Rhizodeposits: An Essential Component for Microbial Interactions in Rhizosphere

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Abstract

Rhizodeposits are essential rhizosphere-associated constituents synthesized by plants that support various biological and physiochemical activities in soil. They significantly influence microbial root colonization capacity, multiplication of rhizosphere microorganisms, soil microbial activity, soil health and secretion of organic bioactive compounds. Root exudates are a group of vitally important compounds with multifarious functions and are released from the living plant roots. They are a complex group of substances secreted by plant roots consisting of low molecular and high molecular weight constituents. The root exudate composition reflects the opposing-associating trait of plants towards rhizosphere microorganisms. These rhizosphere microorganisms produce a wide range of antibiotics that provide a defence to the host plants against a number of phytopathogens. The root exudates, produced as a part of the rhizodeposition process, exert a direct impact on the biogeochemical cycling of carbon and nitrogen. They help in modulating organic matter decomposition in soil by altering the microbial communities involved in the decomposition of soil organic matter and also affect the soil nitrification process. Root exudates are well known for their activity as chemoattractant and signalling molecules for successful

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interactions between plant and rhizosphere microorganisms. Thus, the current chapter will elaborate on the various roles of root exudates in plant-microbe interaction and rhizosphere functioning, the mechanism of root exudates and the molecular insights of the root exudation process.

7.1 Introduction

7.1.1 Rhizosphere: A Dynamic Ecological Niche Space for Complex Microbial Interactions

The ‘rhizosphere’ which refers to the nutrient-rich region of the soil surrounding the plant roots is a metabolically active and diversely rich hot spot for microorganisms, considered to be the most complex ecosystem on Earth. The various biological and chemical processes occurring in the rhizosphere soil is solely influenced by the roots. The rhizosphere represents the most complex and metabolically active region of the soil which controls plant-microbe interactions. The complexity of the rhizosphere region varies with the variation of plant genotypes and also with the age and architecture of plant roots. Apart from the domain, the width of the rhizosphere region also depends on the plant species. The rhizosphere microzone differs from the bulk soil (commonly known as edaphosphere) in terms of increased microbial population and metabolic activity and also due to higher accessibility of plant root exudates. Over the years, efforts have been made to restructure and regenerate the definition of rhizosphere so as to depict three regions, which include the endorhizosphere, the rhizoplane and the ectorhizosphere. The endorhizosphere, as the name suggests, refers to the apoplastic space between the cells and includes the root cortex and the endodermal cells. The rhizoplane refers to the intermediate region or the root surface adjacent to the roots. The ectorhizosphere is the topmost zone of soil that surrounds the plant roots (De-la-Pena and Loyola Vargas 2014).

The rhizosphere microbiome is a complex, highly dynamic microbial assemblage under the control of a number of environmental factors. Soil and plant genotypes are equally crucial in shaping the rhizosphere microbiome via recruitment of soil microorganisms from the bulk soil. Even during a pathogen attack, the host plant actively takes part in selecting a specific group of microbial cells from the rhizosphere microbial community to control and inhibit the infection. This is how disease suppressiveness is triggered in soil despite the presence of virulent soil pathogens. Disease suppressiveness is solely due to the involvement of soil microbial communities and the intense microbial activity in the rhizosphere zone which is activated with an onset of a disease (Mazzola 2002). The recruitment of specific antagonistic microorganisms from the rhizosphere during pathogen invasion was studied and elaborated by Mavrodi et al. (2012). For example, under circumstances of pathogen attack in wheat plants, that is, *Gaeumannomyces graminis* var. *tritici* (under irrigated conditions) and *Rhizoctonia solani* (under dry conditions), the major soil-borne pathogens attacking wheat plants, the wheat rhizosphere recruits

2,4-diacetylphloroglucinol (DAPG) producing pseudomonads and phenazine producing pseudomonads to suppress the growth of take-all pathogens *G. graminis* var. *tritici* and *R. solani*. Thus, under conditions that favour pathogen attack, the host plant recruits antagonists from the rhizosphere microzone to suppress the ill effects of pathogens on host plants.

The rhizosphere soil is an indication of a high microbial population, increase microbial diversity and metabolic activity. The diversity and functionality in the rhizosphere soil are mainly owing to the production of root exudates due to the secretion of organic carbon by the roots (Bakker et al. 2013). Plants act as the main source of organic carbon in soil due to physiological and biochemical plant processes such as litterfall, plant senescence and the C loss from the plant roots. These plant-derived C inputs constitute approximately 0.5–10% of the total C fixed in the soil. The soil microbes get chemotactically attracted to the C containing compounds secreted by the plant roots leading to their survival and proliferation in this carbon-rich environment. These root-derived C containing compounds are collectively referred to as rhizodeposits (Farrar et al. 2003).

7.2 Rhizodeposits: A Vital Component for Plant-Soil Linkage

Rhizodeposits are grouped into different classes based on their composition, mode of release or function. They include substances like root exudates, actively released secretions like proteins, mucilage, lysates, secondary metabolites and inorganic molecules, shedded border cells, root cap cells and the ageing root tissue (Bowsher et al. 2018). The rhizodeposits released into the soil are differentially used by diverse components of the soil community that includes the rhizosphere microbial communities and other residing soil fauna. They behave specifically towards a different group of soil microorganisms resulting in their attraction or repulsion (Fig. 7.1). The composition, superiority and quantity of root exudates being released by the host plant vary between the type of plant cultivar, plant developmental stage and also on environmental factors such as soil type, soil pH, temperature and the residing microbial communities. This chapter will spotlight the importance of root exudates, based on the large body of literature, with the aim of unveiling the mechanistic insights of root exudation patterns and the potent roles of root exudates in different dimensions.

7.2.1 Root Exudates: A Multifunctional Compound of the Rhizosphere Microzone

Root exudates are considered to be the most essential among the rhizodeposits for plant-microbe interactions and rhizosphere microbial community structure. The living roots of plants release plant photosynthates that include sugars, carbon compounds, inorganic ions, metabolites and amino acids as root exudates (Badri

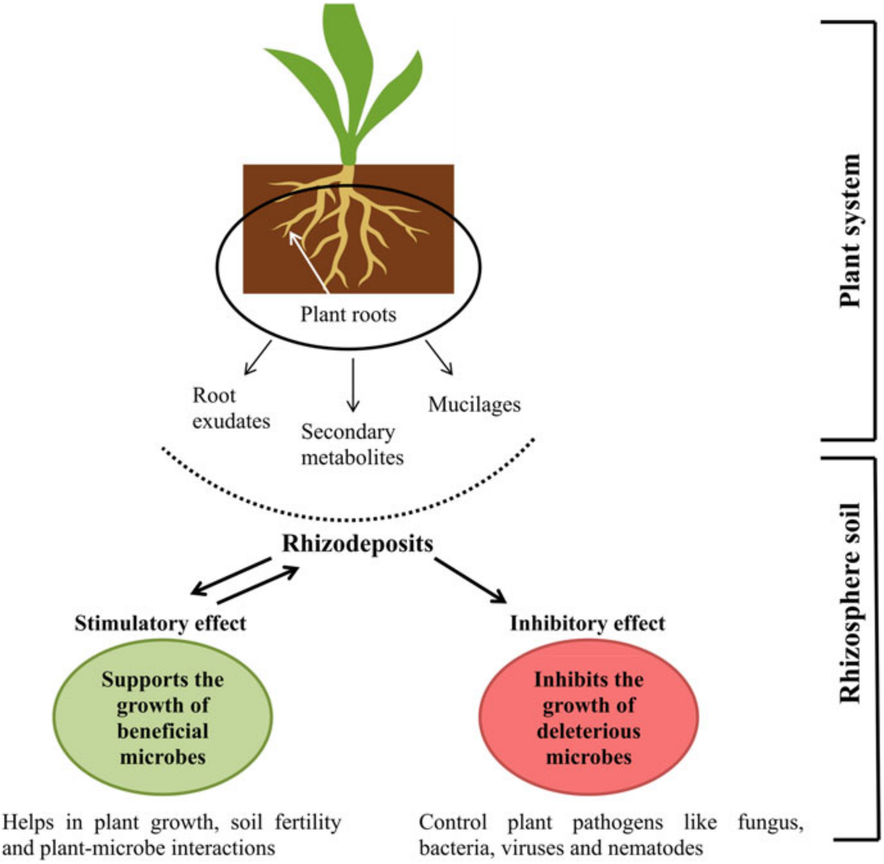

Fig. 7.1 Interaction of rhizodeposits with beneficial or pathogenic rhizosphere soil microorganisms resulting in the stimulatory or inhibitory effects

et al. 2013; Chaparro et al. 2013). The sugars that are present in the root exudates include monosaccharides, disaccharides and five-carbon sugars; amino acids include arginine, asparagine, glutamine, aspartate and cysteine. Root exudates also consists of organic acids such as benzoic acid, acetic acid, ferulic acid, ascorbic acid and malic acid. Apart from the aforementioned constituents, root exudates also contain phenolic compounds and some high molecular weight compounds such as auxin, gibberellin, flavonoids, fatty acids, enzymes, nucleotides, alkaloids, polyacetylenes, tannins, steroids, terpenoids and vitamins (Hayat et al. 2017) (Table 7.1). Root exudates are classified into two groups: the high molecular weight (HMW) compounds such as proteins, terpenoids, vitamins and polysaccharides and low molecular weight (LMW) compounds such as amino acids, sugars, phenols, organic acids and other plant metabolites. The HMW compounds are not easily utilizable by soil microorganisms but make up the majority of C present in the root exudates,

Table 7.1 Different potential roles of root exudates and the compounds detected in root exudates (adapted from Dakora and Phillips 2002; Haichar et al. 2014)

Component in root exudates	Functions	Detected components in root exudates
Amino acids and phytosiderophores	Nutrient source, acts as a chemoattractant and helps in chelating poorly soluble mineral nutrients such as Fe, Al and Ca phosphate	a- and b-alanine, proline, Asparagine, valine, threonine, aspartate, tryptophan cysteine, ornithine, cysteine, histidine, glutamate, arginine, glycine, homoserine, isoleucine, phenylalanine, leucine, -Aminobutyric acid, lysine a-Aminoadipic acid, methionine, serine and homoserine
Organic acids	Nutrient source, acts as a chemoattractant, helps in chelating poorly soluble mineral nutrients and induces the expression of *nod* gene, soil acidifiers and Al detoxifiers	Citric, glutaric, oxalic, malonic, malic, aldonic, fumaric, erythronic, succinic, ferulic, acetic, butanoic, butyric, syringic, valeric, rosmarinic, lactic, glycolic, trans-cinnamic, piscidic, formic, aconitic, pyruvic, vanillic and tetronic acids
Sugars and vitamins	Replaces phosphates from rocks making them available for microorganisms, promotes microbial and plant growth	Glucose, deoxyribose, oligosaccharides galactose, biotin, maltose, thiamine, ribose, niacin, xylose, raffinose pantothenate, rhamnose, riboflavin, arabinose and fructose
Phenolics, inorganic ions and gases	Nutrient source, chemoattractant molecules, microbial growth promoters, *nod* gene inducers as well as *nod* gene inhibitors, Al detoxifiers, chelators of poorly soluble mineral nutrients and resistance	Liquiritigenin, luteolin, daidzein, 4′,7-dihydroxyflavanone, genistein, 4′,7-dihydroxyflavone, coumestrol, 4,4′-dihydroxy-2′-methoxychalcone, eriodictyol, 4′-7-dihydroxyflavone, 3,5,7,3′-tetrahydroxy4’methoxyflavone, Naringenin, isoliquiritigenin, 7,30-dihydroxy-4′-methoxyflavone, umbelliferone, (+)- and (−)- catechin
Proteins and enzymes	Catalysts for P release from organic molecules, biocatalysts for organic matter transformations and plant defence	Acid/alkaline, phosphatase, amylase, invertase, protease, PR proteins, lipases, beta-1,3-glucanases

while the LWC compounds are readily utilizable, more diverse and are accompanied by a wide array of significant functions.

The root morphology serves as an important criterion in influencing the overall make-up and composition of root exudates. The ageing portions of the plant roots were known to exude more of organic acids, while the root tips of primary and lateral roots secrete more of amino acids (McDougall 1968; Rovira 1969). Each part of the plant roots is specialized for the secretion of different compounds as part of root exudates (Frenzel 1957, 1960). For instance, the meristem or the root apex secretes glutamic acid, valine, leucine and phenylalanine as root exudates while the outer layers of the root cap cells and root hair cells are specialized in the secretion of mucilage. Mucilage secretion can also occur due to degradation of the root epidermal cells. Aspartic acid is secreted overall by the entire root system. The zone following the root tip region is considered to be the primary site for root exudation in plants (Badri and Vivanco 2009).

Root exudation by the plants is due to the tremendous root pressure at the growing root tips in order to push their way through the soil. The root exudates mediate multipartite interactions in the rhizosphere region. They behave as a food source attracting neutral, beneficial and pathogenic soil microorganisms. As a response, the host plant introduces compositional modulations that cause the recruitment of beneficial soil microbes, thereby inhibiting/suppressing the pathogenic ones to avoid the flourishing of the non-beneficial microbial community in the rhizosphere microzone as well as defending the plants from pathogens (Zhang et al. 2009).

Root exudations occur by both active and passive transport systems wherein LMW compounds are transported by the process of direct passive diffusion. The movement of these compounds depends on cell membrane permeability, intracellular fluidic pH and polarity of the molecules that are being exuded by the plant roots while the HMW compounds are transported via membrane-bound transporter proteins including the ATP binding cassette (ABC) transporters (Badri et al. 2009; Yuan et al. 2018). Additionally, substrates such as indoles, pyrrolidines, quinolines and isoquinolines belonging to different classes of alkaloids produced by plants; flavonoids and phenolic acids that refer to plant-derived phenolic compounds and antimicrobials are transported from the living roots to the rhizosphere via multidrug and toxic compound extrusion (MATE) active transporters by using ion electrochemical gradient (Weston et al. 2012).

The movement of exuded root secretions in soil depends on diverse factors such as the quantity of root exudation, the nature of root secretions, the receptiveness of the compounds by the soil microorganisms for microbial assimilation and degradation, the nature and quantity of clay in the soil and the total water load of the soil. The zone that extends up to 1–2 mm from the root is considered the distance that is travelled by the root exudates. This rhizosphere microzone observes the maximum microbial load due to the high influence of root exudates that comprises sugars, organic acids and amino acids (Rovira 1969).

7.2.2 Factors Influencing Root Exudation Pattern

There are a number of factors that influence the exudation of compounds from the living plant roots. Soil moisture, plant biotype, microorganisms residing in the vicinity of the roots, damage to the living plant roots and the prevailing environmental conditions influence and modulate the root exudation pattern in plants.

The quality and quantity of root exudation vary among plant species. For instance, both the root exudates of wheat and barley plants contain sugars but the difference in both the exudates occurs in the case of certain sugars such as galactose, glucose and rhamnose, which is due to species variation. Variations in root exudation among species may be due to fluctuations in the distribution potential of the photosynthates which serve as a basic substrate for root exudates. Apart from plant biotype, plant root architecture also influences the exudation pattern as well as the distribution capacity of photosynthates. The morphological characteristics of roots including the surface area of roots, the root branching type, root tip density or the size of the root system determine the rate and extent of the distribution of photosynthates in soil. The absorbing roots that include the primary roots exhibit higher physiological activity than the xylem and phloem vessels present in the plant roots. These roots help in the exchange of materials across the plant roots. These differences in the architecture of the absorptive roots among species or within species, that is, the overall root architecture, play a decisive role in determining the root exudation rates (Yang et al. 2020). Additionally, the leaf habits also exhibit a strong influence over the root exudation pattern of plants. For instance, the studies undertaken by Sun et al. (2017) and Wang et al. (2019) have observed that there occurs higher exudation in deciduous trees than the evergreen trees, which was due to the differences in the leaf habit of both the plants.

Furthermore, environmental conditions and soil characteristics exert a strong relationship on the root exudation pattern of plants through direct or indirect effects. In consideration of environmental conditions, soil warming or an increase in soil temperature plays a crucial role in root exudation patterns. Several studies have investigated its influence on root exudation. Husain and McKeen (1963) have reported that the exudates obtained from strawberry plants grown at 20–30 °C contained higher amounts of amino acids than those grown at 5–10 °C. But the influence of soil warming on root exudation varies from plant to plant. For example, Schroth et al. (1966) observed that root exudation from cotton and bean plants was higher at a temperature of 37 °C, whereas it was lower in case of pea plants. In the case of pea plants, the exudation rate was observed to be higher at 27 °C. A similar pattern was observed for *Vicia faba* plants where the exudation of tannins and phenolics showed a profound increase at 30 °C, which was comparatively low when grown at 4 °C (Bekkara et al. 1998). An increase in temperature influences the root exudation pattern not only quantitatively but also qualitatively. Reports suggest that differences in the release of exudates due to temperature variations were due to alterations in the permeability of the cellular membranes or changes in cellular metabolism. Lower metabolic energy at lower temperatures allows substances to leak out of cells (Hale et al. 1971). Light intensity is one of the other factors responsible for exudation variations in plants. It modifies the exudation rate of secondary metabolites because of alterations in the biological phenomenon of photosynthesis. For instance, a few studies have reported that root exudation strictly depends on diurnal rhythms, which means an increase in root exudation during the light periods while declining during dark periods (Watt and Evans 1999). For example, Hughes et al. (1999) have reported that under light conditions the root exudates of *Alnus glutinosa* (L.) contain more of flavonoid content than the root exudates that were produced during dark conditions. As for tomato and subterranean clover plants, a similar root exudation pattern was observed. Clover plants grown under diurnal light exuded more serine, glutamic acid and a-alanine as part of root exudates than those growing under shady (60%) conditions. In the case of tomato plants, levels of aspartic acid, glutamic acids, phenylalanine and leucine in exudate were high during light periods, which were reported to be reduced by shading (Rovira 1969). Soil moisture significantly influences the exudation patterns in plants. As in the case of high soil moisture, there is less availability of oxygen in the soil, which results in hypoxia. Under hypoxic conditions, there occurs a shift in the respiration process from aerobic to anaerobic. This shift in respiration results in the accumulation of ethanol, lactic acid and alanine at phytotoxic levels in the plant root system (Rivoal and Hanson 1994). The plants defend themselves from the harmful effects of accumulated ethanol and lactic acid by secretion of a wide range of metabolites as part of root exudates (Xia and Roberts 1994).

Any damage whether physical or chemical to the living plant roots can cause significant changes in root exudation patterns. The extent of influence on root exudation is more pronounced for physical damage to roots than chemical ones. Physical damage to the plant roots can occur during digging, trenching or roto-tilling within the root area of the existing plants, whereas chemical damage occurs due to the excessive application of chemicals to the plants. There are studies suggesting that physical damage can cause a sharp increase in the release of amino acids by 73–120% in comparison to the intact, undamaged root system (Ayers and Thornton 1968). In addition to amino acids, physical damage to plant roots can also significantly influence carboxylate exudation in plants (Tiziani et al. 2020). In reference to chemical damage, Martin (1957) has reported that there was increased exudation of root exudates (scopoletin) from oat and wheat roots (C^{14}-1abeled organic compounds) (McDougall and Rovira 1965) when immersed in distilled water in comparison to the nutrient solution. Distilled water is hypotonic while a plant cell is hypertonic. So, when a plant cell is placed in distilled water, water moves from the outside of the cell to the inside, resulting in cell swelling which leads to increased membrane permeability. Thus it can be observed that both physical and chemical damage influences root exudation patterns in plants although the influence shown due to physical damage was more pronounced than that of chemical.

7.2.3 Mechanism of Root Exudation and Genes Involved

Root exudation is a biological process involving multiple mechanisms facilitating transport of soil C to the living plant roots and its release to the surrounding soil. The C produced in the source organs in the phloem is translocated by a specialized mechanism known as Munch’s pressure-driven mechanism that drives the phloem mass flow by use of a pressure gradient in the phloem (Liesche and Schulz 1930). It works principally based on the turgor pressure difference that exists between sink and source organs. During phloem unloading, the low molecular weight compounds are diverted to the phloem pericycle where they are unloaded and eventually move out of the phloem pole pericycle. The high molecular weight compounds like protein compounds remain restricted to the phloem pole pericycle. In no time, the low molecular weight molecules move out of the plant roots to the surrounding soil environment. In order to do so, these molecules need to move across the plasma membrane to reach the apoplast. The plasma membrane is permeable to small, gaseous molecules, while it is impermeable to larger, charged as well as uncharged polar molecules (e.g. glucose) (Canarini et al. 2019).

The small polar molecules and the uncharged molecules are transported through simple passive diffusion using the permeability nature of the lipid membrane as a criterion. The movement of smaller molecules through the lipid membrane is solely dependent on the electrochemical gradient between the source and the sink. The electrochemical gradient helps in the translocation of the molecules from the cytoplasm of root cells to the vicinity soil. The larger molecules pass through the membrane by interacting with specific transmembrane proteins, which is known as facilitated diffusion. These proteins help in transiting the molecules by forming small pores through the lipid bilayer or phospholipid bilayer membrane (Sasse et al. 2018). The efflux of the larger compounds such as sugars, amino acids and organic acids can also take place through specific efflux pumps and channels. A few of the transporters have been characterized for amino acids such as Usually multiple acids move in an out Transporter (UMAMIT), Cationic Amino acid Transporter (CAT), Lys His Transporter (LHT), Glutamine Dumper transporters (GDU) (Pratelli et al. 2010; Besnard et al. 2016). Similarly, for the transport of sugars, transporters like Sugars will be eventually exported as Transporter (SWEET), Sucrose Transporter (SUTs) and Monosaccharide Transporters (MUTs) (Hennion et al. 2019) and organic acid transporters such as Multi-drug And Toxic compound Extrusion/citrate Transporters (MATE) and Aluminum-activated Malate Transporters (ALMT) (Wu et al. 2018) have been characterized. Excretion of high molecular weight metabolites by roots can also take place via vesicular transport (Badri and Vivanco 2009). The newly synthesized secondary metabolites are transported by the vesicles to other storage compartments or the plasma membrane for efflux. This process of exudation of metabolites involving vesicles is known as exocytosis. In some cases, the allelopathic compounds secreted by the plant roots are cytotoxic to plant cells. These allelopathic compounds are separated from the cytosol by membrane-bound vesicles by a process known as vesicular trafficking. Vesicular trafficking and exocytosis are known to be involved in combating attacks by plant pathogens (Grotewold 2001).

Ion channels are responsible for the secretion of carbohydrates and carboxylate ions such as malate and oxalate. These exuded compounds are transported across the lipid membrane through a transport mechanism mediated by proteins. The most widely studied transporter is the aluminum-activated-malate transporter (ALMT). They consist of a group of proteins, responsible for several physiological plant processes like exudation of organic acid in the presence of toxic Al^{3+} ions in the soil, conferring aluminium tolerance in plants under aluminium stress conditions (Sharma et al. 2016). For instance, the organic acid (OA) anions were known to render Al^{3+} resistance to plants under Al toxicity, but their exudation from the plant roots involves a cascade of events. The cascade starts with Al^{3+}/H^+ activating unknown receptors. Activation of the receptors results in an increase of cytosolic Ca^{2+} ions which activate the calcium sensor proteins or calmodulin. The activated calmodulin protein binds to the glutamate decarboxylase enzyme converting it from an inactive form to an active form. The activated form of glutamate decarboxylase enzyme converts glutamate to ɣ-aminobutyric acid, which is involved in the regulation of expression of ALMT1 activity in *Arabidopsis thaliana* plants. In *Arabidopsis,* Al-tolerance genes such as *AtALMT1*, *AtMATE*, *ALS3* and different H^+ tolerance genes are regulated by zinc finger protein sensitive to proton rhizotoxicity1 (STOP1). STOP1 is considered a core component for controlling Al and H^+ tolerance in *Arabidopsis,* while STOP2 regulated by STOP1 protein confers only H^+ tolerance in *Arabidopsis* due to low expression of *AtMATE* and *ALS3* genes. In addition to these, there are a few other factors like calmodulin-binding transcription activator2 (CAMTA2) that is involved in the regulation of expression of the *AtALMT1* gene (Kobayashi et al. 2014). Just like in *Arabidopsis*, in the case of *Oryza sativa*, the *ART1* gene encodes for a transcription factor that is involved in the regulation of 31 downstream genes implicated in Al tolerance. Briefly, Al tolerance in rice is basically due to the involvement of a number of genes that are associated with the process of detoxification of Al at different cellular levels (Tsutsui et al. 2011). The downstream genes that are regulated by *ART1* were characterized to be STAR1 and STAR2 (SENSITIVE TO AL RHIZOTOXICITY1) encoding ATP binding and transmembrane domain of a bacterial-type ATP-binding cassette transporter, Nrat1 (Nramp Al transporter 1), located in the plasma membrane of the root cells and functions as a transporter for trivalent Al into the plants which is essential for the prior step of final Al detoxification, OsALS1, CDT3 and OsFRDLA1 encoding an Al-induced MATE transporter. The ALMT transporters are not the only ones that confer stress tolerance in plants but there are MATE active transporters that also confer tolerance in plants against different stresses (Liu et al. 2009). MATE transporters play a vital role in the transport of a wide variety of molecular substrates, hormones and secondary metabolites (Takanashi et al. 2014). These are the independently activated transporters that confer stress tolerance to plants and are actively involved in citrate exudation.

Secretion of root exudates can also take place via proteins located in the root plasmatic membrane through an active transport mechanism. The active transport mechanism consists of two classes of membrane transporters, namely, ABC and MATE transporters. The root exudation from the living roots involving proteins occurs in three different situations depending on their specificity: transporters that are involved in the secretion of various metabolites, membrane transporters that are involved in translocation of different metabolites to the rhizosphere soil and the unique and highly specific transporters that are involved in the exudation of compounds from plant roots (Jones and George 2002; Orelle et al. 2018). The ABC group of transporters are considered the primary transporters while the MATE transporters are considered the secondary active transporters, and this is due to the fact that the former utilizes the energy from ATP (adenosine triphosphate) hydrolysis while the latter uses electrochemical gradient from the transportation of compounds across the membrane (Weston et al. 2012).

7.3 Root Exudates Mediating Belowground Interactions

Root exudates play a vital role in the root rhizosphere region. Through the exudation of a wide range of compounds as root exudates, the plant roots can structure the soil microbial community and regulate their existence in the immediate vicinity of the roots. Moreover, root exudates can help the soil microbiota in coping up with herbivores, stimulating the process of plant-microbe symbioses, modulating the soil physical and chemical properties and playing a pivotal role in the growth suppression of different pathogenic microorganisms and competing for plant species (Nardi et al. 2000; Walker et al. 2003).

7.3.1 Root Exudates Mediating Plant-Microbe Interactions

From the previous literature, it is well known that plant roots are the most potent source for the recruitment of soil microbes. These soil microbes help in promoting the growth of the plants, protecting the host plant from diverse plant pathogens and increasing plant tolerance to abiotic stress conditions. The predominant factor that helps the host plant to recruit rhizosphere soil microbes are the root exudates which commute with the rhizosphere-residing beneficial microbes while inhibiting the non-beneficial soil microbes.

7.3.1.1 Root Exudates: An Essential Chemoattractant for Microbial Host Root Colonization

Plants exude high levels of C as root exudates that behave as chemoattractant for bacteria. Most of the motile bacteria direct their movement in response to these chemical gradients, a bacterial response known as chemotaxis, for initiating a communication between the plant roots and the soil bacteria and colonizing the root region of the host plants (root colonization). The chemotactic response of bacteria increases their root colonization efficiency in the rhizosphere. The various molecules exuded by the plants help in initiating a positive bacterial chemotaxis towards different host plants leading to root colonization (Brencic and Winans 2005). Bacterial chemotaxis is initiated by the binding of a signalling molecule to a chemoreceptor. This transmembrane chemoreceptor which is responsible for bacterial chemotaxis is also known as methyl-accepting chemotaxis protein and consists of a number of domains. The transmembrane consists of a periplasmic or cytosolic ligand-binding domain, cytoplasmic region consisting of HAMP (histidine kinase, adenyl cyclase, methyl-accepting chemotaxis protein [MCP] and phosphatase) linker and a signalling domain. The ligand-binding domain is responsible for binding extracellular compounds. Once the ligand binds itself to the binding LBD, autophosphorylation of the histidine kinase CheA gets altered, which in turn transfers the phosphoryl groups to the response regulator CheY. Subsequently, the generated CheY-P permits its interaction with the flagellar motor to control cell swimming or tumbling to ultimately mediate chemotaxis (Feng et al. 2018). Existing literature reported bacterial chemotaxis towards various molecules exuded by host plant roots as root exudates mediated by specific chemoreceptors in establishing plant-microbe interaction following host root colonization (Webb et al. 2014; Allard-Massicotte et al. 2016).

Root colonization is one of the most important factors that aids in plant-microbe interaction. Root colonization is considered a key process that controls plant growth and induces systemic tolerance against different biotic and abiotic stresses (Sachdev and Singh 2018). The metabolites and the other organic secretions as a part of root exudates favour microbial colonization of root surfaces. Root colonization occurs when several groups of soil bacteria form microcolonies or biofilms on root surfaces. Biofilms are an assemblage of microbial communities embedded in a matrix of extracellular polymeric compounds (Bogino et al. 2013). The extent of biofilm formation varies between different root regions. In accordance with the previous literature, the depth and thickness of microbial biofilms are higher in the apical region of the roots than in ageing or mature root regions. This is due to the fluctuations in the composition of the root exudates and nutrient availability at the root plane or specific secretion of antimicrobials from the root tip (Rudrappa et al. 2008).

7.3.1.2 Root Exudates as Signalling Molecules

The organisms in the rhizosphere region interact with each other as well as plants via chemical communication established in the rhizosphere microzone. The plants secrete a wide array of metabolites as a response to altered gene expression, which is a result of signalling molecules secreted by the rhizosphere microorganisms. Overall, plants produce a compositionally diverse array of more than 100,000 different low molecular mass natural products known as secondary metabolites. In this chapter, we will explain a few of the molecules that are involved in legume-rhizobia, plant-AMF and actinorhizal plant-Frankia interactions.

Rhizobia

Bacteria belonging to the Rhizobiaceae family produce flavonoids and non-flavonoid signalling molecules that play a significant role in symbiotic interactions. The symbiotic interaction between any strain of bacteria belonging to the Rhizobiaceae family and legume is the result of a molecular interaction based on the signal molecules produced and secreted by both the associated partners involving a succession of recognition events. Initially, the interaction starts with the exudation of signal molecules by the host plant that expresses the genes involved in the process of nodulation.

Flavonoids are a group of plant secondary metabolites that are well known for their activity in plant-microbe interaction. They are synthesized via the central phenylpropanoid pathway and the acetate-malonate pathway. Flavonoids consist of two benzene rings connected by a three-carbon linking chain. They consist of two aromatic rings which are synthesized by different biosynthetic pathways. The flavonoids are categorized into different subgroups based on their molecular structure including flavonols, flavones, flavanones, isoflavonoids, chalcones, catechins, anthocyanidins and dihydroflavonols. There are several studies that have reported its role in in vitro nodule formation process using reporter genes (Shaw et al. 2006). The legume roots are known to secrete flavonoids into the surrounding soil. The quantity and concentration of the flavonoids increase with the presence of *Rhizobium* species in the soil. The flavonoid molecule behaves as a signalling molecule expressing the *nod* genes in rhizobia. The expressions of nod genes are responsible for the synthesis of Nod factors that initiate the nodulation process (Haichar et al. 2012). The Nod factors are lipochitooligosaccharides that act as signalling molecules triggering a sequence of events in host plants such as root hair curling or shepherd's crook, infection thread formation to allow the entry of rhizobia to the host root cells and nodule development (Cullimore et al. 2001). The process of nodule formation is regulated by both rhizobia and the plant and involves mechanisms that are controlled by two factors, that is, nodule numbers and nodule position (Sasse et al. 2018). The existing literature suggests that Nod factors induce certain flavonoids to initiate nodule formation through their action as auxin transport inhibitors. By inhibiting auxin transport inhibitors, there involves a local accumulation of auxin at the nodule initiation site initiating the development of nodule primordial. Similarly, the non-flavonoid molecules are also involved in inducing the expression of *nod* genes. There are several studies that documented the activity of various non-flavonoid molecules in inducing the expression of *nod* genes. For example, trigonelline and stachydrine from alfalfa seeds (Phillips et al. 1992), aldonic, erythronic and tetronic acid (Gagnon and Ibrahim 1998), xanthones (Yuen et al. 1995), vanillin and isovanillin from wheat seeds (Le Strange et al. 1990) can induce expression of *nod* genes in *S. meliloti* by activating the regulatory NodD protein, nod genes in *Mesorhizobium loti*, *Rhizobium lupini*, and *Sinorhizobium meliloti, B. japonicum, Rhizobium* sp. respectively

Frankia

Actinorhizal symbiosis is a type of symbiotic interaction occurring between actinobacterium Frankia and dicotyledonous plants. The symbiotic interaction between the two partners initiates with the infection process. As in *Rhizobium*, 'shepherds crook' is also observed in *Frankia*, but unlike *Rhizobium* Nod factors, the extracellular deforming factors in the case of *Frankia* are quite different both structurally and functionally (Bagnarol et al. 2007). As in the case of *Rhizobium*/ legume interaction, the main factor is the host-derived flavonoids that help the rhizobia to interact specifically with their hosts, and similar is the case with *Frankia*. The root hair curling in *Frankia* is initiated on interaction with the host root filtrate. There are few studies that have correlated the strain specificity in *Myricaceae-Frankia* symbiosis with root phenolics. The main root exudates that were affected by *Frankia* inoculation are phenols, flavonoids and hydroxycinnamic acids. The existing literature suggests that flavonoids determine the microsymbiont specificity as the host plant adapts to their secondary metabolism in accordance with the compatibility status of bacterial strains (Popovici et al. 2011). There are studies that reported that *Frankia* inoculation to host plant *A. glutinosa* activates the genes coding for phenyl ammonia lyase (pal) and chalcone synthase (chs), involved in flavonoid biosynthesis. Similarly, the study by Auguy et al. (2011) revealed that

Frankia interacts with the tropical tree *Casuana glauca* Sieb. ex Spreng. and results in the activation of eight *Casuana glauca* genes coding for enzymes involved in flavonoid biosynthesis.

Arbuscular Mycorrhizal Fungi (AMF)

Arbuscular mycorrhizae are found to colonize the majority of land plants. Mycorrhizal colonization of plant roots is mediated by controlled exudation by the plant roots and sensing of specific secondary metabolites released by the roots. During plant root colonization, the roots communicate with the mycorrhizal association in a complex way. The mycorrhizal fungi obtain a substantial fraction of soil C as a primary source of energy for the metabolic activities in the soil while at the same time benefitting the plants by delivering soil nutrients in return. One of the crucial steps in AMF development in plant roots is the formation of extraradical hyphae induced by signal molecules exuded by plant roots that initialize AMF-induced symbiosis. The signalling molecules secreted by the plant roots as a result of AMF interaction are known as strigolactones.

Strigolactones are known as branching factors exuded by plant roots. They are well known for their activity in stimulating fungal hyphae branching in symbiotic AMF. Strigolactones also help in signalling directional growth of AMF towards roots. Most important, strigolactones are considered an important signal molecule for the establishment of the AM symbiosis (Akiyama and Hayashi 2006). Strigolactones are synthesized from the carotenoid pathway and any alterations in the carotenoid mechanism affect strigolactone synthesis which ultimately affects AMF-host interaction. Recently it was reported that strigolactones play a crucial role even at a later stage of the AMF-plant interaction, when the fungus is already established in the root (Steinkellner et al. 2007).

7.3.1.3 Root Exudates as Carbon Cycling Activator and Nitrification Inhibitor

The exuded materials from the plant roots contain high amounts of C compounds that directly impact the rhizosphere microbial population. Root exudates can provide the rhizosphere microorganisms with precursors that are essential for phytohormone synthesis. Studies reported that plant exudates also contain higher quantities of aminocyclopropane-1-carboxylic acid (ACC) which serves as the main source of carbon and nitrogen for the rhizosphere microbes. This was shown by *acd*S expression by root exudates. Living plant roots also exude certain sugars such as glucose and sucrose that are involved in exopolysaccharides production, which is an essential step in microbial biofilm formation (Haichar et al. 2012). For instance, on growing *Paenibacillus polymyxa* in a culture medium containing a high concentration of sucrose, a high level of levan production was observed. Levan is a naturally occurring fructan present in many plants and microorganism species. High levels of sugar induce the expression of gene *sacB* involved in levan synthesis. Thus, it was clearly understood that the exuded sucrose from the root apex of wheat roots in the rhizosphere ecosystem can easily induce the expression of the *P. polymyxa sacB* gene (Bezzate et al. 2000). These Exopolysaccharides play a pivotal role in legume-rhizobia interactions via taking part in microbial biofilm formation around the plant roots. Since EPS can be produced at high levels of sugar concentration (that is either glucose or sucrose), it points out to facts that (a) root exudates contain a high concentration of these molecules and (b) in the presence of gene expression inducer bacteria may produce EPSs with low glucose or sucrose concentrations. Plant roots exude a wide array of organic substances as a part of root exudates. The organic compounds exuded by the roots were reported to accelerate the process of decomposition of soil organic matter (SOM) with the help of soil-dwelling, rhizosphere-associated microorganisms. The increased solubilization of soil nutrients depends solely on the activation of rhizosphere microbial activity by labile C released by roots. The existing literature suggests that some of the primers like root exudates, even at meagre amounts, can stimulate SOM turnover, which increases nutrient availability, especially nitrogen or phosphorus to plants (Jones et al. 2004; Cheng et al. 2014).

The nitrification process is a key step in the global nitrogen cycle that links the oxidation of ammonia to the loss of fixed nitrogen in the form of dinitrogen gas brought about by specific nitrifying microbial activity. The process involves converting a non-utilizable form of N in the soil to a simple, readily utilizable form that contributes significantly towards plant productivity and environmental quality. The existing literature demonstrated the importance of using recombinant luminescent bacterial strains (*Nitrosomonas europaea*) to monitor nitrification inhibitors released from plant roots (Subbarao et al. 2007). Among the cereals, legume crops, groundnut, pearl millet and sorghum showed detectable biological nitrification inhibition (BNI) in root exudates while among pasture grasses, *Brachiaria humidicola* (Rendle) Schweick and *B. decumbens* showed the highest BNI capacity. In another study, Zakir et al. (2008) have reported for the first time the root exuded compound methyl 3-(3-hydroxyphenyl)propionate (MHPP) responsible for BNI by sorghum. Similarly, Subbarao et al. (2013) have reported a root exuded compound, sorgoleone, 1-p-benzoquinone (exuded from sorghum roots) to contribute significantly to the BNI capacity in sorghum.

7.3.1.4 Role of Root Exudates in Nutrient Deficiency

The living plant roots produce various organic and inorganic compounds to enhance the adaptation rate of plants to different environmental conditions. The exudation of organic compounds by the plant roots increases with a decrease in soil nutrients. Plants increase their exudation of organic compounds into the rhizosphere under nutrient deficiency. Under Fe deficit conditions, plants exude phytosiderophores into the rhizosphere to adapt to the prevailing condition. Herbaceous or woody plants acquire Fe from the soil by secretion of phytosiderophores that facilitates in acquiring of ferrated-phytosiderophore complexes aided by a highly precise and efficient nutrient uptake system (Römheld 1991; von Wiren et al. 1994, 1995). The rate of root exudation increases is positively related to the tolerance of a plant species to Fe deficiency. Under Fe deficiency, the Fe-deficiency tolerant plant genotypes show more root exudation rates than the plant genotypes sensitive to Fe deficiency (Rengel 2002). The process of phytosiderophore release and its uptake by the plants is solely under genetic control (Römheld and Marschner 1990). Several genes are involved in the biosynthesis of phytosiderophores and their precursor nicotianamine that codes for the enzyme nicotianamine synthase (Higuchi et al. 1999). According to the literature, Fe deficiency demands more phytosiderophore production than that under Zn deficiency (Rengel et al. 1998; Walter et al. 1994). This implies to effortless, undeviating and less complicated series of events that are involved in the phytosiderophore triggering process in Fe deficiency than the highly complex triggering process in case of Zn deficiency. Plant genotypes that are tolerant to Zn and Fe deficiency are reported to exude a lesser amount of phytosiderophores than the Zn and Fe sensitive ones in order to increase mobilization of Zn and Fe from sparingly soluble sources (Rengel 2002).

7.3.2 Other Novel Functions of Root Exudates

Root exudates are known to involve in different positive and negative types of interactions that include interactions between plants, plant and soil microorganisms and also between plants, soil microbes and nematodes (tritrophic interactions). Plant -microbe interactions is one of the most common interactions that exist in the rhizosphere microzone which illustrates the tritrophic interactions and the role of root exudates in these interactions. There are a few studies that explained the tritrophic interactions and their occurrence, which is when both the partners the soil microbes and nematodes act synergistically to stimulate growth in plants. A study by Horiuchi et al. (2005) demonstrated that soil-dwelling nematode *Caenorhabditis elegans* helps in establishing a positive connection between roots and soil rhizobia resulting in healthy and high nodulation in legumes. Briefly, the study elucidated the role of *C. elegans* in initiating plant-microbe symbiosis. On the release of plant root volatiles, the nematode, *C. elegans* carry the bacterium to the roots of the legumes resulting in the initiation of plant-microbe symbiosis.

Root exudates contain compounds that are known to exert direct influence on shaping the rhizosphere microbial community. The different components in root exudates show positive chemotactic responses in bacteria and the capacity for different microbial species to utilize and compete for substrates (Somers et al. 2004). For example, in one of the reports by Naim (1965), it was documented that the microbial density in the root apex of Libyan desert grass (*Aristida coerulescens*) was significantly higher than the microbial population found at the base of the plant. A similar pattern was observed for wheat roots (Van Vuurde and Schippers 1980). Looking at the colonizing pattern shown by the microbial communities, it was suggested that this was due to the exudation of certain rhizodeposits predominantly at the root tip. These include root exudates and lysates that is highly predominant at the bases of plant roots.

Furthermore, plant roots secrete a wide range of inhibitory substances as secondary metabolites that help the host plants to cope with different bacterial and fungal pathogens in response to inducers that initiate a defence response (Walker et al. 2003). Under natural conditions, plant defence responses remain constantly stimulated but exudation of secondary metabolites by plant roots such as saponins, glucosinolates and hydroxamic acids accounts for the resistance or the susceptibility of particular plant species/cultivars to root pathogens. There are several studies that have highlighted the antimicrobial activity exhibited by LMW compounds and the plant defence proteins which are released as a part of plant root exudates. For instance, Lanoue et al. (2010) reported that the barley root system secreted phenolic compounds such as vanillic acid, p-coumaric acid and with antimicrobial activity under *Fusarium* attack. Similarly, during *Pseudomonas aeruginosa* infection of basil roots, the basil root system secreted rosmarinic acid that exhibited antibacterial activity against *P. aeruginosa* under in vitro conditions. Flavonoids were recently reported to show a significant inhibitory effect against different bacterial and fungal plant pathogens. Flavonoids were considered to be an important molecule for conferring resistance to plants against different phytopathogens. The chemiosmotic potential between cytoplasmic matrix and vacuole acts as the primary driving force for the transport of flavonoid molecules to the plant infection site. At the site of infection, the flavonoids induce hypersensitivity reaction and programmed cell death. The antimicrobial activity of flavonoids depends on their ability to inhibit microbial adhesion and the inactivation of cell envelope transport proteins. They can disrupt the microbial membrane, alter membrane permeability and inhibit cell envelope and nucleic acid synthesis by forming hydrogen bonds with the stacking of nucleic acid bases, electron transport chain and ATP synthesis (Mierziak et al. 2014). Additionally, plant roots secrete various proteins to protect the plant against different soil-borne pathogens. For instance, Park et al. (2002) have reported that the roots of the plant *Phytolacca americana* (pokeweed) are well known for their ability to secrete various plant defence proteins including PAP-H. PAP-H is a ribosome-inactivating protein (RIP) that helps in the inhibition of protein synthesis by acting on the ribosome in a highly specific order. They also exhibit in vitro N-glycosidase activity against fungal ribosomes, whereby they can recognize and depurinate fungal ribosomes.

Root exudates have also been shown to alter the genetic make-up of the microbial communities (Baudoin et al. 2003) and enhance the number of pollutant degraders in rhizosphere soil (Joner et al. 2002). Marschner et al. (2002) in one of their studies examined the changes in microbial community profile associated with roots varying in architecture and maturity as a result of variations in root exudation pattern using DGGE analysis. DGGE analysis revealed a prominent difference in microbial communities on the basis of the root type which ultimately affects the compositional content of root exudates. The significant differences in fungal and bacterial community structure were recognized to be the difference in organic acid production by both the communities. For instance, the fungal community is known to produce high concentrations of citric acid, while the bacterial community produces *cis*-aconitic and malic acid in addition to citric acid. In relation to root exudates stimulating hydrocarbon degrader populations in rhizosphere soil, Cebron et al. (2011) have observed that the major microbial strains in a phenanthrene contaminated soil were *Pseudoxanthomonas* sp. and *Microbacterium* sp. before the addition of root exudates, but on the addition of root exudates of ryegrass, the growth of

Pseudomonas sp. and *Arthrobacter* sp. were also favoured. This suggests that root exudates have a direct impact on enhancing the microbial diversity of any contaminated piece of land while increasing the abundance of PAH-RHD$_{\alpha}$ gene containing microorganisms for faster remediation of PAH contaminated sites. Secondary plant metabolites, a key component of rhizodeposits, also play a crucial role in plant survival in environments contaminated with different hydrocarbons such as polyvinyl chloride (PVC) and polyaromatic hydrocarbons (PAHs). There are studies reporting that the presence of high concentrations of secondary plant metabolites in the rhizosphere ecosystem enhances the number of pollutant degraders in rhizosphere soil (Donnelly et al. 1994).

7.4 Conclusion and Future Perspectives

The current chapter highlighted a few of the research findings to understand the mechanistic insights of exudation-related plant-microbe interactions as well as rhizosphere functioning. Overall, the chapter provided an illustrated explanation based on the research findings to establish the root exudates as key mediators for successful interaction between plants and rhizosphere microbes in the rhizosphere microzone. But due to a bottleneck in a comprehensive understanding of root exudates chemistry, there is a lack of information and knowledge about belowground plant-microbe interactions. Although several components of root exudates have been characterized, studied and explained in detail, the metabolic profiling of the root exudates has not been explored in detail except for a few components such as organic acids, flavonoids and fatty acids. This can be majorly due to the inadequacy and limitation of technology to isolate and characterize the minute portions of the natural products that are highly alterable in nature.

Moreover, experimental works corresponding to spatiotemporal pattern study of root exudates are mostly under axenic or monoxenic laboratory conditions and thus require more attention for conducting *in-planta* studies to understand the mechanistic insights of root exudates in belowground plant-microbe interactions as well as their dynamic role in plant growth and development. Although much is known in regard to the role of root exudates in an interactive activity, a still more is required to have a good understanding of the exudation pattern of different plant roots belonging to different species, the variations in exudation with respect to plant age, soil type, environmental parameters and rhizosphere microbiome. Furthermore, the fate of root exudates in rhizosphere soil and the function of these exuded materials in microbial physiology and functions have not been explored in detail. Thus there is a huge scope for researchers to undertake metabolomic studies to improve the understanding and knowledge of the same. Moreover, it opens up several opportunities for the researchers to take up studies to understand the interlink between bacterial gene expression and the nature of exuded material from the living plant roots.

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