Effect of Root Exudates on Rhizosphere Soil Microbial Communities

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Abstract
The rhizosphere is an area of soil surrounding plant roots in which soil's most of the reactions occur. The rhizosphere is divided into three zones: endorhizosphere, rhizoplane, and ectorhizosphere. The two vital properties of soil rhizosphere are rootexudates and soil microbes. Root exudates are the chemical compounds that aresecreted by roots and act as a source of food for soil microbes and play an important rolein soil microbe and plant interaction. The soil microbes include bacteria, fungi and actinomycetes which are important for plant growth development and health of plants. The main aimof this review paper to provide an insight to the recent progress made in studies the interactions between plants and rhizosphere microbes through plant root exudates, focusing on how root exudates and focus, onimpact of root exudates on rhizospheric interactions at plant microbiome levels.
Keywords: Microbiome, rhizoplane, rhizosphere, root, exudates

Introduction

The rhizosphere is the area of soil roots where most of the reactions are affected by plant roots (Bashir *et al*., 2016). It is about 1–2 mm wide with no distinct boundaries (Brimecombe *et al*., 2007). The term rhizosphere was coined by Hiltner (1904) to describe the portion of soil in which microorganisms-mediated processes take place under the influence of root system (Susanne, 2016). Interactions between plant roots and microbial communities in the rhizosphere are critical for functions and traits related to plant growth, development and health (Berendsen *et al.,* 2012; Mendes *et al*., 2013). Plant roots release a huge variety of chemical compounds to attract and select microorganisms in the rhizosphere which induce different mechanisms by which plant associated microorganisms influence plant growth and development (Huang *et al*., 2014). Plant-microbe interactions play important roles in a number of vital ecosystem processes, such as carbon sequestration and nutrient cycling (Singh *et al.,* 2004).The root exudates acts as a signaling messenger that initiates and intimates physical and biological communication between the soil microbes and plant roots. Root-mediated rhizospheric communication is grouped into two categories: negative and positive interactions (Mendes *et al*., 2011; Elsas *et al*., 2012). Positive interactions involve communication of plant roots with certain plant growth-promoting rhizobacteria (PGPR). These plant roots produce certain chemicals that act as signals and attract certain microbes and stimulate chemotaxis (Thimmaraju *et al*., 2008). Positive interactions of root exudates also include growth enhancers that enhance growth of neighboring plants and help in cross-species signaling. The negative interaction of root exudates includes secretion of insecticidal and nematicidal compounds, phytotoxins, and secretion of antibiotics (Bais *et al.*, 2006).The main aim of this review; is to understand soil microbe and plant interaction mediated by root exudates for enhancing sustainable agriculture.

Rhizosphere

Rhizosphere is the zone of soil immediately adjacent to roots that supports high levels of microbial activity. It has also been defined as the zone that includes the soil influenced by the root along with the root tissues, supporting large active groups of microorganisms (Morgan *et al*., 2005; Geetanjali and Jain, 2016). The rhizosphere is broadly divided into the three zones, named as endorhizosphere, rhizoplane and ectorhizosphere (Clark, 1949). The endorhizosphere consists of root tissues including cortical cells and the endodermis. Rhizoplane is the area of root surface where soil microbes and soil particles interact. It comprises of the cortex, epidermis, and mucilage. The thirdzone is ectorhizosphere which is formed from soil particles adjacent to roots (**Figure 1**). Besides these three fundamental zones, some other layers are also found which include the mycorrhizosphere, rhizosheath, and bulk soil (Linderman, 1988; Gobat *et al.*, 2004;). Mycorhizosphere is the region inhabiting the mycorrhizal association of plants. Rhizosheath is the strongly adhering dense layer and consists of root hairs, mucoid layer, soil particles, and soil microbes. Bulk soil is the portion of soil which is not the component of rhizosphere (Brundrett, 2009; Lambers *et al*., 2008) Thus, rhizosphere is considered as a unique region distinct from the bulksoil.

Rhizophere being an active region of microbial diversity is considered as the hot spot of soil microbes (Jones and Hinsinger, 2008).The rhizosphere only extends a few millimeters from the root surface (Girlanda *et al*., 2007). However, it contains upto 10^{11}microbial cells per gram of roots (Berendsen *et al*., 2012), with the collective microbial community being referred to as the rhizo-microbiome (Mendes *et al*., 2013). The intense and complex communication among microorganisms plays a fundamental role in recruiting and shaping the microbial community in the rhizosphere (Venturi and Keel, 2016). The rhizo-microbiome is important for plant health (Khan, 2006) and is able to influence the structure of the microbial community (Venturi and Fuqua, 2013). The rhizosphere is also called as human gut microbiome for plants and is considered as the lavish fountain in the arid region (Mendes *et al*., 2011). Rhizosphere has the greater combined genome than that of plant and thus it is called as plant's second genome (Bron *et al*., 2012). Several reports have shown that the difference in microbial communities between the bulk and rhizosphere soil of land plants (Lundberg *et al*., 2012; Peiffer *et al*., 2013). Recently Edwards *et al*. (2015) investigated the microbial communities inhabiting the rice field ecosystem and concluded that the microbes within the rice root interior, the rhizoplane and the rhizosphere had considerable variation. In addition, the microbial communities in various zones, such as rhizosphere, anoxic bulk soil, and oxic surface soil have been reported (Grobkopf *et a*l., 1998; Ludemann *et al*., 2000; Lu *et al*., 2004; Asakawa and Kimura, 2008; Breidenbach and Conrad, 2015; Lee *et al*., 2015).

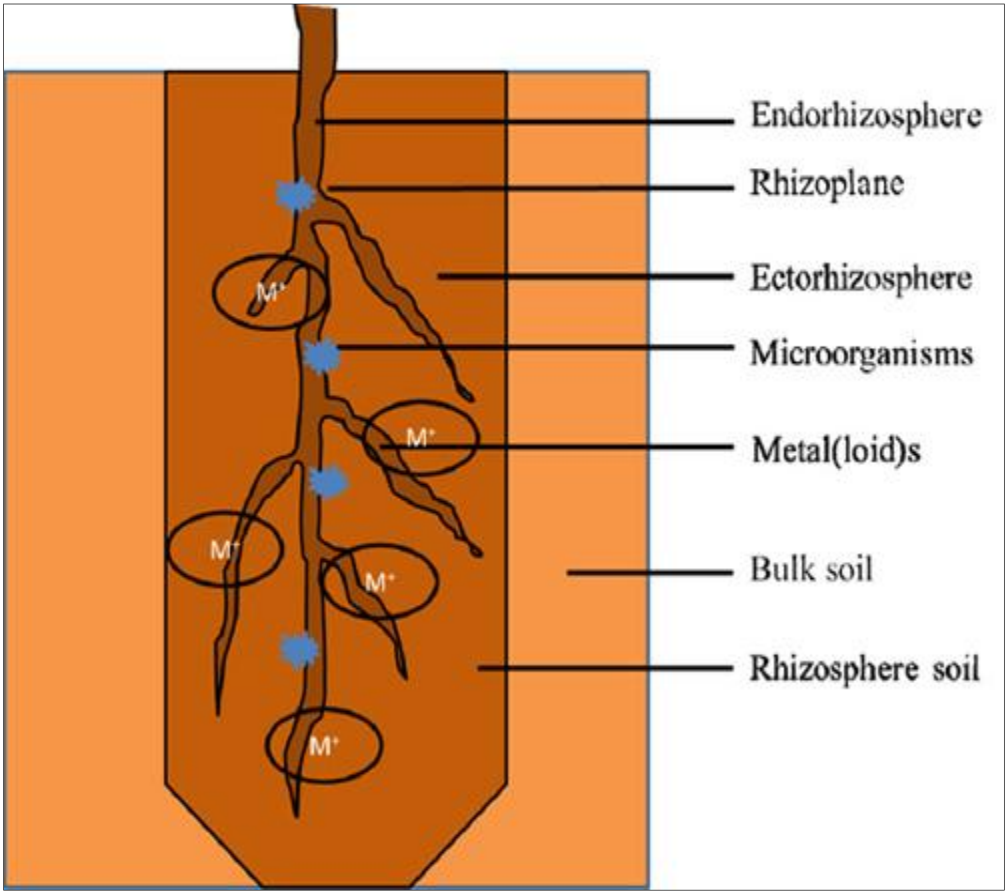

Figure 1: A simplistic diagram of rhizosphere (Seshadri *et al.*, 2015)

Root exudates

Besides providing the mechanical support, the plant roots assist in water and mineral nutrient uptake, which includes the functions like synthesis, secretion and accumulation of diverse group of chemical compounds (Flores *et al*., 1999) which plays a vital role as source of chemicals in soil root ecosystem (Bias *et al*., 2001). These chemical compounds released from intact and healthy roots are referred as root exudates which are relatively important in mediating the communication of plants with soil microbes (Bias *et al.*, 2004; Weir *et al.*, 2004; Broeckling *et al.*, 2008). Plant roots exude a broad range of compounds into the rhizospheric soil. Generally it has been found that microorganisms in rhizosphere live under conditions of "nutrient starvation" and are thus constantly looking for nutrients. The most important nutrient sources excreted by roots are organic acids (citric, malic, succinic, oxalic and pyruvic), carbohydrates (glucose, xylose, fructose, maltose, sucrose, ribose), amino acids, fatty acids, proteins, enzymes, nucleotides and vitamins (Ben, 2015). Some of the processes occurring by the roots in the rhizosphere such as root exudates are still unknown (Hawes *et al*., 2000). Root exudates mostly include sugars, amino acids, peptides, vitamins, nucleotides,organic acids, enzymes, fungal stimulants, and also someother compounds which help in plant water uptake, plant defense, and stimulation(Pate *et al*., 2001 ; Pate and Verboom 2009 ; Taylor *et al*., 2009). Sugars, organic acids, lipids, flavonoids, enzymes, amino acids, proteins, aliphatics, and aromatics are examples of primary substance found within the root exudates (Shukla *et al.*, 2011).

Among these, the organic acids have been found of great importance because of its role in providing substrate for microorganisms and acting as intermediate in both biological and chemical reactions in the soil (Wutzler and Reichstein, 2013).

Root exudates can be divided into two categories: low molecular weight compounds which include amino and organic acids, sugars, phenolic compounds and other secondary metabolites and high molecular weight compounds e.g. polysaccharides and proteins (Badri and Vivanco, 2009).Various environmental factors such as soil type, pH, temperature, nutrient availability and the presence of microorganisms determine the quality as well as quantity of root exudates (Shukla *et al.*, 2011; Xue *et al*., 2013). Mostly at the root tips concentration of exudates is found to be greater and at the sites of lateral branching, decreasing with increasing distance from the root surface (Marschner *et al*., 2011). Different microbial communities can be generated by the diversity in root exudates, specific to each plant species (Huang *et al*.; 2014).

Impact on rhizoflora

Root exudates represent an essential component of communication with rhizosphere-inhabiting microorganisms for plants, a wide range of substrates andsignaling molecules are produced by plants for this communication. Overall, it has been found that plants producea diverse array of more than 100,000different low molecular weight compounds known as secondary metabolites (Bais *et al*., 2004; Mathesius, 2010), which in turn can alter the microbial diversity, the communication among bacteria, secreting compounds that mimic bacterial signals of quorum sensing (Gao *et al*., 2003). Root exudates can mediate rhizospheric interactions (plant-microbe and microbe-microbe) by recruiting beneficial specific microorganisms such as PGPR (plant growth promoting rhizobacteria), mycorrhizal fungi or nitrogen-fixing bacteria (Haung *et al*., 2014). Plants can also use exudates to defend themselves against pathogens (Neil *et al*., 2012).

Numerous studies have revealed that plants can control and form the selection of microbes by secreting specific substrates of root exudates that shape the rhizosphere microbial community (Bakker *et al.*, 2012). For example, application of *p*-coumaric acid (a known root exudates substrate) to cucumber seedlings grown in soil increased bacterialand fungal community profusion, changed the efficiency and structure of rhizosphere bacterial and fungal communities, and overall increased the mass of a soil-borne pathogen of cucumber (Zhou and Wu, 2012). The profusion of the bacterial taxa *Firmicutes*, *Beta-proteobacteria*, and *Gamm-aproteobacteria* and of the fungal taxa *Sordariomycete* and *Zygomycota* also increased in the cucumber rhizosphere, showing that these bacterial and fungal groups involved in the degradation of *p*-coumaric acid. Another cucumber root exudate compound (vanillic acid) shifted the soil microbial communities of cucumber (Zhou and Wu 2013). Badri *et al*. (2013) observed the addition of different natural chemicals derived from *Arabidopsis* root exudates added to the soil produced distinct rhizosphere microbial communities that appeared to have the ability to degrade atrazine. The structure of bacterial communities in a field planted with six potato cultivars at three growth stages (young, flowering, and senescent) were examined by DNA-based pyrosequencing (Inceoglu *et al*., 2012). Furthermore, members of *Pseudomonas*, *Beta*-, *Alpha*-, and *Delta-proteobacteria* were more abundant under different ecological conditions than were members of the *Acidobacteria*. A meta-transcriptomics comparison of the microbial communities in wheat, oat, and pea revealed that fungi were highly enriched in the pea rhizosphere compared with that of other crops (Turner *et al.*, 2013). A study of the dynamics of rhizosphere microbial community structure and function showed that rice-planted soil had significantly different bacterial and fungal communities than those of unplanted soil (Hussain *et al*., 2012). Marton *et al*. (2016) also investigated the influence of root exudate flavonoids on the soil bacterial communitystructure and identified members of the community that change their relative abundancein response to flavonoid exudation.

Conclusion

Numerous microorganisms are present in the rhizosphere, and they form a complex community which are connected with each other and with the external environment. Many of the major compounds found in the root exudates are likely to be present throughout the rhizosphere and are important in structuring rhizosphere microbial communities as well as the plant health in enhancing the sustainable agriculture.

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