixation and better yield of crops such as pea, chickpea and pigeon pea [74, 75].

Beneficial effects of PGPR have been extensively exploited for economic gains in the recent years. PGPMs may act as biofertilizer [76] and/or phytostimulators [77]. The activity and effects of beneficial rhizosphere microorganisms on plant growth and health are well documented for bacteria belonging to the *Proteobacteria* noticeably *Pseudomonas* and *Burkholderia*, *Firmicutes*, *Actinobacteria* and fungi *viz.* *Trichoderma*, *Gliocladium* and nonpathogenic *Fusarium oxysporum*. *Pseudomonads* are common colonizers of plant tissues and traditionally known to be the major component of many rhizosphere communities. *Pseudomonas sp.* have been broadly studied for their ability to reduce the development of various soil-borne plant pathogens through production of different antimicrobial compounds [78], competition for the nutrients in the root exudates [79] and induction of the plant defense mechanisms [80]. Multiple strains of fluorescent *Pseudomonads viz.* *Pseudomonas fluorescence*, *Pseudomonas putida*, *Pseudomonas chloraphis* were shown to improve plant growth in absence of pathogens by mechanisms such as directly solubilizing insoluble P sources [81] and/or regulating the concentration of plant growth regulators namely indole-acetic-acid or 1-amino-1-cyclic-carboxylate (ACC) deaminase [82, 83]. *Bacillus species* offer several advantages over fluorescent *Pseudomonads* and other Gram-negative bacteria as seed inoculants by protecting against root pathogens by virtue of their ability to form endospores [84] and producing broad-spectrum antibiotics. There is a growing list of reports demonstrating rhizosphere colonization and root disease control by *B. cereus* UW85, *B. megaterium* B153-2-2 and *B. subtilis* GB03 which are involved in controlling damping-off in alfalfa and cotton and *Rhizoctonia* root-rot disease in soybean [85-87].

TRANSLATING KNOWLEDGE INTO TECHNOLOGY

Studies in rhizosphere research have undoubtedly improved our ability to steer the knowledge into

technological applications in agriculture, ecological engineering and nature restoration. The applicability of PGPR in agriculture has been steadily increased as they offer the opportunity to replace chemical fertilizers, pesticides and mineral nutrients [88]. Cultivation of plant genotypes that can thrive on biotic and abiotic soil resources may also serve as an alternative in sustainable agriculture. This involves engineering plants with a higher level of resistance to pathogens *via* diverse mechanisms. For example, plants expressing bacterial acyl-homoserine lactonase and producing 5'-O-glucosyltransferase at an increased rate were shown to harbor enhanced resistance to plant pathogen, *Pectobacterium carotovorum* [89, 90]. Recent studies on the rhizosphere ecology of non-cultivated plant species has increased an awareness of reconstructing soil structure by ecological engineering of soil biota. Rhizoremediation can provide a cost effective and environmentally sustainable "Green Technology" for the breakdown of petroleum contaminants from the soil. Carboxylates comprise a significant component of the root exudate mixture and it is hypothesized that these compounds may enhance biodegradation of petroleum hydrocarbons by promoting microbial activity by providing energy source. Future research involving the use of advanced techniques such as SIP combined with powerful metagenomic approaches will greatly improve our ability to understand microbial-carboxylate dynamics and aid in the improvement of rhizoremediation as a viable remediation strategy [91].

CONCLUDING REMARKS

This minireview aims to consolidate our current understanding of chemistry and biology of rhizosphere with regard to both host plant and the residing microbial community with an emphasis to appraise the role of root exudates in shaping rhizobiota. It also highlights the beneficial interactions between plants and different PGPM and BCA. This information, collectively, may serve as foundation for further research towards development of novel methods in sustainable agricultural practice. Despite the historical commitment and attention to the soil microbiome, its study has not kept pace with the recent surge of research activity as that of human microbiome. Plant microbiome is often termed as the second genome of plant and it is to be remembered that plant-microbe interaction is a "dialogue" rather than a unilateral relationship. Further investigation unraveling the 'specific' interactions in the rhizosphere will benefit the fundamental understanding of plant biology and provide stability of food production.

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

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